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Natural Streams and the Legacy of Water-Powered Mills

Robert C. Walter*† and Dorothy J. Merritts*†

Gravel-bedded streams are thought to have a characteristic meandering form bordered by a self-formed, fine-grained floodplain. This ideal guides a multibillion-dollar stream restoration industry. We have mapped and dated many of the deposits along mid-Atlantic streams that formed the basis for this widely accepted model. These data, as well as historical maps and records, show instead that before European settlement, the streams were small anabranching channels within extensive vegetated wetlands that accumulated little sediment but stored substantial organic carbon. Subsequently, 1 to 5 meters of slackwater sedimentation, behind tens of thousands of 17th- to 19th-century milldams, buried the presettlement wetlands with fine sediment. These findings show that most floodplains along mid-Atlantic streams are actually fill terraces, and historically incised channels are not natural archetypes for meandering streams.

The meandering gravel-bedded stream bordered by a self-formed, fine-grained floodplain emerged as the characteristic river form based on pioneering studies in mid-Atlantic and western streams of the United States (*1*–*4*). Today, this ideal—of alternating pools and riffles along sinuous channels with gravel point bars and fine-grained overbank floodplain deposits—guides a multibillion-dollar stream restoration industry (*5*, *6*). Many streams in the low-relief, tectonically inactive mid-Atlantic Piedmont of the United States are deeply incised, with steep eroding banks, and carry anomalously high amounts of suspended sediment (*7*). Fine-grained deposits bordering many eastern streams are thicker than would be expected from just their recent flood deposits (*1*, *3*). These Holocene deposits typically form broad surfaces, referred to as the "valley flat," that were interpreted as floodplains formed by a combination of migrating, meandering stream channels and overbank deposition of silts and clays (*1*, *3*, *8*). The geometry of single-channel meandering streams has been viewed as the result of self-adjusting hydraulic variables in response to changing discharge and sediment load, and agriculture and urbanization have been cited widely as the causes of recent aggradation and degradation (*1*, *3*, *4*, *8*–*10*). This pattern of stream development and morphology has been considered as typical of streams and rivers in stable landscapes.

We observe that crests of breached, historic milldams merge with valley-flat surfaces and that most modern streams are incised deeply below this surface. This observation led us to hypothesize that a rapid, regional transformation of stream valleys had occurred in eastern North America, from widespread aggradation as a result of damming (base-level rise) to subsequent incision and bank erosion due to dam breaching (base-level fall). We propose that valley sedimentation not only resulted from accelerated hillslope erosion caused by deforestation and agricultural development (*8*, *11*) but also was coupled with widespread valley-bottom damming for water power, after European settlement, from the late 17th century through the early 20th century. Damming was essential to the extensive trapping of sediment in broad valley flats that correspond to reservoir surfaces.

We test this hypothesis by examining the following lines of evidence: (i) historical accounts of widespread, intensive water-powered milling that impacted most first- to third-order streams in the mid-Atlantic region; (ii) historical maps showing multiple dams and ponds, and our observations in the field and from light detection and ranging (LIDAR) data of aggradation in these ponds that caused sedimentation upstream into tributaries and swales; (iii) historical, geological, and geochemical data showing rapid sedimentation in valley bottoms during the period of early land clearing; (iv) field observations and remote-sensing data, including LIDAR, showing that downstream-thickening wedges of sediment grade to milldam heights and, hence, that dams produced temporary, higher base levels; and (v) field observations and laboratory data showing that the morphologies and functions of presettlement streams were substantially different from those of modern streams. We revisited the same streams and specific reaches used in early studies that pioneered modern fluvial geomorphology, including fundamental ideas regarding meander migration, floodplain formation, hydraulic geometry, and fluvial response to land clearing. These streams include the Brandywine River (in Pennsylvania and Delaware) and Seneca Creek, Watts Branch, and Western Run (in Maryland) (*1*–*4*, *8*, *9*, *11*), all of which lie within the Piedmont physiographic province of the mid-Atlantic region. In all, we studied Piedmont streams in 20 watersheds throughout Pennsylvania and Maryland (drainage areas from 11 to 1230 km^2; fig. S1).

