AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2014)
Published online in Wiley Online Library
(wileyonlinelibrary.com). DOI: 10.1002/aqc.2432

Ecology, management, and conservation implications of North American beaver (Castor canadensis) *in dryland streams*

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ABSTRACT

1. After near-extirpation in the early 20th century, beaver populations are increasing throughout many parts of North America. Simultaneously, there is an emerging interest in employing beaver activity for stream restoration in arid and semi-arid environments (collectively, 'drylands'), where streams and adjacent riparian ecosystems are expected to face heightened challenges from climate change and human population growth.

2. Despite growing interest in reintroduction programmes, surprisingly little is known about the ecology of beaver in dryland streams, and science to guide management decisions is often fragmented and incomplete.

3. This paper reviews the literature addressing the ecological effects and management of beaver activity in drylands of North America, highlighting conservation implications, distinctions between temperate and dryland streams, and knowledge gaps.

4. Well-documented effects of beaver activity in drylands include changes to channel morphology and groundwater processes, creation of perennial wetland habitat, and substantial impacts to riparian vegetation. However, many hypothesized effects derived from temperate streams lack empirical evidence from dryland streams.

5. Topics urgently in need of further study include the distribution and local density of beaver dams; consequences of beaver dams for hydrology and water budgets; and effects of beaver activity on the spread of aquatic and riparian non-native species.

6. In summary, this review suggests that beaver activity can create substantial benefits and costs for conservation. Where active beaver introductions or removals are proposed, managers and conservation organizations are urged to implement monitoring programmes and consider the full range of possible ecological effects and trade-offs.

Received 02 July 2013; Revised 04 November 2013; Accepted 17 November 2013

KEY WORDS: riparian; habitat management; restoration; reintroduction; mammals; vegetation; alien species; impoundment; erosion

INTRODUCTION

Once driven to near extinction, over the past century populations of North American beaver (*Castor canadensis)* and Eurasian beaver (*Castor fiber*) have rebounded to inhabit much of their former geographic range. Hunting restrictions

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combined with deliberate reintroductions contributed to this conservation success (Nolet and Rosell, 1998; Baker and Hill, 2003); however, increases in beaver range and population size also raise new questions for ecosystem management. Beaver are widely recognized as ecosystem engineers with major influence on landscape form and the structure of aquatic ecosystems. Beaver dams create lentic habitat, promote landscape heterogeneity, and alter stream hydrology, sediment dynamics, and nutrient cycling (Naiman *et al*., 1986), with numerous implications for flora and fauna (Rosell *et al*., 2005). There is an emerging interest in employing or mimicking this remarkable engineering power in stream management efforts (DeVries *et al*., 2012; Pollock *et al*., 2012), but beaver activity can also conflict with other ecological management goals or create significant economic damage (Nolet and Rosell, 1998). Discussions over whether and where to promote beaver populations (Longcore *et al*., 2007; Carrillo *et al*., 2009) are now at the forefront of the conservation debate, leading to new questions about the historical distribution, abundance, and ecological effects of beaver.

Although the ecological effects of beaver activity have been thoroughly studied (Naiman *et al*., 1986; Rosell *et al*., 2005), the majority of research has been conducted in temperate river systems, while little attention has been devoted to beaver within more arid environments (see Supplementary material, Table S1). Regions with an arid or semi-arid climate, formally defined by the ratio of precipitation to potential evapo-transpiration, are collectively described as 'drylands' (MEA, 2005). Given the limited contemporary presence of the Eurasian beaver in drylands, owing to widespread extirpation centuries ago (Nolet and Rosell, 1998), this review focuses on the North American beaver (but see Supplementary Material, Appendix 1). In North America, drylands make up most of the land area of the western United States and Mexico (Figure 1). Major ecoregions of this vast area include arid warm deserts (Sonoran, Mojave, and Chihuahuan); cold desert sagebrush steppes of the Great Basin and the Columbia–Snake River Plateau; tablelands of the Colorado Plateau; grasslands of the more arid western half of the Great Plains; and dry shrublands, grasslands, and

