APPLIED ECOLOGY

Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes

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Gravel-bed river floodplains in mountain landscapes disproportionately concentrate diverse habitats, nutrient cycling, productivity of biota, and species interactions. Although stream ecologists know that river channel and floodplain habitats used by aquatic organisms are maintained by hydrologic regimes that mobilize gravel-bed sediments, terrestrial ecologists have largely been unaware of the importance of floodplain structures and processes to the life requirements of a wide variety of species. We provide insight into gravel-bed rivers as the ecological nexus of glaciated mountain landscapes. We show why gravel-bed river floodplains are the primary arena where interactions take place among aquatic, avian, and terrestrial species from microbes to grizzly bears and provide essential connectivity as corridors for movement for both aquatic and terrestrial species. Paradoxically, gravel-bed river floodplains are also disproportionately unprotected where human developments are concentrated. Structural modifications to floodplains such as roads, railways, and housing and hydrologic-altering hydroelectric or water storage dams have severe impacts to floodplain habitat diversity and productivity, restrict local and regional connectivity, and reduce the resilience of both aquatic and terrestrial species, including adaptation to climate change. To be effective, conservation efforts in glaciated mountain landscapes intended to benefit the widest variety of organisms need a paradigm shift that has gravel-bed rivers and their floodplains as the central focus and that prioritizes the maintenance or restoration of the intact structure and processes of these critically important systems throughout their length and breadth.

INTRODUCTION

Rivers and their riparian corridors are known to play an important role in regional biodiversity (*1*), but the mechanisms sustaining ecological integrity are less well understood across disciplines. Gravel-bed rivers, which commonly occur in the valley bottoms of heavily glaciated mountain systems (Fig. 1), such as those found in the Rocky Mountains of North America, the Alps of Europe, the Andes of Patagonia, the Southern Alps of New Zealand, and the high Himalayas of Asia, are particularly characterized by dynamic fluvial processes that constantly change and renew the surface and subsurface of the river's valley floor (*2*, *3*). In the glaciated regions of the Rocky Mountains, essentially from the Yellowstone area in northwestern Wyoming, United States, to Yukon, Canada, gravel-bed rivers are disproportionately important to regional biodiversity and to landscape-scale ecological integrity. Research conducted in this mountain region, across a wide variety of fields in ecology and diverse taxa, has highlighted the importance of these gravel-bed rivers to an unexpectedly high proportion of the region's aquatic, avian, and terrestrial species. Although gravel-bed river floodplains play a disproportionately important role in sustaining native plant and animal biodiversity, they have also been disproportionately affected by human infrastructure and activities (*4*). In northern Rocky Mountain landscapes, dams, diversions, agriculture, flood control, exurban development, and transportation corridors are but a few of the vast array of human-mediated direct and indirect factors that affect river processes. First principles of ecosystem management (*5*) focus on the protection and conservation of the most diverse and the most productive places to maintain viable populations of native species and ecosystem types. Maintaining evolutionary and ecological processes (*6*), including disturbance regimes (*7*), hydrologic processes (*2*), nutrient cycles (*8*), and connectivity across spatial and temporal scales (*9*), is central to sound conservation. Because gravel-bed rivers and especially floodplains are focal points for biodiversity in maintaining viable aquatic, avian, and terrestrial populations, we need to focus on their conservation, with particular attention to the processes that maintain them in space (across the valley floor) and time (over decades and centuries).

This review provides insights into the ecological importance of gravel-bed river floodplains in glaciated mountain landscapes and is unique in the breadth of its focus. This effort considers the full continuum of species and processes that gravel-bed rivers support, from microbes and meiofauna within the subsurface of the gravel-bed river floodplain up to vertebrate taxa, including amphibians, fishes, birds, mammals, ungulates, and large carnivores. We make the case that the ecological importance of gravel-bed river floodplains as regulators of mountain landscapes has been overlooked because of the strong disciplinary approaches taken with classic fields in hydrology, geomorphology, ecology, and conservation biology. Simply put, syntheses between hydrologists, avian ecologists, freshwater biologists, and large-mammal ecologists have been rare on this subject.

Here, we synthesize decades of disciplinary research into an interdisciplinary review of the evidence for gravel-bed rivers and their floodplains as essential focal points of biodiversity and productivity and as corridors for connectivity across the glaciated mountain landscapes of

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Fig. 1. The Flathead River in southeastern British Columbia. Image illustrates the breadth of the gravel-bed river floodplain system and the hydrogeomorphic relationship between the surrounding catchment and the spatial and temporal complexity of the shifting habitat mosaic. The white arrow spans the width of the floodplain in this river segment (H. Locke, Yellowstone to Yukon Conservation Initiative).

the northern Rocky Mountains. We examine the role of natural processes in maintaining diverse, viable, and interconnected populations of native species that are challenged to adapt to climate change and other human stressors. We review the underlying research in hydrology and geomorphology that sets the stage for ecological interactions on gravel-bed floodplains, where aquatic and terrestrial habitats are intimately intertwined. We explain why we believe that gravel-bed rivers and their floodplains are the ecological focal point of habitat complexity and biodiversity in glaciated mountain landscapes and the "arena" for ecological interactions between and among species. We conclude with the argument that research and management of river ecosystems have too often been approached from a narrow perspective of the river as just a channel plus a narrow riparian ecotone adjacent to it. We argue that river conservation and restoration efforts that consider only the river channel while largely ignoring an expansive floodplain will not be effective at achieving local- or regional-scale benefits. Similarly, efforts to protect upland systems and wildlife that do not address fracturing and connectivity of the river system to uplands will also be compromised. In glaciated mountain systems, conservation efforts intended to benefit a wide spectrum of plants and animals across the landscape must prioritize intact structures and processes throughout the length of gravel-bed rivers and the width of their floodplains.

THE GRAVEL-BED RIVER AND FLOODPLAIN ECOSYSTEM

Hydrogeomorphic complexity and connectivity

Broad U-shaped river valleys are characteristic of glaciated mountain landscapes where large alpine valleys have been deepened and enlarged in response to Pleistocene glaciation (*10*). Three linked hydrogeomorphic domains are found in these U-shaped valleys: canyons, lakes, and gravel-bed floodplains. The distribution of these domains depends on the underlying bedrock, the width of the valley, and the history of glacial advances and gravel deposition. Where a valley is narrow and bedrock is near or at the surface, the river will cut a canyon and flow as a single channel down a steep gradient. Where the valley is broad, the valley floor may be either filled with water, creating a lake, or filled with glacial and alluvial sediments, creating a gravel-bed floodplain. Often, these hydrogeomorphic domains will alternate and reappear several times as a river makes its way down the valley (*11*). Rivers in canyons support comparatively less biodiversity than floodplain segments because the narrow, linear river corridor of confined river segments has much less physical complexity and habitat diversity. By contrast, the gravel-bed floodplains on the same river system are extremely complex, creating an extraordinary diversity of habitats that support diverse communities of aquatic, avian, and terrestrial species (*12*, *13*).

In the Yellowstone to Yukon (Y2Y) region glaciers, snowfields and rainfall feed into the valley's surface water and groundwater. Flow volume in the river channel varies markedly by season, with the spring flood period providing most of the annual stream flow and with lower volumes in late summer, fall, and winter, barring unusual weather events. During the annual spring snowmelt, high volumes of water have enough energy to mobilize gravel and cobble bed sediments, scour river channels, and cut banks on the outer edge of river bends while depositing sediments to create gravel bars on the inside edge. This process, called cut-and-fill alluviation, is dynamic and, over many years, produces a legacy of sorted and unsorted cobbles and gravels distributed across the surface and subsurface of the entire floodplain. Thus, the channel changes both its shape and location repeatedly over time (*14*). Occasionally, during flood disturbance events, the river will completely change its channel as waters flow across the floodplain surface, cut a new channel, and leave behind an abandoned channel. These multiscale disturbance processes create a mosaic of cobble, gravel, and finer deposits across both the surface and the subsurface of the floodplain (*3*). For example, large cobbles with few interstitial fines are created by sediment mobilization during flood events and then get buried as the channel migrates, creating subsurface, heterogeneous flow networks (*15*). Across the surface of the floodplain, the mosaic of habitats is expressed in different successional stages, including new channels, very old channels, ponds, barren gravel bars, young vegetation stands, and gallery old-growth forests that are hundreds of years old (Fig. 2). The complex mosaic of surface and subsurface habitats is interconnected longitudinally with the river slope, laterally from the river channel across the floodplain, and vertically from the river channel into the subsurface gravels (*16*).

