Great Expectations: Deconstructing the Process Pathways Underlying Beaver-Related Restoration

CAROLINE S. NASH⬤, GORDON E. GRANT, SUSAN CHARNLEY, JASON B. DUNHAM, HANNAH GOSNELL, MARK B. HAUSNER, DAVID S. PILLIOD, AND JIMMY D. TAYLOR

Beaver-related restoration is a process-based strategy that seeks to address wide-ranging ecological objectives by reestablishing dam building in degraded stream systems. Although the beaver-related restoration has broad appeal, especially in water-limited systems, its effectiveness is not yet well documented. In this article, we present a process-expectation framework that links beaver-related restoration tactics to commonly expected outcomes by identifying the set of process pathways that must occur to achieve those expected outcomes. We explore the contingency implicit within this framework using social and biophysical data from project and research sites. This analysis reveals that outcomes are often predicated on complex process pathways over which humans have limited control. Consequently, expectations often shift through the course of projects, suggesting that a more useful paradigm for evaluating process-based restoration would be to identify relevant processes and to rigorously document how projects do or do not proceed along expected process pathways using both quantitative and qualitative data.

Keywords: beaver, stream restoration, conservation, monitoring and evaluation

The North American beaver (*Castor canadensis*) is renowned as an ecosystem engineer with the ability to transform hydrologic, geomorphic, and ecological processes within stream ecosystems through the construction of dams (Naiman et al. 1988, Jones et al. 1994, Collen and Gibson 2001, Wright et al. 2002, Ecke et al. 2017). Historical reports describe near ubiquitous presence of beavers throughout North America prior to European settlement (Seton 1909, 1929, Jenkins and Busher 1979), but most populations were extirpated by the nineteenth century because of fur trapping and habitat conversion for agriculture (Hays 1871, Shaw and Fredine 1971, Johnston and Chance 1974). Beaver populations were largely restored throughout their historical distribution across North America in the twentieth century (Müller-Schwarze 2011). However, their century-long absence has been hypothesized as one of several factors contributing to the degradation of streams, particularly low order, intermittent and ephemeral headwater streams found throughout the western United States, where channel incision is prevalent (Marston 1994, Butler and Malanson 2005, Bull 1997, Pollock et al. 2007).

Recent efforts to reverse this degradation have resulted in rapidly growing numbers of beaver-related restoration (BRR) projects in the western United States and elsewhere (Macdonald et al. 1995, Beechie et al. 2010, Halley et al.

2012, Pollock et al. 2014, Pilliod et al. 2018, Wohl et al. 2019). BRR, a process-based restoration strategy (*sensu* Beechie et al. 2010), seeks to reestablish or replicate the process of beaver dam building on degraded stream systems using tactics ranging from the translocation of beavers to streams where dams are desired, to building artificial structures that mimic beaver dams, to restoring riparian vegetation to attract beavers and provide them with food and materials with which to build dams (figure 1; Pollock et al. 2017, Pilliod et al. 2018).

The fundamental idea behind process-based restoration in rivers and streams is that channels have degraded because processes thought critical to sustaining these freshwater ecosystems have either been eliminated, or their rates or magnitudes have changed (Kondolf et al. 2001, 2006, Palmer et al. 2005, Beechie et al. 2010). In principle, if these processes are restored at some historically relevant rates and magnitudes, stream ecosystems should recover accordingly. Compared with engineered stable channel forms (Wohl et al. 2015), process-based restoration tactics are often inexpensive and relatively low tech, making them more scalable and therefore potentially more effective at achieving restoration goals (Nagle 2007, Pollock et al. 2017, Silverman et al. 2019).

With only a few exceptions (e.g., Bridge Creek, Oregon; Pollock et al. 2007, Bouwes et al. 2016, Weber et al. 2017),
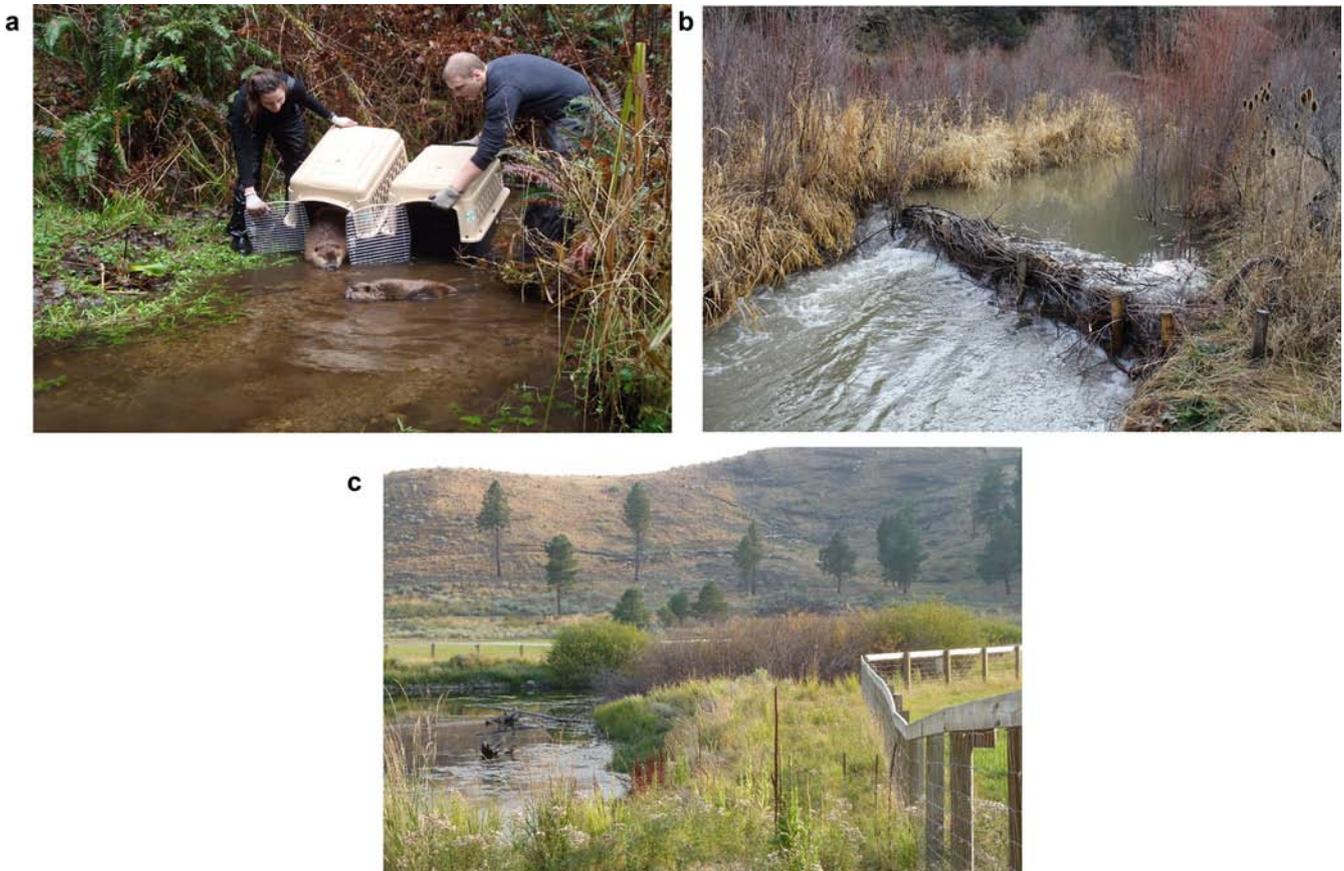
Figure 1. BRR employs three distinct tactics that aim to increase the distribution and number of beavers, beaver dams, or structures that mimic the function of beaver dams. (a) The most reported BRR tactic in the western United States is beaver translocation (Pilliod et al. 2018), where nuisance beavers are captured and relocated to areas in which dams are desired. Photograph: USDA National Wildlife Research Center. (b) The second most reported BRR tactic is to install in-stream structures intended to either function like beaver dams or promote dam building and maintenance by beavers. These artificial structures are constructed with a variety of methods and materials, resulting in diverse and often inconsistent nomenclature (i.e., figure 1; Pilliod et al. 2018) Photograph: USDA National Wildlife Research Center. (c) A third BRR tactic is riparian vegetation restoration, which encourages the reestablishment of riparian shrubs and trees used by beavers by actively planting species thought to promote beaver colonization and dam building, and excluding other browsers or altering livestock management, including the use of fencing. Photograph: Susan Charnley.

BRR projects have seldom been conducted with rigorous pre- and postproject monitoring due largely to monitoring costs, because these can exceed restoration costs (Pilliod et al. 2018, Johnson-Bice et al. 2018, Lautz et al. 2019). In the locations in which BRR has been monitored, the projects are reported as having successfully achieved goals (e.g., Bouwes et al. 2016, Weber et al. 2017), contributing to its broad appeal in popular accounts (Goldfarb 2018). Whether and to where these outcomes might be transferable remains unknown, in part because of the limited geographic scope of intensive monitoring (Johnston-Bice et al. 2018).

Evaluating the effectiveness of any process-based restoration approach, including BRR, requires answering two focal questions: Did the restoration tactic recreate critical processes at effectual rates, and did the reestablishment of these processes create the desired biophysical and, subsequently,

ecological conditions? Evaluating effectiveness therefore requires identifying these desired condition (i.e., expected outcomes), as well as the critical processes thought necessary to establish those conditions. More fundamentally, it requires deciding whether it is the objective or the means by which the objective is achieved that matters most (e.g., Gregory et al. 2012).

The concept of contingency (*sensu* Gould 1989) is a useful way to understand process-based restoration and to manage expectations around potential outcomes of BRR. Contingency in natural systems suggests that every eventual outcome may be explainable in hindsight, but is often difficult or impossible to predict looking forward because of the critical role of historical antecedents and unanticipated intervening factors. Therefore, although certain elements of a restoration project might proceed along well-articulated

Table 1. Case studies of BRR included in this study.

Project location and type	Year started	Land ownership	Source
Bridge Creek, Oregon: beaver dam analogues and riparian vegetation restoration	2007	Federal	Bouwes et al. 2016, Davee et al. 2019, Pollock et al. 2014, Weber et al. 2017
Silvies Valley Ranch, Oregon: low rise artificial beaver dams built from rock, gravel, and soil (aka rock check dams) and riparian vegetation restoration	2001	Private	Davee et al. 2017
Camp Creek, Oregon: beaver dam analogues, channel-spanning wood jams, riparian vegetation restoration	2016	Federal	Armichardy 2017, USDA FS 2016, Charnley et al. 2020
Scott Valley, California: beaver dam analogues	2014	Private	Charnley 2018
Elko County, Nevada: riparian vegetation restoration	early 1990s	Federal and private	Charnley 2019
Eastern New Mexico: beaver dam analogues and translocation	circa 2012	Private	Wild 2017

and relatively predictable paths, the ultimate outcomes associated with a project can be influenced by processes beyond the spatial, temporal, and physical scope of the project, including those influenced by place, sequence of events, and human response. A rigorous process-expectation framework that articulates the contingencies embedded in a restoration strategy from the outset can provide a roadmap to this complex suite of interactions and help set reasonable expectations.

In the present article, we present such a framework to systematize our present understanding of how common BRR tactics might lead to expected outcomes. We first identify commonly expected outcomes from a sample of BRR project case studies (table 1) and restoration guidance documents and construct a process-expectation framework. We then explore the contingency implicit within this framework on the basis of a literature review as well as the experiences of people participating in the case study projects. This framework is not comprehensive, but provides a roadmap by which the explicit and implicit causal links embedded in BRR can be articulated and examined against our current knowledge base and, therefore, set expectations.

Such an assessment is timely as increasing investments are being made in BRR to address wide-ranging natural resource priorities. In the American West, policymakers are already being challenged to develop policy guidance for BRR without a systematic understanding of its consequences to ecosystem health, downstream water users, and infrastructure. Managing expectations regarding the scale at and conditions under which BRR *can* fulfill these expectations is essential to ensure such projects are well suited to local biophysical and social conditions, implemented at effective scales, and communicated in a way that builds trust among landowners, practitioners, regulators and scientists.

A process-expectation framework for BRR

We organize our analysis of BRR around common project goals—expected outcomes—because their specification ultimately sets expectations about what restoration can accomplish and at what scale (Ehrenfeld 2000). To understand how BRR is expected to work, we deconstructed common narratives describing BRR into a framework describing the sequence of processes by which each BRR tactic is expected to produce outcomes (figure 2). The processes we outline in figure 2 reflect expectations and contingencies related to how BRR *should* work, not necessarily how it *does* work in practice.

