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Land before water: The relative temporal sequence of human alteration of freshwater ecosystems in the conterminous United States

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1 **Land Before Water: The Relative Temporal Sequence of Human Alteration of Freshwater**

2 **Ecosystems in the Conterminous United States**

3 **Abstract**

4 Human alteration of ecosystems prior to Euro-American contact in the area that became the
5 conterminous United States disproportionately affected terrestrial systems compared to
6 freshwater systems, primarily through the use of fire and agriculture in some regions of the
7 United States. After circa 1600 AD, trapping of beaver, along with intensive modification of
8 rivers and wetlands for navigation, mining, flood control, power generation, and agriculture,
9 substantially altered river corridors throughout the country. River corridor here refers to
10 channels of all sizes, from headwater streams to very large rivers, and includes floodplains and
11 wetlands associated with channels. We contend that ecosystem alteration by humans prior to
12 and during Euro-American settlement changed from predominantly terrestrial to both
13 terrestrial and freshwater in a manner that was time-transgressive with Euro-American
14 colonization and U.S. settlement between the 17th and 19th centuries. The extent and intensity
15 of post-Euro-American alteration of freshwater environments in the United States have
16 resulted in widespread river metamorphosis toward more geomorphically and ecologically
17 homogenous systems. Recognition of the rapidity and ubiquity of this alteration, and the
18 consequent instability of many contemporary river corridors, should underpin contemporary
19 river management.

20 **Introduction**

21 At the start of the 21st century, many scientists question whether the cumulative
22 impacts of human use of resources and alteration of ecosystems are exceeding the limits of
23 sustainability for human survival (Rockström et al., 2009; Steffen et al., 2015). Human
24 manipulations clearly exceeded the limits of sustainability for the hundreds of species that have
25 gone extinct within the past five centuries (IUCN, 2007). As rates of extinction have accelerated
26 during the past century, a grim contest has developed among claims for the ecosystems and
27 groups of organisms with the highest rates of extinction. Are the tropical rainforests, with their
28 astonishing biodiversity, experiencing the greatest loss of diversity (Canale et al., 2012), or are
29 amphibians in diverse environments disappearing the most rapidly (McCallum, 2007)?
30 Unfortunately, freshwater fauna in North America are a contender in this contest, with
31 projected future rates of extinction five times greater than the rate for terrestrial fauna
32 (Ricciardi and Rasmussen, 1999). A diverse and complicated history of wetland drainage, river
33 engineering, water pollution, and introduced species underlies high rates of freshwater species
34 extinctions, but it is worth considering when some of the human alterations of freshwater
35 ecosystems began relative to those of terrestrial ecosystems. Here, we review how humans
36 began altering the terrestrial environments of North America prior to the modern imperial and
37 national eras, but discuss how it was only during the intensive industrial development of North
38 America by people of European descent that freshwater environments were substantially
39 altered.

40 Early explorers and settlers from Europe perceived North America as a wilderness
41 completely unaffected by human activities, a perception that Denevan (1992) referred to as the
42 pristine myth. This perception was tenacious and long-lived, but extensive research has now

43 established that pre-Columbian societies altered at least some portions of terrestrial
44 ecosystems in what is now the United States prior to Euro-American settlement via burning,
45 settlements, and subsistence activities (e.g., Butzer, 1990; Denevan, 1992; Vale, 1998, 2002).
46 Although Native American irrigation techniques physically modified river corridors in certain
47 parts of North America such as the U.S. Southwest (e.g., Doolittle 1992, 2009), we contend that
48 pre-Columbian societies had a much smaller impact on river corridors compared to the
49 terrestrial landscape of North America. In contrast, Euro-American settlement resulted in rapid
50 and significant alterations of both terrestrial landscapes and river corridors in a variety of ways.

51 This paper reviews existing literature on human alterations of terrestrial and freshwater
52 ecosystems prior to and following settlement of the conterminous United States by people of
53 European descent, with an emphasis on freshwater alterations after Euro-American settlement.
54 Native American here refers to people whose ancestors migrated eastward to North America
55 from Asia and were present in North America prior to Euro-American settlement. Euro-
56 American here describes people who migrated directly from Europe or whose ancestors
57 migrated westward to North America from Europe. We use 1600 AD as a time boundary for
58 considering ecosystem alteration prior to and following Euro-American settlement, although
59 the time of initial direct and indirect contacts between Euro-Americans and Native Americans
60 varied among different regions of the United States and North America. Discussion of the
61 effects of human alteration of freshwater ecosystems focuses on river corridors, which include
62 channels regardless of size, floodplains, and floodplain wetlands, but also briefly reviews lakes.
63 We suggest that understanding the broad patterns of timing in human modifications of

64 terrestrial and freshwater ecosystems provides important insight for managing and protecting
65 these ecosystems.

66 **Human alterations of ecosystems prior to Euro-American settlement**

67 The contention that Native Americans altered terrestrial ecosystems to a greater extent
68 than freshwater ecosystems is based on extensive scholarship focused on diverse geographic
69 regions within the United States, as reviewed briefly in the next two sections.

70 ***Alteration of terrestrial ecosystems***

71 Studies of prehistoric societies from various regions of the United States clearly indicate
72 that many Native American communities significantly altered terrestrial ecosystems. Fire was
73 widely used in diverse ecosystems to improve access to animals; improve or eliminate forage
74 for animals on which people depended for food; drive and encircle animals; increase the
75 production of gathered foods; and clear forest vegetation for garden plots or enhance
76 conditions for favored fruit and mast trees (Pyne, 1982; Krech, 1999; Abrams and Nowacki,
77 2008). Historical sources document these practices from at least some environments in New
78 England (Cronon, 1983; Parshall and Foster, 2002), other portions of the eastern United States
79 (Abrams and Nowacki, 2008), the Cumberland Plateau (Delcourt and Delcourt, 2004), across the
80 prairies (Wohl, 2013b) and some environments within the Intermountain West (e.g., Baker,
81 2002), to parts of California (Solnit, 1994; Parker, 2002). As Krech (1999) notes in his book on
82 Native American environmental practices, deliberate burning "... may indeed have been the
83 most prevalent tool employed by Indians to manipulate their environment ..." (p. 110). The
84 environmental effects of deliberately set fires varied between ecosystems and depended on

85 how frequently and over what extent people used fire, and environmental scientists continue
86 to debate the relative importance of human versus climate controls on fire regimes in diverse
87 areas, as well as local versus regional effects of fire (e.g., Vale, 2002; Marlon et al., 2013; Munoz
88 et al., 2014). Nonetheless, terrestrial ecosystems in much of the United States were at least
89 partly influenced by this form of human-induced disturbance.

90 Changes to terrestrial ecosystems associated with deliberately set fires included altered
91 type of vegetation cover (e.g., dense forest versus open woodlands or grasslands); altered
92 species composition of plant communities (increased fires favored more fire-tolerant species)
93 and of animal communities associated with those plants; altered carbon and nutrient stocks
94 (Turner, 2010; Buma et al., 2014; McLauchlan et al., 2014); and alterations of water and
95 sediment yield to freshwater ecosystems (Shakesby and Doerr, 2006). The magnitude and
96 spatial extent of all these potential changes in response to deliberately set fires varied as a
97 function of the severity, frequency, and spatial extent of the fires, and much of the ongoing
98 debate about Native American use of fires centers on the details of fire severity, frequency, and
99 spatial extent.

100 Husbandry of selected herbaceous and woody plants, and deliberate planting and
101 tending of crops, also affected some terrestrial ecosystems. Native Americans grew a variety of
102 crops, but maize formed the central focus of most prehistoric agriculture. Maize was introduced
103 to the southwestern U.S. from Mexico by 2100 BC (Merrill et al., 2009) and spread from there
104 to the eastern United States. Prehistoric people in arid and semiarid regions of the Southwest
105 developed several techniques for growing crops, including seepage fields downslope from
106 springs; water-table fields in wetlands; irrigation ditches such as at Montezuma Wells in

107 Arizona, USA; mulching to retain moisture; rock-bordered grids to alter the movement of wind
108 and/or water; and low stone terraces known as trincheras on hillslopes (Doolittle, 2000).

109 Native American agriculture, like Euro-American agriculture, involved replacing native
110 land cover with cultivated plants. Native Americans in the area that became New England used
111 fire to clear patches within the forest, then planted the patches for approximately a decade
112 until soil fertility began to decline. Annual reoccupation of fixed village and planting sites also
113 depleted the supply of firewood in the vicinity and early Euro-American colonists wrote of
114 thousands of acres of treeless land around Native American settlements (Cronon, 1983).
115 Estimated Native American population densities were seven times greater in grain-growing
116 communities in southern New England than in communities in northern New England that
117 relied solely on hunting and gathering (Cronon, 1983).

118 Pre-contact Native American cultures across large portions of the United States outside
119 of New England and other agricultural areas such as the upper and central Mississippi River
120 valley (Delcourt and Delcourt, 2004) and the Southwest relied primarily on hunting and
121 gathering rather than intensive agriculture, which limited alteration of terrestrial ecosystems.
122 Population density and the intensity of cropping also varied through time within agricultural
123 regions, creating associated fluctuations in the intensity of ecosystem alteration. However,
124 agricultural communities significantly altered at least portions of surrounding terrestrial
125 ecosystems.