Throughout the year, water is constantly flowing out of the river channel and into the gravels below and laterally beyond the channel (that is, "hyporheic zone," from the Greek *hypo*, meaning "under," and *rheic*, meaning "river"). This river-origin water extends across the U-shaped valley bottom, often from valley wall to valley wall and often hundreds of meters to more than a kilometer laterally from the river channel (*17*). The water that flows in and out of the channel, both vertically and laterally, reappears as upwelling springs directly in the river or in other lateral features such as side channels, springbrooks, and pond habitats on the surface of the floodplain. Water can travel hundreds of meters per day through the floodplain gravels. River water that flows in and out of the channel and the subsurface alluvium creates an extraordinary diversity of ecological niches within the gravel-bed river floodplain. During summer, surface waters heated by solar radiation are cooled by hyporheic groundwater discharge to the surface, creating spatial heterogeneity of water temperatures across the floodplain. The wide variety of temperature regimes is a function of solar warming in the main channel and shallow shorelines and the cool groundwater upwelling into those same habitats (Fig. 3A) (*18*). During winter, those locations that are summer-cooled become winter-warmed, which prevents

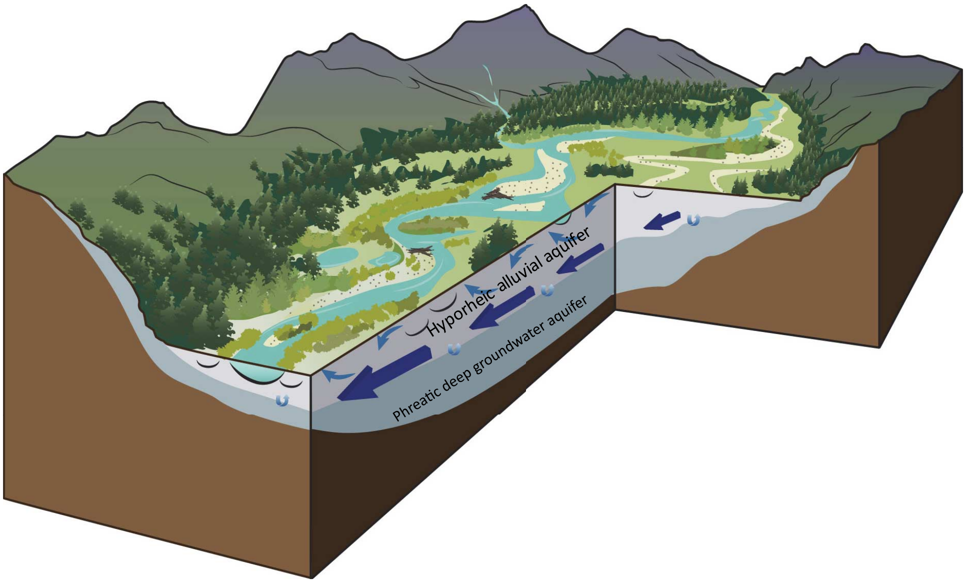

Fig. 2. The three-dimensional structure of the gravel-bed river. Illustration shows the longitudinal, lateral, and vertical dynamics of the floodplain system. The floodplain landscape is created and maintained by biophysical processes that lead to a complex and dynamic habitat mosaic at the surface and in the subsurface. In this cutaway view, the hyporheic alluvial aquifer, characterized by river-origin water flowing through the gravel subsurface, is shown from valley wall to valley wall. The larger blue arrows signify the hyporheic waters that develop at the upper end of the floodplain and flow through the gravel substratum to discharge into the surface at the lower end of the floodplain following long flow pathways. The smaller arrows near the surface illustrate the water exchange between the surface waters and the upper hyporheic waters in the shallow bed sediments that occurs repeatedly along the length of the floodplain. The smaller U-shaped arrows at the interface between the hyporheic zone and phreatic groundwaters illustrate the small exchange that occurs between the hyporheic zone and deeper, phreatic groundwaters that are stored for longer periods of time. The black crescents represent the legacy of cut-and-fill alluviation, characterized by highly sorted open-network cobble substrata with interstitial flow pathways left behind as the river channel moves laterally on the floodplain surface (E. Harrington, eh illustration, Missoula, MT).

the river water in that reach from becoming frozen as anchor or surface ice (*19*).

Nutrients, microbes, and aquatic insects in the gravel

It is broadly understood that river channels support aquatic life and the cycling of nutrients. However, outside of the discipline of stream ecology, it is not as widely appreciated that nutrient-rich waters below and lateral to the channel support a complex food web composed of microbes, mesofaunal crustaceans, and aquatic insects that are hydrologically connected to the river and dependent on the surface water and groundwater exchange. Simply put, most terrestrial ecologists assume that the river and aquatic interface is confined to the river channel. However, the expansive nature of the river corridor in floodplain reaches leads to the aquatic habitat diversity of these unconfined reaches being much higher than that of confined river reaches, subsequently leading to a significantly higher diversity in the aquatic food web (*17*, *20*).

Downwelling water from the river channel into the gravel-bed subsurface carries both particulate and dissolved organic matter (*20*). Oxygen concentrations in the river water are near saturation as the water enters the gravel. At the point of entering the subsurface, particulate organic matter is trapped and filtered from the water. This concentration of particulate organic matter at the oxygen-rich points of downwelling supports abundant and productive communities of microbes and particulate-feeding aquatic insects (*20*). The dissolved organic matter continues to travel into the gravel with the subsurface water. As this water moves through the subsurface gravels, the oxygen becomes depleted by microbial decomposers, which release both CO_2 and biologically available forms of nitrogen and phosphorus (*21*). These bioavailable nutrients flow through the subsurface gravels to reemerge at the surface in springbrooks, ponds, and backwaters, or they may upwell directly into the river channel. Bursts of algal growth occur where these nutrients, which are carried by upwelling of the hyporheic groundwater, come to the surface (Fig. 3B) (*22*). Grazing aquatic insects achieve high densities and growth rates at these sites of high algal growth (*19*).

Many small crustaceans and large aquatic insects spend early stages of their life histories in these nutrient-rich subsurface gravels throughout the gravel-bed river floodplain, again hundreds of meters lateral to the river channel (*17*), reflecting the expansive nature of the alluvial, hyporheic aquifer. They are nourished not only by the dissolved organic matter carried into the gravels by downwelling river water but also by the decomposition of organic matter (such as coarse woody material) that has been buried in the gravels by cut-and-fill alluviation. This buried organic matter forms concentrated sites of decomposition and microbial activity, including anaerobic methanogenic bacteria that account for as much as 99% of energy flow in some species of the hyporheic food web (Fig. 3C) (*23*). The aquatic insects that live in the gravel can be found from valley wall to valley wall and from the top to the bottom of the floodplain in the spaces between the cobbles created by periodic rolling of the rocks through hydrogeomorphic processes. These aquatic insects return to the river channel through the interstices in the gravels and then emerge and reproduce. Hyporheic invertebrates can form a significant portion of the total production of