We included the three most common tactics among BRR practices, determined through an inventory of these practices (Pilliod et al. 2018): beaver translocation, the use of artificial structures, and riparian vegetation restoration. To create our process-expectation framework (figure 2), we linked these tactics to expected outcomes identified from narratives describing the justification for and consequences of BRR in technical guidance documents, published case studies, and peer-reviewed literature (tables 1 and 2). We summarized expected outcomes in table 3. Five of the six case studies are based mainly on research conducted by two of the authors that focused on BRR in rangeland environments of the western United States with current or historical livestock grazing. Research methods included semistructured interviews with 86 people involved in BRR projects across the five sites including ranchers, landowners, agency staff, and staff of nongovernmental organizations to document their perspectives on, and experiences with, BRR. Individual reports were developed for four of the case studies (Davee et al. 2017, 2019, Charnley 2018, 2019), and the results across the five sites were synthesized in Charnley and colleagues (2020). We draw on these publications in the present article.

Across the included case studies, the desired outcome from BRR was rarely beavers alone but was rather contingent on what beavers were expected to do to the landscape—that is, construct dams that then change hydrogeomorphic and ecological conditions. As one rancher put it, "a beaver equals water storage" (Charnley 2019). However, growing numbers of BRR projects involve process pathways that do not require beavers at all (e.g., artificial structures mimicking
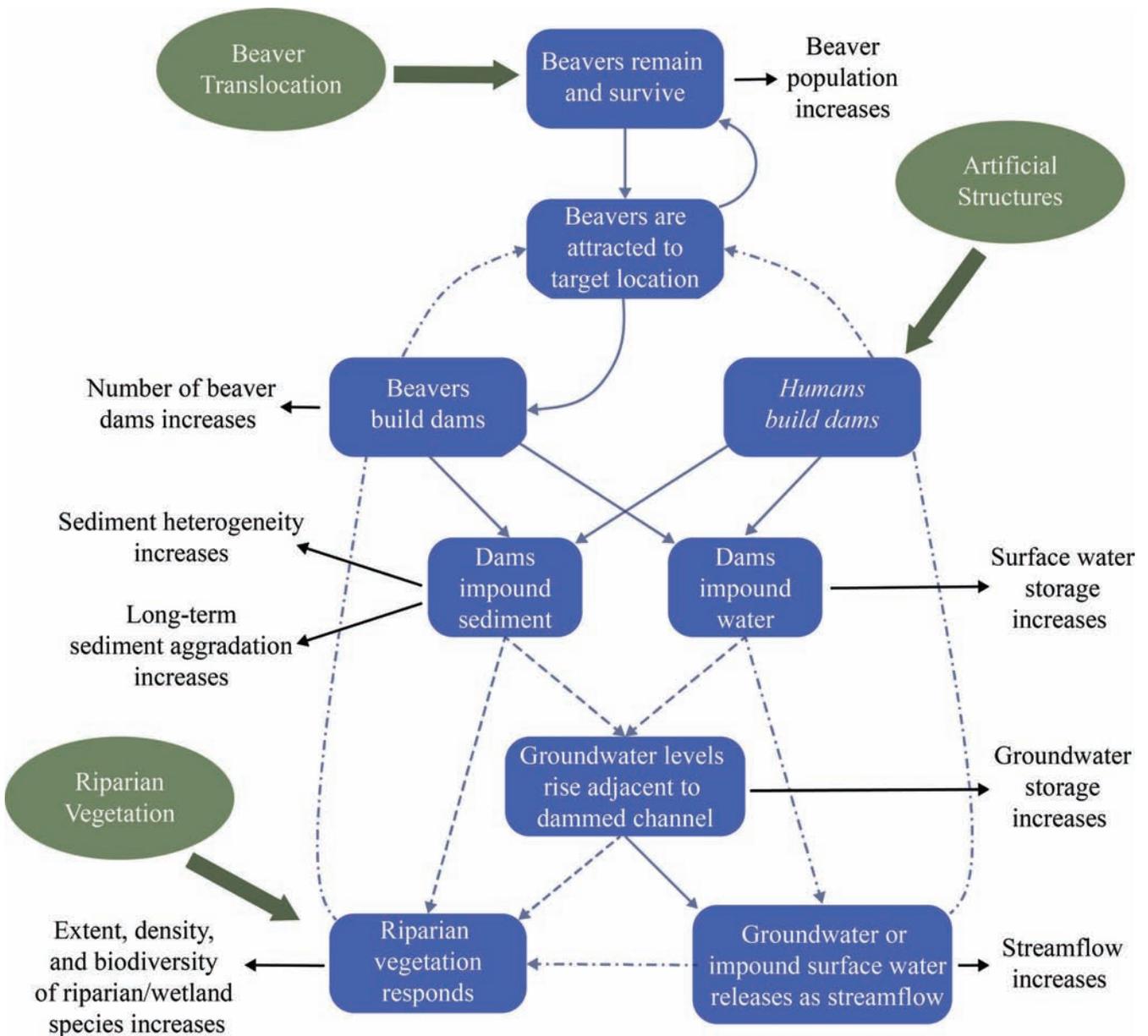
Figure 2. Flow chart documenting the sequence of processes (the blue boxes and the arrows with solid lines) that must occur for each BRR tactic (the green circles and the black arrows) to achieve commonly expected outcomes (the black text). The arrows represent the sequence in which the steps must occur: The solid lines indicate a causal relationship; the dashed lines indicate that one of two mechanisms can lead to the next step, and a dot-dash line indicates that the preceding step can amplify the following step, but it is insufficient to lead to changes on its own. For example, an increase in sediment deposition can increase the surface area in which riparian vegetation can grow, but only if the water table has also risen to provide plant-available water. The processes outlined in the present article reflect expectations about how BRR should work on the basis of stated project goals, not necessarily how it does work in practice.

beaver dams). Dam building is therefore only the primary process that BRR seeks to reestablish, whether by encouraging beavers to build dams or humans building artificial structures. There are wide-ranging and sometimes implicit or conflicting expectations about the subsequent processes that dam building will introduce or amplify. As such, we separate identified processes into those linking BRR tactics

to dam building and those linking dams (built by beavers or humans) to expected outcomes. We also distinguish between the process pathways resulting from longer- versus shorter-lived dams.

To illustrate the logic behind this framework, for beaver translocation (tactic) to increase dam building (expected outcome), beavers must survive, remain within the release

Table 2. BRR project goals for each case study.

Project Location	Socioeconomic	Ecological	Hydrogeomorphic
Bridge Creek, Oregon		Restore streams to improve salmonid habitat to and increase their populations of threatened species (esp. Columbia River steelhead, *Oncorhynchus mykiss*)	Reduce erosion and stream channel incision to increase floodplain connectivity
Silvies Valley Ranch, Oregon	Develop a low-cost restoration tool, reduce regulatory barriers to BRR	Restore riparian habitat mimicking what beavers created to promote fish recovery, increase beaver populations, and improve habitat for wildlife and livestock	Restore degraded and incised stream channels
Camp Creek, Oregon		Improve and increase spawning and rearing habitat for salmonids (especially juvenile Columbia River steelhead, and Chinook salmon, *Oncorhynchus tshawytscha*), increase beaver habitat and promote recolonization, reestablish woody riparian vegetation	Reduce incised stream channel width, reconnect streams to floodplains and side channels, create pools, raise water table increase water discharge during low flow periods
Scott River Basin, California	Demonstrate the value of BDAs as a watershed restoration tool in California	Improve in-stream habitat for salmonids (esp. SONCC coho, *Oncorhynchus kisutch*)	Improve in-stream flows, raise groundwater levels, reduce stream incision
Elko County, Nevada	Promote grazing practices compatible with stream restoration and fish recovery	Restore aquatic and riparian habitat to promote recovery of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*)	
Eastern New Mexico	Increase livestock forage productivity, demonstrate compatibility of beavers and ranching, demonstrate value of beaver for restoration	Increase and improve riparian vegetation, improve riparian function and resilience, reintroduce beavers to stream system	Reduce stream channel incision, increase amount of water in stream systems, reconnect stream to floodplain, elevate water table

Table 3. Project goals and expectations of BRR.

Goal	Expectations
Increase beaver populations	Numerically increase beavers
	Numerically increase beaver dams
Alter sediment dynamics	Increase amount of sediment stored in channel
	Reduce or stop vertical erosion
	Increase the heterogeneity of in-channel geomorphic features
	Increase lateral erosion
Improve water availability	Increase surface water storage
	Increase groundwater storage
	Increase streamflow downstream of projects
Improve riparian/wetland habitat	Increase the extent, density, and biodiversity of riparian/wetland species
Recover populations of fish and wildlife species of concern	Numerically increase aquatic species of concern
	Expand physical habitat for aquatic species of concern

Note: We distinguish between goals and expectations using the same distinction between goals and outcomes in structured decision-making (Gregory et al. 2012). Namely, although goals are stated in language closest to that used by project participants, expectations are stated in quantitative terms that relate to measurable metrics.

location, and build dams. For beaver translocation to improve water availability by increasing late summer stream-flow, however, beavers must survive, remain upstream of the locations in which increased flow is desired, and build dams there. Furthermore, constructed dams must impound water, groundwater must rise near where the dam was built, and either the surface water or groundwater must discharge as streamflow in the late summer at rates greater than those documented before restoration. For these changes to persist

beyond a year, the dams must persist or be maintained as well. For these changes to occur at broader spatial scales, so too must the dam building, water impoundment, and dam persistence.

Embedded in figure 2 are myriad contingent pathways linking BRR tactics to expected outcomes. Although the data are still too scant to attach probabilities, outlining these contingent relationships allows us to evaluate each process against available data, consider implicit assumptions,

attribute reported outcomes to causal mechanisms, and highlight the conditional nature of the processes on which BRR relies. In the following sections, we first evaluate the processes necessary for each BRR tactic to spur dam building, then look to how dams (built by beavers or humans mimicking beavers) change ecosystem processes and conditions. The data presented therein are not meant to be exhaustive but, rather, illustrative of key processes driving BRR outcomes, whether successful or not.

How do BRR tactics promote dam building?

All BRR tactics fundamentally assume that the absence of beavers is limiting dam building and that beavers, once present, will build dams. Each tactic, however, makes different assumptions as to the factors limiting beavers and the processes necessary for their reestablishment:

Beaver translocation aims to increase the number of dams by moving beavers to a location in which dams are desired. Beavers are then expected to form colonies, establish and defend territories, and either begin to build dams or maintain existing structures. The fundamental assumption is that beavers' absence is limiting dam building.

Riparian vegetation restoration aims to increase the number of dams by improving the quantity and quality of riparian vegetation available to beavers for food and dam building. This often also includes limiting access to riparian vegetation by browsing ungulates. Changes to vegetation and grazing or browsing are expected to encourage beavers to move to the area, and subsequently conduct activities as in beaver translocation. The fundamental assumption is that insufficient or unsuitable vegetation is limiting beavers and, therefore, dam building.

Artificial structures—specifically, small dams or impoundment structures built by humans—increase the number of dams by changing the hydrogeomorphic conditions in a stream reach. Artificial structures can include beaver dam analogues (BDAs), which are typically built by weaving small-diameter woody material between posts and sometimes include additional earthen fill behind them, and in-stream structures variably called rock dams, check dams, weirs, or artificial beaver dams (ABDs), which are built entirely of earthen materials. Artificial structures categorically increase the number of dams in a river reach. Hydrogeomorphic changes that result are expected to influence the capacity of the site to grow enough riparian vegetation for beaver food and dam building. Artificial structures are also sometimes used when channels are so incised that floodwaters remain between banks, easily breaching any beaver dam building that does occur on its own. Changes to hydrogeomorphic conditions and vegetation are often expected to encourage beavers to move to the area, and subsequently conduct activities as in beaver translocation. The fundamental assumptions are that biophysical conditions are directly limiting the survival of dams because of hydraulics that emerge in deeply incised channels, or that they are limiting riparian vegetation, which is limiting beavers and, therefore, dam building.

Findings and first principles. In this section, we explore the critical processes linking each of the tactics listed above to sustained dam building by beavers, as is outlined in figure 2, using available biophysical and social data.

Translocation and dam building. For translocation to lead to dam building, beavers must survive, establish, and build dams (figure 2). It is difficult to generalize regarding the probability of survival following translocation of beavers, because it is likely to depend on the type of release employed, the local habitat, and the broader landscape (Moehrenschlager and Lloyd 2016). Recently published guidelines offer suggestions to potentially enhance survival and occupancy (Pollock et al. 2017). Success rates of various release tactics in terms of survival and persistence are not yet well documented in peer-reviewed literature, and likely vary widely.