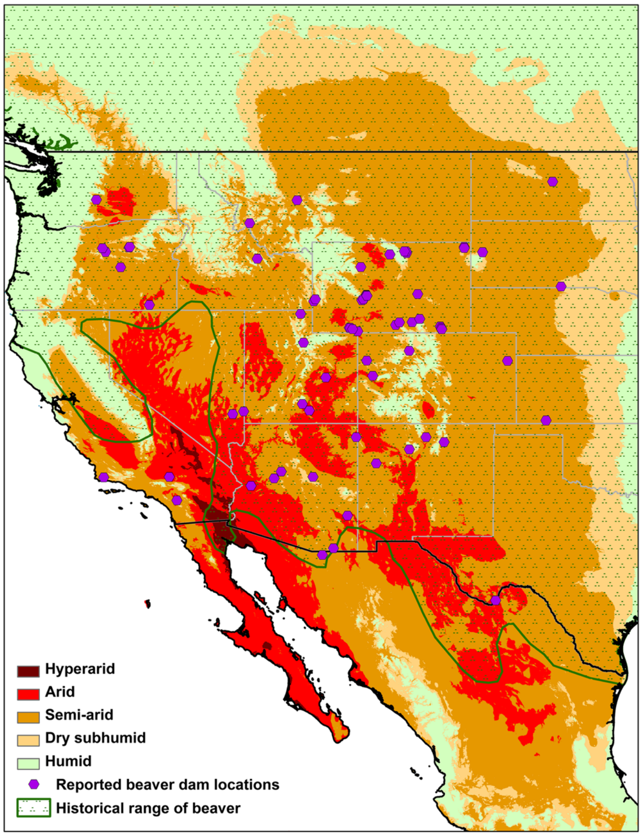

Figure 1. Approximate historical range of North American beaver in western North America and reported locations of beaver dams in drylands. Climate zones are based on an aridity index (MEA, 2005); regions with a hyperarid, arid, or semi-arid climate (i.e. aridity index ≤ 0.5) are considered drylands in this paper. Sources: Trabucco and Zomer (2009) (aridity data) and Patterson *et al.* (2007) (beaver range map).

forests of southern California and northern Mexico (CEC, 1997). The aim of this paper is to synthesize commonalities among the effects of beaver inhabiting the broad range of habitats characterized by aridity, but it should be emphasized that there is great ecological variability within drylands, as well as between dryland and temperate regions.

The return of beaver poses new challenges and opportunities for conservation in dryland streams and wetlands. Biodiversity of drylands tends to be disproportionately concentrated in aquatic and riparian ecosystems: in dryland regions of western North America riparian areas are estimated to cover less than 2% of total land area, yet they support species diversity comparable to upland areas (Knopf *et al*., 1988). Water demand to support growing urban centres and agricultural development is already high, and water withdrawals threaten riparian ecosystems and vulnerable aquatic species (Stromberg, 2001). These stresses are expected to grow more acute in the near future: climate change forecasts predict more drought, reduced rainfall, and reduced stream flow for the desert South-west (Seager *et al.*, 2007), while predicted human population increases will only increase demand for water (Sabo *et al.*, 2010). Extensive loss and alteration of wetland habitat due to human disturbance make these systems a priority for conservation and restoration.

There is a growing sentiment among scientists and resource managers that beaver engineering offers one approach to counteract some conservation threats to dryland streams. Beaver dams increase water storage, raising the local water table and potentially supplementing low stream flows during dry seasons. Beaver ponds can provide habitat for rare species or promote growth of riparian vegetation (Pollock *et al.*, 2003). In present times, beaver dams may perform additional ecological functions such as filtration of toxins or nutrients and control of excessive erosion resulting from human land-use practices (Pollock *et al.*, 2007; Gangloff, 2013). Beavers are returning to ecosystems that bear little resemblance to historical conditions: widespread river regulation has fundamentally altered the function of dryland river ecosystems (Stromberg, 2001), declines of entire native biota and spread of non-native species has altered community dynamics (Pool *et al.*, 2010), and development has shifted priorities for managing river systems. The challenge is to understand the ecological function of beaver in this contemporary dryland landscape.

Opinions and beliefs are strongly divided on the ecological value of beaver in contemporary landscapes. Current approaches to dryland beaver management range from beaver promotion (e.g. reintroduction as part of stream restoration; Fredlake, 1997) to active removal (e.g. to protect riparian vegetation; Mortenson *et al.*, 2008), and there is disagreement over whether the benefits of using beaver in dryland riparian management outweigh the costs (see 'Birds' below). Scientific knowledge and consensus are urgently needed to guide decision making about managing beaver in drylands, but the available science is scattered and often limited in scope. A standard reference on North American beaver notes that '[a]n important research need is to develop independent lines of evidence about how beaver affect ecosystem structure and function over the full range of ecological conditions inhabited by the beaver, especially in the less well-known communities such as southeastern forests, western shrub-steppe, and desert grasslands' (Baker and Hill, 2003; p. 306). In response to this need, the objectives of this paper are: (1) to synthesize published research related to the ecology and management of beaver in drylands; (2) to highlight the ways in which beaver ecological function may differ between arid and semi-arid ('dryland') and humid ('temperate') regions; and (3) to identify the most important knowledge gaps and propose a new research agenda for dryland beaver ecology. Our hope is that current and future science will guide management of beaver in order to conserve valuable dryland stream and riparian ecosystems.