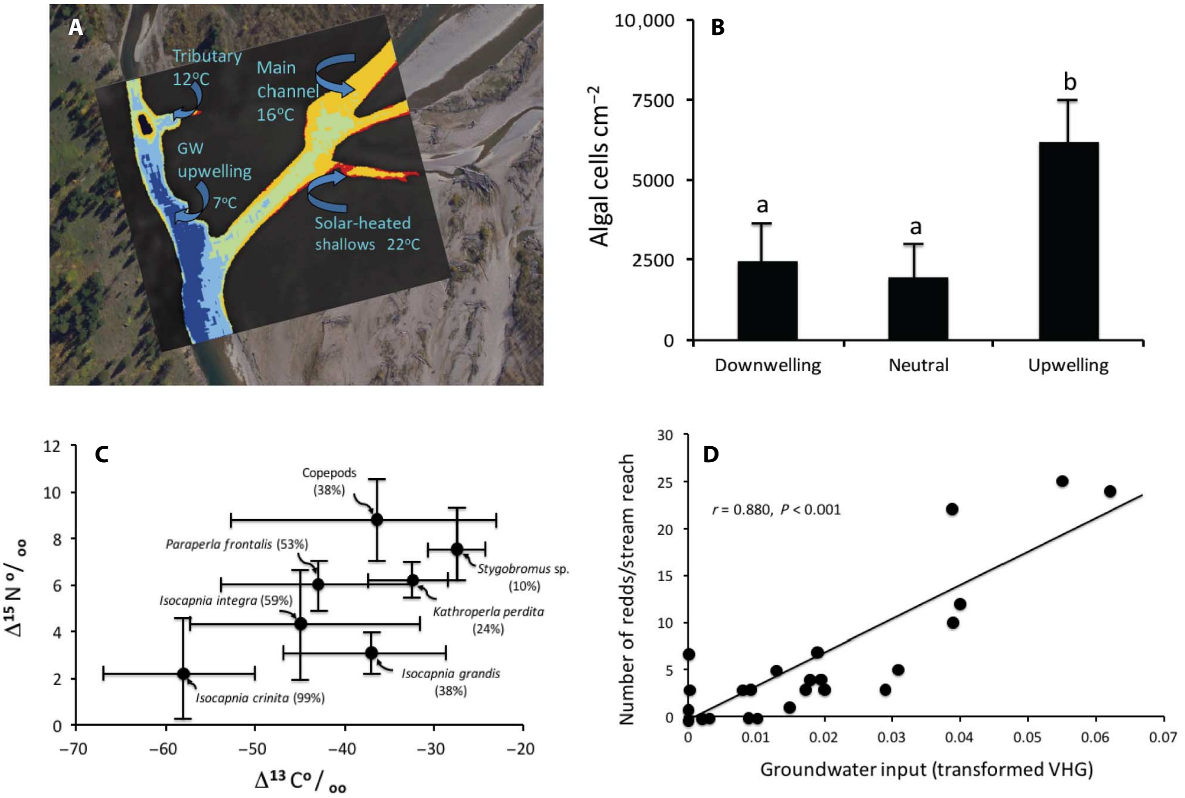

Fig. 3. Biophysical characteristics of gravel-bed floodplains. (**A**) Near-infrared image georeferenced with a high-resolution image showing classified temperatures of an upwelling location on a gravel-bed river floodplain. GW, groundwater. (**B**) Total abundance (±1 SD) (in cells per square centimeter) of substratum from cobbles at points of downwelling (n = 52), neutral (n = 19), and upwelling (n = 49) on a gravel-bed floodplain. Significant difference indicated by different letters above bars [$P < 0.05$, analysis of variance (ANOVA); $P < 0.05$, Tukey's test]. (**C**) Stable isotope biplot for major invertebrate taxa (±1 SD). All taxa have d^{13}C signatures that are more depleted than river dissolved or particulate organic matter. The extreme shift for some organisms is the likely contribution of methane through methanotrophs. Percent contribution of methane to those taxa in the hyporheic food web is shown in parentheses. (**D**) Relationship between groundwater recharge from the hyporheic zone on a gravel-bed floodplain stream reach and the number of bull trout redds (egg pockets) per stream reach. VHG, vertical hydraulic gradient.

invertebrates of the river (*17*) and, thus, directly affect higher levels of the river food web, including fishes, amphibians, birds, and bats and other mammals (*9*).

Native fishes and floodplain fluvial processes

Many of the habitats that are essential for growth, survival, and persistence of native fishes in the Y2Y region are found exclusively on gravel-bed river floodplains. This is particularly true for native and threatened or endangered salmonids, such as the bull trout (*Salvelinus confluentus*) and the westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) that occupy gravel-bed river floodplains for their entire lives or travel hundreds of kilometers to seek out these areas to complete their life cycle (*24*). Trout and other native fishes are dependent on cool water in the summer and unfrozen conditions in the winter, keying into a fundamental character of the groundwater and surface water interaction with the hyporheic zone, as discussed above. Moreover, salmonid reproduction is heavily concentrated in habitats directly associated with groundwater upwelling from the subsurface into the gravels of the river channel (*19*, *25*). In such upwelling sites, incubation temperature is ideal, and there is well-oxygenated water and a sufficient flow to carry away nitrogen waste products from the incubating embryos. Adult female trout construct their redds (that is, nests for incubating eggs) in gravels that have been rolled and swept clean of fine sediments, first by fluvial processes during the spring snowmelt flood and then, again, by the spawning fish. Thus, a suitable spawning habitat is dependent not only on cool water per se but also on the hydrologic process of flooding and the groundwater–to–surface water exchange that is maintained by the shifting habitat dynamics of the gravel-bed river floodplains on the alluvial valley floor (Fig. 3D) (*25*).

The habitats created by fluvial processes on and in the gravel-bed river floodplains are essential not only for spawning but also to the rest of the life cycle of native salmonids. Juvenile salmonids typically use side channels, springbrooks, and low-velocity shoreline habitats for early rearing and feeding (*26*), whereas subadult and adult fishes require deep, complex areas of the channel with channel-edge vegetative cover for feeding and protection from predation (*27*). Trees that fall in the river channel through the process of cut-and-fill alluviation create pools and structures and provide shade that is important during the summer months (*28*). Groundwater upwelling from the floodplain gravels creates an ideal overwintering habitat because of the relatively warm, ice-free conditions provided by hyporheic return flows to the river (*19*). Alluvial valley segments support relatively higher levels of genetic diversity and abundances of native salmonids (*29*), underscoring the importance of these habitats as "biological hot spots" for evolutionary potential (that is, adaptive capacity), resiliency to environmental change, and overall persistence.

Amphibians in ephemeral floodplain habitats

Amphibian reproduction requires pond and nearshore channel environments with specific thermal and hydroperiod conditions (that is, the length of time that surface water is present). Often overlooked is the fact that, in glaciated mountain environments, the greatest diversity of thermal and hydroperiod conditions is found among the ponds and disconnected backwaters of gravel-bed river floodplains. Many amphibians select ephemeral ponds for breeding to avoid predation. The short hydroperiod of such ephemeral ponds prevents predatory fish from accessing the same habitat that amphibians select for eggs and immature aquatic stages. However, to exploit these ephemeral habitats, larval amphibians must grow and develop rapidly before the water disappears. Pond habitats on the open floodplain that are created by the spring flood receive direct sunlight and can be warmed to >25°C, yet have bottom temperatures of <7°C because of subsurface groundwater entering the bottom of the pond through the gravels. Ponds in paleochannels that thread through an adjacent forest tend to be much cooler from top to bottom because of shading by the surrounding mature vegetation and the upwelling of groundwater. This array of thermal and hydroperiod conditions supports not only a diverse amphibian assemblage (*30*) but also high levels of intraspecific genetic diversity and plasticity in phenotypic expression (*31*).

Disturbance and vegetation diversity across the floodplain

The ecological importance of vegetation to aquatic ecosystems has been widely studied (*32*, *33*). However, riparian vegetation is often considered as a relatively narrow band (that is, 25 to 50 m in width) next to the channel, whereas the relevance of plant communities that extend across the floodplain is ignored in the context of "vegetation in the riparian zone." This understanding is inaccurate and is now realized to be too limited. On the gravel-bed river floodplains of the Y2Y region, riparian plant communities extend hundreds of meters to kilometers from the active channel to the lateral edges of the floodplain (see Fig. 1). Water from the river channel downwelling into the hyporheic zone of the floodplain and then flowing subsurface from lateral edge to lateral edge of the floodplain nourishes the trees and other plants (*34*). The combination of these nutrient pulses with multiscale disturbance of cut-and-fill alluviation, larger-scale flood disturbance history, and fire disturbance creates a highly productive and biodiverse vegetation community.