Where it has been systematically documented, the survival of translocated beavers is typically less than 50%, with 35%–57% of predator-related mortality occurring within the first week after release (McKinstry and Anderson 1997, Petro et al. 2015). Beavers also commonly move from their release site. A study in eastern Oregon observed that 78% of relocated individuals moved away from release sites (Scheffer 1941). Of 114 translocated beavers in Wyoming, 58 (51%) moved more than 10 kilometers (km) from their release sites (McKinstry and Anderson 2002). Known maximum distances moved from release sites were 29.2 km in western Oregon (Petro et al. 2015), 48 km in Colorado (Denney 1952), 76.2 km in Wisconsin (Knudsen and Hale 1965), and 238 km in North Dakota (Hibbard 1958). McKinstry and Anderson (2002) evaluated beaver translocation as a tactic by which to improve riparian habitat in Wyoming and considered releases successful in 13 of 14 sites when translocated beavers reproduced. Their efforts required multiple releases per site and an average of 17 beavers released at each site before young were born; however, they did not determine if sites remained occupied after the study (McKinstry and Anderson 2002). Dittbrenner (2019) evaluated the hydrologic effects of beavers in headwater streams in Washington following translocation with a softer release strategy, whereby temporary lodges and food were placed at release sites. Their efforts also required that they release multiple colonies per site to achieve occupation lasting beyond a year, because of depredation and emigration (Dittbrenner 2019).

There are fewer cases documenting rates of dam building following translocations. In New Mexico, one project translocated four beavers to an unoccupied site in which BDAs had been constructed and temporary lodges and supplemental food provided (Wild 2017). Only one beaver remained on site in a bank burrow and the remaining three left the release site. In the Oregon Coast Range, 38 radio-marked beavers were translocated to stream reaches with geomorphic characteristics similar to sites with high dam densities in the same watershed (less than a 3% gradient, 3–4 meters

(m) bankfull width, 25–30 m valley floor width and without neighboring colonies). Not all surviving beavers built dams, and none of those built persisted through high winter discharges (Petro et al. 2015). In northwest Washington, 22 colonies (69 beavers) were released to 13 unique sites; 5 sites had dam building activity that resulted in ponded water for at least 1 year (Dittbrenner 2019).

Riparian vegetation restoration and dam building. For riparian vegetation restoration to lead to dam building, beavers must be attracted to the site in which vegetation is restored, persist in restored reaches, and build dams. The few documented reports about beavers occupying reaches following restoration or increased riparian cover suggest positive results. At several sites in the northern Great Basin, the density of beaver dams associated with grazing exclosures or changes in grazing management to reduce pressure on riparian areas was higher relative to locations in which conventional grazing management was practiced (Baker et al. 2012, Swanson et al. 2015, Small et al. 2016, Fesenmyer et al. 2018). At these sites, the increased dam density was attributed to improvements in riparian condition (Swanson et al. 2015, Charnley 2019). In other locations in which riparian vegetation favored by beavers is less limited, riparian restoration may not affect beavers; in one western Oregon study, woody riparian plantings were consumed by invasive nutria (*Myocastor coypu*) rather than beavers living in the area (Sheffels et al. 2014).

The specific process pathways that drive changes in beaver dam building rates following riparian vegetation restoration remain unclear. Do rates of dam building increase because beaver populations increase, or because existing beavers start building more dams? If the latter, was the behavioral change because of increasing riparian biomass, the absence of competition from cattle, the presence of specific species, or other changes outside the scope of BRR?

Artificial structures and dam building. Building artificial structures is, categorically, a one-time means of reintroducing dam building that will persist for as long as humans continue to build or maintain them. For artificial structures to lead to dam building *by beavers*, however, beavers must be attracted to and establish populations in sites in which the structures were built, then build new or maintain existing dams. Increases in beaver activity were observed at four of the five case study sites that used artificial structures, including beaver dam building at four project locations. For example, in the Scott River Basin, California, participants observed beaver activity at all six restoration sites, beaver maintenance at 5 of 18 BDAs, and beaver dam building at one site (Betsy Stapleton, Scott River Watershed Council, Etna, California, United States, personal communication, 24 May 2020). This rise in activity was attributed to the BDAs and improved riparian conditions in areas in which livestock have been mostly excluded for over 20 years (Charnley 2018). Project participants also mentioned that all but one of the six sites

have factors that limit full beaver occupancy, concluding that "it takes more than building a BDA to make a site desirable to beavers" (Betsy Stapleton, Scott River Watershed Council, Etna, California, United States, personal communication, 24 May 2020).

In eastern Oregon, beaver presence reportedly increased over the decade since artificial beaver dams were built, as did the presence of beavers around the structures (Davee et al. 2017). The rise in beaver activity was attributed to a combination of artificial beaver dams creating desirable hydrologic conditions, riparian plantings, and changes to beaver trapping practices on the ranch (Davee et al. 2017). The contributions of operational changes (e.g., grazing management) to the outcomes reported from artificial structure installations were difficult to isolate and warrant further experimentation.

Whether artificial structures spur dam building is similarly variable. At sites in southwestern Washington (MacCracken and Lebovitz 2005) and eastern Oregon, fewer than 10% of artificial structures were used as foundations for dam building by beavers (the total number of structures built was 55 and 363, respectively). These changes occurred over a period of 3–10 years (Washington and Oregon, respectively) following the construction of artificial structures. No data were provided on dam building outside of project areas. At sites in New Mexico, the reintroduced beaver neither attempted to add to nor maintained the artificial structures (Wild 2017). As of 2020 in the Scott River Basin, California, observers noted one natural beaver dam built across the six restoration sites over the course of 6 years (Betsy Stapleton, Scott River Watershed Council, Etna, California, United States, personal communication, 24 May 2020). In Bridge Creek, Oregon, rates of structure occupancy were not reported, but there was a documented 800% increase in the number of dams following the installation of artificial structures ($n = 121$; Bouwes et al. 2016). It is unclear whether this figure includes the artificial structures or not.

The question of who—beavers or humans—will rebuild or maintain dams following initial construction remains underreported and characterized. In some cases, although it is hoped that artificial structures will spur beaver dam building, it is expected that the artificial structures alone will be sufficient to create the desired biophysical outcomes. Indeed, in some cases beaver occupancy is considered unlikely *until* artificial structures have been present long enough to create biophysical conditions that could support beavers. In either case, it is worth considering who is expected to do the maintenance in the event the initial set of artificial structures neither creates the desired change nor attracts beavers to do the secondary set of work.

Interpretation and some guiding principles around beaver dam building for restoration. It is clear from the published data that several critical processes linking BRR to desired outcomes are largely site specific, as might be expected. In this

section, we integrate the available research on beaver ecology as it pertains to BRR processes into a few key guiding principles.

Many streams already have beavers, with contradictory effects. Although beavers may still be limited in their abundance and distribution at some locations because of direct and indirect human influences (e.g., removal and habitat alteration, respectively), there are other places where beavers are widespread and abundant. Concerns over the decline in North American beaver in the early 1900s led to regulations controlling harvest, and live-trapping programs in the mid-1900s successfully helped reintroduce the beaver to most of their former range (Baker and Hill 2003). Beaver populations are thought to have fully recovered in some areas in which commensurate vegetation changes have also occurred (Ingle-Sidorowicz 1982), although habitat loss through agricultural conversion and expanding development has restricted populations in other areas (Hall 1981). Beaver populations have reestablished in portions of southern California and the Colorado River system into Mexico, although some of these populations are considered marginal (Landin 1980).

The relative population levels at which conflict emerges between beavers and humans in different landscapes remains an open question. Beaver populations have increased so much in some locations as to be considered a nuisance (Charnley et al. 2020). In the Western Great Lakes region, for example, beavers are often considered a threat to the viability of certain cold water salmon and trout fisheries because of the siltation of spawning gravels and movement barriers for species (e.g., brook trout; *Salvelinus fontinalis*) that spawn during lower flows (Johnson-Bice et al. 2018). One-sided actions such as trapping bans have changed stakeholders' levels of acceptance and increased human–wildlife conflicts with beavers in some locations (Jonker et al. 2006, 2009). Knowledge and implementation of nonlethal tools such as flow devices (Taylor and Singleton 2014) have been shown to help reduce unwanted flooding while keeping active beaver colonies and their dams in desired areas.

Some BRR projects appear to have achieved expected outcomes precisely because of a preexisting, dam-building population of beavers. Research using radio-marked beavers found evidence that beavers at Bridge Creek, Oregon, were at or near carrying capacity prior to restoration, with numbers of dams ranging from zero to 20 per territory (Maenhout 2013). Surveys completed before treatment with BDAs documented beavers building anywhere between 30 and 103 dams per year (Demmer and Beschta 2008). Following the installation of artificial structures, a new channel was scoured outside the project area during high flows, on which the reported increases in beaver dam building were observed (Bouwes et al. 2016). Dam building in the restoration area may have therefore occurred because the new channel created more viable stream length for a beaver population in search of new dam sites.

Not all beavers build dams. Often, beavers are thought to be absent if there is not active dam building in an area, because dam building is so closely associated with perceptions of the species (Jones et al. 1994, Wright et al. 2002). Dam building is not, however, a universal behavior associated with North American beaver, but one that emerges to facilitate survival at sites with insufficient water availability for refuge. As central-place foragers (Orians and Pearson 1979, Fryxell and Doucet 1991, McClintic et al. 2014), beavers require protection from predators at their lodge or bank den. Beavers build dams to create open water protection from predators, access to bank dens or lodges for rest and kit rearing, and food caching in extreme winter conditions (Baker and Hill 2003). When these needs can be met in the absence of dams, such as in lakes and larger rivers, beavers often forgo dam building. This points to a potential upper threshold of stream size above which BRR is unlikely to promote dam building (Persico and Meyer 2013, Levine 2016). Absence of dam building may therefore not necessarily reflect an absence or limitation of beavers, but could indicate that beavers' survival does not require dams at that location. This may explain the limited number of additional beaver dams built in reaches treated with artificial structures (e.g., MacCracken and Lebovitz 2005).

But when beavers do build dams, it is driven by survival needs. Beavers build dams when it is advantageous to their survival, but exactly when and where is subject to several contingencies, including vegetation, geomorphology, and how beavers react to these and other influences (Barnes and Dibble 1988, Johnston and Naiman 1990, Suzuki and McComb 1998, Gibson and Olden 2014, Touihr et al. 2018, Macfarlane et al. 2017, Lapointe St-Pierre et al. 2017, Ritter et al. 2020). North American beaver are generalist herbivores that exploit a wide range of foods and environmental conditions (Jenkins 1975, 1981). Cues causing beavers to occupy sites can differ from those that encourage dam building, just as plants chosen for food may differ from those used to construct dams (Barnes and Mallik 1997).

Some have hypothesized that availability of woody plants controls beaver occupancy, although this has not yet been systemically evaluated at large scales (Gibson and Olden 2014). Touihr and colleagues (2018) warned that large scale predictive models may lack the characteristics of riparian vegetation that can be identified by field sampling. Using remotely sensed data, Macfarlane and colleagues (2017) found that vegetation was a top predictor of beaver dam-building capacity in Utah. In contrast, Lapointe St-Pierre and colleagues (2017) found that mean stream gradient and cover of nonforested land within 100 m of the stream were the top variables influencing dam abundance across a large forested landscape in Quebec. It can often be difficult to accurately identify the vegetation that initially drew beavers to an area because beavers alter vegetation so greatly through their foraging and dam building activities (Barnes and Dibble 1988, Johnston and Naiman 1990, Suzuki and

McComb 1998, Ritter et al. 2020). As such, vegetation cues on their own appear site specific and difficult to generalize as drivers of beaver dam building (Touihr et al. 2018).

In addition to the potential influences of vegetation, there are physical constraints on where and when beavers build dams. Beaver dams are typically observed in a narrow range of geomorphic conditions (Touihr et al. 2018), because they are often limited by high stream power at one end (Smith 1998, Demmer and Beschta 2008, Persico and Meyer 2009, Dittbrenner et al. 2018), and minimum discharge at the other (Wolff et al. 1989, Persico and Meyer 2013). Dams built in streams with higher gradient, narrower channels and valleys, and flashier hydrographs are likely to wash out more quickly, whereas dams built in flatter, wider areas with lower flood peaks often persist longer (e.g., McComb et al. 1990, Barnes and Mallik 1997, Suzuki and McComb 1998, Petro et al. 2018). As water availability declines, beavers might be expected to relocate to areas with more water that offer protection, food, and rearing sites, raising critical questions about where North American beaver might be expected to continue building dams as climate change alters the distribution and availability of surface water (Palmer et al. 2009, Dierauer et al. 2018). During prolonged Holocene droughts in the Yellowstone River, Persico and Meyer (2013) found limited evidence of beaver dam building on smaller streams, whereas Levine (2016) documented dam building during the same droughts on larger streams nearby. Petro and colleagues (2018) evaluated local macro- and microhabitat conditions in relation to dam building by beavers and concluded that presence of large deep pools may be necessary for beavers' survival before and during construction. At a broader extent, the type of flow regime (Poff et al. 1997) is likely important for driving patterns of dam construction in space and time by beavers, but comparative studies are lacking.

