Geomorphology 157–158 (2012) 88–98

Contents lists available at ScienceDirect

Geomorphology

journal homepage: www.elsevier.com/locate/geomorph

The role of large predators in maintaining riparian plant communities and river morphology

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A R T I C L E I N F O

Article history:
Received 4 March 2011
Accepted 29 April 2011
Available online 17 June 2011

Keywords:
Channel morphology
Bank erosion
Riparian vegetation
Ungulates
Predators
Trophic cascades

A B S T R A C T

Studies assessing the potential for large predators to affect, *via* trophic cascades, the dynamics of riparian plant communities and the morphology of river channels have been largely absent in the scientific literature. Herein, we consider the results of recent studies involving three national parks in the western United States: Yellowstone, Olympic, and Zion. Within each park, key large predators were extirpated or displaced in the early 1900s and subsequent browsing pressure by native ungulates initiated long-term declines in recruitment (i.e., growth of seedlings/sprouts into tall saplings and trees) of palatable woody species and impairment of other resources. Channel responses to browsing-suppressed riparian vegetation included increased widths of active channels via accelerated bank erosion, erosion of floodplains and erraces, increased area of unvegetated alluvium, channel incision, and increased braiding. A reduced frequency of overbank flows indicated these rivers have become increasingly disconnected from historical floodplains because of channel widening/incision. Results from Zion National Park also identified major biodiversity affects (e.g., reduced abundance of plant and animal species). Although these studies were conducted in national parks, results may have implications concerning riparian plant communities, biodiversity, and channel morphology for streams and rivers draining other public lands in the western US. It is on these lands that native and introduced ungulates have often heavily utilized riparian areas, largely in the absence of key predators, with significant consequences to plant communities and channels.

1. Introduction

The morphology and dynamics of alluvial channels is normally a function of flow regime, the quantity and character of sediment in transport, the composition of material comprising the bed and banks, and riparian vegetation. Of these factors, early texts in fluvial geomorphology (e.g., Leopold et al., 1964; Morisawa, 1973; Gregory, 1977; Richards, 1982; Knighton, 1984) emphasized physical processes as determinants of channel morphology and provided limited insights regarding the potentially important role of vegetation. This emphasis on physical processes led Hickin (1984) to conclude that a need existed for studies designed to isolate the influence of vegetation on channel morphology and rates of channel migration.

To illustrate recent patterns of research in fluvial geomorphology, we undertook a search of the GeoRef database using keywords "channel" and "morphology" that identified a total of 3151 entries; by additionally including "vegetation" in the search we obtained only 260 entries (8% of 3151). Of these 260 entries, nearly 95% were published after 1984 and indicate that authors of early fluvial geomorphology publications had limited information to synthesize with respect to vegetation and its potential role in channel dynamics. In recent years, however, a broadening awareness or riparian plant communities has found them (a) to provide important information as indicators of channel adjustments and form (e.g., Hupp and Bornette, 2003) and (b) to effectively influence the morphology of alluvial channels (e.g., Bennett and Simon, 2004). Furthermore, an abundant ecological literature details the structure and functioning of riparian plant communities (e.g., Cummins, 1974; Gregory et al., 1991; Ohmart, 1996; Naiman and Decamps, 1997; Baxter et al., 2005).

When large predators, such as gray wolves (*Canis lupus*) or cougars (*Puma concolor*), are present in an ecosystem, they may affect both the behavior and population size of ungulate (hooved mammal) prey such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and others. The presence of these apex carnivores can limit ungulate herbivory, thus preventing significant impacts to the composition, structure, and functioning of native plant communities (Ripple and Beschta, 2004a). This top-down forcing and progression of direct and indirect effects across successively lower trophic levels represents a "trophic cascade" (Paine, 1980; Terborgh and Estes, 2010).

As Euro-Americans extended their influence across the western United States (US), any effect that Indians may have had on mammal populations via hunting or habitat modification (e.g., through the use of fire) decreased. In addition, Euro-American settlement of the western states displaced or extirpated large predators from much of

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doi:10.1016/j.geomorph.2011.04.042

their original range (Laliberte and Ripple, 2004; Ripple and Beschta, 2005). For example, widespread poisoning, trapping, and hunting during the late 1800s and early 1900s, in combination with a concerted effort at predator eradication by federal agencies, fragmented cougar ranges and almost completely extirpated gray wolves and grizzly bears (*Ursus arctos*). These reductions in large predator distributions raise several important questions concerning riverine ecosystems of the western US: What are the effects, if any, to the structure and functioning of riparian plant communities following the loss of large predators? Are additional consequences likely with regard to channel morphology?

Although the trophic cascades associated with large predators in terrestrial ecosystems of the conterminous US has been little studied, research is beginning to provide important insights with respect to ecosystem changes that might occur in their absence (Fig. 1). Thus, our objective herein is to provide a synthesis of recent research relative to how riparian plant communities and channels are affected by the absence of key predators. To do so, we focus primarily on results from three national parks (NP) in the western US: Yellowstone NP in the northern Rocky Mountains, Olympic NP in the coastal Pacific Northwest, and Zion NP in the canyonlands of southern Utah.

2. Predators, prey, plants, and channels

Yellowstone, Olympic, and Zion NPs are widely separated geographically (Fig. 2) and each has a distinctive geology, topography, climate, and hydrology (Table 1). For each park, historical records and publications were used to identify when large predators were extirpated or displaced, subsequent changes in native ungulate populations, and descriptions of flora before and after large predator loss. From a trophic cascades perspective, the principal "predator–prey" species of interest were "wolves–elk" in Yellowstone and Olympic NPs and "cougar–mule deer" in Zion NP. Field measurements were used to assess contemporary characteristics of riparian vegetation and river channels; historical photographs were used to assess changes in these characteristics. Study reaches in Yellowstone NP were predominantly located in elk winter range whereas year-round habitat use by elk occurred at sites in Olympic NP. Study reaches in Zion NP were located along canyon bottoms that provided year-round habitat for mule deer.

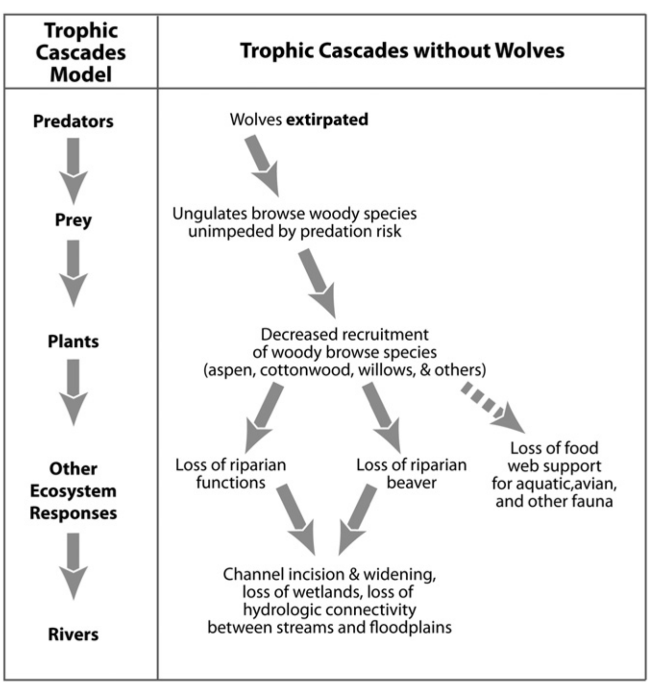

Fig. 1. Top-down perspective of how extirpation of wolves can cascade through lower trophic levels (ungulate prey and plants) to eventually affect the character of river systems.
Adapted from: Ripple and Beschta, 2004a.