METHODS

Systematic literature review

A formal review of the peer-reviewed literature was conducted according to a search protocol that aimed to maximize transparency and repeatability while minimizing bias. Results from standardized keyword searches in ISI Web of Knowledge and Google Scholar were screened by title, abstract, and, when necessary, full text (see Supplementary Material, Table S2 for search terms) to identify papers meeting the following criteria: (1) published in English-language, peer-reviewed journals, in year 2012 or earlier; (2) relevant to the ecology and management of beaver (papers dealing solely with physiology, palaeontology, epidemiology, or providing no information beyond beaver presence, were excluded); (3) study was conducted in a dryland region (Figure 1); and (4) study reported empirical data or original analyses. Reference lists were used to identify additional eligible sources not located by the original search, but no attempt was made to locate all such sources systematically. Grey literature sources are discussed in the text when relevant, but they are not included in the formal results list (Supplementary Material, Table S3).

Dam locations and density

All sources explicitly reporting presence of beaver dam(s) in a dryland location (including locations provided by unpublished data or casual reports) were collected opportunistically, to provide an indication of the full range of beaver dam occurrence. Where available, reports of beaver dam density from dryland streams were also collected. Eligible dam density reports included (1) a longitudinally continuous survey for all beaver dams present in a stream segment; and (2) reporting of both number of dams (rather than number of colonies) found and total stream length surveyed. In some cases this information was obtained by contacting authors. A similar opportunistic search for density reports from temperate streams provided a comparison with dryland streams.

Data from Oregon Department of Fish and Wildlife Aquatic Inventories Project surveys (1990–2011) of both dryland and temperate streams throughout the state of Oregon permitted a more systematic, broad-scale assessment of beaver dam density. Survey data reported the total number of beaver dams present in wadeable stream segments (ODFW, 1997). For this paper each stream survey segment was classified as either dryland or temperate (Figure 1). Survey segment length and beaver dam density were compared between dryland and temperate streams using Student's *t* test. The analysis was restricted to streams with at least one reported beaver dam (all survey reaches from the same stream were aggregated into a single survey segment) to ensure that all habitat considered was at least broadly suitable for beaver dam construction. All analyses were performed using R version 2.13.1 (R Development Core Team, 2011).

DISTRIBUTION AND STATUS

History and status of North American dryland beaver populations

During the 19th century, British and American trappers ventured west through North America in search of beaver pelts; although the majority of their effort was concentrated on temperate montane regions, the desert South-west also supported a thriving fur trade (Weber, 1971). Accounts by early trappers suggest that beaver were present and often abundant on most perennial dryland streams and wetlands. James Pattie, for example, described trapping beaver through southern Arizona in the 1820s (Pattie, 1905), and Peter Skene Ogden reported large beaver populations along parts of the Humboldt River in northern Nevada in 1829: 'In no part have I found beaver so abundant. … The trappers now average 125 beaver a man and are greatly pleased with their success' (Ogden, 1971).

By the end of the 19th century, this intensive trapping effort had drastically reduced or extirpated many beaver populations throughout North America (Naiman *et al*., 1986). In Arizona, for example, beaver were entirely extirpated from the San Pedro, Santa Cruz, and lower Salt and Gila rivers (Hoffmeister, 1986). A 1931 report from New Mexico notes the relative absence of beaver from numerous locations where they were formerly abundant:

> In 1903 [the author] also visited the headwaters of the Pecos River and found that [beaver] were still occupying some of the streams in that region….There were old cuttings along many of the other streams, but in most cases the beaver had been entirely trapped out… (Bailey, 1931; p.215).

Loss of beaver was widely recognized as a problem by the turn of the century, and legislation protecting beaver was followed by deliberate reintroductions in many areas, beginning in the early 20th century (Baker and Hill, 2003). In general beaver numbers have increased over the past 60 years, and currently beaver occupy much of their historical North American range (Baker and Hill, 2003; Pollock *et al*., 2003). However, population densities may be low, and beaver remain absent from many areas of former occupation, especially areas with urban or agricultural development (McKinstry and Anderson, 2002; Baker and Hill, 2003; Carrillo *et al*., 2009). Currently, numerous conservation groups and government agencies advocate increasing dryland beaver populations as part of a riparian conservation strategy (Fredlake, 1997; Wild, 2011).