Altogether, the literature indicates a range of results and contexts that may determine outcomes surrounding dam building; stronger and broader conclusions await further study. The wide range of reported outcomes reinforces the importance of recognizing assumptions and contingencies implicit in expectations about how beavers will behave.

How do dams lead to expected outcomes?

An increase in dams in itself is rarely the objective for BRR restoration. Desired outcomes are usually linked to physical or ecological changes to stream ecosystems that dams are expected to produce. Although many expected outcomes are ultimately related to improving habitat, those improvements are contingent on how the presence and type or types of dams will affect the movement and storage of water and sediment. Within BRR, dams may be constructed by beavers, by humans or both. BDAs and ABDs have been variably and inconsistently defined in the literature (figure 1b; Pilliod et al. 2018), but are similar in their intent to influence beaver activity or attempt to spur processes similarly to how beaver-constructed dams might (e.g., Ecke et al. 2017). Beaver-constructed dams are similarly if not more variable

than artificial structures in the materials used for construction and the duration over which they persist (e.g., Demmer and Beschta 2008). We use the term *dam* through the rest of this section to refer both to beaver dams and artificial structures, except where explicitly stated otherwise.

Regardless of who builds dams and how, expected influences on streams are strongly contingent on how many dams are built, their density and size, and—critically—how long they and the processes they spur persist on the landscape. We provide general descriptions of two process-pathways along which dams are expected to create outcomes in the context of the incised stream systems for which BRR is often invoked (e.g., Pollock et al. 2014), recognizing that both sets of processes may be present within a natural beaver dam complex (Hafen et al. 2020).

The first commonly invoked process pathway indicates that dams will breach with some regularity (figure 3a). One study of natural beaver dams on Bridge Creek, Oregon documented that 89% of beaver dams ($n = 161$) breached within a 5-year window, with 79% of the breached dams creating new geomorphic bedforms within inset floodplains (Demmer and Beschta 2008). Often, dynamic artificial structures are designed so that, when they breach, they will encourage the erosion of steep vertical banks nearby, whose sediment is expected to aggrade inset floodplains, creating fresh bars and surfaces for riparian vegetation (e.g., Pollock et al. 2007). This lateral erosion is expected to widen inset floodplains and decrease the stream power of floods, making it more likely any subsequently built dams will last longer (Pollock et al. 2014). As such, encouraging frequent breaching is sometimes seen as a step on the process pathway toward creating geomorphic conditions more conducive to longer-lived dams that are expected retain water and sediment over a time frame long enough to raise inset floodplains nearer their historical floodplains or terraces. It is expected that either beavers will maintain and build on artificial structures following initial breaches or that wood from the breached artificial structures will collect further downstream as jams, propagating the effect of the initial structure.

Ecologically, the process of frequent breaching is expected to create pulses of flow to scour fine sediment, leaving coarser particles (e.g., gravel, cobbles, boulders) behind. Such coarse bed sediment materials may be more desirable for use by species such as Pacific salmon for spawning, for improved conditions to support in-stream macroinvertebrates, or other ecological functions (Wood and Armitage 1997).

A second process pathway indicates that dams are regularly maintained and are, consequently, longer lived (figure 3b). Studies of natural beaver dams have documented some dams that were continuously maintained could create chains of ponds (Hazell et al. 2003) or fill completely to form meadows (Ives 1942, Demmer and Beschta 2008, Westbrook et al. 2011, Polvi and Wohl 2012). Often, artificial structures intended to be longer lived are built of earthen materials and rock in addition to or instead of wood to better retain
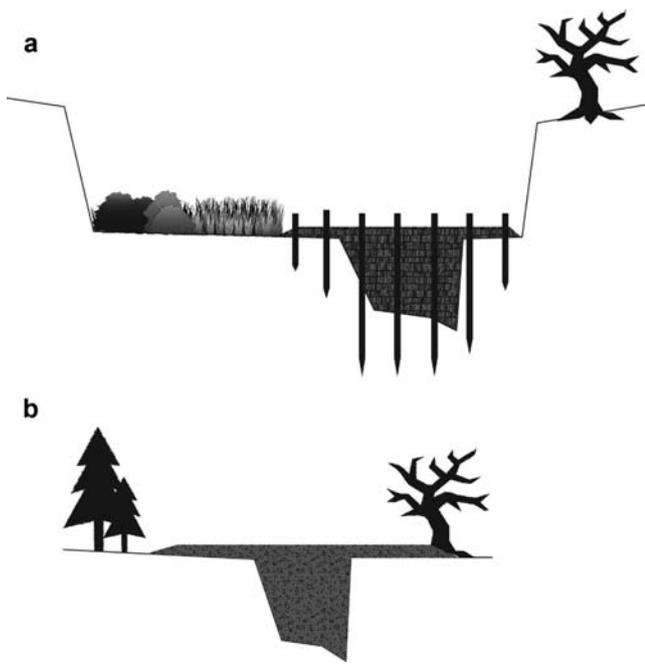
Figure 3. Artificial structures built to mimic beaver dams fall along a spectrum on the basis of their intended design life: (a) Artificial structures expected to be dynamic are commonly placed on channels within well-developed inset floodplains, where there can be considerable existing riparian vegetation to use when building the structures. Their objective is often to erode steep vertical banks laterally to harvest sediment and introduce heterogeneity to geomorphic forms within the inset floodplain. In some cases, the objective is to harvest enough sediment laterally to completely fill the inset floodplain back to an elevation nearer its historical floodplain or terrace. (b) Longer-lived structures are commonly placed in gullies that have limited inset floodplain development, very deeply incised channels, and in locations with limited vegetation. Their goal is typically to collect water and sediment behind the structure to gradually fill the channel to an elevation nearer its historic floodplain. In some cases, the structures are built in a single phase in which the structure completely fills the gullies, whereas others project plans assume it will take multiple phases of filled structures to raise the bed elevation back nearer that of the historic floodplain or terrace.

incoming water and sediment. If the initial structure is shorter than the channel was deep, it is typically expected that subsequent dam building on top of filled pools will gradually raise the channel bed back to the level of the terrace (e.g., Pollock et al. 2014). If the initial structure is the same height or slightly taller than the channel was deep, it is expected that the filling of the single dam will accomplish so-called floodplain reconnection. In both cases, it is expected that raising the levels of surface water in the channels will increase the frequency with which floodwaters spread onto adjacent floodplains, raise adjacent groundwater levels, and

encourage frequent surface and groundwater flooding. As such, regular maintenance against complete breaches is critical to ensuring that in-channel surface water levels remain high enough to keep the channel hydrologically connected to its floodplain. If these dams breach and water drains, there may be benefits within the inset floodplain akin to those expected from more dynamic dams, but hydrogeomorphic conditions on the historical floodplain will likely revert to their predam condition.

Ecologically, maintained dams are expected to retain fine sediment and therefore produce a potentially very different geomorphic setting than systems with frequent structure breaches (e.g., increased fine sediment on the stream bed upstream of dams), which may have benefits for a host of species or life stages that depend on them (e.g., Gonzalez et al. 2017). The increased groundwater levels are expected to create favorable conditions for the reestablishment of wetland and riparian vegetation across valley floors, potentially benefiting a different suite of species and ecosystem functions.

In both cases, the persistence of any one dam is considered less important for accomplishing expected outcomes than the persistence of processes (e.g., flooding, lateral erosion) spurred by the larger network of dams.

Findings and first principles. In this section, we explore the critical processes linking dams to desired outcomes of BRR (figure 3), as is outlined in figure 2 using available biophysical and social data.

Dams and sediment processes. Within BRR, dams alter sediment processes along one of the two aforementioned process pathways—long-term collection of in-channel sediment behind dams or repeated breaches that harvest sediment by eroding banks laterally (figure 2). Dams can also increase overbank sedimentation if their presence results in increased frequency, magnitude and duration of flooding (Westbrook et al. 2011, Levine and Meyer 2014). In all cases, dams will collect sediment while they remain in place, often resulting in complex depositional forms and stratigraphy (e.g., Stratton and Grant 2019). When a dam breaches, some or all of that sediment is evacuated and moved downstream. Studies of partially breached natural beaver dams have documented upstream sediment stabilizing behind the remnant dam as vegetation becomes established, creating bars or islands (e.g., Demmer and Beschta 2008, Levine and Meyer 2014, Pollock et al. 2007). As such, the persistence of dams is a central control on the degree to which they can influence geomorphic processes and, subsequently, generate expected outcomes (Butler and Malanson 2005). Along dynamic process pathways, the network of dams must continue eroding and impounding sediment for however long it takes to raise the inset floodplain nearer the historical floodplain (i.e., Pollock et al. 2014). Along maintenance process pathways, the dams must be maintained for however long it takes to directly aggrade the same volume of water and sediment.

The variable life spans of dams and the diverse environments in which they are built result in wide ranges of short-term sedimentation rates. In watersheds with high sediment yields and dams that persist for a few years, dams may collect a considerable depth of sediment, particularly if the area experiences wildfires (e.g., 0.47 m in year 1, Pollock et al. 2007). In other watersheds in which sediment yield is low or dams breach frequently, sediment accumulation may be limited (Levine and Meyer 2014, O'Connor et al. 2014).

The influence of beaver dams on sedimentation over longer periods of time (which may be necessary to fill deeply incised channels) is harder to identify given the variability of beaver-induced depositional processes (Kramer et al. 2012) and lack of longitudinal data on persistence of multiple dams and types of dams (Hafen et al. 2020). Often, the only places in which beaver-aggraded sediment remains in the geologic record are locations with downstream grade controls that create long-term depocenters. Polvi and Wohl (2012) collected data from such a location, finding that beaver dams were responsible for 32%–53% of the postglacial sediment that accumulated upstream of terminal moraines in the Rocky Mountains. In locations in which North American beaver were known to be present during the Holocene, however, only limited volumes of valley bottom sediment could be attributed to beaver dams except in glacial scour depressions with exceptionally low gradients (Persico and Meyer 2013). This suggests that larger-scale geomorphic controls influence the sediment trapping efficiency of beaver dams over timescales long enough to influence valley floor morphology (e.g., Beeson et al. 2018). As such, the capacity of a dam to change geomorphic setting is influenced *by* the initial geomorphic setting.

Dams and surface water. Dams alter surface water processes by introducing a grade break that slows and impounds surface water, thereby increasing the surface area and depth of water and increasing the frequency of flooding and the extent of flooded areas during high flows. Dams hold surface water for as long as they are in place and intact, with an obvious volumetric tradeoff between sediment and water storage behind the dam. Dams can also promote surface and ground water storage on floodplains locally to the structure if floodplains are present. All these factors undoubtedly contributed to reported increases in surface water storage behind dams and in nearby depressions by BRR project participants following the increase in dam building on their properties (Charnley 2018, 2019, Charnley et al. 2020). This was generally viewed positively, because the surface water was available late into summer, addressing concerns around intermittent streams limiting habitat for aquatic species and late-season water sources for livestock, fish, and wildlife. Nevertheless, the increase in surface water was also sometimes viewed negatively because it occasionally led to flooding of roads, trails, hay fields, and riparian pastures (Charnley 2018, 2019). Natural beaver dams are variably reported as both contributing to local and downstream flooding (e.g., Butler

1989) and attenuating and reducing downstream flooding (e.g., Nyssen et al. 2011, Puttock et al. 2017, Westbrook et al. 2020), whereas the effects of the artificial structures commonly used in BRR on downstream flooding are not yet as well documented (e.g., Walder and O'Connor 1997). In general, dams will moderate floods if they or their adjacent floodplains are not already saturated prior to flooding or if the floodwaters are spread onto floodplains and slowed down (Burns and McDonnell 1998, Westbrook et al. 2020).