2.1. Yellowstone National Park

The upper Gallatin Basin along the northwestern corner of Yellowstone NP experiences a continental climate with winters that are characteristically cold and most annual precipitation occurs as snowfall (Table 1). Annual peak discharge of the Gallatin River normally occurs during springtime snowmelt. Because significant amounts of snow accumulate at higher elevations each winter, the Gallatin elk herd migrates towards lower-elevation terrain in the valley to satisfy foraging needs during the fall, winter, and early spring. This winter range has forested and shrub-steppe hillslopes with willows (*Salix* spp.) dominating riparian plant communities along valley bottoms.

Yellowstone NP was established in 1872. While increased protection of most wildlife species soon followed, wolves continued to be persecuted and were eventually extirpated by the mid-1920s (Lovaas, 1970; Weaver, 1978). Historical reports for the upper Gallatin chronicle a general suppression of woody browse species by elk following the loss of wolves, including impacts to willows in riparian areas and aspens (*Populus tremuloides*) in uplands (Lovaas, 1970; Halofsky and Ripple, 2008). Although the Gallatin elk population initially increased after the loss of wolves, their numbers have generally declined since the 1930s because of (a) an annual harvest, by hunters, of elk that leave the park and (b) losses from periodic starvation during severe winters because of an elk-damaged winter range (Peek et al., 1967). Whereas willows occupied much of the Gallatin River floodplain in 1924, considerable browsing-caused suppression and mortality of willows occurred in the following years and bank erosion became a prominent feature of the channel. A chronosequence of photographs for the years 1925, 1949, and 1961 illustrate continued deterioration of willow communities following the loss of wolves (Fig. 3; see also Fig. 1 in Beschta and Ripple, 2006a).

Three reaches along the Gallatin River were selected for measuring channels and floodplains (see Fig. 2 in Beschta and Ripple, 2006a). Reach A, the "control" reach, was located upstream of the winter range. This reach normally experienced relatively little foraging pressure from elk during winter periods and has retained an intact riparian plant community of willows and sedges (*Carex* spp.) throughout the 20th century. Reaches B and C (treatment reaches) were located within the elk winter range and, following the loss of wolves, experienced significant foraging pressure from elk each winter (Patten, 1968; Lovaas, 1970). At each study reach, four channel cross-sections were surveyed for calculating bankfull discharge (m^3/s) using Manning's equation (Beschta and Ripple, 2006a). Discharge–frequency relationships for rivers in southwestern Montana (Parrett and Johnson, 2004) were then used to estimate the return period (years) associated with the bankfull discharge at each cross-section.

Inspection of 1979–99 aerial photographs indicated Reach A (control) had experienced little change in planform morphology over this period of record (Beschta and Ripple, 2006a). Aerial photographs for Reaches B and C (treatment) had a more extended period of coverage (i.e., 1947–99) and showed a general shift in planform morphology over time. Originally a sinuous, single-thread channel in 1947, the Gallatin River subsequently began to experience increased lateral movement, decreased sinuosity, increased active channel width, and an increased amount of unvegetated alluvium. Inspection of channels upstream and downstream of Reaches B and C on the 1947–99 aerial photos indicated similar channel changes were occurring as well as increased braiding (i.e., channel splitting around unvegetated bars and islands).

The average ratio of bankfull width/depth for Reach B (118 m/m) was considerably greater than Reach A (42 m/m), the control reach,

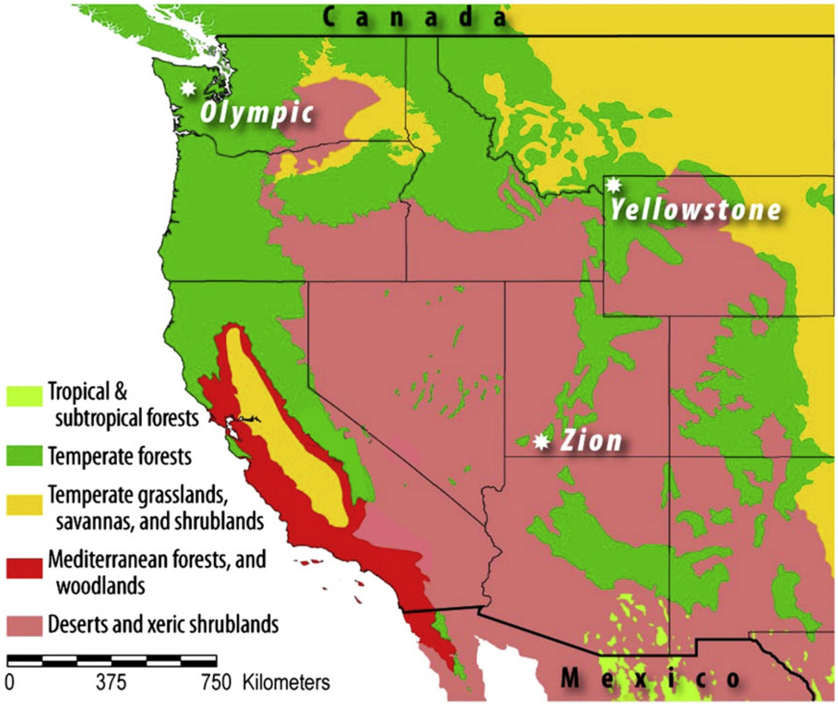

Fig. 2. Location of Yellowstone, Olympic, and Zion National Parks and associated biomes in the western United States. Adapted from Olson et al. (2001).

whereas average bankfull width/depth for Reach C, which was experiencing channel incision, was 39 m/m, a value similar to that of the control reach (Beschta and Ripple, 2006a). Bankfull flows in Reach A had an average return period of 3.2 years whereas average return periods for bankfull flows at Reaches B and C were 33.4 and 9.1 years, respectively (Fig. 4). The greater return periods for Reaches B and C appear to be the result of increased cross-sectional areas from streambank erosion and/or channel incision that have occurred in recent decades.

2.2. Olympic National Park

The Hoh, Queets, and Quinault Rivers originate at elevations of over 2000 m in the Olympic Mountains that occupy the center of the Olympic Peninsula. From their headwater sources, these rivers steeply descend to an elevation of ~300 m and then continue westward along relatively low-gradient channels with broad floodplains and alluvial terraces before ultimately discharging into the Pacific Ocean. Annual peakflows usually occur from October through February during extended periods of heavy rain, or rain-on-snow. Coastal rain forests of the western Olympic Peninsula contain several deciduous and coniferous tree species as well as a varied understory shrub community (van Pelt et al., 2006). These highly productive forests also provide physical habitat needs and food-web support for nearly 230 wildlife species (Quinault Indian Nation and US Forest Service, 1999).