Milldam history. Dam building for water power in the eastern United States began in the

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late 1600s and persisted until the early 1900s. Dams and races that delivered water from the pond upstream of a dam were built to run iron forges, furnaces, mining operations, and—most commonly—mills; we refer to all of these water-powered activities as milling. Before the adoption of steam engines during the late 19th century, every mill required a milldam reservoir to supply a relatively constant head and reliable supply of water. Early American settlers brought milling technologies from Europe, where thousands of water-powered mills lined streams as early as 1100 CE (*12*) [see supporting online material (SOM) text, table S4, and fig. S5]. Milling intensified with economic growth in early America, and dozens of mill acts dating to the 1700s encouraged mill and dam building. Our analysis of historic records in Lancaster County, Pennsylvania, for example, indicates that peak mill development was from 1780 to 1860, but water-powered milling extended from 1710 to 1940. Our county-by-county compilation of U.S. manufacturing census data reveals >65,000 water-powered mills in 872 counties in the eastern United States by 1840 (*13*) (Fig. 1). Water-powered milling was especially intensive in the mid-Atlantic Piedmont region along and west of the fall line, where stream gradients are conducive to milldam construction and shipping ports of the Coastal Plain are in close proximity (e.g., Wilmington, Delaware; Philadelphia, Pennsylvania; and Baltimore, Maryland). The Piedmont provided the bulk of manufacturing and agricultural goods to port cities and a large portion of the wheat and flour for mid-Atlantic shipping (*14*, *15*).

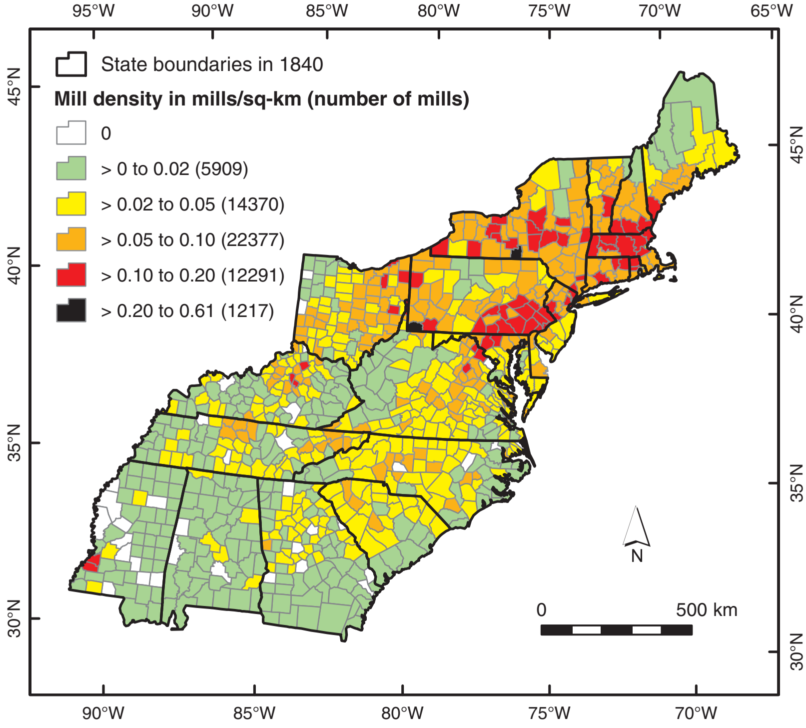

Fig. 1. Density of water-powered mills along eastern U.S. streams by 1840 by county (872 county boundaries are shown for 1840). The highest densities are in the Piedmont and the Ridge-and-Valley physiographic provinces of Maryland, Pennsylvania, New York, and central New England.

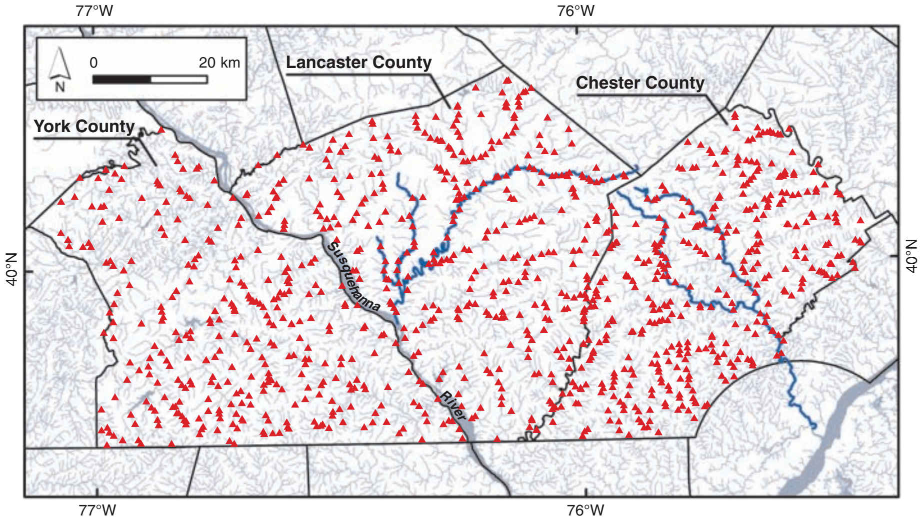

Fig. 2. Historic 19th-century milldams (triangles) on Piedmont streams in York, Lancaster, and Chester counties, southeastern Pennsylvania, located from >100 large-scale township maps dating to 1876 (York), 1875 (Lancaster), and 1847 (Chester). The total number of dams shown is 1025. Main stems of Conestoga (Lancaster) and Brandywine (Chester) rivers are highlighted in dark blue.