Whether, when, and how surface water stored behind dams discharges to the stream depends largely on the drainage pathways available. Surface water can drain over the top of a dam, through gaps in the dam itself, or via hyporheic flow under and around the dam to downstream reaches. Overtopping occurs when inflow above the dam exceeds the sum of throughflow and hyporheic flow, such as during peak flows, and will cease as flows decline. Water draining through the dam itself is subject to a fundamental trade-off; the more water that drains, the shorter the period of flow augmentation lasts. Increased hyporheic flow in the vicinity of dams has been documented but typically involves small volumes of water relative to mainstream flow (Lautz et al. 2006, Lautz et al. 2010, Briggs et al. 2012). Hyporheic flows may, however, play other ecologically important roles such as clearing fine sediment from gravels, increasing the heterogeneity of water temperature, and increasing nitrate uptake (White 1990, Majerova et al. 2015, Fanelli and Lautz 2008).

Increasing late season water availability is both a common expected outcome for BRR projects and a frequently reported outcome (Collier 1959, Charnley 2018, 2019, Charnley et al. 2020). However, *increased surface water* can refer to hydrologically different changes: an increase in the flux of water (streamflow), stored water (e.g., backwater behind a dam), or both. Ultimately, the volume of water in these systems is governed by precipitation and conservation of mass; although dams can affect the volume of water stored in a given location and the timing of its release, they cannot increase the water available to the system.

Though increasing late-season water availability is often a key motivator for BRR projects, the influence of these practices downstream flow dynamics remains one of the most poorly characterized outcomes. This is, in part, because it can be challenging to measure low flows in small channels in which BRR is often carried out, let al.one detect statistically significant change outside error bounds and noise (e.g., Nash et al. 2019). These difficulties are compounded by limited funding sources available to monitor projects, and project timelines that can limit or eliminate baseline data collection.

To date, only five biophysical studies have included instantaneous subdaily discharge measurements associated with beaver dams before and after their installation. Woo and Waddington (1990) observed that reaches downstream of dams with gaps at their bases had higher discharge for 7–10 days relative to reaches upstream of the dam, indicating short-term flow augmentation from fast-draining
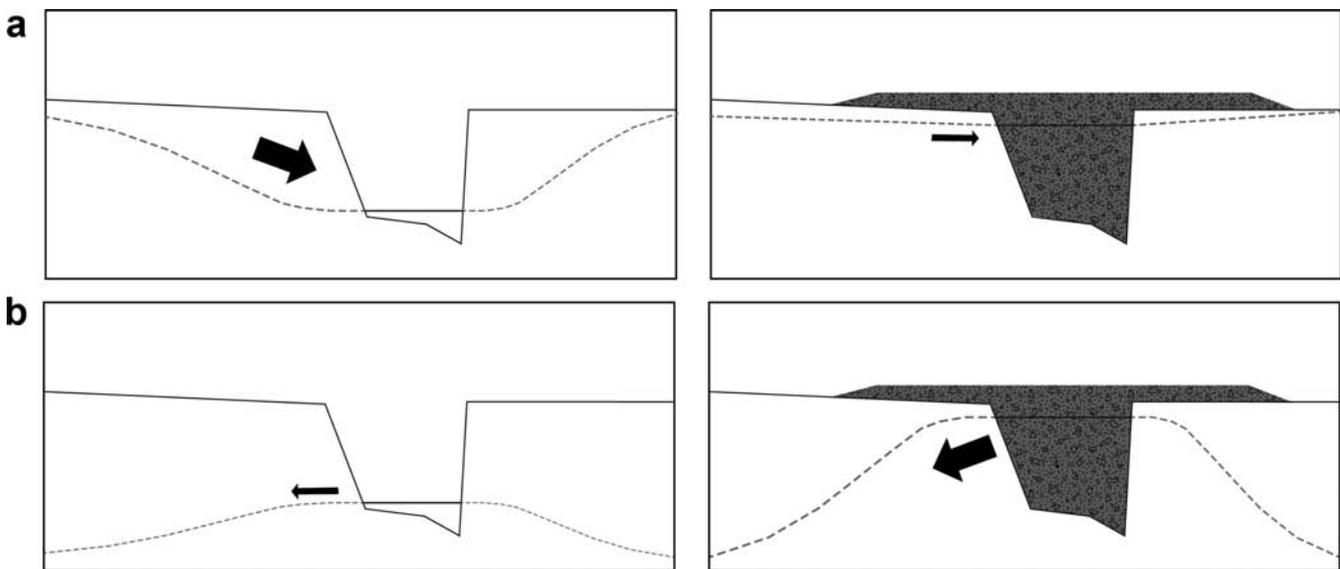
Figure 4. Dams influence local groundwater processes differently depending on antecedent conditions. The solid line represents surface water levels; the dashed grey line represents groundwater levels; the arrows represent direction and relative magnitude of exchange. (a) In gaining reaches, where groundwater is discharging to the stream, dams raise the elevation of the point of discharge, decreasing the gradient over which groundwater flows, decreasing rates of discharge. (b) In losing reaches, where streamflow recharges groundwater, dams raise the elevation of the point of recharge, increasing the gradient over which groundwater flows, increasing rates of recharge.

dams with gaps at their bases. Nyssen and colleagues (2011) reported similarly short-term increases to streamflow following winter storms downstream of reaches that contained beaver dams compared with reaches without any beaver dams. Without predam data, however, it is difficult to disentangle the influence of beaver dams relative to baseline watershed properites (McDonnell et al. 2018). Puttock and colleagues (2017) describe similar event-scale flow attenuation downstream of beaver dams, and otherwise report that streamflow below dams was generally lower than above owing to increased water storage behind the dam and in surrounding floodplains. Conversely, Majerova and colleagues (2015) used dilution gaging to measure the change in discharge moving downstream through a 750 m reach with 10 beaver dams and reported that the construction of the dams resulted in a net change from losing to gaining between March and October. The authors acknowledged that irrigation dynamics may have influenced these values, although the change because of beaver dams persisted beyond irrigation season. Subsequent work at the same site revealed a more complex and contingent set of outcomes, however. Clark (2020) reported that beaver dams tended only to increase baseflow discharge when the dams were relatively young but reverted to neutral or losing conditions as ponds silted in and overbank flooding occurred less frequently. This suggests changes to baseflow dynamics may be contingent both on climatic variables independent of the dams, as well as the geomorphic response of the channel *to* the dams. This emphasizes the need for longer-term,

continuous up- and downstream discharge monitoring before, during and following the implementation of BRR.

Dams and groundwater. Dams affect groundwater by raising surface water levels and changing the gradient along which groundwater drains, contingent on preexisting hydrogeology and water distribution. In hydrologically gaining reaches—where groundwater discharges into the channel (figure 4a), dams raise the point of discharge, reducing hydraulic gradients and flow rates, thereby causing higher groundwater levels in floodplain aquifers. In hydrologically losing reaches—where surface water recharges groundwater (figure 4b), dams raise the source point elevation, increasing hydraulic gradients and infiltration rates and causing more water to drain out of the channel to groundwater. In some settings, dams can drive a localized change from losing to gaining around the impoundment (Majerova et al. 2015). As was noted, dams can also promote increased overbank flooding upstream, which can recharge floodplain aquifers provided there is a floodplain aquifer to recharge. Such recharge generally occurs during the wet season when floodplain aquifers may be fully charged already.

The participants in four of the case study projects observed higher water tables around BRR sites, particularly near artificial structures and persistent beaver dams. This outcome was valued by ranchers adjacent to the project sites for increasing the productivity and extent of riparian vegetation, which created better forage locally for livestock (Charnley 2018, 2019, Davee et al. 2017). It is worth noting that these

benefits arise from an increase in consumptive water use, which removes water from the system. The project participants suggested that changes near the dams were greatest, although some reported observable changes spanning wide (400 m) floodplains (Davee et al. 2017). This is consistent with several reports documenting rising groundwater levels following the construction of beaver dams (Lowry 1993, Westbrook et al. 2006, Burchsted et al. 2010, Karran et al. 2018). Westbrook and colleagues (2006) describing persistently higher water table elevations as far as 300–600 m from beaver dams, whereas Karran and colleagues (2018) reported beaver dams stabilized already high water tables in a stream-adjacent fen.

Other studies have reported little to no change to the water table following dam building (Woo and Waddington 1990, Burns and McDonnell 1998, Gurnell 1998, Collen and Gibsen 2001, Feiner and Lowry 2015, Scamardo and Wohl 2020). In a few cases, extensive clay strata limited recharge to floodplain aquifers (e.g., Feiner and Lowry 2015, Scamardo and Wohl 2020). In others, extremely coarse valley fill was unable to hold water very long and rapidly transmitted it elsewhere (e.g., Burns and McDonnell 1998).

Interpretation and some guiding principles for dams to achieve desired outcomes. It is clear from the published data that several critical processes linking dam building to expected outcomes are controlled by geomorphic setting, local climate and geology, and the number and type of dams. In this section, we integrate the available research on how beaver dams and artificial structures influence stream systems into a few key guiding principles that might help projects in any location assess the most appropriate set of actions given their conditions.

Intact dams will create certain outcomes irrespective of location. Intact dams will store water and sediment for the duration of their life and, in so doing, alter local gradients driving surface and groundwater flow. All intact dams have finite storage volumes and will therefore be subject to trade-offs between water and sediment storage, as well as existing storage and flood mitigation. When dams breach, they typically release stored water, some stored sediment, and can cause downstream flooding. This may be beneficial (e.g., depositing fresh sediment on floodplains, aggrading downstream channel beds with wood and sediment) or may lead to negative consequences (e.g., depositing fine sediment in spawning areas for amphibians and fishes, creating downstream incision) depending on the watershed in question, fill material and dynamics of the dam breach. When surface water levels revert to predam conditions, so too will the surface–groundwater gradients and hyporheic flows.

Dams involve trade-offs; a dam cannot store water and drain it, too. For a dam to store water, it must reduce in-stream flow by intercepting discharge; for a dammed reach to increase downstream discharge above baseline conditions, it must release previously stored water. Humans control the timing of this relationship in engineered dams, with outlets that are opened and closed to optimize discharge and storage. Leaky dams offer no such control. Drainage is greatest when the upstream water level is much higher than downstream; drainage diminishes as this head differential does as well (i.e., peak flows, low flows). A leakier dam can drain greater magnitudes of streamflow, but in so doing it will quickly drain its storage (e.g., 7–10 days; Woo and Waddington 1990, Nyssen et al. 2011). A more impermeable dam can store water later into the summer precisely because it does not release much of that water as streamflow. The increased storage of water behind dams also increases evaporation, and dams that create changes in riparian and valley floor plant communities do so, in part, because they have increased the amount of groundwater available for plant use (transpiration) and groundwater evaporation (Loheide and Gorelick 2005, Hammersmark et al. 2008, Marshall et al. 2013, Essaid and Hill 2014, Nash et al. 2018). Any water transpired by plants or lost through evaporation is no longer available for streamflow in that reach. Any selection of goals or outcomes must be cognizant of these inherent trade-offs.

What a dam does depends on where (geomorphically) it is built. Although a beaver dam and artificial structure might function similarly once constructed, the decision to where either gets built is subject to separate contingencies. Although humans can have certain expectations for BRR, beavers behave according to the proximate and ultimate drivers that influence all animals (Lima et al. 1996). Accordingly, where beavers construct dams and how they build them will be driven primarily by these influences, with outcomes for conditions desired by humans being a by-product of these activities. Conversely, artificial structures can be built wherever humans desire, including in locations beaver might not otherwise be able or choose to build.

Across a landscape or riverscape (Fausch et al. 2002), topography, channel dimensions, and flow regime interact to provide some control over the magnitude and direction of outcomes that result from a dam holding back water and sediment (Grant et al. 2003). Certain relational patterns among these variables exist across landscapes (e.g., Schumm 1977), although there are often as many exceptions to these patterns as there are rules. It is useful to consider the position of these various geomorphic knobs at a given site and consider the scale of the channel intended for restoration with BRR as fundamental factors in setting both the scale and type of expectations (figure 5).