Widespread hunting of predators, ungulates, and other wildlife occurred as Euro-Americans began settling the western portion of the Olympic Peninsula in the 1890s (Morgenroth, 1909). In 1909 Mt. Olympus National Monument was created (becoming Olympic NP in 1938) for the primary purpose of protecting elk and their habitat. Wolves, originally considered common on the peninsula, continued to be persecuted and were extirpated by the early 1920s (Ratti et al., 2004). With elk protected from human hunting, wolves absent, and other large predators suppressed, the elk population rapidly increased. Heavy browsing of riparian vegetation and winter losses of elk from starvation along the western rivers of the park began to occur in the 1920s (Webster, 1922; Sumner, 1938). Whereas the rivers of the Olympic Peninsula have historically supplied important habitat for anadromous salmon (*Oncorhynchus* spp.) and trout (*Salvelinus* spp.), declines in wild fish runs during the 20th century have been observed for the Hoh (Bakke, 2009) and upper Quinault (Quinault Indian Nation and US Forest Service, 1999) Rivers.

Red alder (*Alnus rubra*), black cottonwood (*Populous trichocarpa*) and bigleaf maple (*Acer macrophyllum*) are the primary deciduous

Table 1
General characteristics of the parks and study areas.

National Park	Year of park establishment	Park area (km^2)	Study area elevation (m)	Climatic conditions[a] Temp. (°C)	Precip. (cm)	Snowfall (cm)	NPP (kg/m^2)
Yellowstone	1872	8983	~2000	1.7	34	240	1.3
Olympic	1909	3743	<100	9.9	300	33	2.1
Zion	1918	593	~1300	16.3	38	23	1.1

[a] Long-term air temperature, precipitation, and snowfall averages based on annual data from the following weather stations: Yellowstone NP (Lamar Ranger Station, WY; n = 60 years), Olympic NP (Forks, WA; n = 60 years), and Zion NP, (Zion Park Headquarters, UT; n = 80 years); NPP = net primary productivity in kg of dry biomass/m^2/year (Bachelet et al., 2000; Daily et al., 2000).

trees occurring along rivers in western Olympic NP. Although young red alder plants are relatively unpalatable to elk, the seedling and sprouts of black cottonwood and bigleaf maple, species with very different autecologies, are highly palatable. Thus, we determined historical patterns of cottonwood and maple recruitment (i.e., growth of seedlings/sprouts into tall saplings and trees) to evaluate long-term patterns of elk herbivory. The age structure, or number of trees by date of establishment, for black cottonwood and bigleaf maple along the Hoh, Queets, and East Fork Quinault Rivers indicated that recruitment began to decline soon after the extirpation of wolves as an enlarged elk population increasingly utilized riparian vegetation as a source of browse (Fig. 5). Even though elk populations subsequently decreased, browsing impacts in riparian areas have intensified over time and in recent decades elk herbivory appears to have largely terminated recruitment of black cottonwood or bigleaf maple along these rivers.

Wetted width, active channel width, and the presence/absence of multiple channels (used to calculate the % of a reach that was braided) were measured on 1994 orthophotos at 0.25-km intervals ($n = 32$ measurements per reach) along 8-km reaches of the Hoh, Queets, and East Fork Quinault Rivers (Table 2). The ratio of active channel width to wetted width was also calculated for each reach. For comparative purposes, these same measurements were compiled for 8-km reaches of the Clearwater and lower Quinault Rivers, both outside the park. The Clearwater catchment is located between the Hoh and Queets catchments whereas the lower Quinault River occurs downstream of Lake Quinault and is, thus, buffered by the lake from any upriver changes in large wood or sediment production that may originate within the park (Beschta and Ripple, 2008).

Whereas average wetted widths were similar for the 8-km long reaches inside and outside the park (46 vs. 44 m, respectively), braiding occurred along 37% of reaches inside the park versus only 2% for those outside the park, a nearly 20-fold difference (Beschta and Ripple, 2008). Furthermore, the ratio of active channel width to wetted width for reaches inside the park ($\bar{x} = 3.0$ m/m) was double that of rivers outside the park ($\bar{x} = 1.5$ m/m). Overall, active channels inside the park were typically wider than those outside the park and had approximately four times as much bare alluvium. An example of the wide and braided channel morphology that are now characteristic of rivers within the western portion of Olympic NP is shown Fig. 6.

2.3. Zion National Park

Canyons and valleys of Zion NP have been largely formed by long-term down-cutting of streams and rivers through Jurassic rock units of the Markagunt Plateau. Annual peakflows can be generated by several mechanisms, including rapid melt of accumulated winter snowfall, convective storms during the summer, or infrequently occurring subtropical depressions in late summer–early autumn. Along the valley bottoms of Zion NP, riparian gallery forests are typically dominated by Fremont cottonwood (*Populus fremontii*) with willows and other shrubs common in understory plant communities.

In the late 1800s and early 1900s, native vegetation along the North Fork of the Virgin River in Zion Canyon had been impacted by grazing of domestic livestock and the agricultural practices of ranchers and homesteaders. Zion NP was established in 1918 and by

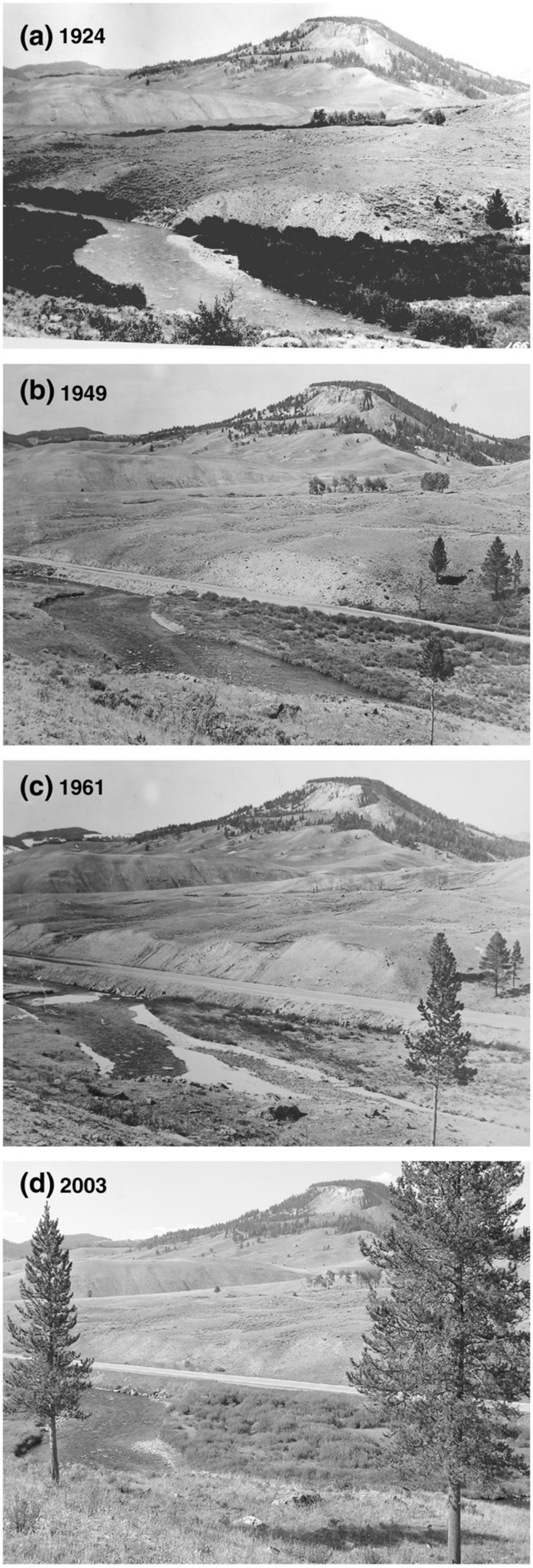

Fig. 3. Photo chronosequence of the Gallatin River and its floodplain showing the status of riparian willow communities in (a) summer of 1924, (b) summer of 1949, (c) late spring of 1961, and (d) summer of 2003. Riparian vegetation associated with the floodplain shows progressive degradation from 1924 through 1961 because of high levels of elk browsing following wolf extirpation in the mid-1920s. Also, conifer "high-lining" (i.e., removal of lower branches by elk browsing), not evident in the right center of the 1924 photo, is visible in the 1949 and 1961 photos. In 2003, 7 years after wolf recolonization, willow communities along the Gallatin River floodplain are beginning to recover.
Adapted from: Ripple and Beschta, 2004b.