Historic maps show locations of mill buildings, millponds, and races dating to early American history, and historic photos of dams date to the late 19th century. Lancaster, York, and Chester counties, Pennsylvania, have large-scale mid- to late 19th-century historic maps from which we located 1025 milldams (Fig. 2), which is similar to the number of mills recorded in the 1840 U.S. manufacturing census. From county historical societies and the Pennsylvania commonwealth's inventory of dams, we acquired photographs and records of hundreds of historic milldams. The Pennsylvania Department of Environmental Protection (PA DEP) has an inventory of about 8400 dams in the commonwealth, of which 4100 are breached, and estimates that 8000 to 10,000 more might exist (*16*). These estimates result in an average density of 0.14 to 0.15 dams per km^2 for the commonwealth of Pennsylvania. The possibility of 16,000 to 18,000 dams in Pennsylvania is consistent with the ~10,000 mills listed for Pennsylvania in the 1840 U.S. manufacturing census, considering that mill and dam building continued throughout the 19th century. In Chester County, Pennsylvania, for example, which includes much of the drainage area of the Brandywine River, the 1840 U.S. manufacturing census lists 379 water-powered operations, and our examination of historic maps from the 1840s to the 1860s revealed at least 377 dams. The Brandywine Valley contained "the most notable concentration of mill industries in the colonies," with 60 paper mills alone in 1797 (*17*). Using 1840-era county boundaries, we calculate a density of 0.19 milldams per km^2 in Chester County, which is only slightly greater than the density of water-powered mills in other Piedmont counties of Pennsylvania, Maryland, and Virginia calculated from the 1840 U.S. manufacturing census data.

Our field observations and LIDAR analysis (n > 200 millpond reaches) for the Conestoga, Brandywine, and Codorus Rivers (among others) in Pennsylvania, and for Western Run, Seneca Creek, Watts Branch, and the Monocacy River in Maryland (figs. S1 to S4), demonstrate a series of aggradational wedges of fine-grained sediment that thins and extends upstream of dams on all of these streams for several kilometers. Aggradational impacts extended upstream to many undammed tributaries as well, as a result of backwater effects.

Low stream gradients (0.001 to 0.004 in the Piedmont) and low to moderate dam heights controlled milldam spacing; typically, one dam was placed every 2.4 to 5 km along the Brandywine, Conestoga, and Codorus rivers, Seneca Creek, and Western Run. Historic photos and our field observations indicate that early milldams spanned entire valley bottoms of what are now first-, second-, and third-order streams (fig. S3). Such streams comprise greater than 70% of stream length in the region, and damming them would have a substantial impact on a large portion of watersheds, including upstream tributaries. Milldam heights were generally 2.5 to 3.7 m. Direct step calculations (*18*) imply that flow velocity would have been reduced by as much as 60% at least 1 to 3 km upstream of milldams (flow reduction is impacted to a greater extent by higher dams and/or lower stream gradients). Our estimates of trap efficiencies (*19*) of >60% for Piedmont reservoirs suggest that sedimentation rates would have been high during periods of accelerated soil erosion. Various early American mill acts that regulated the raising of dams and compensation for flooded lands, both of which were common occurrences, also indicate that milldams had well-known backwater effects on valley bottoms (see SOM text). Because of these backwater effects, later mill acts were passed to control mill crowding (*17*, *20*) (see SOM text). Historical accounts also show that milldams altered the original stream ecology: (i) In 1731, settlers tore down a milldam on the Conestoga River because it was ruining the local fishing industry, and (ii) in 1763, a petition cited complaints regarding the abundance of milldams on the Conestoga River “as destroying the former fishery of shad, salmon, and rock fish, which were before in abundance, and the tributary streams had plenty of trout—all now gone” (*21*).

Stream sediments. Based on geochemical and stratigraphic analysis of sediments exposed in stream banks (~100 sites) and samples from 45 backhoe trenches and >110 hydraulic cores in adjacent fill terraces, we constructed a composite stratigraphic profile for a representative Piedmont stream (first to third order) (Fig. 3). Similar profiles have been described throughout the Piedmont, from South Carolina to Pennsylvania (*8*, *22*–*24*). The bedrock (weathered) valley floor typically is overlain by: (i) a thin (<0.5-m) bed of angular to subangular quartz-rich gravel; (ii) a thin (<0.5- to 1-m), dark (black, 10YR 2/1), organic-rich silt loam; and (iii) a thick (1- to 5-m) pale to yellowish brown sequence of fine sand, silt, and clay [commonly referred to as silt loam and clay loam; U.S. Department of Agriculture (USDA)/Natural Resources Conservation Service classification]. Exceptions to this typical sequence occur where stream channels were diverted along valley walls (e.g., to drain valley bottoms for agriculture) or where stream beds were mined for metal ores and gravel.