126 The ongoing debate about the spatial extent and intensity of ecosystem alteration by
127 Native Americans prior to Euro-American settlement indicates the difficulty of quantifying
128 prehistoric human effects on terrestrial ecosystems. Generalizing across the conterminous

129 United States, Native American alterations were less extensive and intensive than subsequent
130 Euro-American alterations because Native Americans had lower population densities, simpler
131 technologies, and lack of integration into global commercial markets and hence lower demands
132 for resources. Consequently, Native American alterations of water and sediment yields from
133 uplands, as well as of plant and animal communities, were for the most part less intense and
134 less persistent than subsequent Euro-American alterations. Native Americans did alter some
135 terrestrial environments, however, in ways that can be detected in geological and archeological
136 records (e.g., Delcourt et al., 1998).

137 ***Alteration of freshwater ecosystems***

138 In contrast to the alteration of terrestrial ecosystems through the localized use of fire
139 and planting of crops in diverse regions of the United States, there are few examples of Native
140 American communities significantly altering freshwater ecosystems. People in specific regions
141 depended on fish, mussels, wild rice, and other freshwater organisms for a substantial portion
142 of their nutrition, and at least wild rice appears to have been cultivated to some degree
143 (Doolittle, 2000). There is no evidence, however, that the methods used to obtain these foods
144 substantially altered the morphology of rivers, lakes, or wetlands, or the flow regime of rivers.
145 The Hohokam of central Arizona, one of the most impressive and well-studied prehistoric
146 Southwestern agricultural societies, provide an example of the lack of substantial alteration of
147 freshwater ecosystems.

148 The Hohokam built the largest canal system in pre-Columbian North America during the
149 10th to 15th centuries (Doolittle, 1992; Krech, 1999). Scattered villages used a variety of

150 agricultural techniques and at least some of the settlements relied on irrigated agriculture, with
151 crops grown in floodplains using water diverted from rivers. Archeologists disagree on
152 Hohokam population numbers through time. Canal networks built and used during different
153 time intervals make it difficult to infer how much water might have been diverted from the Salt,
154 Gila, Verde, Santa Cruz, and other rivers in the region. However, there is no evidence that the
155 Hohokam diverted enough water to change river processes downstream from their diversion
156 points, and they did not build dams or large water retention structures (Krech, 1999).

157 Exceptions to the lack of Native American alterations of freshwater ecosystems come
158 from relatively densely populated agricultural societies in the eastern half of the United States.
159 Archeological sites scattered across the eastern United States and the Mississippi Valley
160 indicate that maize-based agriculture helped to support relatively high population densities and
161 more intensive alteration of upland and riparian ecosystems for agriculture. Removal of natural
162 land cover changed water and sediment yields from uplands in a manner recorded in alluvial
163 sediments. Lake and floodplain stratigraphy from some sites along the Illinois and Mississippi
164 Rivers indicates increased sedimentation associated with upland farming during the Archaic
165 Period (8,000-600 BC) and with farming in the valley bottoms of the Mississippi drainage during
166 the Woodland Period (600 BC to AD 1050) (Green and Nolan, 2000). Population density and the
167 style and importance of agriculture relative to hunting and gathering varied through time. Large
168 settlements and intensive agriculture reached an apogee during the Mississippian Period (AD
169 850-1450), which gave rise to sites such as Cahokia on the Mississippi River near St. Louis.
170 Sedimentation at an archeological site at the confluence of Raymondskill Creek and the
171 Delaware River and at other sites in eastern North America suggests an episode of increased

172 sedimentation in freshwater environments (floodplain, tidal-marsh, lacustrine) during A.D.
173 1100—1600 in association with maize crops (Stinchcomb et al., 2011). With the exception of
174 river corridors within a few regions of the Mississippi River drainage basin, however, Native
175 American agriculture did not significantly increase sedimentation along river networks across
176 the conterminous United States (James, 2011).

177 The combined picture that emerges from scattered archeological sites is one of
178 temporal and spatial fluctuations in sedimentation in freshwater ecosystems as population and
179 land use locally increased and decreased over time intervals of centuries to millennia. After
180 circa A.D. 1600, the combined effects of climate change, Euro-American diseases, and Euro-
181 American invasion substantially reduced Native American population levels in the eastern
182 United States and displaced people westward. Relatively densely settled prehistoric
183 communities locally influenced wetlands and riparian areas through farming in riparian areas
184 and increased sedimentation, but, with the exception of the Hohokam, these communities did
185 not develop irrigation networks and there is no evidence that they altered channel morphology
186 or flow regime on the rivers they lived along. Based on the use of fire and upland agriculture by
187 Native American communities in at least some types of terrestrial ecosystems across the United
188 States, and the spatially and temporally limited effects of Native American agriculture on
189 sedimentation in freshwater ecosystems, we generalize Native American alteration of
190 ecosystems as affecting predominantly upland, terrestrial environments.

191 **U.S. rivers circa 1600 AD**

192 Before reviewing Euro-American alteration of freshwater ecosystems in the United
193 States, it is useful to describe the condition of these ecosystems prior to intensive Euro-
194 American settlement of the country and after many centuries of occupation by Native
195 Americans. Most rivers, floodplains, and wetlands throughout the conterminous United States
196 had a substantially different appearance than they do today. First, much more of the landscape
197 was seasonally or perennially inundated (Vileisis, 1997). Diverse wetlands along river corridors
198 and elsewhere – marshes, swamps, lakes, ponds, fens, mires, prairie potholes, playas – were
199 more abundant and larger. Writing of New England as it appeared in 1633, for example, William
200 Wood described swamps 30 to 50 km wide (Cronon, 1983). Spatially extensive black soil layers
201 characteristic of organic matter accumulating in the reducing environment of riverine wetlands
202 inundated by beaver ponds indicate the past location of marshes and swamps, as described for
203 extensive portions of valley bottoms across the eastern and Midwestern United States (e.g.,
204 Morgan, 1868; Mills, 1913; Dugmore, 1914). Other historically extensive swamps such as the
205 Black Swamp (~4200 km² in extent) along Ohio’s Maumee River were likely facilitated by large
206 accumulations of downed wood from trees blown over during tornadoes (Kaatz, 1955).
207 Naturally occurring wood rafts – concentrations of wood extending along many kilometers of
208 river channel and persisting for decades to centuries – blocked the passage of flood waters and
209 created flooded bottomlands along rivers as varied as Louisiana’s Red River, the Manistique
210 River of Michigan, Otter Creek in Vermont, Ohio’s Maumee River of Ohio, the Guadalupe River
211 of Texas, and the Willamette River of Oregon (Wohl, 2014).

212 Some of the nation’s major aquifers, such as the Ogallala (Basso et al., 2013), had much
213 higher water tables. Many riparian water tables, especially in arid and semiarid regions, were

214 higher (e.g., Stromberg et al., 1996; Falke et al., 2011). Springs and seeps were more common
215 and discharged more water. Floods were unregulated, spilling across extensive bottomlands for
216 weeks to months at a time in environments as diverse as Florida (Douglas, 1947), Illinois
217 (Steele, 1841), the lower Mississippi (Schramm et al., 2009), rivers of the Great Plains fed by
218 snowmelt from the Rockies (Wohl, 2013b), California's Central Valley (Ingram and Malamud-
219 Roam, 2013) and western Oregon and Washington (Sedell and Luchessa, 1981).

220 Smaller rivers in forested environments in many cases resembled a staircase of ponds
221 created by sequential beaver dams along the channels. From the smallest creeks to the great
222 rivers such as the Ohio, Illinois, Atchafalaya, and lower Mississippi, rivers in forested
223 environments contained abundant wood in the channel and across the floodplain (Wohl, 2014).
224 The earliest written descriptions from channels in New England and the Southeast across the
225 Great Lakes region to the Pacific Northwest emphasize the enormous quantities of individual
226 logs, jams, and enormous wood rafts in rivers. Along with beaver dams on small rivers and
227 floodplains, all of this instream wood slowed the passage of high discharges, forcing water
228 across the floodplain and into secondary channels, as well as into the subsurface to recharge
229 riparian aquifers and help to maintain wetlands. Beaver dams and logjams also facilitated
230 lateral channel migration and formation of secondary channels, which further enhanced the
231 formation of riparian wetlands.

232 Channels of all sizes were much more physically complex than we are used to seeing
233 today. From prairie creeks and small rivers of the Mid-Atlantic Piedmont that flowed along
234 marshy swales with multiple, subparallel, poorly defined channels (Walter and Merritts, 2008),
235 to large rivers of the Great Plains with braided sections (Williams, 1978; Nadler and Schumm,

236 1981) and large rivers of the Pacific Northwest with anastomosing planform (Collins et al.,
237 2002), river channels were commonly diffuse and poorly defined. Early explorers, from Louis
238 Hennepin on the Illinois River in 1679 to Mark Twain navigating the Mississippi River during the
239 1850s (Twain, 1883), and Army engineers on the Willamette River in 1870, complained of the
240 difficulty in following the main course of a river. In arid regions such as central Arizona,
241 channels that are now dry and deeply incised were perennial rivers that supported riparian
242 forests and beaver colonies (Rea, 1983; Webb et al., 2014). Across the United States, river
243 corridors were wetter and more spatially heterogeneous at scales from individual river
244 segments to entire watersheds. This physical diversity equated to abundant and diverse
245 habitat, as well as retention of nutrients and organic matter, and supported an enormous
246 biodiversity (Perry et al., 2002).