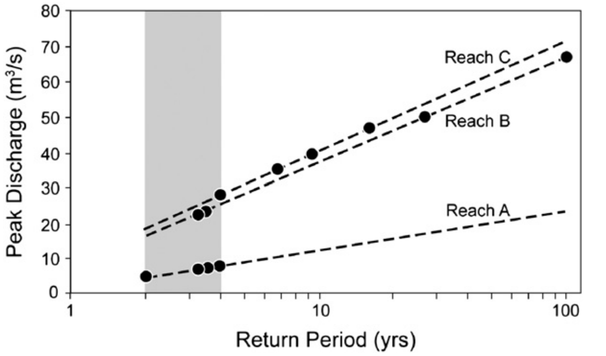

Fig. 4. Discharge–frequency relationships (dashed lines) for Reaches A, B and C of the upper Gallatin River, based on regional equations from Parrett and Johnson (2004). The shaded area encompasses the range of return periods for Reach A (control) and plotted points represent bankfull discharges and associated return periods for four cross-sections within each reach.
Adapted from: Beschta and Ripple, 2006a.

the 1920s vegetation recovery along the river was well underway as predators kept the mule deer population at a low level (Presnall, 1938; Smith, 1943). Park development and a dramatic increase in visitors displaced cougars from the canyon in the 1930s and mule deer numbers increased dramatically (Dixon and Sumner, 1939). In the late 1930s and early 1940s the park service began a program of trapping and removing mule deer in an attempt to reduce herbivory impacts associated with these wild ungulates. The agency terminated this program, however, even though the superintendent repeatedly expressed concerns in annual reports about the impacts to plant

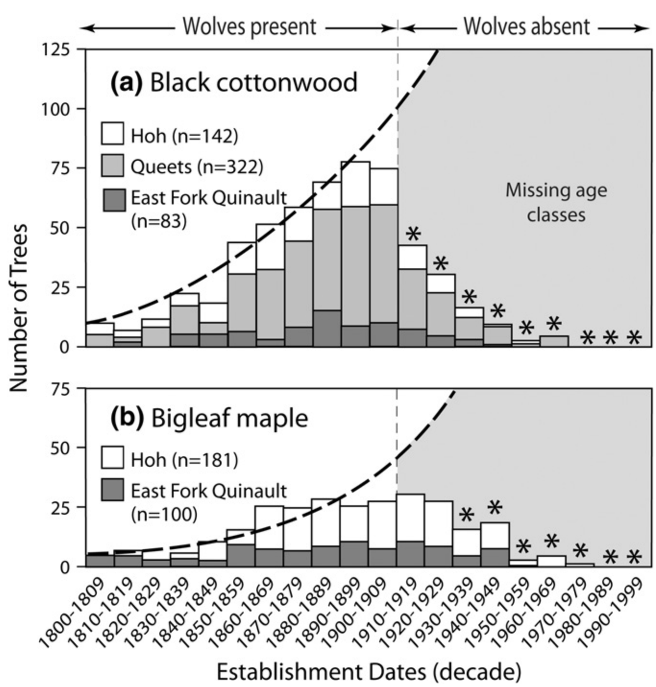

Fig. 5. Age structure of (a) black cottonwood ($n=547$ trees) along the Hoh, Queets, and East Fork Quinault River and (b) bigleaf maple ($n=282$ trees) along the Hoh and East Fork Quinault Rivers, western Olympic National Park, showing decline in tree recruitment following the extirpation of wolves. The exponential function (dashed line) was fitted to measured tree frequencies for the period1800–1910; its extension into the period 1910–2000 represents a general expectation of tree frequencies had wolves not been extirpated. Tree frequencies outside the lower 95% confidence limit are represented by "*".
Adapted from: Beschta and Ripple, 2008.

Table 2
Catchment area and other channel characteristics associated with 8-km long river reaches inside and outside of Olympic National Park in the western Olympic Peninsula (adapted from Beschta and Ripple, 2008). Reach elevation and channel slope measurements from 1:24,000 USGS topographic maps; wetted and active channel width measurements (± standard errors) from 1994 orthophotos (1-m resolution).

Characteristic	Inside park			Outside park	
	Hoh River	Queets River	East Fork Quinault R.	Clearwater River	Lower Quinault R.
Catchment area (km^2)	280	560	205	355	1070
Approximate reach elevation (m)	180	45	150	30	10
Channel slope (m/m)	0.006	0.003	0.005	0.003	0.001
Wetted width of river (m)	52 (±2)	60 (±3)	28 (±2)	31 (±2)	56 (±2)
Active channel width (m)	184 (±15)	155 (±9)	74 (±7)	43 (±2)	82 (±4)