Native cottonwoods (*Populus* spp.) and willows (*Salix* spp.) dominate early succession of gravel-bed river floodplains in the Y2Y region, and their life history traits are tightly linked with the natural flow regime (*35*). Cottonwoods and willows are intolerant of established vegetation, and seedling recruitment requires barren sites newly formed by flood disturbance events and scour, as described above. Although these species are prolific seed producers, the tiny seeds are annually released in a short interval after the spring snowmelt peak and are only viable for a few weeks. The seeds are blown or floated onto moist and barren sites left behind on the exposed cobble bars by the receding river water. After germination, the small seedlings will only survive through the first summer of highly xeric conditions on the bare cobble and gravel bars if the river stage recedes slowly enough for the root elongation to track the falling groundwater zone, which is tightly linked to the river level. If the rate of decline following the peak in the flood hydrograph is too rapid, then seedlings desiccate and die with resulting poor recruitment (*36*). Conifer-dominated stands often eventually replace cottonwood stands in areas of the floodplain that are undisturbed for a long period of time (*14*), and with their lower productivity, conifers also tend to harbor lower biodiversity (*37*). Thus, highly stable floodplains (that is, lacking disturbance flooding) in the Y2Y region become dominated by less diverse and less productive conifers.

Gravel-bed river floodplains contain a complex set of habitats that includes soil moisture ranging from extremely xeric to mesic and hosts an extraordinarily high diversity of plant species. More than 60% of plant species from the floodplain valley floor to the alpine occur on the heterogeneous habitats of the gravel-bed floodplains (*38*). This is because moisture gradients that occur across hundreds of meters of elevation on mountainsides are highly compressed over short elevation differences on floodplains but support similarly diverse species assemblages. These rich and diverse floodplain plant communities are shaped by, and in many cases are dependent on, the natural dynamic processes of the river. Many of the plants of gravel-bed river floodplains are pioneering species that not only are tolerant of flooding but also are actually dependent on the physical disturbance of the cut-and-fill alluviation process that creates open cobble bars for their reproduction (*39*). These plant communities also influence the river's hydrological and geomorphic processes as large trees of old-growth forest patches are eroded, and large wood debris is captured by the river during flood events. The largest wood creates hydraulic complexity with deep scour in one location and high deposition in another (*3*, *28*). Likewise, paleochannels with scour holes become pond habitats with hydric soils and wetland plants. These often occur directly next to floodplain surfaces 2 to 3 m in elevation above the groundwater table, which is directly controlled by the river stage. Thus, old-growth cottonwoods and spruce forests are often seen growing directly adjacent to both the contemporary channel and old paleochannels (*14*).

Avian direct and indirect use of floodplains

Many bird species are known to rely on river corridor habitats. In the Y2Y region, more than 70% of the species diversity is associated with gravel-bed rivers and floodplains to complete part of their life cycle (if not the entire cycle) (*40*). The continuum of floodplain use among bird species in the region ranges from those entirely reliant on near-channel habitats (for example, water and shore birds), to birds that seasonally occupy adjacent riparian forest habitats for breeding activity (for example, flycatchers, wet woodland passerines, and raptors), to short-term inhabitants of the river floodplain during migrations or seasonal temporary users before local connectivity to uplands (for example, neotropical migrants). The highest bird densities (*41*) and greatest bird diversity (*42*) are associated with expansive floodplains containing a variety of aquatic and terrestrial habitats with large and complex patches of deciduous gallery forests intersected by side channels and a range of successional plant communities. The dependence of passerines on riparian vegetation, especially in the semi-arid west, has led ornithologists to refer to gravel-bed river systems as the "aorta" of mountain landscapes (*43*).

The diverse structure and composition of floodplain vegetation that result from fluvial processes lead directly to high bird diversity (*42*). The cottonwood gallery forests, which are highly dependent on fluvial processes, provide nesting and perching sites. Freshly exposed gravels are a critical habitat to spotted sandpipers (*Actitis macularius*) and other shorebirds. Gravel-bed floodplains are also important to birds typically thought of as upland breeding species. Following their spring migration to the Y2Y region, many upland species rely on the gravel-bed river floodplain habitats along the valley floor early in the season before breeding or as they prepare to migrate south in the fall. For instance, ruby-crowned kinglets (*Regulus calendula*), categorized as "coniferous forest specialists," inhabit gravel-bed floodplains during the winter and early spring. Some stay in the coniferous forest adjacent to the floodplain, whereas others move to an upland forest habitat as resources become available for breeding activity later in the spring (*44*). Migrating insectivorous birds prefer floodplains because of the predictable and abundant food resources and a lower predation risk than other environments (*45*). Peregrine falcons (*Falco peregrinus*) that breed in coniferous forests often forage over floodplains (*46*), and although falcons do not rely solely on gravel-bed floodplains, these areas provide critical prey resources (for example, waterfowl, passerines, and shorebirds) that attract and support peregrine populations and those of other raptors.

The arena for ungulate and wolf interactions

Many large mammals, such as moose (*Alces alces*), beaver (*Castor canadensis*), and river otter (*Lutra canadensis*), are obligate users of wetlands, rivers, and floodplain habitats. However, the wide variety of large mammals generally considered as upland species but which rely heavily on gravel-bed river floodplains for many portions of their life histories is often overlooked. Throughout the Y2Y region, large-mammal communities are shaped by elevation, climate, precipitation, and primary productivity gradients created by the mountain ecosystem (*47*). Gravel-bed river floodplains in the region provide the overall highest annual primary productivity (*48*), the earliest appearance of spring-emergent vegetation, and the latest continuance of fresh vegetation in the fall (*49*). Critical grasslands and shrub and aspen stands required for winter maintenance of large ungulates, such as bison (*Bison bison*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.), dominate the vegetation of alluvial fans, which extend onto broader gravel-bed river floodplains at the lower elevation valley bottoms. Gravel-bed river floodplains provide boreal lichens for woodland caribou (*Rangifer tarandus*) and a key habitat for large carnivores such as wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and mountain lions (*Felis concolor*) (*50*, *51*).

Gravel-bed floodplains provide not only critical habitats but also the arena for key ecological interactions among several large mammals (Fig. 4A). Carnivory and herbivory are important ecological processes that affect both gravel-bed river floodplains and upland habitats in mountainous ecosystems (*52*). In the Y2Y region, wolves commonly den along the edge or directly on large gravel-bed river floodplains (*53*). Wolves find preferred materials for denning in gravel and sand deposits along banks exposed by the processes of cut-and-fill alluviation. Gravel-bed floodplains also provide a significant predation advantage to wolves. Spring migratory corridors of their prey, from winter ranges to alpine summer ranges, follow valley bottoms, passing close to active wolf dens (*54*) and increasing the likelihood of successful predation during spring and fall (*55*). In summer, risk of mortality is greatest when ungulates cross lower-elevation valleys between alpine ranges (*55*), whereas during winter, an estimated 40% of all wolf kills within Banff National Park occurred on gravel-bed river floodplains. Moreover, the attraction of ungulates to spring green-up near warmer groundwater upwelling zones may create an ungulate "hot spot" during the time of year when large ungulates are in poor body condition (*56*). These hot spots are then exploited by large carnivores, resulting in the important late winter–early spring spike in mortality of all ungulate species on the gravel-bed floodplains (*57*). Many studies show that ungulates pursued by predators on uplands will descend onto the floodplain of the valley bottom, attempting to use the river as an escape strategy. When this strategy proves unsuccessful, the kill invariably occurs on the floodplain. Thus, in the case of wolves and coyotes, it is particularly disadvantageous for prey to escape by running downhill (*58*).