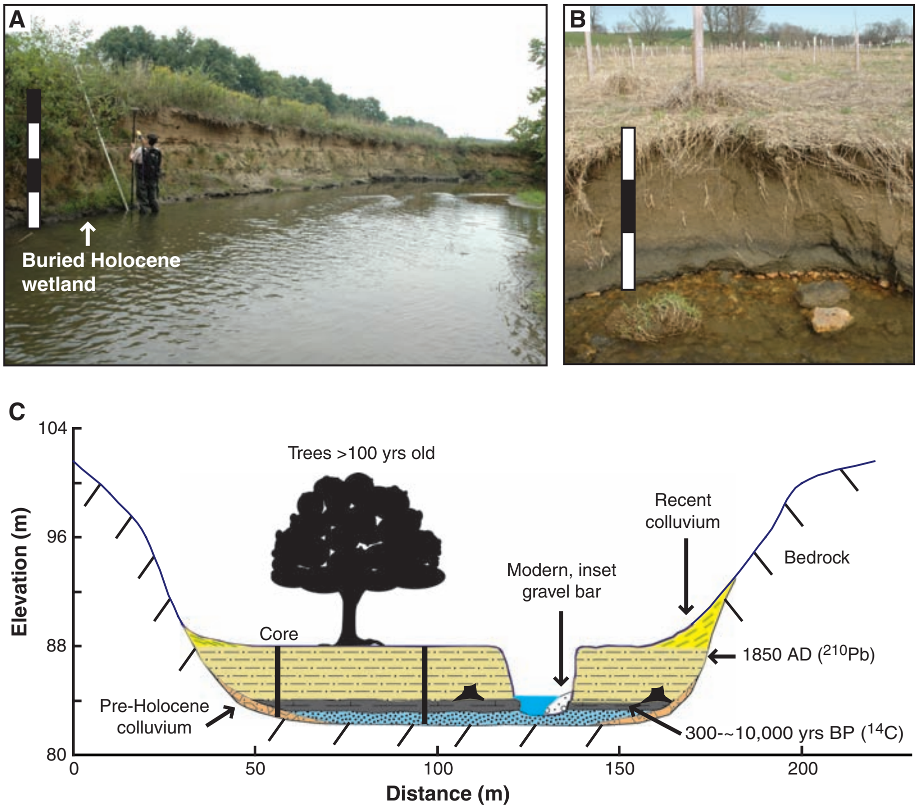

Fig. 3. Streams throughout the mid-Atlantic region (see also figs. S1 and S2) have similar characteristics: vertical to near-vertical banks consisting of 1 to 5 m of laminated to massive fine-grained sediment overlying a Holocene hydric soil and a basal gravel overlying bedrock. (**A**) Western Run, Maryland. (**B**) Big Spring Run, Pennsylvania. Scale bars in (A) and (B) are marked in 0.5-m increments; the banks in (A) and (B) are ~2.2 and ~1.4 m high, respectively. (**C**) Conceptual model based on composite stratigraphy from multiple sites, including stream-bank exposures, trenches, and cores.

We interpret the dark, organic-rich silt loam (2 to 9% by weight total carbon in the <2.0-mm fraction) above the basal gravel as a buried hydric (wetland) soil (tables S1 and S2). Throughout the region, this hydric soil contains abundant, well-preserved woody debris, seeds, nuts, roots, algal mats, and pollen, and sometimes is a peat with mosses. At multiple sites, we observe deciduous tree stumps (which often show evidence of having been logged) rooted in this stratum and corduroy (wooden log or plank) roads upon its surface. The overlying fine-grained, pale brown sediments are lower in organic matter (~1 to 2% by weight total carbon in the <2.0-mm fraction), generally horizontally bedded, typically finely laminated, and contain rare lenses of subrounded gravels and historic artifacts that include brick fragments, cut logs and planks, and pieces of coal. Seventy radiocarbon dates from this buried wetland soil (samples of wood, leaves, or seeds) throughout Pennsylvania and Maryland yield ages ranging from 11,240 to 300 years before the present (table S3), indicating that these soils accumulated and stored organic matter throughout the Holocene epoch. We estimate that these valley-bottom wetlands were efficient carbon sinks, storing from 2.5×10^5 to 1.35×10^6 kg of carbon per hectare that now is buried beneath historic sediment (*25*).