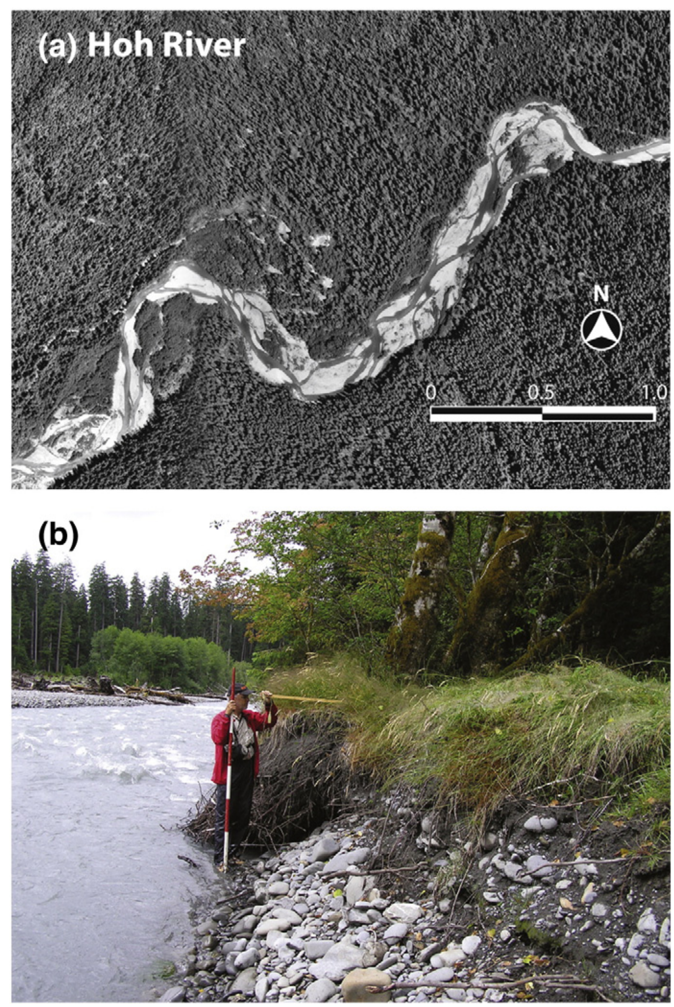

Fig. 6. (a) A 1994 orthophoto showing the Hoh River and its active channel along a portion of the Hoh River study reach (Olympic National Park visitor center is located on the north side of the river near photo center). (b) A 1.8-m high (above water surface) transitional fluvial terrace along the north side of the Hoh River south of the visitor center. The terrace is comprised of coarse gravel/cobble in the lower 1.2 m and grades into sand in the upper 0.6 m. Erosion of these vertical banks during periods of high flow continues to increase the width of the channel as well as increase the input of coarse sediment and organic debris (trees) into the river.
Adapted from: Beschta and Ripple, 2008.

communities that were being caused by mule deer. In contrast, diverse riparian vegetation occurs in the North Creek catchment, an area of limited human visitation and continued cougar presence, located immediately west of Zion Canyon (Ripple and Beschta, 2006a).

The age structure of Fremont cottonwood within riparian areas of North Creek (Fig. 7a, cougars common) showed continuous recruitment over time with more young trees than old ones, a normal feature of healthy gallery forests. In contrast, riparian areas along the North Fork of the Virgin River in Zion Canyon (Fig. 7b, cougars rare) experienced decreased tree recruitment since the 1930s because of heavy browsing by mule deer after cougars were displaced from the canyon (Ripple and Beschta, 2006a).

The frequency of eroding streambanks along the North Fork of the Virgin River (cougars rare) was over 2.5 times that of North Creek (cougars common). In addition, the average width/depth ratio for the North Fork of the Virgin River channel was approximately double that of the North Creek channel (Fig. 8a). The effects of intensive long-term herbivory was also reflected in the reduced occurrence of hydrophytic plants, wildflowers, amphibians, lizards, and butterflies (Fig. 8b). For all of these categories, the relative abundance of indicator plant and wildlife species was much less for riparian areas along the North Fork of the Virgin River (cougars rare) than along North Creek (cougars common). Lastly, native fish densities in the North Fork of the Virgin River were lower relative to those in streams where cougars were "common" (Ripple and Beschta, 2006a).

3. Synthesis

The establishment of Yellowstone, Olympic, and Zion NPs in the western US during the late 1800s and early 1900s created a series of natural experiments (Diamond, 1983) where, except for large predators, wildlife was generally protected. These national parks thus provided important benefits for undertaking research on trophic cascades and channel morphology because potentially confounding effects of various land uses, such as forest harvesting, livestock grazing, agriculture, and others, were either absent or had diminished following park establishment. Conducting research in these parks had an added advantage in that streams and rivers were free-flowing (i.e., undammed) and, thus, riparian vegetation and channels experienced natural hydrologic disturbance regimes. Because these parks were widely separated geographically and had differing climatic and topographic settings, we considered each to represent an independent case study.

3.1. Uncoupling the trophic cascade

Historically, humans have modified many boreal and temperate ecosystems by reducing native animal populations, with large predators especially subject to persecution (Ripple et al., 2010b). As wolves were being extirpated from the western US and cougar ranges increasingly fragmented in the early 1900s, widespread human hunting also devastated many wild ungulate populations. Depleted elk and deer populations, however, were eventually protected in most areas of the West whereas persecution of large predators typically continued. When ungulate populations subsequently began to increase, in the general absence of large predators and with reduced human hunting, impacts to vegetation from irrupting ungulate populations were soon observed (Leopold et al., 1947). The effects included intensively browsed woody species and also reduced diversity of flora, loss of habitat for nongame species, and accelerated soil erosion (Leopold, 1939, 1943).

Plants, although they occupy the lowest trophic level in terrestrial ecosystems, are fundamental to the productivity, sustainability, and functioning of these systems. Thus, when riparian plant communities are significantly altered, the capacity to provide a full range of ecosystem services can be greatly diminished. Results from each of the three parks, and others (Beschta and Ripple, 2009), consistently indicated that major alterations of riparian plant communities occurred from increased wild-ungulate herbivory following the loss of an apex predator, with these effects becoming more severe over

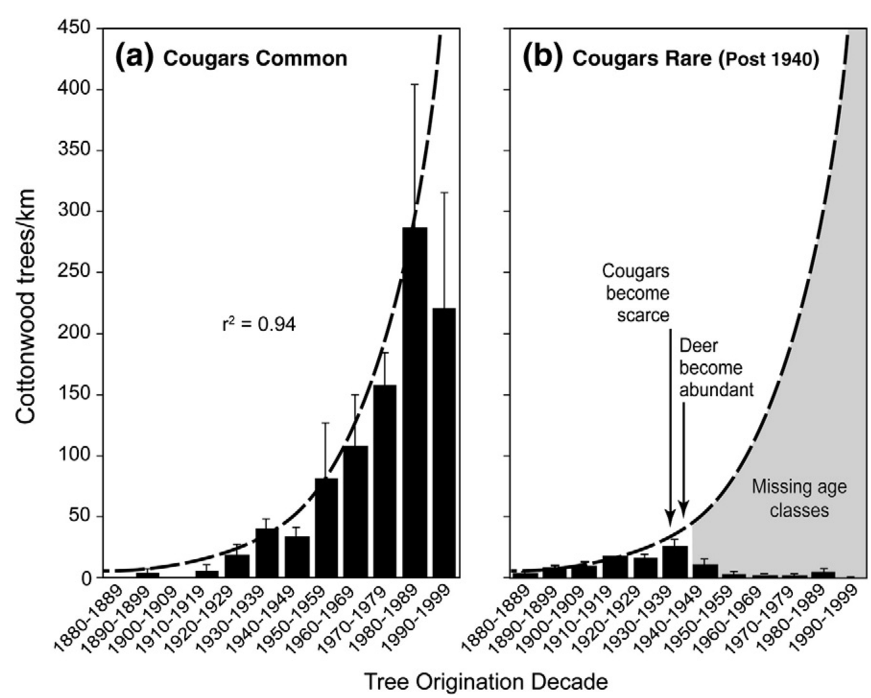

Fig. 7. Age structure of riparian cottonwood along (a) North Creek (cougars common; $n = 777$ trees) and (b) the North Fork of the Virgin River in Zion Canyon (cougars rare; $n = 262$ trees) in Zion National Park. The exponential function (dashed line) was fitted to measured tree frequencies for North Creek study reaches; this same relationship has been plotted along with tree frequencies for the Zion Canyon study reaches illustrating a general cessation of cottonwood recruitment (i.e., missing age classes) after cougars were displaced and deer became abundant.
Adapted from: Ripple and Beschta, 2006a.