The San Pedro River, Arizona, provides a case study for the history of beaver management in a dryland river. Nineteenth century accounts described extensive open marshlands and abundant beaver

(Webb and Leake, 2006), as in James Pattie's description of the San Pedro during his 1825 trapping expedition: '[the river] being very remarkable for the number of its beavers, we gave it the name of Beaver River. At this place we collected 200 [beaver] skins;…' (Pattie, 1905). However, heavy trapping, supplemented by dynamiting of beaver dams in an attempt to reduce mosquito-borne malaria, effectively extirpated beaver from the San Pedro River by the early 20th century (Johnson, 2011). Around the same time, probably due to a combination of climatic conditions and land-use change (including loss of beaver dams), rapid downcutting and arroyo formation drained riparian wetlands (Webb and Leake, 2006). More recently, as one of Arizona's only fully free-flowing rivers and an important site for migratory birds, the San Pedro River has become an important site for riparian conservation in the desert South-west (Stromberg *et al*., 1996; Johnson, 2011). In the 1990s, reintroduction of beaver was proposed as a means to increase perennial surface water, reduce erosion, and improve habitat heterogeneity for other wildlife; in particular, beaver activity could promote development of wetlands more closely resembling historical conditions along the river (Fredlake, 1997). Since reintroduction in 1999–2001, beaver populations have increased, spread, and built dams (Johnson, 2011). Continuing monitoring of ecosystem responses to this reintroduction provides an opportunity to improve understanding of the historical consequences of widespread beaver removal.

Distribution of beaver in dryland streams

The historical range of the North American beaver includes most of the drylands of western North America (Figure 1). Establishing whether beaver were historically present in a region can play an important role in decisions about beaver management (Longcore *et al*., 2007), but the rapid decimation of beaver populations from western North America makes it difficult to determine the precise limits of historical beaver distribution. Borders of the widely cited beaver native range map (Jenkins and Busher, 1979; Figure 1) have been called into question by recent research: although it is widely believed that beaver were historically absent from large areas of California and Nevada (Jenkins and Busher, 1979; USFWS, 2009), Lanman *et al*. (2012) suggest that beaver were in fact present in the dryland Carson and Walker river basins of western Nevada, and a similar review of the evidence indicates that beaver may also be native to arid southern California (M. Pollock, pers. comm.; Lanman *et al*., 2012). In Mexico, Gallo-Reynoso *et al*. (2002) provide evidence for historical and current presence of beaver extending farther south into the Sierra Madre Occidental than is usually included in the beaver native range. Natural variation in beaver populations over time (Baker and Hill, 2003) adds to the difficulty of establishing historical distribution.

Beaver occupy a wide range of aquatic habitats, including streams and rivers, lakes, and wetlands (Baker and Hill, 2003). In drylands, many flowing waters are ephemeral and perennial streams are relatively rare (Levick *et al*., 2008); other important habitat types occupied by beaver in dryland North America include large rivers (Breck *et al*., 2001), the sloughs, backwaters, side channels, and other riparian wetlands in river floodplains (Billman *et al*., 2013), and isolated spring-fed wetlands (Kindschy, 1985). Historical sources document abundant beaver in the marshes and sloughs of the lower Colorado River and Delta, for example (Mellink and Luévano, 1998). In addition, beaver are highly adaptable and make use of developed and novel ecosystems including reservoir shores (Tallent *et al*., 2011), urban environments (Nolte *et al*., 2003) and, especially, the irrigation canals that are common in dryland agricultural landscapes (Hoffmeister, 1986; Demmer and Beschta, 2008). Development of canal networks in arid regions such as California's Imperial Valley has allowed beaver populations to expand into formerly unsuitable territory (Tappe, 1942; Mellink and Luévano, 1998). However, beaver damming of canals frequently leads to their removal as nuisance animals (McKinstry and Anderson, 2002). Most dryland studies focus on beaver in streams and rivers, and information about beaver ecology in other habitat types, especially springs and wetlands, is limited.

Several models have been developed to characterize potential beaver habitat within dryland North America. The Southwest Regional Gap Analysis Project broadly estimates range-wide potential beaver habitat within the south-western United States, based on availability of perennial water, land slope (<15%), and land use (excluding dense urban development; USGS, 2007). A similar model (excluding non-stream habitat types) for the state of New Mexico suggests that large areas of potential beaver habitat are currently unoccupied (Wild, 2011). However, 'relatively little descriptive work (on beaver-habitat associations) has been done in the Southwest' (Wild, 2011; p. 7), and model parameters are of necessity based primarily on studies from temperate regions. Data are needed to evaluate the performance and utility of these and other dryland habitat suitability models.