In general, steeper gradients and increasing discharge tend to increase stream power and decrease dam persistence (Smith 1998, Demmer and Beschta 2008, Persico and Meyer 2009, Dittbrenner et al. 2018), although there are several nongeomorphic drivers that can also influence dam persistence (Hafen et al. 2020). Channels with larger cross-sectional areas relative to incoming discharge are less likely to facilitate overbank flooding and, instead, will concentrate stream
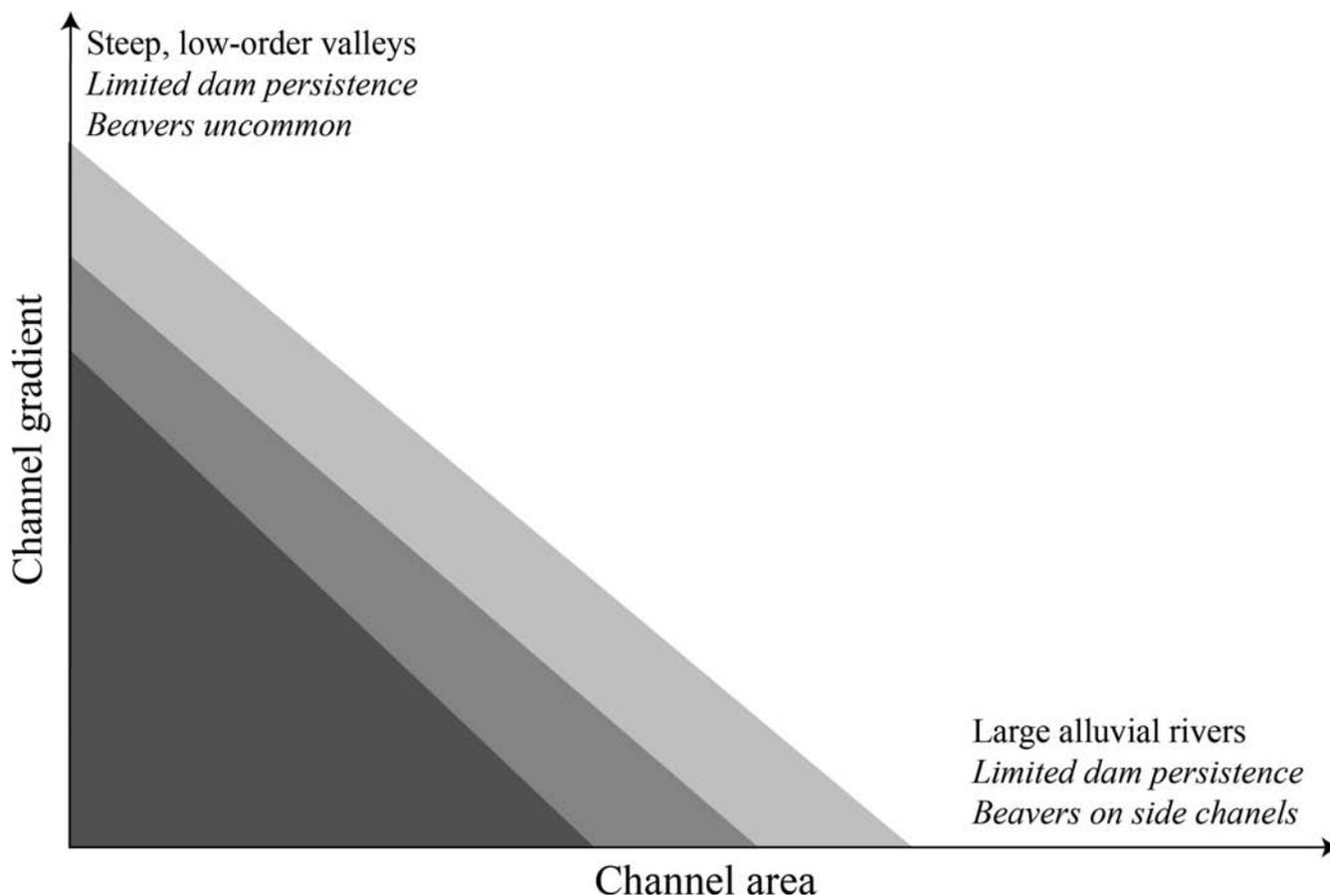
Figure 5. There is a general geomorphic relationship between gradient and channel area as pertains to common limitations to beaver dam building and persistence. Dams, which are ultimately limited by unit stream power, tend not to exist in very steep reaches or in reaches transporting high rates of flow. The breadth of the range of environments in which dams might persist between these two environments, however, is modulated by a number of contingencies at a given location (bidirectional black arrow). Wetter climates, flashy hydrographs, channels with small width:depth ratios and narrow valleys relative to channel widths might tend to decrease the range of environments in which dams can persist by increasing other variables relevant to unit stream power (darker shaded range). Conversely, drier climates, stable (i.e., regulated or groundwater fed) hydrographs, channels with large width:depth ratios and broad valleys might tend to increase the potential range of environments (lighter shaded ranges). Artificial structures, which often use various forms of equipment to stabilize the dam materials, are also able to persist in a broader range of environments. The combination of these variables at a specific site will influence its suitability for BRR. Source: Adapted from figure 2 of McComb and colleagues (1990).

power between their banks. The narrower the channel relative to its depth, the more concentrated the stream power. If floodwaters can overtop a channel's banks, a wider valley floor will provide more accommodation space than a narrower one. Similarly, coarser valley fill typically moves flood recharged groundwater down gradient faster (Burns and McDonnell 1998), whereas fine valley fill may be able to hold more water, although the finest fill (i.e., clay) may hinder recharge (Feiner and Lowry 2015, Scamardo and Wohl 2020).

The breadth of geomorphic conditions suitable for dam building is also influenced by hydrologic regime and the dam design (figure 5). For instance, in a wetter climate, or one with a flashier hydrograph, the range of environments in which a dam might last long enough to spur expected

processes might be constrained relative to a drier environment, where even in steep reaches there may be insufficient water to breach dams. Similarly, given two channels with the same cross-sectional area, a narrower, deeper channel will generate greater unit stream power, therefore also likely constricting the range of geomorphic conditions in which dams might otherwise persist. Humans can build artificial structures beyond the environments to which beavers are confined, because they are less limited by available building materials and can engineer and construct longer-lived structures than a beaver might be able to build in the same environment (e.g., in steeper or larger channels). In these cases it is worth considering whether it is more important that humans select sites using the exact same variables

driving beaver dam building or whether artificial structures represent something more akin to a cross-species technological transfer that might be subject to different site selection principles.

This is not to say one set of environments is better or worse, but rather that geomorphic setting can influence effectiveness of a given process pathway. For instance, wetter environment may have more hydrologic tools to facilitate expected outcomes via frequent breaches, whereas a better strategy in a drier environment may be to perform regular maintenance to conserve what little water and sediment does arrive to the dammed site.

Dams are fluvial discontinuities, with contradictory effects. Dams fundamentally interrupt the longitudinal flow of water, sediment, and nutrients. In certain cases such discontinuities are thought to have contributed to key ecological processes: increasing biodiversity, altering biogeochemical cycles, and organizing bedforms on which aquatic species rely for different life stages (Schlosser and Kallemeyn 2000, Burchsted et al. 2010, Wohl and Beckman 2014, Grant et al. 2016). Nevertheless, water and sediment impounded by a dam—no matter its form—cannot move downstream while it is being impounded. The consequences of this can be aligned with or opposed to expected outcomes: Stored water can support riparian vegetation and improve upstream habitat for many species; more stored sediment can reduce downstream turbidity and improve fish and wildlife habitats. On the other hand, increased water use by vegetation can reduce downstream flows (Hammersmark et al. 2008, Essaid and Hill 2014, Nash et al. 2018) and reduced sediment loads can promote erosion and incision downstream of dams (Grant et al. 2003).

Our growing understanding of the ecological importance of discontinuity must necessarily be balanced with a keen awareness of other expected outcomes that may be disrupted by discontinuity. Working toward rebuilding ecologically beneficial discontinuity will require careful communication and planning along the entire length of the stream, where impacts might be expected, to prevent any unforeseen negative consequences.

Conclusions

BRR is an exciting new frontier in river restoration that represents a fundamental paradigm shift in how scientists and practitioners think about healthy river systems and successful human interventions. As with all restoration, BRR represents a grand experiment testing our understanding of rivers (Wohl 2019) and beavers, and as with all experiments, outcomes and their interpretations rely on our assumptions and expectations.

We have purposefully cast a wide net in our definition of BRR in an effort to understand the myriad forms BRR takes as the community of practice continues to evolve. In many ways, BRR is a repackaging of old techniques with new expectations. Each of the three commonly used tactics (per Pilliod et al. 2018) has a long-standing community of

practice in other disciplines: translocation for wildlife management (Mengak 2018); grazing plans, plantings, and exclosures for rangeland conservation (e.g., CPS 382,391,528,612, NRCS 2020); and small dams for erosion control (e.g., CPS 402, NRCS 2020). The innovation of BRR lies in the centrality of North American beaver to the *narratives* motivating action and the complicated, contingency-laced pathways on which we base our expectations.

We think it is fair to say that beavers themselves are mainly what attract people to BRR. They are classically charismatic macrofauna whose status as ecosystem engineers aligns with the growing movement toward nature-based solutions—letting nature restore itself (Cohen-Shacham et al. 2016). Moreover, the presence of beavers has become emblematic of an image of pre-European ecosystem health and equilibrium. However, numerous BRR process pathways neither involve nor require beavers to achieve desired outcomes (figure 2), and projects are occurring in locations with known limitations to beaver occupancy (Betsy Stapleton, Scott River Watershed Council, Etna, California, United States, personal communication, 24 May 2020) as well as in locations with healthy existing beaver populations (Maenhout 2013). As such, the *beaver* in the name may say less about beavers and more about how we expect rivers to function.

A key expectation requiring consideration in BRR relates to *who* will do the work of restoration: beavers or humans? If beavers are placed at the center of the motivating narrative, they are arguably not well characterized as a pariah or as a panacea, but as self-willed animals whose survival needs often, but not always, align with those of humans. Consequently, it is worthwhile to consider how much space society is truly willing to leave for what beavers want when it does not align with human expectations. BRR is likely to be most successful in those landscapes in which human objectives align with beavers' survival needs (e.g., figure 2). But that may not always be the case, as when beavers do not need dams for their survival and maintain healthy populations in streams in which conditions remain undesirable to human eyes. In this case, unmet expectations are not because of the beavers, but because of a misunderstanding of the broader drivers of stream behavior and function.

The ways in which BRR (and process-based restoration generally) interact with these drivers is intrinsically complex. Restoration outcomes rely on linked chains of processes and contingencies over which humans often have limited control. Some of these processes, such as dams capturing water and sediment, proceed along relatively predictable pathways for which geomorphic controls are generally understood. Others, such as a beaver's decision to build a dam, are more complicated and rest on contingencies related to beaver ecology, project design, location, adjacent land management, ecological response, and the sequence of events that occur after implementation. This may be why most reports of successful BRR projects describe the use of multiple tactics that were maintained and iterated on over many years (e.g., Marshall et al. 2013, Fesenmyer et al. 2018, Davee et al. 2017,

Charnley 2018, 2019). In each of these projects, goals often shifted as stream systems adapted and evolved, pointing to the difficulty and perhaps futility of evaluating success based solely on the specific outcomes expected on initiation of process-based projects.

We propose that a more useful paradigm for monitoring and evaluating process-based restoration may itself be process based (e.g., Gregory et al. 2012). Instead of setting static goals at the outset of a project and evaluating effectiveness at the end, we recommend deconstructing expectations about how a restoration tactic is initially expected to work to achieve outcomes into a process-expectation framework (e.g., figure 2). This systematic framework can then be used to document what happens as a project proceeds, including the point and direction at which the project may deviate from initial expectations, and if or when goals potentially shift. Such a monitoring framework could align well with the adaptive management of such socioecological systems (Stankey 2005, Kingsford et al. 2017).

Such documentation can produce a rich collection of case studies and observations to inform adaptive management actions at a project site, and identify patterns that can help target future research, monitoring, and restoration efforts. More broadly, moving evaluation away from the binary paradigm of success and failure developed for form-based restoration moves BRR toward a greater understanding of *why* restoration projects are—or are not effective at meeting goals and desired outcomes, and whether those goals or expected outcomes are, in fact, appropriate for a given watershed.

Creating rigorous process-expectation frameworks can help synthesize diverse quantitative and qualitative data sets into robust chronicles of restoration outcomes. On farms, ranches, and other working landscapes, diverse data sources can illuminate how management actions unrelated to the specific restoration tactic (i.e., exclosures, operations management, crop rotation) may ultimately influence desired restoration outcomes. Quantitative data can provide checks on qualitative observations, whereas qualitative data can provide context to quantitative records. In this way, process-based evaluation can both test critical scientific assumptions behind current practices and contribute to the evolution of on-the-ground improvements in BRR.

Ultimately, what makes BRR so exciting and challenging are one and the same—the prospect of restoring nature *with* nature. Nature is intrinsically messy and unpredictable, and so successfully implementing BRR asks that practitioners simultaneously state their goals about how they want beavers and landscapes to respond while acknowledging that whether they respond accordingly is not entirely controllable. Humans bring an understanding of how landscapes function, how ecosystems respond and how interventions might benefit others. Beavers bring their adaptive life histories and survival mandates. The landscape allows what it will. The conjunction has the potential to make rivers better—if expectations are managed, relevant processes acknowledged, and luck intervenes along the way.