247 **Human alterations of ecosystems following Euro-American settlement**

248 Native American cultures followed widely different patterns of settlement that affected
249 their impacts on terrestrial and freshwater ecosystems. Pueblo peoples of the southwestern
250 United States lived in the same dwellings and community locations for centuries, for example,
251 whereas other cultures moved seasonally or at other relatively short time intervals. Individual
252 families of European descent followed the westward-moving frontier of settlement across the
253 conterminous United States over a period of decades. Consequently, exceptions exist to any
254 generalization about settlement patterns of either Native Americans or Euro-Americans. With
255 that caveat, we generalize that settlement of the United States by Euro-Americans commonly
256 involved rapid and more intense alteration of terrestrial environments than terrestrial

257 alterations associated with much of the Native American occupation of the land. Euro-
258 Americans were more likely to settle in communities intended to remain in place for decades to
259 centuries, and Euro-Americans were more likely to rapidly undertake intensive and extensive
260 alteration of land cover for profit (e.g., commercial timber harvest or mining). Land cover
261 change also occurred as a side effect of technological developments, such as substantial
262 increases in fire severity and extent in association with sparks from coal-burning railroad trains
263 (Pyne, 1982).

264 Contact with Euro-American communities and associated commercial markets also
265 influenced Native American alteration of terrestrial environments by creating competition for
266 existing land and resource uses; altering the geographic extent and population levels of specific
267 Native American groups; and in some cases integrating Native American communities into the
268 enormous commercial markets of Europe and Asia via exports such as furs (e.g., Du Val, 2006;
269 Fenn, 2014; Davidann and Gilbert, 2016). Initial Euro-American contact led Algonquians and
270 Iroquois in the Potomac River basin, for example, to intensify maize production (Rice, 2009).
271 Access to horses greatly increased the mobility of Native Americans of the Great Plains, creating
272 more extensive and locally intensive alteration of grassland ecosystems, especially where
273 Native American access to adjacent mountains was restricted by Euro-American hunting and
274 settlement (West, 1998). Although Euro-American diseases and warfare greatly reduced Native
275 American population numbers across the United States, Native American peoples did not cease
276 to exist with the start of Euro-American settlement. Instead, Native American impacts on
277 terrestrial ecosystems changed, although the details vary between individual Native American
278 groups and through time.

279 Settlement of the United States by Euro-Americans was also accompanied by many
280 resource uses that affected freshwater environments, most of which occurred nearly
281 simultaneously and were commonly interrelated. These include: beaver trapping; wetland
282 drainage; timber harvest and log floating; placer and lode mining; navigation, river clearing, and
283 channelization; construction of canals; overharvest of freshwater species and fish stocking;
284 construction of dams and water diversions; construction of levees; changes in water and
285 sediment yields from uplands as a result of clearing native vegetation and changing the fire
286 regime; and contamination of surface and ground water via diverse materials ranging from
287 sewage and organic waste to increasingly toxic and persistent synthetic chemicals. The details
288 of which resource use affected freshwater environments in a particular region first and/or most
289 intensively depend on when Euro-Americans first reached the region and the specific
290 characteristics of the region. Commercial timber harvest initiated Euro-American settlement of
291 the northern Great Lakes region, for example, and the modification of channel form and flow
292 regime to facilitate downstream transport of logs constituted the first significant alteration of
293 river corridors in the region. In contrast, agriculture and establishment of towns initiated Euro-
294 American settlement of the eastern seaboard, so that river corridors were first altered through
295 practices such as construction of milldams and drainage of riparian and other wetlands. **Figure**
296 **1** summarizes these patterns.

297 The specific effects associated with a particular category of resource use also changed
298 with time as a result of technological changes. Contamination of surface waters by excess
299 sediment, distillery or slaughterhouse waste, or wood waste from sawmills (Kofoid, 1903), for
300 example, later gave way to contamination by synthetic chemicals such as organochlorine

301 pesticides and PCBs (Kraus et al., 2017). Similarly, the size and operation of 18th-century mill
302 dams differed significantly from the size and operation of 20th-century hydroelectric dams.

303 In the sections that follow we briefly review the diverse human activities that altered
304 freshwater ecosystems during and after Euro-American settlement. Our emphasis is on
305 freshwater ecosystems in order to highlight the contrast between the limited effects on
306 freshwaters by Native Americans and the significant effects on freshwaters by Euro-Americans.

307 ***Beaver trapping***

308 One of the earliest Euro-American influences on natural (rather than human)
309 communities in the United States was commercial exploitation of individual species. In many
310 regions of the United States, beaver trapping was the first substantial alteration of river
311 corridors, and beaver populations were decimated prior to permanent Euro-American
312 settlement of an area. Trapping of beavers provides an especially striking example of how Euro-
313 American activities substantially altered freshwater ecosystems.

314 Ecologists estimate that as many as 400 million beavers (*Castor canadensis*) occupied
315 rivers and wetlands from northern Alaska down into northern Mexico when Euro-Americans
316 first reached North America (Naiman et al., 1988). By building dams, beavers created riparian
317 wetlands that attenuated downstream fluxes of water, fine sediment, organic matter, and
318 nutrients (Naiman et al., 1994; Westbrook et al., 2013; Wegener et al., in press). These effects
319 were recognized by early Euro-American settlers in New England, who prized the fertile soil of
320 valley bottoms formerly occupied by beavers (Cronon, 1983). Beaver-created wetlands
321 supported high diversity of microbes, plants, and animals from insects to mammals (Rosell et
322 al., 2005). Individual beaver meadows – segments of valley bottom with numerous dams and

323 ponds – persisted for thousands of years (Kramer et al., 2012; Polvi and Wohl, 2012) and
324 created resistance and resilience to disturbance within river ecosystems (Hood and Bayley,
325 2008).

326 Having driven Euro-American beavers (*Castor fiber*) nearly to extinction by the 12th
327 century in some parts of Eurasia by the end of the 19th century, the Euro-American fur trade
328 systematically and energetically exploited North American beaver populations starting with
329 eastern North America during the early 17th century and progressing westward. North American
330 beaver populations fell to 6-12 million by the mid-19th century (Naiman et al., 1988). Although
331 beaver populations in Eurasia and North America are gradually recovering and beavers are now
332 actively reintroduced as part of river restoration in both continents, scientists are still trying to
333 understand the cumulative effects of severe beaver-population declines on freshwater
334 environments (Hood and Bayley, 2008; Green and Westbrook, 2009; Johnston, 2012; Polvi and
335 Wohl, 2012, 2013). Among the most significant cumulative effects of substantially reduced
336 beaver activity are declines in habitat and biodiversity (e.g., Bartel et al., 2010; Peipoch et al.,
337 2014) and decreased retention of water, solutes, sediment, and particulate organic matter
338 within river corridors (e.g., Wegener et al., in press) (Figure 2).

339 ***Wetland drainage***

340 Euro-American immigrants to the United States brought with them a cultural history of
341 wetland drainage. The Dutch were pre-eminent at developing techniques to drain wetlands and
342 Dutch engineers taught the English: by 1649, more than 38,000 ha had been drained in England.
343 George Washington’s library included a copy of the 1775 “Practical Treatise on Draining Bogs

344 and Swampy Ground” (Simco et al., 2009). Seventeenth-century Euro-American colonists along
345 the eastern seaboard immediately began altering salt marshes through haying and grazing, as
346 well as draining, diking, and building cities (Baltimore, Philadelphia, Boston, New York,
347 Charleston, and others) on coastal wetlands. Freshwater marshes along rivers such as the
348 Sudbury and Concord in Massachusetts were similarly used for haying as early as the 1630s.
349 These uses of river corridors occurred simultaneously with beaver trapping: more than 10,000
350 beavers were killed in Connecticut and Massachusetts during the 1620s and more than 80,000
351 beavers per year were hunted from the Hudson River and western New York during 1630 to
352 1640 (Vileisis, 1997). The beaver trade ended in New England by 1660 (Cronon, 1983) as the
353 animals largely disappeared from the region as a result of trapping.

354 Farther south, most colonial governments required landowners to improve their land
355 either through cultivation or by clearing and draining in order to gain land title. By the final
356 decade of the 1700s, almost all rice planters from North Carolina south to Florida had moved
357 their plantations down to tidally influenced freshwater rivers, which they altered with elaborate
358 networks of dikes, check banks, flood gates, ditches, canals, drains, and rice-milling dams. These
359 activities altered the hydrology of river corridors sufficiently to create problems with saltwater
360 intrusions (Silver, 1990; Stewart, 2002). Much of this agriculture was simultaneous with floating
361 of cut timber downstream to sawmills. Loggers altered access to interior timber stands by
362 digging canals and draining portions of extensive wetlands such as the Great Dismal Swamp
363 (late 1760s). In the lower Mississippi River valley, swamp forests along river corridors were
364 logged during initial settlement (1717) for valuable timber from bald cypress, then drained and
365 cropped (Vileisis, 1997).

366 As Euro-American settlement proceeded westward, riparian wetlands were not
367 necessarily the first target for croplands, but they were commonly modified within two to three
368 decades of settlement. In the Illinois prairie, for example, John Deere's 1837 invention of the
369 self-scouring, steel-bladed plow allowed farmers to cut through the dense network of
370 grassroots and cultivate the uplands following the initial rush of Euro-American settlers at
371 statehood in 1819. The 1850 Swamp Land Act ceded federal swamplands to Illinois and other
372 states with the intention of facilitating wetland drainage using levees, drains, and ditches
373 (Vileisis, 1997) (Figure 3). Alteration of river corridors proceeded rapidly (Wohl, 2013b). In
374 Illinois, state legislation in 1879 facilitated the organization of levee districts that used state
375 funds to build levees, drain wetlands, and channelize rivers (Landwehr and Rhoads, 2003). To
376 cite another example, Euro-American settlement in western Mississippi began about 1830 and
377 by 1840 settlers were channelizing streams and draining wetlands (Shields et al., 1995).