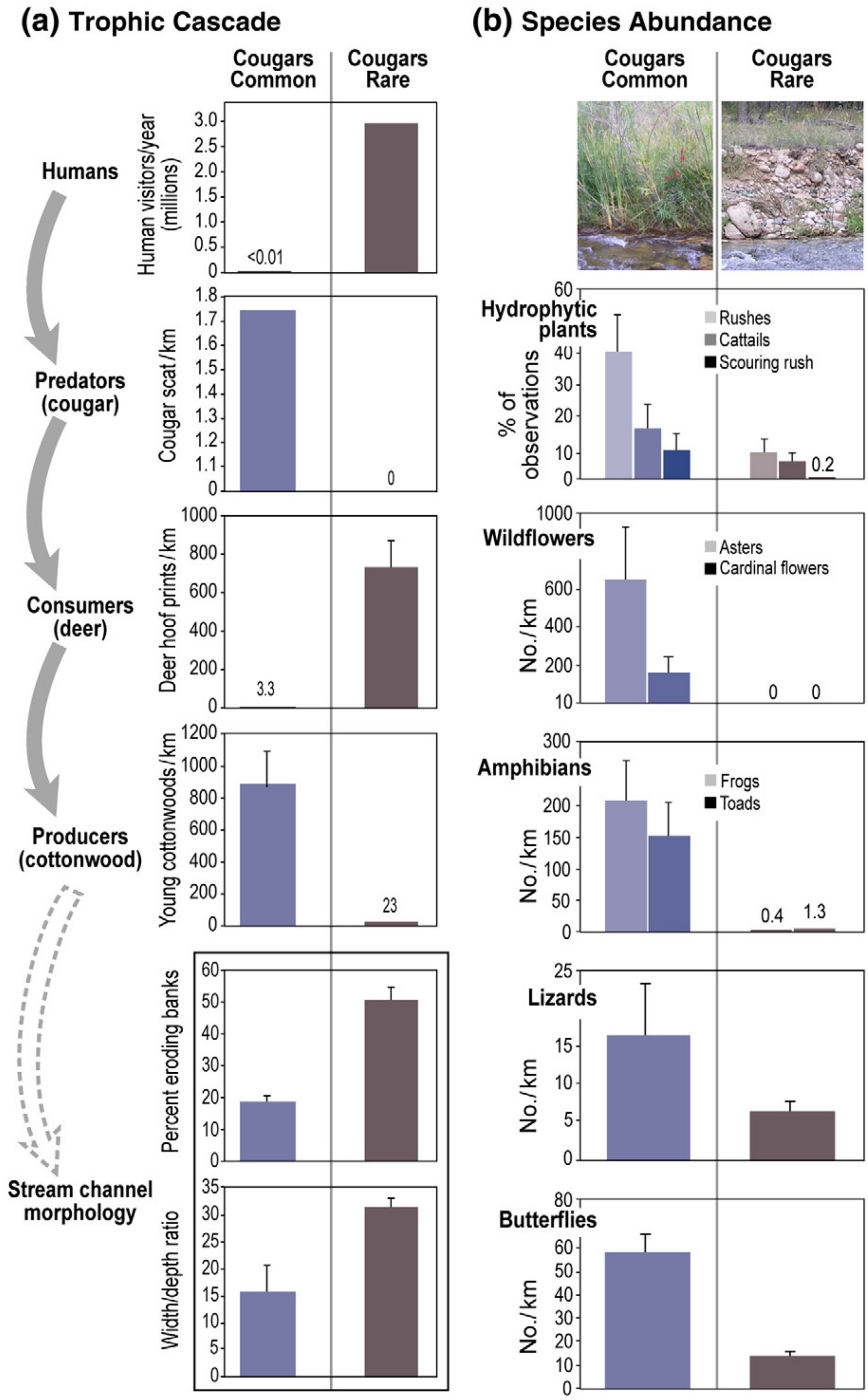

Fig. 8. (a) Trophic cascade indicated by inverse patterns of abundance across trophic levels to stream channel variables, and (b) observed species abundance of biodiversity indicators associated with "cougars common" and "cougars rare" areas of Zion National Park.
Adapted from: Ripple and Beschta, 2006a.

time and often extending to a wide range of plant species. Furthermore, as willow communities along the Gallatin River in northwestern Yellowstone NP were being heavily altered by elk browsing, aspen communities on upslope areas of the upper Gallatin basin were similarly experiencing a browsing-caused decline (Halofsky and Ripple, 2008). As recruitment of black cottonwood and bigleafed maple on floodplains and alluvial terraces of rivers in western Olympic NP deteriorated in the decades following wolf extirpation, comparable impacts to palatable young conifers, such as western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*), also occurred (Fonda, 1974; Harmon and Franklin, 1983; van Pelt et al., 2006; Larson and Paine, 2007). In Zion NP, a decline in recruitment of Fremont cottonwood within gallery forests (Ripple and Beschta, 2006a) was accompanied by impacts to other browse plants along the North Fork of the Virgin River (Presnall, 1938).

In the northern elk winter range of Yellowstone NP, located approximately 50 km east of the Gallatin catchment, long-term changes to cottonwood, willow, and upland aspen communities from elk herbivory following extirpation of wolves in the 1920s have been widely documented (Bailey, 1930; Rush, 1932; Grimm, 1939; Kay, 1990; Chadde and Kay, 1996; Singer, 1996; Ripple and Larsen, 2000; Kay, 2001; Barmore, 2003; Beschta, 2005; Wagner, 2006; Beschta and Ripple, 2009). Additionally, the loss of functional willow communities in the northern range led to abandonment of beaver dams during the 1920–30s with stream incision, unprecedented in the last two millennia, occurring within two decades (Wolf et al., 2007).

In various national parks and areas along the Canadian Rockies, the near elimination of wolves during the mid-1900s allowed intensive elk herbivory to greatly reduce aspen recruitment and severely impact plant communities (Kay, 1997; White et al., 1998; White, 2001; Beschta and Ripple, 2006b). At the edge of the Great Plains, near the Black Hills of South Dakota, the loss of a large predator guild at Wind Cave NP allowed elk and bison (*Bison bison*), even after the elimination of cattle from the park, to curtail recruitment of cottonwood (*Populus* spp.), bur oak (*Quercus macrocarpa*), aspen, and various shrub species (Ripple and Beschta, 2007a). On the Kaibab Plateau of southern Utah–northern Arizona, the loss of cougars and wolves in the early 1900s allowed native mule deer populations to irrupt, thus causing aspen recruitment to plummet (Binkley et al., 2005). The displacement of cougars from Yosemite Valley in Yosemite NP, much like that which occurred with Zion Canyon in Zion NP, allowed the mule deer population to increase (Cahalane, 1941) and initiated a major decline in California black oak recruitment, a decline that has continued through recent decades (Ripple and Beschta, 2008).

Of the nearly 1.4 million square kilometers of public lands in 11 conterminous western states, most occur outside of national parks where aggressive predator control programs have been practiced and where gray wolves, with the exception of recent reintroductions and recolonizations in parts of Idaho, Montana, and Wyoming, have been extirpated for many decades. With the long-term suppression of predators since the early-1900s, wild ungulate numbers have increased greatly in many areas of the West. In addition, domestic livestock grazing has been widespread on public lands for most of the 20th century. For example, approximately one million square kilometers of public land, managed by the US Forest Service and Bureau of Land Management, are generally available for grazing livestock. Thus, plant communities across a major portion of public land in the American West have annually experienced throughout much of the 20th century the combined foraging pressure of domestic and wild ungulates.