References cited

Armichardy D. 2017. Camp creek log weir removal and large wood placement project (2011–2014). Pages 146–151 in Pollock MM, Lewallen GM, Woodruff K, Jordan CE, Castro JM, eds. The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains, version 2.0. US Fish and Wildlife Service.

Baker BW, Peinetti HR, Coughenour MB, Johnson TL. 2012. Competition favors elk over beaver in a riparian willow ecosystem. Ecosphere 3: 1–15.

Baker BW, Hill EP. 2003. Beaver (*Castor canadensis*). Pages 288–310 in Feldhamer GA, Thompson BC, Chapman JA, eds. Wild Mammals of North America: Biology, Management, and Conservation, 2nd ed. Johns Hopkins University Press.

Barnes DM, Mallik AU. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management 61: 1371–1377.

Barnes WJ, Dibble E. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany 66: 40–44.

Beechie TJ, Sear DA, Olden JD, Pess GR, Buffington JM, Moir H, Roni P, Pollock MM. 2010. Process-based principles for restoring river ecosystems. BioScience 60: 209–222.

Beeson HW, Flitcroft RL, Fonstad MA, Roering JJ. 2018. Deep-seated landslides drive variability in valley width and increase connectivity of salmon habitat in oregon coast range. Journal of the American Water Resources Association 54: 1325–1340.

Bouwes N, et al. 2016. Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). Scientific Reports 6: 12.

Briggs MA, Lautz LK, McKenzie JM, Gordon RP, Hare DK. 2012. Using high-resolution distributed temperature sensing to quantify spatial and temporal variability in vertical hyporheic flux. Water Resources Research 48: 16.

Bull WB. 1997. Discontinuous ephemeral streams. Geomorphology 19: 227–276.

Burns DA, McDonnell JJ. 1998. Effects of a beaver pond on runoff processes: Comparison of two headwater catchments. Journal of Hydrology 205: 248–264.

Burchsted D, Daniels, M, Thorson R, Vokoun J. 2010. The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. BioScience 60: 908–922.

Butler DR. 1989. The failure of beaver dams and resulting outburst flooding: A geomorphic hazard of the southeastern Piedmont. Geographical Bulletin 31: 29–38.

Butler DR, Malanson GP. 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71: 48–60.

Charnley S. 2018. Beavers, Landowners, and Watershed Restoration: Experimenting with Beaver Dam Analogues in the Scott River Basin, California. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. Research paper no. PNW-RP-613.

Charnley S. 2019. If You Build It, They Will Come: Ranching, Riparian Revegetation, and Beaver Colonization in Elko County, Nevada. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. Research paper no. PNW-RP-614.

Charnley S, Gosnell H, Davee R, Abrams J. 2020. Ranchers and beavers: Understanding the human dimensions of beaver-related stream restoration on western rangelands. Rangeland Ecology and Management 73: 712–723.

Clark TR. 2020. Impacts of Beaver Dams on Mountain Stream Discharge and Water Temperature. Utah State University.

Cohen-Shacham E, Walters G, Janzen C, Maginnis S, eds. 2016. Nature-Based Solutions to Address Global Societal Challenges. International Union for Conservation of Nature.

Collen P, Gibson RJ. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish: A review. Reviews in Fish Biology and Fisheries 10: 439–461.

Collier, Eric. 1959. Three Against the Wilderness. Dutton.

Davee R, Charnley S, Gosnell H. 2017. Silvies Valley Ranch, OR: Using Artificial Beaver Dams to Restore Incised Streams. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. Research paper no. PNW-RN-577.

Davee R, Gosnell H, Charnley S. 2019. Using Beaver Dam Analogues for Fish and Wildlife Recovery on Public and Private Rangelands in Eastern Oregon. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. Research paper no. PNW-RP-612.

Demmer R, Beschta RL. 2008. Recent history (1988–2004) of beaver dams along Bridge Creek in Central Oregon. Northwest Science 82: 309–318.

Denney RN. 1952. A summary of North American beaver management, 1946–1948. Colorado Game and Fish Department. Report no. 28.

Dierauer JR, Whitfield PH, Allen DM. 2018. Climate controls on runoff and low flows in mountain catchments of Western North America. Water Resources Research 54: 7495–7510.

Dittbrenner BJ, Pollock MM, Schilling JW, Olden JD, Lawler JJ, Torgersen CE. 2018. Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. PLOS ONE 13: e0192538.

Dittbrenner BJ. 2019. Restoration Potential of Beaver for Hydrological Resilience in a Changing Climate. PhD Dissertation. University of Washington, Tacoma, Washington, United States.

Ecke F, et al. 2017. Meta-analysis of environmental effects of beaver in relation to artificial dams. Environmental Research Letters 12: 113002.

Ehrenfeld JG. 2000. Defining the limits of restoration: The need for realistic goals. Restoration Ecology 8: 2–9.

Essaid HI, Hill BR. 2014. Watershed-scale modeling of streamflow change in incised montane meadows. Water Resources Research 50: 2657–2678.

Fanelli RM, Lautz LK. 2008. Patterns of water, heat, and solute flux through streambeds around small dams. Groundwater 46: 671–687.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. BioScience 52: 483–498.

Feiner K, Lowry CS. 2015. Simulating the effects of a beaver dam on regional groundwater flow through a wetland. Journal of Hydrology: Regional Studies 4: 675–685.

Fesenmyer KA, Dauwalter DC, Evans C, Allai T. 2018. Livestock management, beaver, and climate influences on riparian vegetation in a semi-arid landscape. PLOS ONE 13: e0208928.

Fryxell JM, Doucet CM. 1991. Provisioning time and central-place foraging in beavers. Canadian Journal of Zoology 69: 1308–1313.

Gibson PP, Olden JD 2014. Ecology, management, and conservation implications of North American beaver (*Castor canadensis*) in dryland streams. Aquatic Conservation: Marine and Freshwater Ecosystems 24: 391–409.

Goldfarb B. 2018. Eager: The Surprising, Secret Life of Beavers and Why They Matter. Chelsea Green Publishing.

Gonzalez R, Dunham J, Lightcap S., McEnroe J. 2017. Large wood and instream habitat for juvenile Coho salmon and larval lampreys in a Pacific Northwest stream. North American Journal of Fisheries Management 37: 683–699.

Gould S. 1989. Wonderful Life: The Burgess Shale and the Nature of History. Norton.

Grant GE, Schmidt J, Lewis SL. 2003. A geological framework for interpreting downstream effects of dams on rivers. Water Science and Applications 7: 209–213.

Grant GE, O'Connor J, Safran E. 2016. Excursions in fluvial (dis)continuity. Geomorphology 277: 145–153.

Gregory R, Failing L, Harstone M, Long G, McDaniels T, Ohlson D. 2012. Structured Decision Making: A Practical Guide to Environmental Management Choices. Wiley.

Gurnell AM. 1998. The hydrogeomorphological effects of beaver dam building activity. Progress in Physical Geography 22: 167–189.

Hafen KC, Wheaton JM, Roper BB, Bailey P, Bouwes N. 2020. Influence of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence in the intermountain western United States. Earth Surface Processes and Landforms 45: 2664–2674.

Hall ER. 1981. The Mammals of North America, 2nd ed. Wiley.

Halley D, Rosell F, Saveljev A. 2012. Population and distribution of Eurasian beaver (*Castor fiber*). Baltic Forestry 18: 168–175.

Hammersmark CT, Rains MC, Mount JF. 2008. Quantifying the hydrological effects of stream restoration in a montane meadow, northern California, USA. River Research and Applications 24: 735–753.

Hays WJ. 1871. Notes on the range of some of the animals in America at the time of arrival of the whitemen. American Naturalist 5: 25–30.

Hazell D, Osborne W, Lindenmayer D. 2003. Impact of post-European stream change on frog habitat: Southeastern Australia. Biodiversity and Conservation 12: 301–320.

Hibbard EA. 1958. Movements of beaver transplanted in North Dakota. Journal of Wildlife Management 22: 209–211.

Ingle-Sidorowicz HM. 1982. Beaver increase in Ontario: Result of changing environment. Mammalia 46: 167–176.

Ives RL. 1942. The beaver–meadow complex. Journal of Geomorphology 5: 191–203.

Jenkins SH. 1975. Food selection by beavers. Oecologia 21: 157–173.

Jenkins SH. 1981. Problems, progress, and prospects in studies of food selection by beavers. Worldwide Furbearer Conference Proceedings 1: 559–579.

Jenkins SH, Busher PE. 1979. *Castor canadensis*. Mammalian Species 120: 1–8.

Johnson-Bice SM, Renik KM, Windels SK, Hafs AW. 2018. A review of beaver–salmonid relationships and history of management actions in the Western Great Lakes (USA) region. North American Journal of Fisheries Management 38: 1203–1225.

Johnston DR, Chance DH. 1974. Presettlement overharvest of upper Columbia River beaver populations. Canadian Journal of Zoology 52: 1519–1521.

Johnston CA, Naiman RJ. 1990. Browse selection by beavers: Effects on riparian forest composition. Canadian Journal of Forest Research 20: 1036–1043.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373–386.

Jonker SA, Muth RM, Organ JF, Zwick RR, Siemer WF. 2006. Experiences with beaver damage and attitudes of Massachusetts residents toward beaver. Wildlife Society Bulletin 34: 1009–1021.

Jonker SA, Organ JF, Muth RM, Zwick RR, Siemer WF. 2009. Stakeholder norms toward beaver management in Massachusetts. Journal of Wildlife Management 73: 1158–1165.

Karran DJ, Westbrook CJ, Bedard-Haughn A. 2018. Beaver-mediated water table dynamics in a Rocky Mountain fen. Ecohydrology 11: e1923.

Kingsford R, Roux D, McLoughlin C, Conallin J. 2017. Strategic adaptive management (SAM) of intermittent rivers and ephemeral streams. Pages 535–562 in Datry T, Bonada N, Boulton A, eds. Intermittent Rivers and Ephemeral Streams. Academic Press.

Kondolf GM, Smeltzer MW, Railsback SF. 2001. Design and performance of a channel reconstruction project in a coastal California gravel-bed stream. Environmental Management 28: 761–776.

Kondolf GM, et al. 2006. Process-based ecological river restoration: Visualizing three-dimensional connectivity and dynamic vectors to recover lost links. Ecology and Society 11: 5.

Knudsen GJ, Hale JB. 1965. Movements of transplanted beavers in Wisconsin. Journal of Wildlife Management 29: 685–688.

Kramer N, Wohl EE, Harry DL. 2012. Using ground penetrating radar to 'unearth' buried beaver dams. Geology 40: 43–46.

Landin JAB. 1980. Estado actual del 'Castor' (Castor canadensis mexicanus) en el Estado de Nuevo Leon, Mexico. Pages 309–314 in Lund HG, Caballero M, Hamre RH, Driscoll RS, Bonner W, eds. Arid Land Resource Inventories: Developing Cost-Efficient Methods. US Department of Agriculture, Forest Service. General technical report no. WO-28.

Lapointe St-Pierre M, Labbé J, Darveau M, Imbeau L, Mazerolle MJ. 2017. Factors affecting abundance of beaver dams in forested landscapes. Wetlands 37: 941–949.

Lautz LK, Siegel DI, Bauer RL. 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. Hydrological Processes 20: 183–196.

Lautz LK, Kranes NT, Siegel DI. 2010. Heat tracing of heterogeneous hyporheic exchange adjacent to in-stream geomorphic features. Hydrological Processes 24: 3074–3086.

Lautz L, Kelleher C, Vidon P, Coffman J, Riginos C, Copeland H. 2019. Restoring stream ecosystem function with beaver dam analogues: Let's not make the same mistake twice. Hydrological Processes 33: 174–177.

Levine R, Meyer GA. 2014. Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. Geomorphology 205: 51–64.

Levine R. 2016. The Influence of Beaver Activity on Modern and Holocene Fluvial Landscape Dynamics in Southwestern Montana. University of New Mexico.

Lima SL, Zollner PA. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131–135.

Loheide SP, Gorelick SM. 2005. A local-scale, high-resolution evapotranspiration mapping algorithm (ETMA) with hydroecological applications at riparian meadow restoration sites. Remote Sensing of Environment 98: 182–200.

Lowry MM. 1993. Groundwater Elevations and Temperature Adjacent to a Beaver Pond in Central Oregon. Oregon State University.

MacCracken JG, Lebovitz AD. 2005. Selection of in-stream wood structures by beaver in the Bear River, southwest Washington. Northwestern Naturalist 86: 49–58.