378 An estimated 89.4 million ha of wetlands existed in the conterminous United States
379 circa 1780 (Dahl, 1990), even though Euro-Americans had been altering river corridors along
380 the eastern seaboard for more than a century. By 1980, wetlands had shrunk to approximately
381 42.2 million ha. Ten states had lost more than 70 percent of their wetlands by 1980 and 22
382 states had lost more than 50 percent (Dahl, 1990). In the words of a 1973 Congressional report:

383 For the last three-and-a-half centuries Americans have busily settled,
384 developed and cultivated the continent's flood plains. In this, they
385 were more bold than prudent.... They stubbornly refused to recognize
386 a flood plain for what it is.... In Delaware, Maryland, and other
387 middle-Atlantic States, extensive drainage networks were dug by

388 slaves. Later, in the last decades of the 19th century, drainage districts
389 were established and thousands of miles of trenches gouged to dry up
390 wetlands. (CGO, 1973, p. 2)

391 The implications of the diverse forms of wetland drainage were twofold. First, wetlands
392 very effectively attenuate downstream fluxes of water, fine sediment, and dissolved and
393 particulate organic matter. By limiting attenuation and storage of these materials, wetland
394 drainage altered riverine flow regimes, sediment transport, and nutrient availability in ways
395 that stressed aquatic, riparian, and coastal biotic communities. Second, wetlands, including
396 those in river valleys, are disproportionately important sources of habitat and food relative to
397 the area that they occupy in the total landscape (Amoros and Bornette, 2002; Dudgeon et al.,
398 2006). Wetland drainage largely eliminated vital wetland habitat for many species of plants
399 and animals.

400 ***Timber harvest and log floating***

401 From the eastern seaboard to the Great Lakes and across the Intermountain West and
402 the Pacific Northwest, commercial timber harvest commonly began by using existing waterways
403 to float cut logs to collection booms for transport to sawmills (Wroten, 1956; Sedell et al., 1991;
404 Cowan, 2003; McMahon and Karamanski, 2009). This practice began during the first half of the
405 17th century in Maine and New Hampshire (Cronon, 1983) and then moved progressively
406 westward with the Euro-Americans. Although railroads subsequently took over the
407 transportation of cut logs during the 19th century, the use of rivers to transport logs typically
408 lasted for at least a decade in regions initially settled by Euro-Americans during the 19th

409 century. In some regions, log transport on rivers persisted much longer as each new area of
410 forest was opened to timber harvest.

411 Log floating had at least three effects on rivers (Sedell et al., 1991; Cowan, 2003; Wohl,
412 2014). First, the logs themselves altered channel boundaries, dislodging existing instream wood
413 and battering the channel bed and banks and riparian vegetation, particularly when thousands
414 of logs were floated downstream during a single season (Figure 4). Second, channels were
415 commonly modified to facilitate the movement of logs. Overbank areas such as floodplains and
416 secondary channels were blocked, obstructions within the channel such as wood and large
417 boulders or bedrock were blasted out, and small channels were enlarged. Third, splash dams
418 were built on small to medium channels throughout river networks to facilitate log movement.
419 These small, temporary dams were allowed to fill with water and logs and then dynamited to
420 send the logs rapidly downstream in an outburst flood.

421 Log floating and associated channel modifications extended from headwater channels
422 just barely wider than the diameter of a log to the largest rivers in the country. Although log
423 floating typically lasted at most a decade in a given region (until all of the marketable timber
424 had been cut or railroads took over transportation of cut logs), the enlargement and
425 simplification of affected channels has persisted for more than a century (Young et al., 1994;
426 Miller, 2010; Ruffing et al., 2015). Removal of upland and riparian forests during timber harvest,
427 where spatially extensive and intensive (i.e., clearcutting rather than selective cutting), also
428 increased water and sediment yields to adjacent river corridors and lakes (Cronon, 1983). As
429 with other land uses affecting river corridors after Euro-American settlement, the timing of
430 timber harvest and log floating varied among regions. New York State led the nation for volume

431 of timber production in 1859, for example, but peak production shifted to states such as
432 Wisconsin and Minnesota during the 1870s to 1900, before shifting to the Pacific Northwest
433 during the early 20th century (Wohl, 2014).

434 The ecosystem implications of timber harvest and log floating primarily involved loss of
435 habitat abundance and diversity as channels and floodplain wetlands were simplified and
436 laterally disconnected from one another; loss of attenuation of peak flows and storage of
437 nutrients and organic matter as simplified river corridors more rapidly passed material
438 downstream; loss of naturally occurring instream wood and obstructions such as beaver dams
439 that limited longitudinal connectivity and increased lateral and vertical connectivity; and lower
440 biomass and biodiversity of aquatic and riparian organisms as a result of loss of habitat and
441 nutrient retention (Young et al., 1994; Nilsson et al., 2005; Helfield et al., 2007; Ruffing et al.,
442 2015).

443 ***Placer and lode mining***

444 Placer deposits are precious metals such as gold that are mixed with alluvial sediments
445 in river valleys and terraces. Lode deposits are in place within bedrock and can occur as veins of
446 precious metals such as gold and silver within igneous or metamorphic rocks, or in the form of
447 ores such as iron or uranium within sedimentary rocks. Placer deposits are inherently
448 associated with freshwater ecosystems and many types of lode deposits are most accessible
449 within river corridors.

450 By displacing vegetation, soils, and overlying sediments or rock units, both placer and
451 lode mining involved extensive disruption of surface cover and topography, which commonly

452 resulted in substantially increased volumes of sediment entering freshwater ecosystems
453 (Wagener and LaPerriere, 1985; James, 1991, 1994, 1999; Hilmes and Wohl, 1995). Removal of
454 upland forest cover for timber used directly in mining (e.g., timbered ore shafts, fuel for steam-
455 powered stamp mills, charcoal production) and for communities and transportation systems
456 associated with the mining further exacerbated changes in water and sediment yield to
457 freshwater ecosystems (Syvitski et al., 2005), as did construction of water-powered mills.
458 Deforestation commonly occurred extremely rapidly and over large areas in association with
459 mining. A typical furnace associated with iron mining in the eastern and southeastern United
460 States, for example, consumed 0.4 ha of forested land per day while in use (Hart et al., 2008).
461 Increased sediment yields affected river corridors by overwhelming sediment transport capacity
462 and accumulating sediment in channels and on floodplains. Small increases in sediment supply
463 can smother bottom-dwelling organisms or limit the survival of fish (Van Nieuwenhuysen and
464 LaPerriere, 1986; McLeay et al., 1987). Progressively greater amounts of sediment can bury
465 spawning habitat, fill channels and transform them from meandering to braided, fill floodplain
466 wetlands and lakes, and substantially reduce the abundance, diversity, and stability of habitats
467 within the river corridor (Gilvear et al., 1995).

468 Introduction of contaminants such as mercury used to amalgamate placer gold
469 commonly accompanied mining (Singer et al., 2013), further disrupting freshwater ecosystems
470 with an extremely persistent and highly toxic substance. Mercury, in particular, bioaccumulates
471 within individual organisms and biomagnifies within food webs, limiting the health and survival
472 of a wide variety of organisms (May et al., 2000). Other toxic metals and acids associated with
473 the ores containing precious metals were released into streams and rivers, rendering them

474 virtually barren for kilometers downstream. Acid mine drainage is lethal to fish, invertebrates,
475 and algae. In the Rocky Mountain region alone, more than 15,500 km of streams below mines
476 are impaired and unable to support native freshwater communities (Baron et al., 2002).

477 Examples of placer and lode mining that directly affected freshwater ecosystems come
478 from iron mining in many portions of the eastern United States during the 18th and 19th
479 centuries (Swank, 1892; Hart et al., 2008); 19th-century placer and lode mining of gold in the
480 Southern Appalachians (Pardee and Park, 1948); and 19th-century placer gold mining in
481 California's Sierra Nevada (James, 1991) (Figure 5) and the Colorado Rockies (Wohl, 2001).

482 ***Navigation, river clearing, and channelization***

483 Navigation, river clearing, and channelization here refer to a suite of channel
484 modifications undertaken to facilitate the downstream passage of cut logs to sawmills, reduce
485 overbank flooding, and improve navigation for boats from small flatboats and keelboats to
486 commercial steamboats and barges. Prior to the development of extensive railroads after the
487 Civil War (1861-1865), natural waterways and canals formed the most efficient and economical
488 transport network in the United States for moving large volumes of material. After Robert
489 Fulton designed an efficient steamboat in 1807, rapidly accelerating use of these larger boats
490 required extensive modification of rivers to remove the dangerous snags that could quickly sink
491 a steamboat and to create uniform minimum flow depths through dredging.