The capability of domestic livestock, such as cattle and sheep, to significantly alter vegetation and watershed conditions has been widely studied. For example, reviews by Kauffman and Krueger (1984), Platts (1991), and Belsky et al. (1999) found that the grazing/browsing of streamside areas by livestock can have significant effects to the composition and structure of riparian plant communities and soils. Because much of the American West is relatively arid, this increases the likelihood of livestock use in riparian areas and impacts to diverse plant communities (Kauffman and Krueger, 1984). Trimble and Mendel (1995), in their review of the "cow as a geomorphic agent," similarly identified impacts to upland soils and hydrologic processes as well as altered streambanks associated with the foraging and trampling of cattle. Of 17 grazing strategies evaluated by Platts (1991) regarding capability to maintain riparian plant communities for protecting in-stream conditions and fisheries habitat, only three strategies rated "9" or better on a 10-point scale. These three involved closure of riparian areas to livestock use, a fenced riparian corridor to exclude livestock, or short-term use by sheep only. Most of the remaining grazing strategies, the ones commonly used on public lands, rated between 1 and 5, indicating that they were poor to fair, respectively, in maintaining riparian plant communities and the protection these plants provide to streams and aquatic habitats.

3.2. Altered channels

In the absence of an apex predator, studies from the three widely separated national parks highlighted in this paper found that relatively unimpeded herbivory by wild ungulates altered riparian plant communities that, in turn, allowed for major changes to occur in the morphology of channels. Alternative hypotheses for the observed impacts to vegetation and channels changes were explored for each park and ranged from consideration of hydrologic disturbance regimes and climate in Yellowstone NP (Beschta and Ripple, 2006a) and Olympic NP (Beschta and Ripple, 2008) to climate, human interventions, and site attributes in Zion NP (Ripple and Beschta, 2006a). None were able to explain, however, the observed changes in channel morphology.

The geomorphic indicators used to assess possible changes in channels varied between parks and ranged from a hydraulic characterization of cross-sections (Yellowstone NP), an analysis of channel dimensions from orthophotos (Olympic NP), to measurements of channel widths and depths (Zion NP). Yet results indicated a consistent channel response to impaired riparian plant communities—increased bank erosion that eventually led to either a widening of the active and wetted channel, or channel incision. When channel widening and/or incision occur, a reduction in the frequency of overbank flows results and, in turn, contributes to the loss of moist-site riparian plants and a conversion of floodplain plant communities to species that are more tolerant of drier conditions (Chapin et al., 2002; Rost and Rasmussen, 2004). An inability to maintain functional riparian plant communities because of altered moisture regimes is thus likely to encourage additional channel widening.

In the northern range of Yellowstone, aerial photographs of the Lamar Valley only go back to 1954 which is two to three decades after riparian and upland plants had begun experiencing intensive elk browsing (Barmore, 2003; Beschta, 2005). Inspection of the 1954 photos, in combination with coverage in the 1960s, 70s, 80s, and early 90s, however, indicated the active channel of the Lamar River had become increasingly wider over time (thus creating large surface areas of unvegetated alluvium). Over a period of nearly four decades, accelerated streambank erosion has allowed the channel to experience major lateral shifts in location, become increasingly braided, and export large volumes of alluvium from eroding floodplains and terraces to downstream reaches (Fig. 9a). Even though wolves have been reintroduced into the park, an increasing population of northern range bison in recent years continues to impact riparian vegetation and streambanks along the Lamar Valley (Fig. 9b), effects that began decades earlier from elk (Kay, 1990; Beschta and Ripple, 2010; Ripple et al., 2010a). Thus, wild ungulate herbivory in the northern range continues to suppress riparian plant communities in the Lamar Valley and prevents them from helping to stabilize streambanks along the river.

A study of the Little Bighorn River in south-eastern Montana (Beschta, 1998) found that removal of riparian vegetation initiated a period of major channel changes. Over a period of nearly five decades (i.e., 1938–87), measurements from aerial photographs indicated that the original narrow, sinuous, and laterally stable channel changed dramatically. Beginning in the early 1950s, riparian forests of the well-vegetated floodplain were mechanically removed with subsequent grazing of these areas by cattle. Following vegetation removal the widths of active channels increased and channel sinuosity decreased (thus steeping the gradient of the river). In comparison to an upstream reach where vegetation had not been removed, the vegetation-impacted reach became wider, shallower, and increasingly braided. During high flows, accelerated bank erosion of former floodplains increased the width of the active channel and in conjunction with channel down-cutting decreased the occurrence of overbank flows, thus effectively uncoupling the flow regime of the river with its former floodplain. The combined effects of increased active channel width and channel down-cutting resulted, on average, in an estimated loss of 160 m^3 of floodplain soil and alluvium per meter of channel length.

More recently, the role of reduced riparian shrub densities on the stability of floodplains was evaluated for the Clark Fork of the Columbia River in western Montana. Using a process-based model of overbank

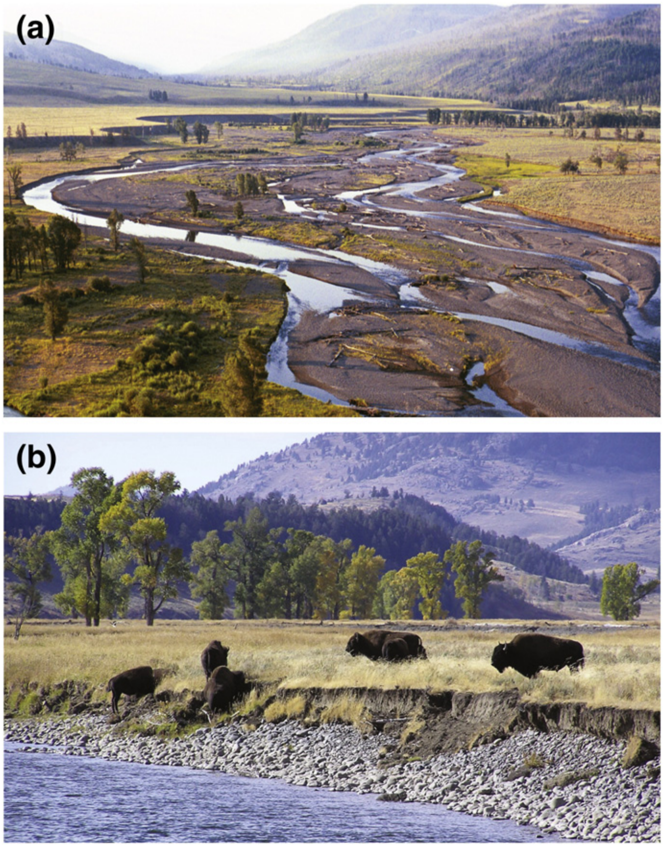

Fig. 9. (a) Up-valley view of the Lamar River from near its confluence with Soda Butte Creek (August 2003). Vertical river banks continue to erode during periods of high flow, wide active channels, expansive areas of unvegetated alluvium, and the generally braided character of channel following the loss of riparian vegetation in previous decades from intensive elk herbivory after the extirpation of wolves. (b) Trampling and high level herbivory in recent years by bison along the Lamar River limit recovery of riparian plant communities and prevent streambanks from stabilizing (September 2009).

flows, Smith (2004) found that dense shrub communities, which historically existed along the Clark Fork, would have been able to maintain a single-thread, meandering channel even during large floods. With a decrease in the density of woody vegetation, however, results of the model indicated that the single-thread channel would become destabilized. Along the Carmel River of California, Groeneveld and Griepentrog (1985) found that groundwater extraction was linked to a decline of riparian vegetation, followed by severe bank erosion. Accordingly, degradation of riparian vegetation, by herbivory or other means, can lead to accelerated bank erosion and altered morphology of an alluvial channel.