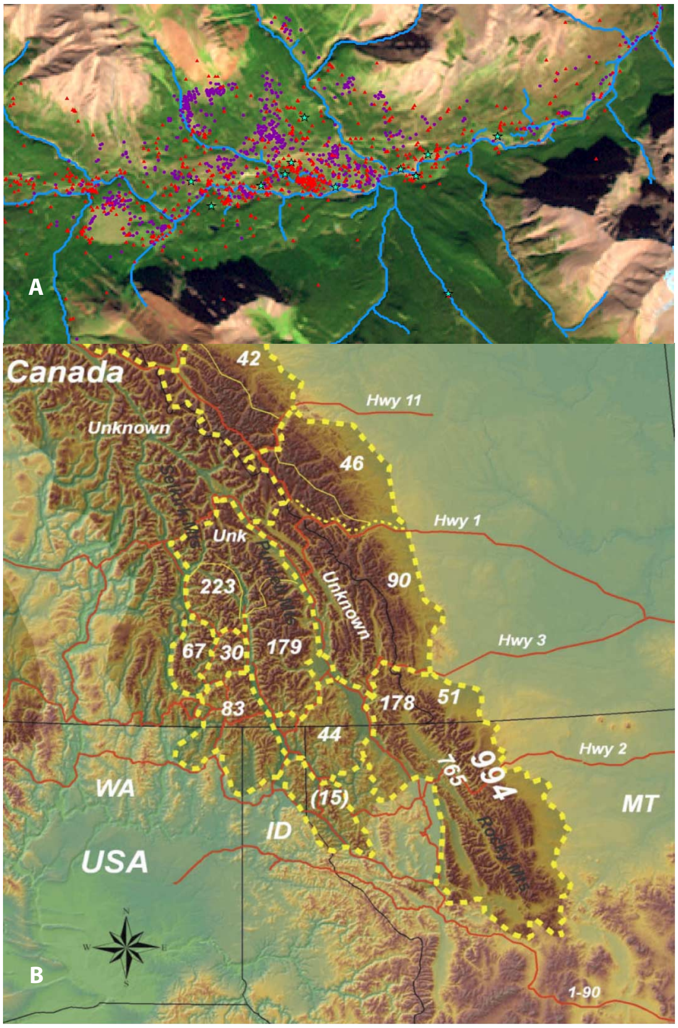

Fig. 4. Elk and wolf frequency distribution on a gravel-bed river floodplain and subpopulations of grizzly bears. (**A**) A spatially explicit frequency distribution of radio-collared elk (purple) and wolves (red) and locations of elk kills by wolves (green stars). (**B**) A map of grizzly bear subpopulations in the United States–Canada transboundary area of the Y2Y region derived from fragmentation synthesis. Numerical values represent subpopulation estimates. The yellow dotted lines delineate fragmentation between subpopulations and follow fragmented gravel-bed river floodplains [modified with permission from the study by Proctor *et al.* (*65*)].

The predation that occurs on gravel-bed floodplains also affects the health and reproduction of cottonwoods on the floodplain and upland aspen forests. Wolf predation on elk, which occurs primarily on gravel bars, is capable of providing top-down controls on elk density in some systems (*52*). Eradication of wolves and other carnivores across the southern half of the region in the 1930s to 1960s led to the extreme overpopulation of large ungulates, in particular elk, throughout many river valleys (*59*). The increased elk numbers, in turn, led to a marked increase in herbivory by elk on woody browse species such as aspen, cottonwoods, and willow, which then cascaded to declines in beaver and other obligates of early willow and mature forest species, such as riparian passerine birds (*52*). The loss of the deciduous cottonwood and aspen forests not only had a direct effect on beaver populations but also had a significant effect on the role large wood has in hydrogeomorphic processes of the gravel-bed river floodplains. In the last several decades, the restoration of wolves in Banff and Yellowstone has reversed the loss of woody browse species on gravel-bed river floodplains (*60*). Results from spatial risk models for Yellowstone National Park and the Ya Ha Tinda and Bow Valley in Banff National Park show that since the 1990s, wolf predation on elk has also resulted in a marked rejuvenation of upland aspen (*52*, *61*).

Predation on ungulates on gravel-bed floodplains also likely results in an overlooked but important source of nutrient flow. The role of salmon as a nutrient subsidy from the marine environment to gravel-bed floodplains around the north Pacific Rim has been well documented (*62*). Similarly, a study on Isle Royale (*63*) showed that the distribution of wolf-killed moose carcasses had strong and persistent effects on terrestrial nutrient cycling by concentrating nutrients at the site of the kill. Work in Yellowstone National Park has shown high pulses of nutrients from carcasses to terrestrial systems. Because predation risk is highest on gravel-bed floodplains, high nutrient concentrations around large ungulate carcasses are likely to reach the aquatic system (*63*).

Floodplains as "connectors and fragmentors" of grizzly bear populations

There was once a large contiguous population of grizzly bears (*U. arctos*) across western North America from Mexico to Alaska. Today, south of Alaska and central and northwestern Canada, the southern part of the Y2Y region holds the remnant distribution in what was the southern half of their North American distribution (*64*). In this area, there is a contracted suite of subpopulations, some of which are small with high conservation risk, whereas others are healthier and act as core anchors to the whole system (*65*). Direct mortality and habitat loss were the initial causes of severe range contraction, but such mortality and habitat loss have been significantly reduced in many areas. Now, population fragmentation is a major threat to the remaining grizzly bears (*65*).

Grizzly bears have ecological characteristics that make them particularly vulnerable to human activities. They occur in sparse densities and have low reproductive rates and male-biased dispersal. In the southern Y2Y region, population fragmentation for grizzly bears is concentrated on gravel-bed river floodplains. Floodplains are critical to grizzly bears for two reasons. The well-known reason is that floodplains are the first areas to green up in the spring and, thus, are disproportionately used when bears emerge from hibernation. The insight that they are critical for reasons of fragmentation is novel. Previously, fragmentation has been a more generalized concern about human transportation and settlement corridors (*65*), but now, we observe that the gravel-bed floodplain portions of these areas are a seasonally critical habitat and paradoxically serve as a source of fragmentation. For grizzly bear populations in southern Canada and the northern United States, the human settlement and transportation corridors within gravel-bed river floodplains and river valleys in general actually define the boundaries of grizzly bear subpopulations (Fig. 4B) (*65*).

The opposite of fragmentation is movement enabled by connectivity. It is important for all wide-ranging species but is especially important for grizzly bears. For grizzly bear populations, female movement is critical. Females provide population viability, and in-migration of females is required to rescue small, fragmented populations from extirpation (*65*). In the Y2Y region, movement of females between mountain ranges is both concentrated (*66*) and most at risk across gravel-bed river floodplains. Female connectivity is not a dash across a human settled valley but a process where female offspring disperse away from their mother into their adult home range that usually overlaps a portion of their maternal range (*67*). Because female grizzly bear dispersal is gradual (*67*) and over relatively short distances (*68*), linkage areas are not narrow movement corridors but need to be large secure areas (that is, kilometers long and across whole gravel-bed river floodplains) where female bears can live portions of their lives with minimal mortality risk.

Where gravel-bed river floodplains are intact in remote places such as the Flathead Valley in southern Canada and the western boundary of Glacier National Park (United States), there is no population fragmentation (*68*). By contrast, in the adjacent but more heavily used Elk River Valley along Highway 3, north of the Flathead watershed, human developments on gravel-bed floodplains have inhibited female movements, although males still cross the valley (*68*). Farther west, human developments in the Nelson, British Columbia, area have completely blocked valley bottom movements of both males and females, leading to genetic differentiation and isolation of the southern Selkirk Mountain population (Fig. 4B) (*65*). These patterns hold across the southern Y2Y region. Both males and females demonstrated reduced movement rates with increasing settlement and traffic. Female movement rates reduced markedly when settlement increased to >20% of a fracture zone. Male movement continues past the 20% level but declines gradually. In highly settled areas (>50%), both sexes had a similar reduction in movements in response to traffic, settlement, and mortality. The result is that several small bear populations that have male-only immigration are not viable over the long term (*65*).