492 It is difficult to over-estimate the extent and intensity of river corridor modification
493 associated with steamboat traffic, which occurred along most rivers of suitable size in the
494 eastern half of the United States during the 19th and early 20th centuries and along a more

495 limited number of rivers in the western U.S. (Wohl, 2014). Desire to enhance steamboat
496 navigation led to: direct modification of channels (removal of millions of logs, dredging,
497 blasting, straightening, blocking off overbank areas); extensive riparian deforestation
498 associated with the need for wood to power the steamboats; greater settlement of remote
499 areas by transporting people and goods to these regions; and federal involvement in river
500 engineering (Harmon et al., 1986; Wohl, 2014). Congressional appropriations for removing
501 wood from rivers date to the very start of the nation, in 1776 (Harmon et al., 1986), but
502 assigning the engineering of inland rivers to enhance steamboat traffic to the U.S. Army Corps
503 of Engineers in 1824 institutionalized these practices (Reuss, 2004).

504 Some of the most sustained efforts at wood removal included dismantling the
505 enormous, naturally occurring wood rafts such as the famous Great Raft on Louisiana's Red
506 River. While present, this accumulation of wood enhanced overbank flows, channel-floodplain
507 connectivity, and the formation of an anastomosing channel planform in which multiple
508 secondary channels branch around vegetated islands before rejoining the main channel
509 downstream (Triska, 1984; Wohl, 2014). This greatly increased the diversity of aquatic and
510 riparian habitats, as well as retaining dissolved and particulate nutrients, and increasing the
511 extent of biologically rich floodplain wetlands.

512 Dredging and straightening channels, although undertaken on a small scale by
513 individuals or local groups for more than a century, also accelerated when the U.S. Army Corps
514 of Engineers began channelizing the Mississippi River in the 1870s (Gillette, 1972) (Figure 6).
515 Channelized systems can reduce overbank flooding within the zone of channelization, but
516 commonly exacerbate flooding and sedimentation downstream. Eroding channels can

517 destabilize an entire watershed by dropping base level for tributaries that then incise, further
518 exacerbating downstream sediment yields and typically reducing the abundance, diversity, and
519 stability of instream and riparian habitats in the affected segments of the river corridor (Shields
520 et al., 1995). Even if channelization is not continued, affected channels can require several
521 decades to become stable again (Simon, 1994).

522 ***Construction of canals***

523 Prior to development of the national railroad network, bulk materials were most
524 efficiently transported via boats on natural rivers and lakes. Spanning the spatial gaps in this
525 natural freshwater transportation network became a priority of early commercial development
526 in the United States, with private companies and various levels of government contributing to
527 the construction of canals (Cowan, 1997).

528 The Erie Canal was the first major water project in the United States. Begun in 1817, the
529 canal linked Lake Erie with the Hudson River (Langbein, 1976). A major problem with the 584-
530 km-long canal was seepage of canal water into adjacent soils and rivers crossing the canal, but
531 expected problems of extensive erosion and flooding were not reported. The Erie Canal may
532 have been responsible for the introduction of the nonnative sea lamprey (*Petromyzon marinus*)
533 or alewife (*Alosa pseudoharengus*) to the Great Lakes, where their introduction disrupted lake
534 food webs and caused severe damage to native lake trout and other native fish populations
535 (Christie and Goddard, 2003).

536 Canals had a relatively short duration as useful transportation networks because of the
537 rapid development of railroads starting in the 1830s (Cowan, 1997). Many of the transportation

538 canals continued to exist for decades, however, creating sources of potential environmental
539 alteration. Other canals were built for different purposes, such as diversion of waste or
540 diversion of water for consumptive uses or for dilution of waste. Canals associated with water
541 diversion for consumptive uses are discussed in a subsequent section of this paper in
542 association with flow regulation. The effects of canals designed primarily for waste disposal are
543 exemplified by the 47-km-long Sanitary and Ship Canal completed in 1900 to link the Illinois
544 River to Lake Michigan. The intent of the canal was to divert wastewater from Chicago into the
545 Illinois River. Prior to construction of the canal, Chicago dumped wastewater into Lake Michigan
546 and extracted drinking water from the lake, leading to repeated outbreaks of cholera (Wohl,
547 2013b). Diversion of sewage into the Illinois River created a downstream-progressing wave of
548 extinction of freshwater organisms (Richardson, 1918; Colten, 1992). The canal is currently of
549 concern as a corridor for the potential invasion of Asian carp species established in the
550 Mississippi River drainage (Sandiford, 2009). Since the 1800s and end of the 20th century, 180
551 non-indigenous aquatic species have become established in the Great Lakes (Van Der Zanden et
552 al., 2009). Many of these species were transported via canals. Exotic species have had impacts
553 on virtually every ecological process and niche, causing a cascade of devastation to native fishes
554 and mussels (Mills et al., 1994). The sea lamprey was catastrophic for native lake trout, causing
555 millions of dollars of losses to commercial fisheries. Alewife populations later decimated the
556 lake whitefish commercial fishery. Alewife subsequently became important prey for introduced
557 salmon. White perch migrating up the Erie Canal are now competing with native fishes for food
558 supplies. Since their introduction in the 1980s, zebra mussels and quagga mussels rapidly
559 displaced native unionid mussels (Mills et al., 1994).

560 The primary environmental alterations associated with canals constructed for diverse
561 purposes are likely to be the stresses that they exert on native freshwater organisms by
562 changing flow regime or providing a pathway for dispersal of pollutants or exotic species. In
563 many cases, these effects persist more than a century after a canal has ceased to serve its
564 intended purpose.

565 ***Overharvest of freshwater species and fish stocking***

566 Most of the commercial exploitation of freshwater species that led to precipitous
567 population declines and associated changes in freshwater ecosystems involved either bivalves
568 or fish. Commonly, commercially harvested species were simultaneously impacted by multiple
569 stressors, including overharvest, habitat destruction, pollution, and introduction of exotic
570 species. Examples of species driven nearly to extinction through these processes include
571 Atlantic salmon in rivers of the eastern United States. An estimated 5-12 million Atlantic salmon
572 (*Salmo salar*) spawned in watersheds from the Connecticut River to northern Labrador at the
573 time of Euro-American contact, but these fish had become scarce by the mid-1700s through the
574 combined effects of overfishing, upland clearance and river sedimentation, and mill dams
575 (Montgomery, 2003). Analogous substantial declines occurred during the 18th century in
576 Atlantic sturgeon (*Acipenser oxyrinchus*), shad (*Alosa sapidissima*), alewife (*Alosa*
577 *pseudoharengus*), and other fish species in the eastern United States as a result of the
578 combined effects of dams that blocked migration routes, overfishing, and sedimentation of
579 river-bed habitat (Walter and Merritts, 2008; Brown et al., 2013). In this context, the ubiquity of
580 dams on nearly every river hosting runs of diadromous fish species is worth highlighting.

581 Similarly, Pacific salmon and steelhead (*Oncorhynchus* spp.) populations in coastal rivers of the
582 western United States (Lichatowich, 1999) have declined severely as a result of habitat loss,
583 altered connectivity and flow regime caused by dams, overfishing, and nonnative, hatchery-
584 raised fish (Nehlsen et al., 1991).

585 Unionid mussels in the Mississippi River drainage provide a second example of
586 overharvest. These mussels were harvested for freshwater pearls and for their shells, which
587 were used to culture pearls and to manufacture buttons and other items. Much of the harvest
588 occurred between 1890 and 1930, until mussel populations were severely depleted. Use of the
589 crowfoot, which consisted of multiple, four-pronged hooks attached to an iron bar that was
590 dragged along the streambed, severely disrupted mussel beds and increased bed erosion and
591 water turbidity (Scarpino, 1985). Commercial harvest of at least 50 species of freshwater
592 mussels in many rivers of the United States began in the 1850s and continues today, with the
593 result that many commercial mussel fisheries are now collapsing, leaving mussel populations at
594 dangerously low levels (Anthony and Downing, 2001).

595 A third example comes from lake sturgeon (*Acipenser fulvescens*) in the Great Lakes,
596 which were abundant prior to the late 1800s and are now estimated to be less than 1% of
597 historic levels as a result of overfishing and other human-induced stressors (DeHaan et al.,
598 2006). Additional examples can be drawn from any commercially exploited fish species in the
599 United States.

600 Fish stocking has also been widespread in the United States since at least 1871, when
601 Spencer Baird oversaw stocking programs across the nation as head of the US Fish Commission.
602 Fish stocking can involve introduction of species from outside of the United States; introduction

603 of U.S. species to different portions of the country where they do not naturally occur; or
604 introduction of native or nonnative species to fish-less lakes. At least some fish introductions
605 have involved simultaneous attempts to eradicate native species viewed as undesirable, with
606 the most infamous example likely being the 1962 rotenone poisoning of 720 km of the Green
607 River in Utah prior to introduction of game fish for recreational fishing (Wiley, 2008).

608 One of the most successful examples of nonnative fish stocking involves the
609 introduction of common carp (*Cyprinus carpio*), which were first brought to the United States in
610 1831, as imports to the State of New York. Baird aggressively promoted carp as a food fish for
611 the farm ponds starting to appear across the eastern and Midwestern U.S. and the fish
612 commission distributed thousands of free carp (Sandiford, 2009).

613 Introductions of species native to different portions of the country are exemplified by
614 the spread of brook trout (*Salvelinus fontinalis*; native to eastern North America) and rainbow
615 trout (*Oncorhynchus mykiss*; native to cold water, North American tributaries of the Pacific
616 Ocean). Introduction of fish to fishless lakes was typically undertaken to create recreational
617 fisheries in high-elevation mountain lakes (Knapp et al., 2001). Today, 60% of all naturally
618 fishless lakes and 95% of larger deeper lakes in western North America contain nonnative trout
619 (Knapp et al., 2001; Bahls, 1992). Other fish species and freshwater organisms also spread to
620 new habitats through accidental introductions.