Availability of perennial water is probably the most important factor governing beaver distribution in dryland streams and wetlands. A survey of beaver occupancy along an eastern Washington stream found that beaver were present only in the lower, perennial reaches (Lind, 2002), but numerous authors report beaver presence on intermittent streams (Ffolliott *et al.*, 1976; Mellink and Luévano, 1998; Albert and Trimble, 2000; McKinstry and Anderson, 2002). It is clear that beaver require a year-round source of water; however, even when the channel is not flowing, stream reaches classified as 'intermittent' may still contain permanent ('perennial') pools of water that can support beaver. Thus habitat models that limit possible habitat to perennial stream reaches may be too conservative, although it is likely that the bulk of dryland beaver occupancy is concentrated along true perennial streams and wetlands.

Availability of riparian vegetation is also believed to influence the distribution of beaver in drylands, where vegetation is often restricted to a narrow riparian corridor (Hoffmeister, 1986; Andersen and Shafroth, 2010) and generally more limited than along temperate streams (MacFarlane and Wheaton, 2013). Riparian vegetation may shape reach-level distribution of beaver in dryland streams: studies have shown close associations between beaver presence and density of willow (see 'Effects of herbivory on native plants' below). Anecdotally, beaver absence or failure to re-establish is often attributed to lack of vegetation (Mellink and Luévano, 1998; Albert and Trimble, 2000). In particular, loss of riparian vegetation owing to livestock or other ungulate grazing, another common feature of North American drylands, may prevent beaver establishment (Baker *et al.*, 2005; White and Rahel, 2008). At a larger scale, however, the hypothesis that availability of vegetation limits range-wide beaver distribution in drylands has not been formally tested.

River regulation by large dams, a primary form of human alteration to dryland river ecosystems, has a complex relationship with beaver ecology. Dewatering downstream of dams can sometimes reduce habitat available to beaver (Mellink and Luévano, 1998); however, flow regulation prevents the large floods that might displace beaver and destroy their dams, and it often increases downstream perennial flow (Andersen and Shafroth, 2010). These hydrologic effects also promote riparian vegetation close to the active river channel, which in turn supports a greater number of beavers (Breck *et al.*, 2001). Construction of Glen Canyon Dam, for example, is thought to have increased the beaver population of the Grand Canyon as result of increased availability of stable riparian habitat (Hoffmeister, 1986). Moreover, flow regulation can permit construction and maintenance of beaver dams at a much greater density than would have been possible historically; this has occurred on the Bill Williams River (Arizona), which provides a compelling example of the relationship between beaver and flow regulation. The extent of historical beaver occupancy of this remote desert river is uncertain, but intermittent surface flow and lack of riparian vegetation are likely to have limited permanent beaver presence, and large floods would have removed any dams with some regularity. However, on the present-day river, dam regulation has maintained perennial downstream flow, mostly eliminated large floods, and promoted dense riparian vegetation; these conditions are highly favourable for beavers and beaver dams. Andersen and Shafroth (2010) calculated that construction of beaver dams over seven flood-free years converted lotic habitat to lentic at a rate of approximately 3%

per year. Current management goals for the river include periodic removal of beaver dams (by controlled floods; Figure 2) in order to maximize habitat diversity and promote establishment of native cottonwood–willow riparian vegetation (Shafroth *et al.*, 2010).

Distribution of beaver dams in dryland streams

Most of the ecosystem engineering abilities attributed to beaver result from construction of beaver dams. Dam-building primarily occurs on small streams, and beaver may also dam secondary channels and backwaters within the floodplain of large rivers (Naiman *et al.*, 1986; Billman *et al.*, 2013). Because of its ecological importance, this review focuses primarily on beaver dam-building in streams. However, not all beavers construct dams: along lakes and large rivers, for example, beavers dig bank dens and make use of the existing deep water (Mortenson *et al.*, 2008). A relatively large proportion of dryland beavers are bank-dwellers rather than dam-builders (Breck *et al.*, 2001), in part because much of the perennial water in arid environments is concentrated in large rivers.

The hydrology of many dryland catchments may also limit persistence of beaver dams. High inter- and intra-annual variation in runoff is characteristic of dryland streams generally, and intense flash floods common in low desert streams would presumably destroy any existing beaver dams (Andersen and Shafroth, 2010). Thus it seems likely that floods and flow variability may limit the distribution, density, or longevity of beaver dams in dryland streams. Beaver dams can be found throughout the range of beaver occupancy, including arid, low-desert streams, although reports from higher-elevation, semi-arid locations are more common (Figure 1). Within broad regional requirements, local channel geomorphology determines specific locations where dam construction is possible (McComb *et al.*, 1990; MacFarlane and Wheaton, 2013). Because so many of the ecological effects of beaver activity depend on dam construction, predicting the consequences of a beaver introduction or population increase will require an accurate prediction of where and in what densities beavers are capable of building and maintaining dams.