In the Y2Y region, floodplains are often in private hands. The paradigm where human settlement patterns usurp entire river valleys could be improved to better serve biodiversity objectives that include large carnivores if portions of these valley systems contain low human densities and are managed for or restored to a condition closer to their natural state (*65*, *68*). Thus, conservation efforts that focus on securing gravel-bed river valley bottom habitat on private land are essential in maintaining healthy connected grizzly bear populations across the Y2Y region (*65*, *68*). Further, for public lands such as the Canadian Flathead where valley bottoms have both an intact gravel-bed river floodplain structure and hydrological processes, conservation management that minimizes human densities, and thus mortality risk and habitat disturbance, is critical for the regional grizzly bear metapopulation to persist.

Synthesis of disturbance and the shifting habitat mosaic

The theory of habitat complexity leading to high species diversity has long been a foundational guiding concept in ecology (*69*, *70*). Connectivity across the landscape and fragmentation between and among habitats have repeatedly been shown as underpinning realities supporting biodiversity and ecological integrity (*6*). Gravel-bed rivers and floodplains form a network of complex habitats and corridors of connectivity distributed across the landscape in temporally dynamic patterns. The floodplain reaches of the river systems in the Y2Y region are distinctly nonlinear and composed of a vast suite of varying aquatic and terrestrial habitats that collectively form a habitat mosaic (*12*, *71*). This mosaic of habitats is maintained through time by the forces of flood disturbance and geomorphic change across the floodplains of a river system (*14*), in which flood pulses of sufficient power to initiate incipient motion of the substratum and maintain cut-and-fill alluviation of the channel and banks (*3*) are a significant annual disturbance among the unregulated gravel-bed rivers of the Y2Y region. However, floodplain habitat mosaics are subject to other important landscape-scale disturbance regimes. Throughout the Rocky Mountains of the United States and Canada, fire also affects floodplain habitat patch composition (*72*). Gravel-bed river floodplains exist at the intersection of disturbance regimes, annual flooding regimes that shape the riverscape, and longer-period fire regimes that shape the landscape, including floodplains (*72*). The dynamic nature of the river (that is, the geomorphic cutting, eroding, and depositing of material) from fine sediments to old-growth trees creates a "shifting habitat mosaic" with complex feedbacks, *n*-dimensional gradients, and temporal variation (*12*), both on the surface and in the subsurface sediments.

Gravel-bed rivers vary greatly, both between rivers and within rivers, along their longitudinal gradient (*73*). Floodplain river segments are vastly more complex and biologically diverse than confined river segments of the same river (*13*). The complex floodplain segments are also focal points or intersections of regional biodiversity. For example, among aquatic insects, floodplain reaches have more than twice the diversity of confined river segments. The region's salmonids spawn almost exclusively in floodplain reaches where there is a combination of complex habitats and surface water and groundwater interaction directly resulting from the relationship between the river and the floodplain. Although occupying less than 3% of the area, more than half of the region's plant diversity can be found on these floodplains (*38*). More than 70% of the region's bird species use floodplain reaches for some critical component of their life histories (*40*). The large, iconic ungulates of the region use river floodplains year-round (*49*) but most extensively in winter, and wolves not only follow the elk or caribou but also den almost exclusively on river floodplains (*54*). Gravel-bed rivers are also the primary corridors connecting otherwise disconnected populations of wide-ranging grizzly bears (*65*).

We conclude that, in the glaciated landscapes of the Rocky Mountains of North America from Y2Y, gravel-bed rivers and floodplains are the central and most important sites of biodiversity and connectivity at the regional spatial scale. From microbes to grizzly bears, disturbance-driven river floodplains support a disproportionate variety of species, affecting the distribution and abundance of the region's biodiversity far beyond the area confines of the floodplains themselves (Fig. 5). These floodplains are also the primary arena where species interactions and critical life history events occur for many aquatic, avian, and terrestrial species. Natural fluvial processes that have shaped these landscapes for millennia are centrally important to supporting the diversity of connected habitats that species of enormous ecological and socioeconomic value rely on. Simplifying floodplains by either hydrologic modification of the power of the river (for example, flood reduction) or geomorphic modification (for example, bank hardening levees or rip-rap) invariably results in loss of biodiversity (*74*). For metapopulations of species as varied as aquatic insects, amphibians, fish, birds, ungulates, wolves, and grizzly bears to persist in the Y2Y region, it will be necessary to focus conservation efforts on these gravel-bed river floodplains and the processes that maintain them.

FLOODPLAINS: COUPLED NATURAL AND HUMAN SYSTEMS

An endangered landform

Floodplains are recognized as among the most endangered landform types worldwide (*75*). Gravel-bed river floodplains are flat, rich, and attractive areas with abundant water for municipalities, agriculture, and recreation. In most mountainous systems, they are the first to be converted to permanent human settlement, agriculture, industry, and transportation corridors (*75*). Although there are many protected areas in the Y2Y region (for example, Yellowstone, Waterton-Glacier, Banff, and Jasper National Parks and Bob Marshall and Frank Church Wildernesses), humans have altered the structure and function of the gravel-bed river floodplains inside, and particularly outside, of these protected areas, and in many ways. Over the past century, we have expended enormous effort to harness and control gravel-bed rivers for power generation, flood control, and irrigation. Many of the region's cities were pioneered along the edge of river floodplains when these rivers were important for commerce. Virtually every city pioneered near a river has deliberately encroached onto the neighboring floodplain and subsequently built levees and hardened structures to prevent flooding and damage to infrastructure. Unfortunately, these prove to be inadequate when very large but highly repeatable floods occur, as seen on the Bow River in Alberta (1927 and 2013), Flathead River in Montana (1896 and 1964), Yellowstone River in Montana (1997 and 2011), and Snake River in Idaho (1927 and 1997).

Worldwide, there has been a marked decline among many species, from amphibians (*76*), to bumble bees (*77*), to marine fisheries (*78*). There are many compounding and additive factors affecting populations that lead to marked worldwide declines across a multitude of species, and loss of ecosystem complexity and connectivity is a significant part of the loss in overall biodiversity and especially of valued native species. In many mountain systems, gravel-bed river systems are vastly transformed and will require strategic restoration to recover their ecosystem function.

Hydrologic and geomorphic modification

The dynamics of the human system that interface with gravel-bed rivers and floodplains superimpose a desire for minimization of environmental risk and maximization of control over nature. The processes through which the natural system affects the human system (for example, flooding and damage to the human infrastructure) and the processes through which the human system affects the natural system (for example, flood control and hardening of river banks) are complex. Dams for hydropower, flood control, and irrigation of agricultural lands are pervasive in mountainous landscapes worldwide (*79*). Dams are generally placed in canyon sections of rivers where bedrock nears the surface and the valley is narrow. Unconfined, open valley river segments are often upriver from these confined reaches that make ideal locations for dams. Historically, in the Y2Y region of the Rocky Mountains, these river segments were critical, high-biodiversity, expansive floodplains supporting the full suite of aquatic, avian, and terrestrial species native to the region, as discussed above. Not only do dams inundate upstream floodplains, but they also interrupt the natural flow regime (*35*) and change the dynamics of hydrogeomorphic processes and disturbance regimes downstream of the dam. This loss of fluvial process results in negative ecological cascades across many species that are reliant on gravel-bed floodplain dynamics to maintain the shifting habitat mosaic