621 Alteration of species present in freshwater ecosystems creates a plethora of effects that
622 ecologists continue to investigate. Among these changes are altered energy subsidies among
623 freshwater, riparian, terrestrial, and marine environments (Cederholm et al., 1999; Baxter et al.,
624 2004). Changes in physical process and water quality can also be associated with the introduced

625 organisms, such as increased turbidity caused by feeding behavior of some types of introduced
626 fish (Zambrano et al., 2001) or changes in lake trophic structure that affect nutrient cycling and
627 water quality (Covich et al., 1999; Schindler and Parker, 2002).

628 Accidental or deliberate stocking of nonnative freshwater species began with Euro-
629 American settlement of each region of the United States (Halvorson, 2011). The peak period of
630 deliberate stocking of nonnative fish species likely occurred between circa 1870 and 1970, but
631 accidental introductions such as those from ship ballast water continue to substantially impact
632 freshwater ecosystems, as exemplified by zebra mussels from Russia (*Dreissena polymorpha*,
633 introduced circa 1988), several carp species introduced from Asia during the 1970s, and species
634 of algae (e.g., *Didymosphenia geminata*), crayfish (e.g., *Orconectes rusticus*), and other aquatic
635 organisms native to specific regions in the United States but now invading other areas of the
636 country.

637 ***Contamination of surface and ground waters***

638 Contamination of surface waters with organic and industrial wastes occurred as soon as
639 Euro-American settlers began commercial exploitation of resources or developed permanent
640 communities. Primary contaminants during the 18th and 19th centuries included human and
641 animal wastes; increased sediment yield from upland soil erosion associated with changes in
642 land cover; and industrial by-products such as sawdust, mercury from placer mining, tannery
643 effluent, or distillery slops (Pisani, 1984; Colten, 1992). Continued development of industry and
644 commercial agriculture during the 20th century dramatically increased the range of
645 contaminants entering surface and ground waters, particularly with rapid advances in the

646 synthesis of organochlorine compounds after circa 1950. National water-quality assessments
647 undertaken during the past two decades indicate ubiquitous contamination of surface and
648 ground waters throughout the conterminous United States (e.g., USGS, 1999; Nowell, 2001;
649 Dubrovsky et al., 2010) as a result of both point sources and non-point sources including
650 atmospheric deposition and terrestrial runoff (Carpenter et al., 1998). Pervasive contamination
651 has resulted in multiple iterations of the Clean Water Act, but the great majority of surface and
652 ground waters in the conterminous United States remain unsafe to drink without treatment.
653 Nutrients from sewage treatment plants, industrial agriculture, and animal feeding operations
654 have caused widespread eutrophication in the United States, leading to substantial loss of
655 biodiversity, increased algal productivity, taste and odor issues, and increasingly harmful algal
656 (cyanobacterial) blooms that are toxic to fish and people. Contamination of surface and ground
657 waters is a primary contributor to the continuing extinction of freshwater species.

658 ***Dams and water diversions***

659 Dams were built for diverse purposes following Euro-American settlement of a region,
660 but many of the earliest were mill dams. As Walter and Merritts (2008) documented for the
661 mid-Atlantic Piedmont, tens of thousands of mill dams were built along smaller rivers during
662 the 17th to 19th centuries. The backwater from each dam extended nearly to the base of the
663 next dam upstream as a result of the proliferation of early milling acts that promoted damming
664 for water power. Each of these dams accumulated a 1-5 m thick wedge of sediment in its
665 backwater, effectively burying the small, anabranching channels that existed within extensive

666 vegetated wetlands prior to damming. Sequences of dams affected river process and form for
667 the entire upstream watershed by changing base level.

668 Mill dams were built within every region of the United States settled by Euro-Americans,
669 primarily with the intent of powering grist mills, saw mills, or early industries. The earliest
670 known commercial dam in the United States is Stockbridge Dam in Massachusetts, built in
671 1640. Although many of the mill dams were abandoned by the late 19th century, the sediment
672 stored behind each dam still affects river corridors. Merritts et al. (2011) document continuing
673 channel adjustments via processes of bank erosion that release much of the fine sediment and
674 nutrients that create problems in downstream depositional environments such as Chesapeake
675 Bay. Geologists describe these continuing channel adjustments as a transient response to past
676 changes in land cover and rise in base level caused by the presence of mill dams (Merritts et al.,
677 2013), but two or more centuries of adjustment is persistent on human timescales.

678 In the western United States, Spanish Catholic missionaries built a diversion dam on the
679 San Diego River in California near the end of the 18th century to provide water for irrigating
680 crops (Anonymous, 1916). In portions of the arid and semiarid western United States initially
681 settled by Euro-Americans during the 19th century, water diversions were the first form of
682 freshwater alteration to follow beaver trapping. The South Platte River drainage in Colorado
683 provides an example. Euro-American settlement of the region accelerated dramatically
684 following the 1859 discovery of placer gold. The earliest settlements were mining towns in the
685 mountains and the earliest water diversions were driven by the need to provide water for use
686 in separating precious metals from sediment in placer deposits (Wohl, 2001). Within less than a
687 decade, agricultural settlements were established along the eastern base of the mountain

688 front, and these uniformly relied on surface water diverted from rivers to irrigate crops. By
689 1876, for example, all of the available surface water had been appropriated in the Poudre River,
690 a tributary of the South Platte, and conflicts were arising from over-appropriation (Wohl, 2001,
691 2013b).

692 A similar history of water diversion for mining and agriculture, along with massive
693 increases in sedimentation along river corridors in association with mining, occurred along the
694 western base of the Sierra Nevada in California (James, 1994, 1999). Some diversion structures
695 simply siphon water from a river channel into a pipe or canal. Many forms of diversion,
696 however, rely on water storage via dams within or outside of channels. In river networks
697 simultaneously experiencing multiple human alterations, such as California rivers with mining in
698 the upper basin and irrigated agriculture in the lower basin, dams within channels can store
699 substantial volumes of human-generated sediment and create delays in the downstream
700 movement of this sediment and associated contaminants to depositional environments such as
701 nearshore areas (D. Merritts, pers. comm., March 2017).

702 Construction of large dams accelerated substantially during the 20th century. By the end
703 of the century, only about 2% of the 5.6 million km of rivers within the United States were
704 unaffected by dams and dams impounded a volume of water approximately equal to the annual
705 continental runoff (Graf, 2001). Among the primary effects of dams large and small on
706 freshwater ecosystems are substantial changes in flow regime; storage of sediment and
707 nutrients; creation of a local base level at the dam and reservoir; loss of migration routes and
708 aquatic and riparian habitat; and changes in water temperature and chemistry and the cycling

709 of carbon, nitrogen, and silica (e.g., Ligon et al., 1995; Nilsson and Berrgren, 2000; Poff and
710 Zimmerman, 2010).

711 In addition to large dams, hundreds of thousands of stock ponds store water, carbon,
712 and nutrients. These human-created water bodies may have replaced some of the effects of
713 lost beaver-created wetlands. Annual burial rates of organic and inorganic carbon tend to be
714 highest in small, eutrophic lakes and impoundments, for example, and the concentration of
715 organic carbon in sediment is greatest in lakes with a low ratio of watershed to impoundment
716 area (Downing et al., 2008). Small water bodies may thus be disproportionately important with
717 respect to organic carbon storage relative to their size. Severe reductions of beaver populations
718 throughout the United States significantly reduced organic carbon storage in beaver ponds,
719 which have the potential for substantial carbon concentrations in pond sediments and adjacent
720 wet riparian areas (Naiman et al., 1986, 1988; Wohl, 2013a; Johnston, 2014). Small agricultural
721 impoundments have greater sedimentation rates than natural lakes (Downing et al., 2008) and
722 have presumably increased sediment storage of carbon in river networks, but the magnitude of
723 carbon storage in small, natural beaver meadows versus small, agricultural impoundments
724 remains unknown.

725 **Levees**

726 Although the great era of federally built levees occurred during the 20th century,
727 individuals and communities built smaller levee systems much earlier. French and Spanish law
728 that regulated early settlement in the lower Mississippi River region, for example, stipulated
729 that each landowner agree to build a levee to protect claimed land before obtaining legal

730 possession (Reuss, 2004). Levee construction along the Mississippi River at New Orleans began
731 in 1717 (NHRAIC, 1992). Levees were commonly built in association with drainage of riparian
732 wetlands as a means of limiting overbank flows that could inundate those wetlands. Levees
733 were also built to assist in manipulating water levels in deliberately inundated areas, such as
734 rice fields along river corridors. In valley bottoms affected by excess sediment from upstream
735 mining, such as rivers draining California's Sierra Nevada, levees were built to limit overbank
736 flooding exacerbated by sediment deposition that raised channel beds by several meters (e.g.,
737 James, 1994). Levee construction in this region accelerated following a major flood in 1862.
738 Continued expansion of levees in regions such as Yuba County, California facilitated
739 urbanization of flood-prone areas that were then inundated by several major floods associated
740 with levee breaks during the 20th and 21st centuries (Montz and Tobin, 2008).

741 Because systematic records of individual or community levee construction were not
742 kept, it is difficult to estimate the spatial extent and effects of levees built prior to the late 19th
743 century. A massive flood on the Mississippi River in 1858 initiated a national flood-control
744 policy focused on levees and this focus did not change until after the 1927 Mississippi River
745 flood revealed its limitations, although levees continued to be built extensively after 1927. No
746 systematic analysis of the extent of levees appears to exist at present, but many rivers are
747 heavily affected. Along the Mississippi River between St. Louis, Missouri and Head of Passes,
748 Louisiana, for example, federal flood-control levees have reduced floodplain area connected to
749 the channel by 70-90% (Flor et al., 2010).