Macdonald DW, Tattersall FH, Brown ED, Balharry D. 1995. Reintroducing the European beaver to Britain: Nostalgic meddling or restoring biodiversity? Mammal Review 25: 161–200.

Macfarlane WW, Wheaton JM, Bouwes N, Jensen ML, Gilbert JT, Hough-Snee N, Shivik JA. 2017. Modeling the capacity of riverscapes to support beaver dams. Geomorphology 277: 72–99.

Maenhout JL. 2013. Beaver Ecology in Bridge Creek, a Tributary to the John Day River. Master's thesis. Oregon State University, Corvallis, Oregon, United States.

Majerova M, Neilson BT, Schmadel NM, Wheaton JM, Snow CJ. 2015. Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. Hydrology and Earth System Sciences 19: 3541–3556.

Marshall KN, Hobbs NT, Cooper DJ. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proceedings of the Royal Society B 280: 20122977.

Marston R. 1994. River entrenchment in small mountain valleys of the western USA: Influence of beaver, grazing and clearcut logging [L'incision des cours d'eau dans les petites vallées montagnardes de l'ouest américain: l'influence des castors, du pâturage et des coupes forestières à blanc]. Géocarrefour 69: 11–15.

McClintic LF, Taylor JD, Jones JC, Singleton RD, Wang G. 2014. Effects of spatiotemporal resource heterogeneity on home range size of American beaver. Journal of Zoology 293: 134–141.

McComb WC, Sedell JR, Buchholz TD. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50: 273–281.

McDonnell JJ, et al. 2018. Water sustainability and watershed storage. Nature Sustainability 1: 378–379.

McKinstry MC, Anderson SH. 1997. Use of Beaver to improve riparian areas in Wyoming. Wyoming water 4: 128–134.

McKinstry MC, Anderson SH. 2002. Survival, fates, and success of transplanted beavers, Castor canadensis, in Wyoming. Canadian Field-Naturalist 116: 60–68.

Mengak MT. 2018. Wildlife Translocation. US Department of Agriculture: Animal and Plant Health Inspection Service.

Miles MB, Huberman AM. 1994. Qualitative Data Analysis: An Expanded Sourcebook, 2nd ed. Sage.

Moehrenschlager A, Lloyd N. 2016. Release considerations and techniques to improve conservation translocation success. Pages 245–280 in Jachowski DS, Millspaugh JJ, Angermeier PL, Slotow R, eds. Reintroduction of Fish and Wildlife Populations. University of California Press.

Müller-Schwarze D. 2011. The Beaver: Its Life and Impact, 2nd ed. Comstock.

Nagle G. 2007. Evaluating "natural channel design" stream projects. Hydrological Processes 21: 2539–2545.

Naiman RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. BioScience 38: 753–762.

Nash CS, Selker JS, Grant GE, Lewis SL, Noël P. 2018. A physical framework for evaluating net effects of wet meadow restoration on late-summer streamflow. Ecohydrology 11: e1953.

Nash CS, Grant GE, Selker JS, Wondzell SM. 2019. Discussion: "Meadow Restoration Increases Baseflow and Groundwater Storage in the Sierra Nevada Mountain of California" by Luke J. H. Hunt, Julie Fair, and Maxwell Odland. JAWRA Journal of the American Water Resources Association 56: 182–185.

[NRCS] National Resources Conservation Service. 2020. Conservation Practice Standards. NRCS. www.nrcs.usda.gov/wps/portal/nrcs/detailfull/national/technical/cp/ncps/?cid=nrcs143_026849.

Nyssen J, Pontzeele J, Billi P. 2011. Effect of beaver dams on the hydrology of small mountain streams: Example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. Journal of Hydrology 402: 92–102.

O'Connor JE, Mangano JF, Anderson SW, Wallick JR, Jones KL, Keith MK. 2014. Geologic and physiographic controls on bed-material yield, transport, and channel morphology for alluvial and bedrock rivers, western Oregon. Geological Society of America Bulletin 126: 377–397.

Orians GH, Pearson NE. 1979. On the Theory of Central Place Foraging. Pages 155–177 in DJ Horn, GR Stairs, RD Mitchell, eds. Analysis of Ecological Systems. Ohio State University Press.

Palmer MA et al. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology 42: 208–217.

Palmer MA, Lettenmaier DP, Poff NL, Postel SL, Richter B, Warner R. 2009. Climate change and river ecosystems: Protection and adaptation options. Environmental Management 44: 1053–1068.

Persico L, Meyer G. 2009. Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park. Wyoming Quaternary Research 71: 340–353.

Persico L, Meyer G. 2013. Natural and historical variability in fluvial processes, beaver activity, and climate in the Greater Yellowstone Ecosystem. Earth Surface Processes and Landforms 38: 728–750.

Petro VM, Taylor JD, Sanchez DM. 2015. Evaluating landowner-based beaver relocation as a tool to restore salmon habitat. Global Ecology and Conservation 3: 477–486.

Petro, VM, Taylor JD, Burnett KM, Sanchez DM. 2018. Methods to predict beaver dam occurrence in coastal Oregon. Northwest Science 92: 278–289.

Pilliod DS, Rohde AT, Charnley S, Davee RR, Dunham JB, Gosnell H, Grant GE, Hausner MB, Huntington JL, Nash CS. 2018. Survey of beaver-related restoration practices in rangeland streams of the western USA. Environmental Management 61: 58–68.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. BioScience 47: 769–784.

Pollock MM, Beechie TJ, Jordan CE. 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the

interior Columbia River basin, eastern Oregon. Earth Surface Processes and Landforms 32: 1174–1185.

Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C. 2014. Using beaver dams to restore incised stream ecosystems. BioScience 64: 279–290.

Pollock MM, Lewallen GM, Woodruff K, Jordan CE, Castro JM. 2017. The beaver restoration guidebook: Working with beaver to restore streams, wetlands, and floodplains, version 2.0. US Fish and Wildlife Service. www.fws.gov/oregonfwo/promo.cfm?id=177175812.

Polvi LE, Wohl E. 2012. The beaver meadow complex revisited: The role of beavers in post-glacial floodplain development. Earth Surface Processes and Landforms 37: 332–346.

Puttock A, Graham HA, Cunliffe AM, Elliott M, Brazier RE. 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively managed grasslands. Science of the Total Environment 576: 430–443.

Ritter TD, Gower CN, McNew LB. 2020. Habitat conditions at beaver settlement sites: Implications for beaver restoration projects. Restoration Ecology 28: 196–205.

Scamardo J, Wohl E. 2020. Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado Front Range, USA. River Research and Applications 36: 398–409.

Scheffer VB. 1941. Management studies of transplanted beavers in the Pacific Northwest. Transactions of the North American Wildlife Conference 6: 320–325.

Schlosser IJ, Kallemeyn LW. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81: 1371–1382.

Schumm SA. 1977. The Fluvial System. Wiley.

Seton ET. 1909. Life-Histories of Northern Animals, vol. 1: Grass-Eaters. Scribner.

Seton ET. 1929. Lives of game animals, vol. 4, part 2: Rodents, etc. Doubleday.

Shaw SP, Fredine CG. 1971. Wetlands of the United States: Their Extent and Their Value to Waterfowl and Other Wildlife. US Department of the Interior Fish and Wildlife Service. Circular no. 39.

Sheffels TR, Systsma MD, Carter J, and Taylor JD. 2014. Efficacy of plastic mesh tubes in reducing damage by the invasive nutria (*Myocastor coypus*) to woody vegetation in a Pacific Northwest urban riparian restoration site. Northwest Science 88: 269–279.

Silverman NL, et al. 2019. Low-tech riparian and wet meadow restoration increases vegetation productivity and resilience across semiarid rangelands. Restoration Ecology 27: 269–278.

Small BA, Frey JK, Gard CC. 2016. Livestock grazing limits beaver restoration in northern New Mexico. Restoration Ecology 24: 646–655.

Smith DW. 1998. Beaver Survey Mammoth, WY. US National Park Service. Report no. YCR-NR-93-3.

Stankey GH. 2005. Adaptive Management of Natural Resources: Theory, Concepts, and Management Institutions. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. General technical report no. PNW-GTR-654.

Stratton LE, Grant GE. 2019. Autopsy of a reservoir: Facies architecture in a multidam system, Elwha River, Washington, USA. GSA Bulletin 131: 1794–1822.

Suzuki N, McComb WC. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. Northwest Science 72: 102–110.

Swanson S, Wyman S, Evans C. 2015. Practical grazing management to maintain or restore riparian functions and values on rangelands. Journal of Rangeland Applications 2: 1–28.

Taylor JD, Singleton RD. 2014. The evolution of flow devices used to reduce flooding by beavers: A review. Wildlife Society Bulletin 38: 127–133.

Touihri M, Labbé J, Imbeau L, Darveau M. 2018. North American beaver (*Castor canadensis* Kuhl) key habitat characteristics: Review of the relative effects of geomorphology, food availability and anthropogenic infrastructure. Écoscience 25: 9–23.

[USDA FS] US Department of Agriculture, Forest Service 2016. Camp Creek Headwaters Project Final Project Report. USDA. www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd534877.pdf.

Walder JS, O'Connor JE. 1997. Methods for predicting peak discharge of floods caused by failure of natural and constructed earthen dams. Water Resources Research 33: 2337–2348.

Weber N, Bouwes N, Pollock MM, Volk C, Wheaton JM, Wathen G, Wirtz J, Jordan CE. 2017. Alteration of stream temperature by natural and artificial beaver dams. PLOS ONE 12: e0176313.

Westbrook CJ, Cooper DJ, Baker BW. 2006. Beaver dams and over-bank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. Water Resources Research 42: W06404.

Westbrook CJ, Cooper DJ, Baker BW. 2011. Beaver assisted river valley formation. River Research and Applications 27: 247–256.

Westbrook CJ, Ronnquist A, Bedard-Haughn A. 2020. Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm. Hydrological Processes 34: 3726–3737.

White DS. 1990. Biological relationships to convective flow patterns within stream beds. Hydrobiologia 196: 149–158.

Wild C. 2017. Beaver reintroduction on private property, New Mexico. Pages 182–187 in Pollock MM, Lewallen GM, Woodruff K, Jordan CE, Castro JM, eds. The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains, version 2.0. US Fish and Wildlife Service. www.fws.gov/oregonfwo/promo.cfm?id=177175812.

Wohl E. 2019. Riverine Legacies. H23A-07. Paper presented at the American Geophysical Union Fall Meeting; 9–13 December 2019, San Francisco, California.

Wohl E, Beckman ND. 2014. Leaky rivers: Implications of the loss of longitudinal fluvial disconnectivity in headwater streams. Geomorphology 205: 27–35.

Wohl E, Lane SN, Wilcox AC. 2015. The science and practice of river restoration. Water Resources Research 51: 5974–5997.

Wohl E, Scott DN, Yochum SE. 2019. Managing for Large Wood and Beaver Dams in Stream Corridors. US Department of Agriculture, Forest Service, Rocky Mountain Research Station. General technical report no. RMRS-GTR-404.

Wolff SW, Wesche TA, Hubert WA. 1989. Stream channel and habitat changes due to flow augmentation. Regulated Rivers: Research and Management 4: 225–233.

Woo MK, Waddington JM. 1990. Effects of beaver dams on subarctic wetland hydrology. Arctic 43: 223–230.

Wood PJ, Armitage PD. 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21: 203–217.

Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96–101.

Caroline S. Nash (cnash@ckblueshift.com) is a principal at CK Blueshift and an affiliate faculty member at Boise State University, in Boise, Idaho, in the United States. Gordon E. Grant is a research hydrologist with the USDA Forest Service Pacific Northwest Research Station, in Corvallis, Oregon, in the United States. Susan Charnley is a research social scientist with the USDA Forest Service Pacific Northwest Research Station, in Portland, Oregon, in the United States. Jason B. Dunham is a supervisory aquatic ecologist with the US Geological Survey Forest and Rangeland Ecosystem Science Center, in Corvallis, Oregon, in the United States. Mark B. Hausner is an associate research professor of hydrology in the Desert Research Institute's Division of Hydrologic Sciences, in Reno, Nevada, in the United States. Hannah Gosnell is a professor of geography in the College of Earth, Ocean, and Atmospheric Sciences at Oregon State University, in Corvallis, Oregon, in the United States. David S. Pilliod is a supervisory research ecologist with the US Geological Survey Forest and Rangeland Ecosystem Science Center, in Boise, Idaho, in the United States. Jimmy D. Taylor is a supervisory research wildlife biologist with the USDA National Wildlife Research Center, in Corvallis, Oregon, in the United States.