We interpret the underlying gravels as derived from long-term (10^6 to 10^7 years) hillslope erosion and denudation of the landscape. Many may have formed from downslope movement associated with episodic periglacial processes and tundra conditions during the late Pleistocene or earlier. The predominance of quartz, a highly resistant mineral, and the position of these colluvial gravels beneath pervasive Holocene interglacial hydric soils support this deduction.

We constrained the timing of millpond sedimentation using ^{210}Pb geochronology (*26*) and historic documents. Analysis at two sites where historic sediment is 1 and 5 m thick indicates that secular equilibrium for ^{210}Pb is reached at a depth of 15 to 20 cm below the surface. This finding indicates that sediments near the surface were deposited by 1850 or earlier and that these slackwater reservoirs reached sediment storage capacity by at least that year (fig. S3). At multiple sites in Maryland and Pennsylvania, we observe groves of large trees estimated to be up to 150 years old on valley fill deposits. This is consistent with fossil seed and pollen evidence showing that a riparian forest became established circa 1850 in an estuary fill deposit in the upper Chesapeake Bay, after peak sedimentation from the watershed occurred between 1840 and 1880 (*27*). Historic air photos dating to the 1930s and maps dating to the early 1800s indicate that ponds diminished in size until the mid- to late 1800s and became stable swamps and meadows thereafter, until dam breaching and incision.

The characteristics of the presettlement sediments and organic material suggest that valley bottoms were broad, forested wetlands (alder shrub-scrub) with small, shallow (<1-m) anabranching and chain-of-pool streams that experienced frequent overbank flow, which is consistent with accounts by early explorers of ubiquitous swampy meadows and marshes fed by springs at the base of valley side-slopes (*28*). The upper surface of the dark hydric soil has low relief and typically extends across valley bottoms [see Fig. 3 and valley cross sections in (*8*, *24*)]. Along a rural section of Western Run northwest of Baltimore, Maryland, for example, we followed the modern deeply incised channel from one side of the valley to the other and mapped a Holocene hydric soil (buried beneath 2 m of historic sediment) for the entire distance; no buried channel deposit was encountered, and at times the hydric soil became more peaty and rested directly upon bedrock. This regional network of small streams and low, vegetated islands within the flood zone was probably impacted heavily by beaver dams and small ponds, which could explain the lack of buried stream channels at all sites observed to date (*29*). Plant fragments and seeds extracted from these buried hydric soils indicate obligate and facultative wetland species, including various hydrophytic trees, shrubs, sedges, rushes, and cresses. Groundwater flow throughout valley-bottom gravels would have supplied a near-continuous base flow to these wetlands.