750 The ecological effects of levees include severing lateral connectivity between channels
751 and floodplains. Fluxes of water and dissolved and particulate nutrients and organic matter

752 sustain biotic productivity throughout a river corridor, and the ability of organisms to physically
753 move between channels and floodplains is critical to the survival of some species of fish and
754 other aquatic organisms (Junk et al., 1989; Bayley, 1991). By confining peak flows to channels
755 rather than allowing water to spread across the river corridor, levees also increase flow velocity
756 within channels, which can alter habitat and nutrient availability for aquatic organisms
757 (Mattingly et al., 1993).

758 ***Changes in water and sediment yields to river corridors***

759 Of all the types of alterations of freshwater ecosystems occurring after Euro-American
760 settlement, change in water and sediment yields to river corridors is the only one present prior
761 to Euro-American settlement, as noted earlier. However, the magnitude of water and sediment
762 entering river corridors increased substantially following Euro-American settlement because of
763 the greater intensity and extent of removal of native upland vegetation. Increased water yields
764 came primarily in the form of greater surface runoff and decreased infiltration, which led to
765 flashier hydrographs, less groundwater recharge, and the drying of springs and ponds (Cronon,
766 1983). Sediment yields to rivers, lakes, and wetlands typically increased by an order of
767 magnitude following removal of native upland vegetation, a scenario documented repeatedly in
768 the stratigraphy of freshwater environments across the United States (Gottschalk, 1945; Happ,
769 1945; Knox 1977; Cooper and Brush, 1993; Köster et al., 2007; James, 2011; James and Lecce,
770 2013; Trimble, 2013).

771 Increased sediment yields and associated aggradation of channels and floodplains
772 commonly drove additional efforts to engineer river corridors by dredging and straightening

773 channels, for example, in an effort to reduce bottomland flooding exacerbated by loss of
774 channel conveyance (Shields et al., 1995). In the eastern half of the United States, increases in
775 sediment yield were initially driven by upland agriculture and associated removal of native
776 vegetation (e.g., Jackson et al., 2005). In the western half of the country, increased sediment
777 yields initially resulted from mining (Gilbert, 1917; James, 1999) or commercial timber harvest
778 (Whitney, 1994), because agriculture was mostly confined to river corridors or low-lying areas
779 to which surface water could be easily diverted. In either scenario, increased sediment yields
780 typically adversely affected the diversity, abundance, and stability of aquatic and riparian
781 habitat.

782 **U.S. rivers circa 1900 A.D.**

783 The cumulative effects of Euro-American alteration of river corridors can be assessed by
784 considering the characteristics of these environments after one or more centuries of Euro-
785 American occupation. By 1900, river corridors across much of the United States had already
786 been extensively altered. Hundreds of millions of beavers had been killed, thousands of
787 hectares of wetlands had been drained, and millions of logs had been removed from river
788 corridors (Harmon et al., 1986; Wohl, 2014), which had also been physically simplified through
789 diverse forms of direct channel engineering.

790 The net effect of these activities was twofold: (1) to reduce the extent of riparian
791 wetlands, both directly through draining wetlands and indirectly by removing or reducing the
792 primary processes responsible for creating riparian wetlands, including beaver dams, logjams,
793 lateral channel movements, and high riparian water tables (Triska, 1984; Patrick, 1995; Vileisis,

794 1997; Wohl, 2014); and (2) to physically simplify and homogenize river corridors.
795 Homogenization resulted from burying original valley bottoms beneath historic sediment within
796 impoundments; straightening and dredging rivers; removing instream obstructions; blocking
797 lateral connectivity to floodplains and secondary channels; and reducing intra- and inter-annual
798 variability in flow through diversions and dams (Poff et al., 2007; Peipoch et al., 2015).
799 Essentially, Euro-Americans did everything they could to make spatially complex and temporally
800 variable natural river corridors more like simple, uniform irrigation canals.

801 Physical simplification of river corridors tends to increase flow velocity and the peak
802 magnitude of floods if dams are not present (Higgs, 1987). These changes in hydrology and
803 hydraulics cause increased erosion of the channel boundaries and sediment transport.
804 Increased channel erosion can result in further wetland drainage as riparian water tables
805 decline and can also reduce ground water recharge for base flow (Schoof, 1980). Numerous
806 studies indicate that physically simplified and homogenized river corridors have lower biotic
807 integrity in terms of species richness, diversity, and biomass (Groen and Schmulbach, 1978;
808 Scarnecchia, 1988; Rhoads et al., 2003; Moyle and Mount, 2007).

809 Mountain streams in the Colorado Rockies provide an example of how physical
810 simplification and homogenization alter biotic communities. Historically, abundant logjams and
811 beaver dams created obstructions with backwaters characterized by greater channel cross-
812 sectional area, deeper flow with lower velocity, finer-grained streambed sediment and storage
813 of organic matter, and enhanced overbank flow and formation of secondary channels (Wohl,
814 2011; Polvi and Wohl, 2013). The spatial heterogeneity associated with logjams and beaver
815 dams facilitates retention of dissolved and particulate nutrients (Day et al., in review), greater

816 abundance and diversity of aquatic habitat, and greater biomass of salmonid fish (Herdrich et
817 al., in review) and aquatic insect predators such as riparian spiders (Venarsky et al., in review).
818 Historical removal of logjams and beaver dams, even where this removal occurred several
819 decades ago, results in contemporary channels with less spatial heterogeneity (Livers and Wohl,
820 2016) and lower levels of biotic productivity (Herdrich et al., in review; Venarsky et al., in
821 review).

822 **20th century acceleration of human effects on river corridors**

823 The 20th century was a period of intense, federally financed river engineering in the
824 form of dredging and channelization, as well as construction of levees and dams (Reuss, 2004).
825 Nearly every major river within the conterminous United States was extensively affected by
826 these direct modifications by the end of the century (Graf, 2001). Although ground water
827 pumping for irrigated agriculture began during the 1880s and 1890s in drier regions of the
828 United States, drilling of wells into shallow aquifers greatly accelerated during the 20th century.
829 Early wells were less than 30 m deep, but turbine pumps developed during the early 1960s
830 allowed irrigation wells to access much deeper ground water. Simultaneous development of
831 center-pivot irrigation systems substantially expanded the extent of irrigated crop lands.
832 Withdrawal of shallow and deeper ground water resulted in drying of springs and small streams
833 in arid and semiarid regions (Falke et al., 2010).

834 The 20th century also saw widespread introduction of algae-enhancing nutrients and
835 persistent pollutants in the form of synthetic chemicals such as pesticides into freshwater
836 environments (Wohl, 2004). As population grew and the industrial and commercial agricultural

837 sectors of the U.S. economy accelerated starting in the 1940s, a national sense of alarm over
838 the extent and intensity of alteration of freshwater ecosystems also grew. This resulted in
839 legislation such as the original Clean Water Act in 1972.

840 In the final decades of the 20th century, concern grew over the potential effects of
841 climate change on river corridors. The specific effects of changing climate vary among different
842 regions of the United States. Systematic records of precipitation and river discharge indicate
843 that some regions such as the Rocky Mountains are growing drier and experiencing earlier
844 melting and a smaller snowpack (Mote et al., 2005; Stewart et al., 2005), whereas other regions
845 such as parts of the northeastern and north-central United States or lower Mississippi Valley
846 are receiving more precipitation (Karl et al., 1996; National Climate Assessment, 2013). Changes
847 in the type, magnitude, frequency, and seasonal timing of precipitation will cascade through
848 freshwater environments, affecting sediment transport, channel morphology and stability,
849 habitat abundance, connectivity, temperature, and nutrient cycling (Covich et al., 1997; Hauer
850 et al., 1997; Rood et al., 2008; Goode et al., 2012; Eby et al., 2014). Combined with other
851 human-induced changes that limit the ability of aquatic organisms to migrate to more suitable
852 habitat, changing climate may prove to be a major stressor of freshwater environments.

853 **21st century movement toward river restoration**

854 The end of the 20th century and the start of the 21st century also saw a major shift in
855 river management toward increased efforts to restore river ecosystems. The pace of dam
856 removals, particularly of small and medium-sized dams, accelerated across the United States.
857 Many of the rivers affected by dam removal have physically stabilized within months to years as

858 sediment stored behind dams is mobilized and redistributed downstream (e.g., O'Connor et al.,
859 2015). Surprisingly, upstream-downstream connectivity for fish and other aquatic organisms is
860 rapidly restored (Pess et al., in press; Torra et al., 2015), although recovery of biotic
861 communities may take longer.

862 River restoration has become a billion-dollar industry in the United States (Bernhardt et
863 al., 2007). Many restoration projects focus on relatively short lengths of channel (e.g., 1-2 km)
864 and emphasize physical reconfiguration (Bernhardt et al., 2005). The ability of these types of
865 projects to restore river ecosystem function and biotic communities is likely to be limited,
866 especially because the projects are typically not coordinated within a river basin or driven by
867 ecological understanding of river function (Bernhardt and Palmer, 2011). Major, federally
868 financed programs designed to restore connectivity within river basins across much larger
869 spatial and temporal scales, such as those undertaken on Florida's Kissimmee River (Whalen et
870 al., 2002) (Figure 7) or the Colorado River in Grand Canyon (Cross et al., 2011), are more likely
871 to enhance river ecosystem functions.