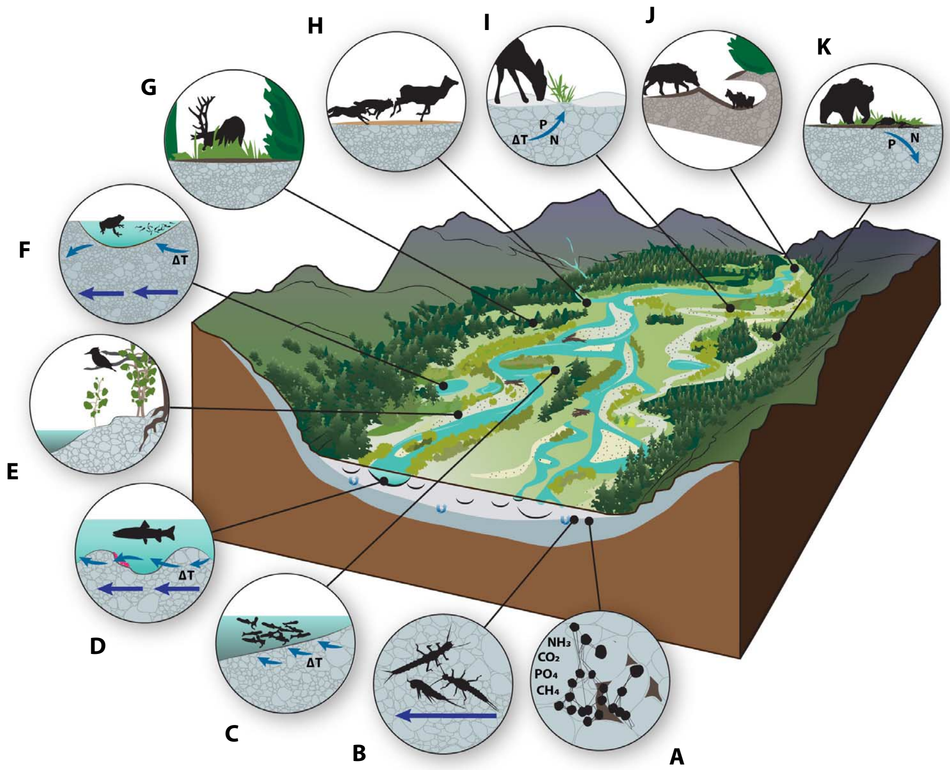

Fig. 5. The gravel-bed river floodplain as the ecological nexus of regional biodiversity. Illustration shows the complexity of the shifting habitat mosaic, the biophysical interactions among organisms from microbes to grizzly bears, and the importance of gravel-bed river floodplains as the nexus of glaciated mountain landscapes. (**A**) Microbes of the interstitial spaces of the gravel bed showing the products of processing of organic matter in the subsurface. (**B**) Crustaceans and insects that inhabit the gravels of the floodplain. (**C**) Temperature modification of surface habitats from upwelling hyporheic zone waters. (**D**) Native fishes spawning in floodplain gravels. (**E**) Riparian obligate birds. (**F**) Amphibian spawning in floodplain ponds and backwaters. (**G**) Ungulate herbivory of floodplain vegetation. (**H**) Wolf predation on ungulate populations. (**I**) Early-spring emergence of vegetation. (**J**) Wolf dens located along floodplain banks. (**K**) Use by grizzly bears and other carnivores as an intersection of landscape connectivity and sites of predation interactions (E. Harrington, eh illustration, Missoula, MT).

and connectivity, locally at the floodplain scale and regionally at the landscape scale. Loss of hydrologic dynamics and flooding is a well-documented cause of cottonwood gallery forest collapse across the region (*36*, *39*). Flow augmentation and temperature modification of dam tail waters likewise markedly affect aquatic populations of river food webs (*80*, *81*). By blocking natural connections, the upstream and downstream impacts of dams include effects on the dispersal and migration of organisms and genetic isolation through loss of migratory populations (*6*).

While private property and public infrastructure on gravel-bed river floodplains are subject to flooding, human infrastructure is also subject to the natural process of cut-and-fill alluviation. As the river moves across the floodplain, banks are cut and sediments are redeposited. Land is lost on one side of the channel and added to the other. Often, sites that experience high stream power that erodes banks are controlled by bank-hardening structures such as rip-rap, levees, and dikes (*82*). The cobble and gravel along the bed and banks of the river that were once mobile become stabilized and more embedded as fine sediments infiltrate the spaces in between the now immobile cobble. The rate of water exchange between the channel and the floodplain surface and subsurface is reduced, and the hyporheic food webs are degraded (*83*). Dams reduce stream power by reducing annual flooding, whereas bank hardening prevents sediment mobilization, especially laterally, and, thus, eliminates the dynamics of the floodplain system. This also results in the eventual collapse of the cottonwood gallery forest, in loss of aquatic habitats across the floodplain, and in cascading negative consequences for aquatic, avian, and terrestrial species dependent on the sustaining dynamics and shifting habitat mosaic of floodplains (*84*). In short, human manipulation of both flow and bank hardening directly affects hydrogeomorphic processes with major negative consequences in maintaining the natural spatial and temporal dynamics of the habitat mosaic on the floodplain that support regional biodiversity and ecosystem-scale ecological integrity (Fig. 6). Nonetheless, while many gravel-bed river floodplains in the region are intensely affected, the Y2Y region provides an unprecedented opportunity to protect and restore many large gravel-bed river systems.

New frontiers in regional-scale conservation

Gravel-bed river floodplains serve as refugia (*85*) and will be critically important under climate change and global warming for a variety of aquatic and terrestrial species. The effects of a rapidly changing climate will further stress habitats and populations that have already been affected by human activities for over a century (*86*). For example, salmonids are especially vulnerable to climate change because their survival is dependent, from eggs to juveniles to adults, on an abundance of clear, cold, connected, and complex habitats that are concentrated

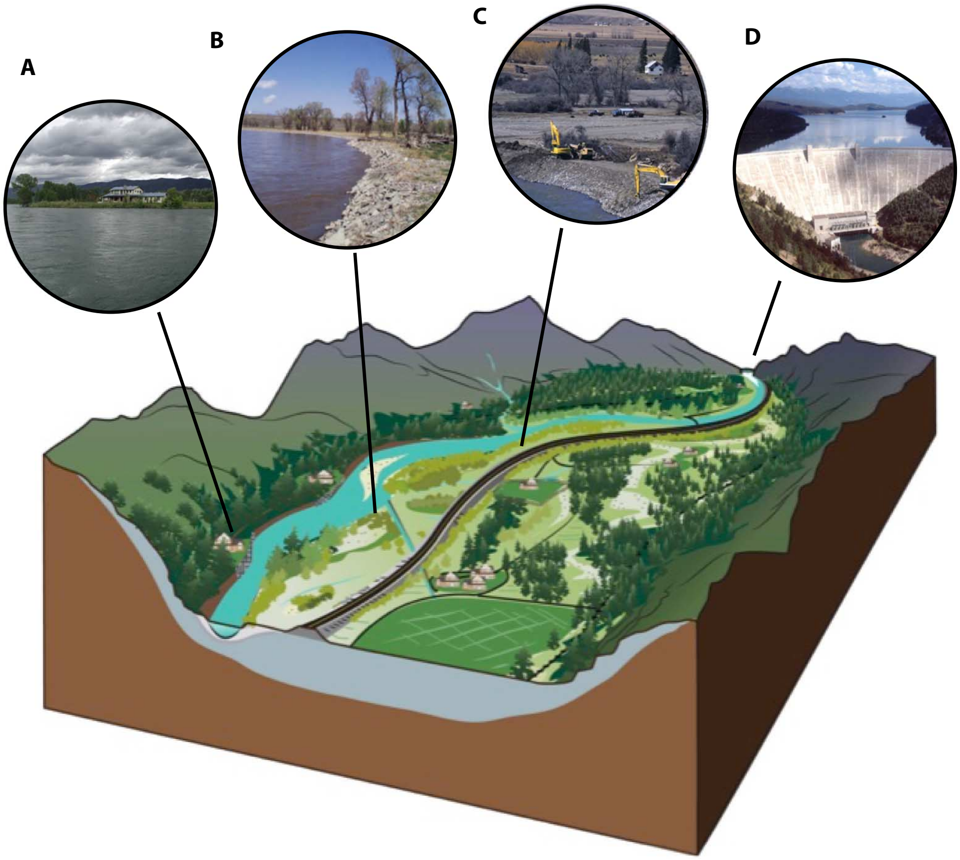

Fig. 6. The gravel-bed river floodplain as affected by human structures. (**A** to **D**) Illustration shows the loss of floodplain natural complexity as a result of human infrastructure shoreline housing and transportation corridor (A), rip-rap as a bank-hardening structure (B), geomorphic modification of levee construction (C), and a dam at the top of the floodplain (D). Note that, in this cutaway view, the hyporheic zone is highly reduced and modified from that shown in Figs. 2 and 5 as the river is converted into a functional single-thread river with little cut-and-fill alluviation across the floodplain. This results in the loss of highly sorted, open-network cobble substrata and further loss of the interstitial flow pathways of the hyporheic zone. When modified, most ecosystem components illustrated in Fig. 5 are significantly reduced or eliminated from the floodplain system (E. Harrington, eh illustration, Missoula, MT).

in their abundance on gravel-bed river floodplains (*19*), specifically because of the disturbance processes that maintain the connectivity of groundwater–surface water interactions and produce pockets of cold water across the mosaic of surface habitats (*87*). The sensitivity of cold-water salmonids is one of the primary determinants of their endangered status. Likewise, birds, ungulates, and large predators are dependent on the complex spatial mosaic of habitats that are affected by human-modified hydrogeomorphic processes (*42*, *50*). Extensive research has clearly shown that riparian and gravel-bed river valley habitats are important for grizzly bears (*64*). However, grizzly bears and gravel-bed river valleys intersect most significantly seasonally and at two less obvious levels. In the presence of human populations and infrastructure, gravel-bed rivers fragment grizzly bear populations, but they can also provide the connectivity to reverse that large-scale fragmentation. The degree to which gravel-bed river valleys are in their natural state plays a major role in determining the conservation status of the regional and subcontinental grizzly bear populations (*65*).