Recently, Macfarlane and Wheaton (2013) developed a model specifically to estimate the potential extent of beaver dam-building activity across a landscape, emphasizing conditions typically found in dryland streams. In addition to availability of perennial water and riparian vegetation, the model incorporates stream power at base flows and at flood levels to predict the effects of stream hydrology on dam construction and persistence. Other studies have found that dam presence in dryland streams is strongly associated with low stream gradient (as in temperate streams; Baker and Hill, 2003), and also with alluvial substrate, gentle bank slopes, and presence of hardwood or riparian vegetation (McComb *et al.*, 1990; Lind, 2002). When riparian trees are not available, beavers may construct dams of willow (*Salix* sp.; Call, 1970), cattails (*Typha* sp.; Andersen and Shafroth, 2010), or even sagebrush (*Artemisia* sp.; Apple *et al.*, 1985), but authors suggest that such dams are likely to be less stable than those constructed with large wood.

Figure 2. Two beaver dams on the Bill Williams River: intact dam (left); and breached dam during an experimental flood (right). Photos: Julian Olden.

The typical hydrology and relatively limited vegetation of dryland streams suggests the hypothesis that beaver dams in dryland streams will be less abundant than in temperate streams. However, dam densities reported in the literature do not support this hypothesis: there is no consistent difference in reported densities between dryland and temperate streams at either small or relatively large scales (Figure 3(a)). However, this collection drew heavily on studies from high-elevation, semi-arid Wyoming, where very high densities have been reported, and the relatively fewer values from fully arid locations are consistently low (Supplementary Material, Table S4). Similarly, data from standardized stream surveys throughout the state of Oregon show no significant difference in mean beaver dam density between dryland (1.07 dams km^{-1}; n = 44) and temperate stream (1.50 dams km^{-1}; n = 329) segments (Student's *t*-test, $P = 0.117$, df = 62; Figure 3(b)), despite a significantly greater mean survey length for dryland (16.2 km) than for temperate (9.0 km) stream segments (Student's *t*-test, $P = 0.002$, df = 49). Together these results indicate that, where dams are built, beaver dams in dryland streams can achieve densities comparable to those found on average in temperate streams, even over relatively large scales (>100 km). However, the few available large-scale beaver dam surveys reported from dryland streams do suggest a tendency for uneven, patchy distribution of dams (McComb *et al.*, 1990; Andersen and Shafroth, 2010; Gibson, unpub. data; but see Call, 1970) compared with a more homogeneous distribution in temperate streams (Johnston and Naiman, 1990). Additional research on beaver dam abundance in dryland streams is needed for a better description of distribution patterns and to quantify the range of dam densities to be expected across a variety of habitat settings.

Beaver modification of dryland streams is a dynamic process that varies in time as well as in space. In eastern North America, beaver dams tend to be stable landscape features, some persisting as long as a century (Burchsted *et al.*, 2010). In dryland streams, however, floods and variable stream discharge usually preclude such longevity; in addition, variable discharge can produce wide fluctuations in dam density over time. Over 17 years of biannual beaver dam census in a small central Oregon stream, the total number of dams present on 32 km of stream ranged from 9 to 103. No individual dam persisted more than 7 years, and most were breached within 2 years or less (Demmer and Beschta, 2008). Dam longevity varies with environmental setting: in high-elevation, semi-arid