872 **Water before land vs land before water**

873 To return to the idea proposed at the start of this paper, the body of research
874 summarized in preceding sections illustrates how Native Americans primarily altered limited
875 portions of terrestrial ecosystems across the United States, whereas Euro-Americans rapidly
876 and thoroughly altered both terrestrial and freshwater ecosystems. The timing and magnitude
877 of alteration of terrestrial versus freshwater environments following Euro-American entry into a
878 region depended on the specific resources initially exploited by these immigrants (Figure 1). In

879 some cases, upland resources such as mineral deposits or timber were exploited first, although
880 removal of minerals commonly increased sediment yield to river corridors and cutting of timber
881 typically involved extensive, essentially simultaneous, modification of rivers. In humid climates,
882 agriculture typically began on uplands because bottomlands were saturated for substantial
883 portions of the year. In arid and semiarid climates, Euro-American agriculture typically began in
884 riparian areas and relied on extensive modification of river channels and flow regimes (e.g.,
885 Worster, 1985; Wohl, 2001). Even where initial Euro-American activities focused exclusively on
886 uplands, the effects on freshwater environments were commonly rapid and significant because
887 of the lack of any sediment control in regions where native vegetation was removed for mining,
888 timber harvest, grazing, or cropping.

889 The speed and magnitude of change in sediment yields and responses of river corridors
890 depended primarily on two factors. The first was the spatial extent, intensity, and speed of
891 changes in land cover. The second influential factor was the resistance and resilience of the
892 portion of the landscape and river network under consideration (Webster et al., 1975;
893 Brunsden and Thornes, 1979; Brunsden, 2001). Even in relatively small watersheds of a few
894 hundred square kilometers, headwater portions of the river corridor can respond more rapidly
895 and in different manners than mainstem or downstream portions of the river corridor (e.g.,
896 Trimble, 2013).

897 Quantitatively comparing the magnitude of Native American alterations of terrestrial or
898 freshwater ecosystems to the magnitude of Euro-American alterations is difficult because of
899 limited quantitative data for the initiation and duration, spatial extent, and intensity of
900 alterations associated with each group of people, as well as important differences among

901 geographic regions within the United States. There is no question, however, that all forms of
902 ecosystem alteration increased substantially with Euro-American settlement of the United
903 States. Although many of the alterations associated with Euro-American settlement occurred
904 nearly simultaneously in terrestrial and freshwater ecosystems because of the synergy in
905 resource use between uplands and river corridors (e.g., cutting upland timber and floating cut
906 logs down rivers), we feel justified in making the broad generalization that freshwater
907 ecosystems were minimally altered by human occupation of the United States prior to Euro-
908 American contact. This situation changed dramatically as soon as Euro-American commercial
909 interests created a demand for beaver fur and accelerated once Euro-Americans began to settle
910 in the United States. Consequently, when attempting to evaluate 'water before land' versus
911 'land before water' in the context of either Euro-American settlement and resource use alone
912 or Euro-American alterations relative to those of Native Americans, the most appropriate
913 formulation varies between diverse geographic regions of the United States. As a whole,
914 however, Euro-Americans altered freshwater ecosystems earlier in their history of occupation
915 of a geographic area and to a greater extent than Native Americans.

916 The contemporary effects of this extensive Euro-American alteration of freshwater
917 ecosystems across the conterminous United States appear in the form of accelerated extinction
918 of freshwater species (Ricciardi and Rasmussen, 1999); chronic problems with surface-water
919 quality in rivers and lakes (e.g., GAO, 2013); increasing flood damages despite more than a
920 century of focused efforts to reduce flood hazards (Cartwright, 2005); and increasing shortages
921 of water for human consumptive uses (GAO, 2014). Although some of these problems stem
922 partly from other causes (increased flood damages, for example, also reflect increasing

923 population and infrastructure within floodplains (Cartwright, 2005)), they have helped to make
924 river and wetland restoration a commercial market worth well over a billion dollars a year in
925 the United States (Bernhardt et al., 2007). In this context, it is helpful to understand the history
926 of human alterations of freshwater ecosystems and to use this history to gain insight into the
927 form and function of these ecosystems through time.

928 Today the extent of both terrestrial and freshwater ecosystem modification in the
929 conterminous United States is nearly total, although the alteration took place at different
930 times. Recovery, too, of terrestrial and freshwater systems, is displaced in time and space. Land
931 in the eastern U.S. was cleared for Euro-American agriculture and timber and charcoal
932 production starting in the 1600s and during the period 1820-1880 more than 80% of the land
933 was open (Foster, 1992). Abandonment and reforestation started in 1850 and increased
934 progressively through the early 20th century, approaching complete reforestation circa 1940.
935 Although these second-growth and sometimes third-growth forests differ, in terms of processes
936 such as carbon fluxes and nutrient retention (Turner, 2010), from forests with a history of only
937 natural disturbance, tree regrowth has restored many of the functions provided by pre-
938 settlement forests. Restored functions include changing how precipitation inputs move through
939 and across hillslopes (Jones, 2000); stabilizing hillslopes by intercepting precipitation and
940 increasing soil cohesion through roots (Johnson et al., 2000); and helping to retain organic
941 matter and nutrients in upland environments (McLauchlan et al., 2014).

942 Recovery of freshwaters, where this has occurred, is only a few decades old at most. The
943 rate of dam removals is increasing (O'Connor et al., 2015) and river and wetland restoration are
944 widely attempted, with varying success (e.g., Wohl et al., 2015b). Rivers can respond rapidly to

945 some restoration actions such as dam removal or restored connectivity (Doyle et al., 2005).
946 However, recent syntheses suggest that many restoration projects are of limited success for at
947 least four reasons. First, the scale of restoration does not begin to match the scale of land use
948 in most watersheds (Bernhardt and Palmer, 2011). Second, the ecological function of rivers
949 remains impaired by well-established invasive species (Yard et al., 2011), persistent
950 contaminants (Bernhardt and Palmer, 2007), and increasingly warmer temperatures. Third,
951 persistent legacy effects of land use may have moved the freshwater ecosystem into a
952 degraded alternative stable state (Heffernan, 2008; Wohl and Beckman, 2014; Livers et al., in
953 review). Fourth, it is typically not feasible to restore primary input variables such as natural flow
954 (Poff et al., 1997), sediment (Wohl et al., 2015a), or wood regimes (Wohl, 2017). In the absence
955 of dynamic input regimes, river ecosystems are unlikely to fully recover physical complexity that
956 can support ecosystem functions present prior to Euro-American settlement.

957 Schumm (1969) introduced the phrase *river metamorphosis* to describe a complete and
958 typically rapid alteration of river form and function in response to human activities such as flow
959 regulation. Schumm referred specifically to rivers of the Great Plains, which transformed from
960 wide, shallow, braided channels with minimal woody riparian vegetation to relatively narrow,
961 deep, meandering channels with extensive riparian forests as a result of diversions that reduced
962 peak flows and increased base flows. Analogous metamorphoses occurred in wide, shallow,
963 diffuse channels of marshy regions such as the Everglades (Wohl, 2004) or the mid-Atlantic
964 Piedmont (Walter and Merritts, 2008), where channel engineering and dams created more
965 confined, channelized flows. Brierley et al. (2005), contrasting human alteration of rivers in the
966 Old and New Worlds, proposed that removal of riparian vegetation and instream large wood

967 following Euro-American settlement of the New World rapidly reduced the buffering capacity of
968 riverscapes and effectively lowered the thresholds governing channel stability, such that rivers
969 became highly sensitive to change. Writing primarily of rivers in Australia, Brierley et al. (2005,
970 p. 41) noted that “The short lag time between disturbance and metamorphosis, typically
971 measured in terms of a few decades [during Euro-American settlement], ensured that once
972 critical trigger events were experienced it was exceedingly difficult for systems to recover.” Our
973 personal observations of rivers in the conterminous United States and the written and
974 photographic records of these rivers during the past two centuries support this interpretation.
975 As a result of rapid, thorough, and extensive changes in inputs (water, sediment, large wood,
976 nutrients, contaminants), physical configuration, and biotic communities during Euro-American
977 settlement, river corridors cannot fully or completely return to being physically and biologically
978 diverse ecosystems that are resistant and resilient to various disturbances. Recognition of this
979 relatively recent, fundamental, and ubiquitous alteration of river corridors and river ecosystem
980 functions during the past two centuries should underlie river management in the United States.

981 One of the most important considerations in the context of river management is
982 reflected in the observation of Brierley et al. (2005) that rapid change in variables controlling
983 river form and process creates continuing instability and limits resilience to change. River
984 corridors experience natural, abrupt disturbances such as floods, droughts, or wildfires.
985 Individual portions of a river network can have greater or lesser resistance to these
986 disturbances and exhibit differing degrees of resilience in recovering from the disturbance
987 (Townsend et al., 1997; McCluney et al., 2014). The rapid, widespread, and continuing
988 disturbances created by Euro-American alterations of uplands and river corridors since 1600

989 have reduced resistance and resilience of rivers throughout the United States, thus increasing
990 the vulnerability of freshwater ecosystems to ongoing changes such as warming climate.
991 Recognition of the ubiquity of changes in river corridors is also critical. There are almost no
992 naturally functioning river corridors remaining in the conterminous United States (e.g., Graf,
993 2001), which highlights the vital importance of protecting those that do remain.

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