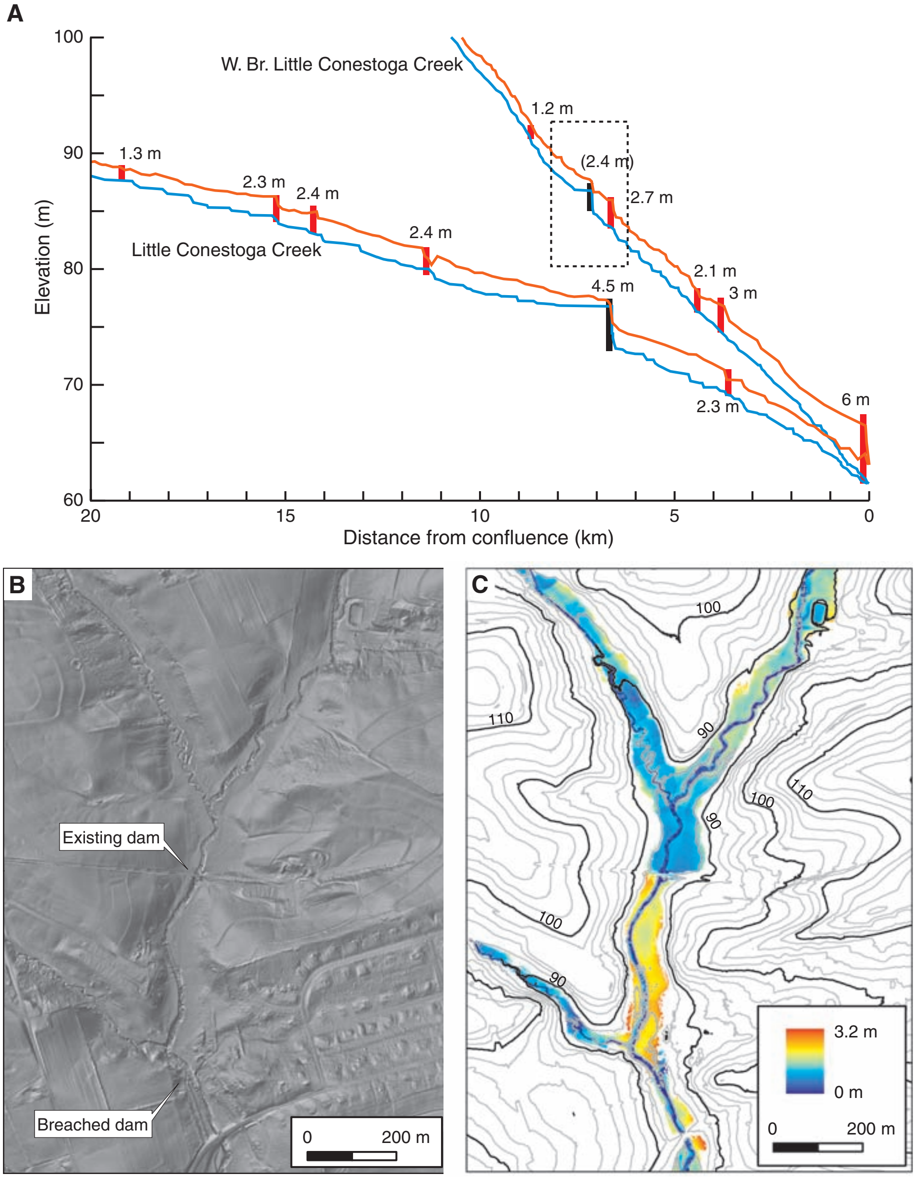

Fig. 4. Methods for locating dams and assessing their impact on reservoir sedimentation, subsequent channel incision, and bank erosion with high-resolution LIDAR. (**A**) Long profile of Little Conestoga Creek and West Branch Little Conestoga Creek extracted from LIDAR-derived DTM (digital terrain model), depicting locations of milldams (black and red vertical bars). The lower (blue) line for stream profiles approximates the water surface, whereas the upper (red) line approximates banks above streams (i.e., reservoir fill surface). Dams shown in black are still in place; those in red are breached, some only partially. The influence of dams on relative terrace height is apparent, such as at kilometer 7, where the Lake Mill dam is still in place on the Little Conestoga. The area in the dashed box is illustrated in (B) and (C). (**B**) Hillshade rendering of LIDAR-derived DTM clearly depicts the low-gradient relict millpond surface along the valley corridor. Note that channel incision occurs upstream of the breached dam (denoted at bottom) but not upstream of the partially breached dam ("existing dam," denoted in middle). This difference is documented in (**C**), which maps the height of the terrace surface above the stream water surface. Upstream of the breached dam, the terrace is up to 3.2 m above the water surface, rising upward toward the dam in the downstream direction. Upstream of the unbreached dam, the terrace height is less than 1 m. Light and dark gray contour lines in (C) are 2- and 10-m intervals, respectively.

Recent responses. In the past 100 years, many historic dams have been breached as mills were abandoned. Breaching has led to incision of streams into the milldam reservoir sediments and to locally heavy erosion of steep stream banks. High-resolution (15-cm-vertical) LIDAR data for the Conestoga River and Western Run indicate that dam height controls stream-bank height (via depth of incision) above the water surface (Fig. 4). These remote-sensing observations are consistent with our field studies, which encompass a much greater area. Fill terraces increase in height downstream toward the tops of breached dams and then drop to the level of backwater effects from the next slackwater reach downstream. By mapping channel banks on high-resolution digital orthophotos from the early 1990s to 2005 for Lancaster and York counties, Pennsylvania, we estimate that bank erosion rates are >0.2 m/year locally and at least 0.05 m/year along many stream reaches upstream of 20th-century dam breaches. In Maryland, stream cross sections monitored for 41 years in a study of meander migration and floodplain formation near the headwaters of Watts Branch, Maryland (*2*, *9*), are located <1 km upstream of a breached 19th-century dam, which was not recognized by previous workers. This dam supplied water from a millpond to Wootton's Mill, which operated until 1905 (fig. S4). Our historic research indicates that the dam breached sometime between 1905 and 1952. The higher valley-flat surfaces upstream of the dam are interpreted here as fill terraces rather than floodplains, even though they might receive occasional overbank flow. Although previous workers interpreted late 20th-century enlargement of the channel to upstream urbanization, we propose that enlargement was a natural response to dam breaching and incision.

Where dams are unbreached or partially breached, deep incision has not yet occurred, and streams are shallow and wide as they spill over the historic dams. In some cases, more recent dams have been constructed within incised channels near the site of older breaches; many of these second-generation dams are also breached. In Pennsylvania, these inset dams typically were constructed in the late 1800s to early 1900s.