3.3. Loss of biodiversity and ecosystem functions

Although riparian areas comprise only about 1–2% of the land area in the western US, they normally provide critical habitat and food for a diversity of wildlife (Kauffman et al., 2001; Baker et al., 2004). For example, nearly two-thirds of neotropical migrant birds depend upon riparian vegetation during the breeding season (Bureau of Land Management, 1998). Where high levels of grazing and browsing of riparian areas have occurred over time, major impacts to terrestrial (e.g., wildlife habitat, food webs, microclimates) and aquatic (e.g., water quality, bank stability, channel morphology) ecosystems have been a common consequence (Elmore and Beschta, 1987; Platts, 1991; Ohmart, 1996; Belsky et al., 1999; National Research Council, 2002; Kauffman and Pyke, 2005). Beaver (*Castor canadensis*), considered a keystone species in stream systems (Wright et al., 2002; Pollock et al., 2003), usually cannot exist where riparian plant communities experience high rates of browsing from either wild (Baker et al., 2005) or domestic (Fouty, 2003) ungulates.

The geomorphic transformation of alluvial channels *via* accelerated bank erosion and/or incision, sometimes in conjunction with channel aggradation in downstream reaches, can have pronounced ecological consequences. Some of these effects were documented in Zion NP where the abundance of various species of hydrophytic plants, lizards, amphibians, butterflies, and fish were drastically reduced as herbivory from deer decimated riparian plant communities, altered channels, and degraded terrestrial and aquatic habitats (Fig. 8). A review of invertebrate studies (Baxter et al., 2005) indicated that the riparian zones and adjacent streams are closely connected by reciprocal fluxes of invertebrate prey where terrestrial invertebrates can provide up to half the annual energy budget for drift-feeding fishes such as salmonids. In turn, the emergence of adult insects from rivers can constitute a substantial component of the energy needs of riparian consumers such as birds, bats, and spiders. Accelerated bank erosion and channel widening (Figs. 6 and 9) increasingly fragment these linkages.

As streambanks erode, the mixing of coarse streambed sediments, with an influx of finer sediment during floodplain erosion, decreases the median size and sorting of sedimentary material on the bed and makes them relatively mobile (Smith, 2004). This increased mobility during lower flows makes benthic habitats less habitable for many insect larvae that normally live within the interstices of the coarse bed sediments. Even where streambeds remain stable, the intrusion of fines associated with increased sediment transport can effectively fill gravel interstices and cause deterioration in benthic habitats (Beschta and Jackson, 1979). Eroding streambanks and wider channels also allow for increased stream temperatures because of shallower depths and lack of shading canopy cover as well as a loss of vegetatively-stable overhanging banks typically used as cover and refugia for fish (Platts, 1991; Beschta, 1997). A loss of vegetation along streambanks and floodplains further decreases habitat values for birds, beaver, and other terrestrial and aquatic wildlife, and effectively truncates allochthonous inputs to a stream that can be a major source of organic carbon for aquatic organisms (Gregory et al., 1991; Ohmart, 1996; Berger et al., 2001; Dobkin et al., 2002). Thus, the cascading effects of excessive herbivory of riparian plants can significantly alter the basic structure and function of riparian and aquatic ecosystems.

Because herbivory-altered ecosystems are a common feature along many western streams and rivers, recovering the resiliency and ecosystem services that such systems would normally provide represents a major opportunity and challenge (National Research Council, 1992; Beschta, 1996; Kauffman et al., 1997; Hill and Platts, 1998; Verry et al., 1999; National Research Council, 2002; Wissmar et al., 2003). In the case of Yellowstone NP, the reintroduction of wolves in the winters of 1995–96, after seven decades of absence, appears to have reestablished a tri-trophic cascade of wolves–elk–plants and initiated the recovery of willow and aspen in portions of the Gallatin winter range as well as a spatially patchy recovery of cottonwood, willow, and aspen in the northern range of the park (Ripple and Beschta, 2006b; Beschta and Ripple, 2007; Beyer et al., 2007; Ripple and Beschta, 2007b; Halofsky et al., 2008; Beschta and Ripple, 2010). For example, along Blacktail Deer Creek in the northern range, canopy cover over the stream increased from <5% prior to wolf introduction to between 14 and 75% by 2003 along three sample reaches (Beschta and Ripple, 2007). Whether gray wolves can have similar ecosystem effects in other areas of the northern Rocky Mountains where reintroductions or recolonizations have occurred remains to be documented.

For those areas of the West where riparian ecosystems have been significantly altered by wild or domestic ungulates and top predators are unlikely to recolonize, reducing the impacts of ungulates needs to be a high priority if the recovery of riparian plant communities is to occur. Whereas improvements in riparian plant communities can often be attained relatively quickly when levels of herbivory are reduced, recovery of highly altered channel systems is likely to require a longer period of time.

4. Conclusions

Early biologists, such as A. Leopold, E.L. Sumner, V.H. Cahalane, and others, who observed the degradation of ecosystems in the early to mid-1900s, often expressed concern in their writings about the on-going alteration of plant communities following the loss of large predators. In some cases, they also identified the occurrence of accelerated soil erosion when terrestrial vegetation was heavily altered by intensive ungulate herbivory. Yet, they were generally unable to foresee the changes in streams and rivers that were to follow the loss of large predators, as the capability of riparian plant communities to function was increasingly disrupted by large herbivores. With the exception of the studies described herein, we are unaware of any previous reports indicating that the removal of top predators might create cascading effects through the ungulate prey to plants such that the morphology of stream and river channels are significantly altered.

Even today, we suggest that fluvial geomorphology, hydrology, and related fields are only beginning to recognize that functionally intact plant communities can play a fundamental role in the character and morphology of streams and rivers (e.g., GeoRef database). Whereas great strides have been made in these fields regarding an improved understanding of physical processes such flow mechanics, sediment transport, flow frequency and magnitude as well as regional assessments of hydraulic geometry and channel patterns, increased integration is needed with ecologists, botanists, and other biologists for whom the integrity of riparian plant communities and the geomorphology of channels takes on an added dimension.

In retrospect, the widespread loss of apex predators and increased herbivory from ungulates in the western US over the last century appear to have initiated major ecosystem effects that have eventually contributed to altered biological and physical attributes of many streams and rivers. The recent Yellowstone experience, however, indicates such effects may be reversible in areas where ecologically effective populations of previously removed apex predators can again be re-established. In areas where recovery of such predators is not possible, controlling the potential impacts associated with ungulates needs to be a high priority if the productive capacity and functioning of riparian plant communities and aquatic ecosystems is to be restored.

Acknowledgments

We appreciate the critical comments and suggestions provided by two anonymous reviewers.

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