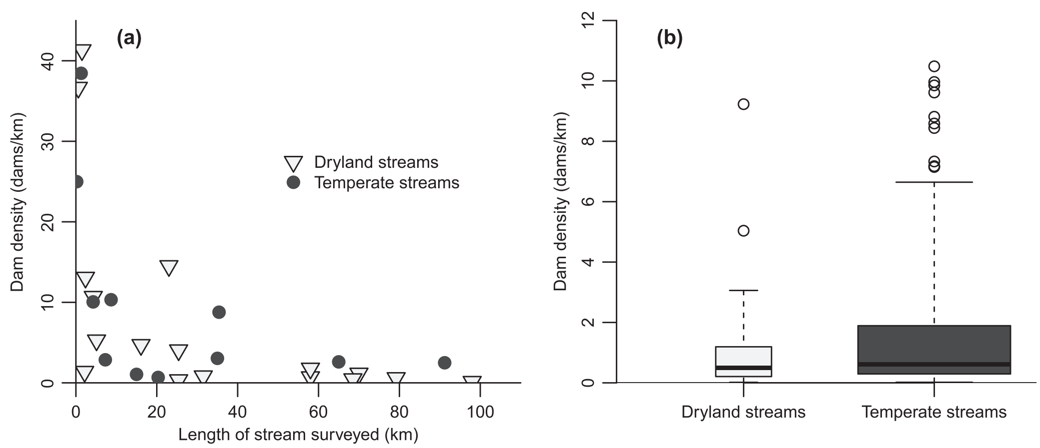

Figure 3. Comparisons of beaver dam densities reported for dryland and temperate streams. Panel (a) shows beaver dam densities reported in the literature, as a function of total stream length surveyed. Light-grey triangles indicate densities from dryland streams and dark circles represent temperate streams. Not shown is an extreme dryland value of 25.6 dams km^{-1} over 145 km (Call, 1970). Density sources are listed in Supplementary Material, Table S4. Panel (b) shows a boxplot of beaver dam densities reported for standardized stream segment surveys from dryland (n = 44) and temperate (n = 329) streams distributed throughout Oregon, USA. Stream length of survey segments ranges from 2–200 km (dryland streams) and from 2–275 km (temperate streams). Boxplots show median, interquartile range (IQR), 3 times IQR (whiskers), and outliers; box widths are proportional to the square root of the number of observations in each group. Data source: ODFW (1997).

Wyoming, for example, most beaver dams were found to be between 5 and 19 years old (Call, 1970), while dams in the desert San Pedro River (Arizona) usually wash out each year in seasonal monsoon floods (Johnson, 2011). However, dam longevity also depends on channel morphology, which may change over time in response to climatic or anthropogenic factors (Cluer and Thorne, 2012; see also 'Geomorphology' below). Historical marshes on the San Pedro River, for example, may have been capable of supporting much more stable beaver dams than do contemporary entrenched channels (see 'History and status' above).

Beginning to quantify the relationship between stream discharge and dam failure, Andersen and Shafroth (2010) found that flood pulses of about $60\,m^3\,s^{-1}$ (relative to base flow of $\sim 1\,m^3\,s^{-1}$) damaged at least 50% of monitored beaver dams below Alamo Dam on the Bill Williams River (Arizona). Fewer dams were damaged in a $37\,m^3\,s^{-1}$ flood pulse – but 'significant' damage to beaver dams was observed at discharge as low as $5\,m^3\,s^{-1}$, suggesting that even relatively small managed floods may affect beaver dam function. This study also showed that dams were quickly rebuilt even following flushing floods large enough to obliterate all dams.

ABIOTIC EFFECTS

Geomorphology

Beaver dams play a significant role in shaping the morphology of river channels (Pollock *et al.*, 2003). Fundamentally, construction of a beaver pond increases the extent of surface water and lentic wetland habitat; this function may have particular ecological significance in drylands, where wetland habitat is rare (McKinstry *et al.*, 2001). Beaver ponds sometimes maintain perennial surface water or wetlands in otherwise intermittent stream channel segments (Albert and Trimble, 2000; McKinstry and Anderson, 2002), which can promote a stable riparian community and provide a water source for wildlife and livestock during the dry season (Call, 1970; Demmer and Beschta, 2008). In many temperate streams, beaver ponds typically fill with sediment over time and eventually develop into beaver meadows or other wetland landforms (Burchsted *et al.*, 2010), but this longevity is unlikely for beaver dams in flood-prone dryland streams (see 'Distribution of beaver dams' above). Despite high rates of dam failure, however, former beaver dams on a central Oregon stream were associated with increased channel sinuosity, diverse wetland habitats, and pool–riffle complexes resulting from sediment deposition within former ponds (Demmer and Beschta, 2008). Westbrook *et al.* (2011) documented a similar effect in a temperate montane stream characterized by frequent dam failure during high flows: both presence and breaching of beaver dams increased heterogeneity in sediment deposition and riparian vegetation on floodplain terraces. Microhabitat complexity associated with even short-lived beaver dams may promote aquatic biodiversity (Billman *et al.*, 2013).

The ability of beaver ponds to trap and retain sediment has proved useful in restoration of incised stream channels, a common problem for dryland streams. Channel incision, typically following land-use change such as development or introduction of livestock grazing, is associated with rapid erosion, lowering of the water table, severed connectivity with the floodplain, elimination of riparian vegetation, and loss of fish habitat (Pollock *et al.*, 2007). Encouraging beaver dam construction can be a technique to restore functioning of these channels. Pollock *et al.* (2007) studied the process in detail on Bridge Creek in semi-arid central Oregon; sediment accumulation behind beaver dams indicated relatively rapid aggradation of the stream channel and reduction in channel slope associated with the dams. In a similar study from semi-arid Idaho, DeVries *et al.* (2012) documented increased frequency of overbank flows (i.e. hydrologic connectivity with the floodplain) around artificial structures constructed to imitate beaver dams. These studies demonstrate that beaver dams can effectively speed up the relatively slow process of aggrading incised streams sufficient to reconnect them with abandoned terraces.