Stream ecosystems worldwide are increasingly affected by multiple stressors that lead to an overall reduction in biodiversity (*74*). Throughout North America, ecological restoration of streams and rivers has primarily focused on increasing habitat heterogeneity or complexity to promote restoration of biodiversity losses (*88*). The most common practice in stream restoration has been the reconfiguring of channels and adding physical structures such as boulders, large wood, and channel-spanning weir structures to enhance structural heterogeneity and restore biodiversity. However, these approaches have been shown to be largely unsuccessful (*88*). Lack of success has been attributed to streams that are sensitive to a suite of stressors that are often cumulative, including impacts from urbanization, agriculture, deforestation, invasive species, flow regulation, water extractions, and mining.

Although managers should critically diagnose the stressors that affect an impaired stream and primarily invest in resources to solving problems that will most likely limit restoration, a central goal of conservation across mountain regions should be the restoration of the natural spatial and temporal dynamics that sustain gravel-bed river processes. This is not to suggest that impacts from mining, forest practices, or urban runoff are not distinct problems (*89*, *90*), which must be addressed. However, on floodplain segments in particular, channel reconfiguration and structures introduced by riverscape managers are actually counterproductive if they interfere with channel migration and cut-and-fill alluviation. This means taking real steps to remove hydrologic constraints to flooding regimes, allowing sufficient power in the river to mobilize the gravel and remove geomorphic constraints to river channel migration, such as rip-rap, levees, and even well-intentioned habitat structures, to restore the dynamics of the floodplain habitat mosaic. Successful river restoration and renaturalization have been achieved along tens and even hundreds of kilometers of gravel-bed river by reengaging naturalized hydrogeomorphic regimes and achieving floodplain dynamics (*84*, *91*, *92*).

Important pressures and unresolved questions

Conservation management decisions during the next decade will have an enormous effect on native biodiversity (*93*, *94*). Here, we have made the case that protecting and restoring gravel-bed river floodplains in glaciated mountain environments such as Y2Y are of major importance to large landscape conservation efforts that seek to protect biodiversity and ensure ecosystem resilience and resistance to human encroachment, other human stressors, and the complicating factors of altered flow and temperatures associated with climate change. For example, as society considers the global implications of climate change, many are looking for solutions in reduction of CO_2 loading to the atmosphere. Hydropower is now being touted as a "green technology" energy source, having a "no or low" carbon loading footprint (*95*). However, this can be very short-sighted. We must not impose an action to solve one problem, such as global atmosphere carbon loading, while introducing hugely unintended negative consequences on other systems (for example, gravel-bed river floodplains) and, thus, amplifying one of the fundamental reasons we have concern for climate change, namely, the loss of regional and global biodiversity. As air temperatures and cold water habitats warm throughout the Y2Y and other mountain regions, managers can mitigate potential adverse consequences to wildlife and plants by protecting, reconnecting, and restoring gravel-bed river floodplains and their functional processes that maintain ecosystem structure over extended time and space (*96*).

Another growing pressure on gravel-bed rivers, and thus a significant threat to their ecological role in regional biodiversity, follows from human demographics. The Rocky Mountain region of North America has one of the fastest-growing human populations in both the United States and Canada (*97*, *98*). Exurban housing developers are attracted to floodplains for their amenities, including proximity to the biodiversity that is threatened by those same developments. Property values reflect these preferences, and subsequently, strong political pressures are often applied to permit development on flood-prone areas. However, such developments are anathema to maintaining natural processes or renaturalization of flow regimes and geomorphic processes for conservation purposes, because homeowners demand "protection" from the river and its natural processes that create the environment and biodiversity that attracted them onto the floodplain in the first place. Urban and exurban expansion creates very specific challenges, whereas farmers, ranchers, and the Department of Transportation (at both state and provincial levels) continue to rip-rap and levee-off channel shorelines to prevent property and infrastructure losses. Invariably, actions to restrict the river channel on floodplains are catastrophic to sustaining local and, ultimately, regional biodiversity because processes dependent on renewed gravel surfaces are eventually lost to succession without regeneration, and connectivity to both subsurface and surface floodplain habitats are severed.

On the near horizon, there remain unresolved questions regarding gravel-bed river floodplains and continued and growing threats to their survival as foci of regional biodiversity and productivity, especially among the coupled natural and human system responses to climate change and population growth and redistribution. Thus, the overriding question remains, "How do we resolve the enormous gap between what scientists know to maintain and restore functioning floodplain and gravel-bed river systems and the neglect by land-use managers, energy planners, and society as a whole to values and vulnerabilities of these biodiverse floodplain systems that represent the ecological nexus in glaciated mountain regions?" The first step is a synthetic understanding across disciplines that gravel-bed river floodplains in mountain landscapes have a disproportionate concentration of diverse habitats, nutrient cycling, productivity, and water supply that is critically important to a vast array of aquatic, avian, and terrestrial species at the landscape and regional scales. Second, gravel-bed river floodplains have also been disproportionately negatively affected by human infrastructure and use. This scientific understanding and implementation of conservation policies that reflect this understanding will require a paradigm shift from conservationists and river managers to prioritize the maintenance or restoration of intact structures and processes throughout the length and breadth of gravel-bed rivers and their floodplains.

Future research needs and hypotheses

It is at the interface of classic disciplines where interesting and novel insights are being discovered in conservation. We need comprehensive ecosystem assessments of gravel-bed rivers to include integrated analysis of floodplains across multiple spatial and temporal scales, including important ecological attributes such as landscape conditions integrated with climate impacts and human-induced drivers, to understand the vulnerability of gravel-bed river floodplains to ongoing and future human stressors. Future work should include developing cause-and-effect relationships between gravel-bed rivers and uplands that are derived from changes that originate in gravel-bed river systems, to strengthen society's understanding of these ecosystems and inform how they might be restored to their proper functioning condition. There will continue to be increasing human effects in mountain zones worldwide. These will continue to be focused in the river valleys. We need to understand how the pressures from further development and population growth will be complicated by climate change with regional warming. We need to understand how the alteration of the magnitude and seasonality of river flows will affect the timing of critical life history events of aquatic, avian, and terrestrial populations that rely on gravel-bed river systems. There is abundant evidence that floodplains are critical areas supporting species diversity in glaciated mountain landscapes. However, we know much less about how the varied and dynamic physical conditions in these floodplains influence intraspecific genetic and ecological diversity. For example, does the physical habitat diversity on floodplains promote fine-scale patterns of local adaptation that we do not see elsewhere in the landscape? Finally, our paper highlights the need for synthetic research that moves beyond studying focus taxa or species assemblages (for example, community ecology that addresses only vegetation or only birds) or habitat types (for example, riparian forests). To learn about the complex interactions among ecosystems and their components across landscapes, we need an improved understanding of how subsidies flow from rivers to ridge tops and vice versa. It is through this expanded understanding that we will have the potential to greatly improve conservation and management practices.

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