Increasing channel width at a breached dam site on the Brandywine River during the past ~100 years is consistent with 671 repeat measurements of fair to excellent quality for less than bankfull discharge at the Chadds Ford U.S. Geological Survey (USGS) gage station, which is located between two closely spaced breached milldams (see SOM text). Our analysis of these data indicates that the ratio of width to discharge for a given discharge range increased from 0.4 to 0.5 between 1908 and 2007. This increase yields an estimate of at least a 10-m increase in channel width, likely resulting from bank erosion, since 1908 and is consistent with (i) our mapping of bank erosion along this reach, (ii) air photos from 1937 to the present that show channel widening, and (iii) the marked rise in suspended sediment loads recorded at this gage station from 1964 to 1978 (USGS data; see SOM text). Similarly, we calculate a power function exponent of 0.26 for the relation between width and discharge at the Chadds Ford gage station, whereas an analysis of hydraulic geometry relations in 1955 yielded an exponent of 0.17 (*3*). A 50% increase in this exponent during the past ~50 years is consistent with channel evolution by lateral erosion and long-term widening after incision in response to dam breaching (*30*).

Similar to earlier studies (*2*, *3*, *8*), our measurements of sediment size indicate that modern channel-bed sediments are much coarser grained (coarse sands and gravels) than the fine sediments (mostly silt and clay and some sand) that are exposed along stream banks. We attribute this difference not to a meandering stream that deposits gravel in bars and silt and clay on floodplains during overbank flow but rather to increased flow velocities and shear stresses that accompany deep incision of streams into fine-grained millpond sediment. After dam breaching, incised channels have shear stresses >5 to 10 times as high as those of presettlement streams (shear stress is proportional to water depth and slope) and, consequently, are capable of transporting Pleistocene gravels that eroded from the buried toes of hillslopes (Fig. 4). Further, bank erosion removes not only vast amounts of postsettlement alluvium but also wide areas of Holocene wetland soils and Pleistocene basal gravels that covered stream valleys in this region since the end of the last ice age.

To assess the impact of bank erosion on sediment load of the modern streams, we collected ^{137}Cs data on sediments from several southeastern Pennsylvania streams and stream banks. Cesium-137, produced by atmospheric nuclear bomb testing, reached its peak production in 1963 and ceased in the mid-1970s with the banning of atmospheric bomb tests. This non-natural isotope readily infiltrated surface sediments and is strongly adsorbed onto the surfaces of fine-grained soil particles (*31*, *32*). It thus provides a metric for sediment loads and surface erosion (*33*). Comparison with suspended load data from gage stations indicates that 30 to 80% of suspended sediment is derived from bank erosion (*25*). Historic stream-bank sediments, which we measured at 15 sites, also have high levels of total carbon, nitrogen, and phosphorus, ranging from 0.5 to 3.1% (C), 400 to 2100 parts per million (N), and 340 to 958 ppm (P); thus, bank erosion is contributing to the high nutrient loads of many of these streams (*25*). These results are consistent with bank erosion rates and with sediment and nutrient loads measured in other watersheds in the United States and around the world (*34*–*36*).

Conclusions. We conclude that fluvial aggradation and degradation in the eastern United States were caused by human-induced base-level changes from the following processes: (i) widespread milldam construction that inundated presettlement valleys and converted them into a series of linked slackwater ponds, coupled with deforestation and agricultural practices that increased sediment supply; (ii) sedimentation in ubiquitous millponds that gradually converted these ponds to sediment-filled reservoirs; (iii) subsequent dam breaching that resulted in channel incision through postsettlement alluvium and accelerated bank erosion by meandering streams; and (iv) the formation of an abandoned valley-flat terrace and a lower inset floodplain. This evolution explains why so many eastern streams have bankfull (discharge) heights that are much lower than actual bank heights. Assessments of bankfull discharge are crucial to estimates of flood potential and to design criteria for stream restoration.

Early workers considered western and eastern streams in the United States to have similar origins and forms [compare with plate 2 in (*1*)]. However, western streams are in a more tectonically active region, generally have high stream gradients, and carry substantial bed-load fractions, whereas eastern Piedmont streams are in a tectonically quiescent region, have low stream gradients, and largely did not carry gravel (or even much fine sediment) during the Holocene before formation of modern incised channels. Formation of gravel bars in the wake of eroding, meandering channels, followed by overbank deposition of fine sediment, was not the natural process of floodplain formation in the eastern United States before mill damming and subsequent channel incision after dam breaching. Valley bottoms along eastern streams were characterized by laterally extensive, wetland-dominated systems of forested meadows with stable vegetated islands and multiple small channels during the Holocene. These findings are consistent with research on streams in the Pacific Northwest, which revealed that large woody debris from forested riverine areas was critical to geomorphic processes and habitat before logging, channel clearing, and ditching during the late 1800s to early 1900s (*37*–*39*). In particular, logjams blocked channels and led to the formation of side channels and floodplain sloughs, producing multiple anabranching channels and riverine wetlands that are in stark contrast to the large, single channels that exist in these streams today.

Our results explain the unusually thick deposits of fine sediment in stream banks relative to the limited amount of modern overbank deposition (*1*, *3*). They also explain the lack of levees on mid-Atlantic streams (*1*); the great contrast between fine stream-bank and coarse stream-bed material; the observation that eastern (incised) streams, in comparison with western streams, change little in width as discharge increases at a station (*3*, *10*); and the anomalously high suspended sediment and nutrient loads measured in Piedmont streams (*7*).

Postsettlement milldam construction and millpond sedimentation were rapid and pervasive. This process inundated, buried, and sequestered presettlement wetlands and altered regional stream functions probably within two generations of settlement. Our field and historical research shows that stream valleys were once lined with millponds, which then silted in to form broad, flat bottom lands. The modern, incised, meandering stream is an artifact of the rise and fall of mid-Atlantic streams in response to human manipulation of stream valleys for water power. Our results indicate that a substantial portion of modern suspended sediment and nutrient loads could be due to dam breaching and erosion of reservoir sediment, which is consistent with studies of recent dam removals elsewhere in the United States (*40*, *41*).

These conclusions change the interpretation of hydraulic geometry in eastern U.S. streams that is based on the archetype of an “ideal meandering river form” and imply the need to reconsider current procedures for stream restoration that rely on reference reach conditions and the assumption that eroding channel banks are natural and replenishable. The current condition of single gravel-bedded channels with high, fine-grained banks and relatively dry valley-flat surfaces disconnected from groundwater is in stark contrast to the presettlement condition of swampy meadows (shrub-scrub) and shallow anabranching streams described here.

This work has implications for interpretation of alluvial sedimentation and stream channel form and evolution in Europe as well as in the United States. Tens of thousands of mills existed throughout Europe by the 18th century, and it is possible that European streams have been responding to anthropogenic base-level rise and fall for up to a millennium (SOM text and fig. S5). We propose that widespread mid- to late medieval alluviation and burial of pre-Roman organic-rich soils observed in "all lowland and piedmont river valleys in Britain and much of Northern Europe" (*42*) might have been the result of mill damming.

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Supporting Online Material

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Lhx2 Selector Activity Specifies Cortical Identity and Suppresses Hippocampal Organizer Fate

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The earliest step in creating the cerebral cortex is the specification of neuroepithelium to a cortical fate. Using mouse genetic mosaics and timed inactivations, we demonstrated that *Lhx2* acts as a classic selector gene and essential intrinsic determinant of cortical identity. Lhx2 selector activity is restricted to an early critical period when stem cells comprise the cortical neuroepithelium, where it acts cell-autonomously to specify cortical identity and suppress alternative fates in a spatially dependent manner. Laterally, Lhx2 null cells adopt antihem identity, whereas medially they become cortical hem cells, which can induce and organize ectopic hippocampal fields. In addition to providing functional evidence for Lhx2 selector activity, these findings show that the cortical hem is a hippocampal organizer.

Classic genetic analyses in *Drosophila* have described the roles of "selector" genes (*1*–*3*), which drive developmental patterning events by cell-autonomously specifying cell identity, suppressing alternative fates, regulating cell affinity, and positioning developmental borders that often serve as secondary signaling centers. The LIM homeobox gene *Lhx2*—a vertebrate ortholog of the well-described *Drosophila* selector gene *Apterous* (Ap) (*1*)—has been postulated to act as a selector gene in the developing mouse cerebral cortex (*4*). Lhx2 is expressed in cortical precursor cells but not in the adjacent telencephalic dorsal midline, which consists of choroid plexus epithelium (CPe) and the intervening cortical hem, a secondary source of bone morphogenetic protein (Bmp) and wingless-int (Wnt) signals (figs. S1 and S4) (*4*, *5*). Previous studies indicate that the hem is required for hippocampal induction and/or expansion (*6*, *7*), but evidence that the hem is sufficient to induce and organize hippocampal tissue has been lacking. Conventional Lhx2 null embryos ("standard" knockout, or sKO) (*8*) possess excessive hem and CPe at the expense of hippocampus and neocortex (*4*, *5*). Although this is consistent with a selector gene phenotype, the basic issue of cell autonomy