However, the geomorphic effects of beaver dams vary depending on channel morphology, which may fluctuate over time (Cluer and Thorne, 2012). Dams constructed within incised channels are less likely to create overbank flooding and geomorphic complexity such as braided channels than are dams in an unimpaired, low-gradient floodplain (Johnson, 2011; Pollock *et al*., 2012). Furthermore, there is a positive feedback relationship between dams and channel form: stable beaver dams promote aggradation and overbank flooding, which spreads and dissipates flood energy across the floodplain; within incised channels, however, concentrated flood energy typically washes out beaver dams in their first year (Demmer and Beschta, 2008; Johnson, 2011; Pollock *et al*., 2012), thus preventing development of the stable beaver colonies that might counteract the incision. Artificially stabilizing beaver dams or dam-like structures within incised channels has been proposed as a management technique to break the incision cycle and enhance the restoration potential of beaver dams (Apple *et al*., 1985; Pollock *et al*., 2012).

Hydrology

A number of studies indicate the importance of dryland beaver ponds in groundwater processes that shape patterns of discharge and riparian vegetation. Groundwater monitoring along a central Oregon stream showed increases in groundwater surface elevation (i.e. water table), groundwater storage potential, and aquifer recharge surrounding a beaver dam (Lowry, 1993), and anecdotal reports indicate a similar increase in water table elevation associated with construction of new beaver dams on the San Pedro River, Arizona (Johnson, 2011). In a semi-arid Wyoming stream, where beaver dams were associated with increased hyporheic exchange, Lautz *et al*. (2006) also found that the effect of dams varied with geomorphic setting: in gaining reaches, water diverted to the subsurface by a beaver dam re-entered the main channel shortly below the dam, but in losing reaches, water was diverted to deeper, longer-term flow paths. These effects are generally consistent with studies from temperate streams (Rosell *et al*., 2005), but may take on a new importance in the different ecological context of water-limited dryland stream ecosystems.

The most intriguing aspect of the relationship between beaver ponds and groundwater dynamics in dryland streams is the potential for the elevated water storage to increase stream flow during dry seasons, potentially converting downstream hydrology from intermittent to perennial. Chronic low-flow conditions are a common feature of dryland streams, and increasing loss of surface flow to climate change and human use is a primary conservation concern for many dryland streams (Seager *et al*., 2007; Levick *et al*., 2008). Advocates for beaver reintroduction frequently cite more stable, perennial flow as a benefit to be provided by beaver dams (Fredlake, 1997; Wild, 2011); unfortunately, very few data are available to evaluate this hypothesis. Some anecdotal reports, from both temperate and dryland streams, suggest instances where beaver dams did convert intermittent streams to perennial flow (reviewed in Pollock *et al*., 2003). Studies monitoring beaver reintroductions in drylands have reported that beaver ponds maintained perennial standing water (see ‘Geomorphology’ above), but no data are available to evaluate downstream effects on discharge. In addition, construction of beaver ponds may affect stream water budgets by changing evaporative processes (Andersen *et al*., 2011). Research is needed to quantify the relationships between beaver dams and hydrologic processes in dryland streams.

In contrast to their ability to maintain flow during drought conditions, beaver dams may also reduce stream velocity and erosive power during peak flows. Somewhat limited empirical evidence from temperate streams supports this hypothesis (reviewed in Pollock *et al*., 2003; Rosell *et al*., 2005), but few data are available from dryland streams. Where management goals include reducing erosion or sedimentation, promotion of beaver dams may be an effective strategy (DeVries *et al*., 2012). However, in many dryland river systems, large peak flows are important in conservation of native fish (Rinne and Miller, 2006) or plant (Stromberg, 2001) communities. In this case dam-building activity may counteract management goals, although beaver dams are unlikely to have a significant effect on large magnitude, infrequent floods.

Water quality and chemistry

High water temperature is a primary management concern for water quality in many dryland streams, in particular with respect to endangered salmon and trout. In general beaver dams are thought to increase water temperatures owing to increased water surface area, longer residence time, and decreased shading (Rosell *et al*., 2005), although cooler water temperature due to deep pools and increased willow shading has also been cited as a potential benefit to be provided by beaver activity (Wild, 2011). Evidence for thermal effects of beaver dams in dryland streams is mixed. Water temperatures in a south-east Oregon stream were consistently slightly warmer within beaver ponds than in neighbouring unimpounded reaches (Talabere, 2002), but in the cool tailwaters below Alamo Dam on the Bill Williams River (AZ), Andersen *et al*. (2011) found no consistent trend in water temperature within beaver ponds. It is interesting that both Lowry (1993) and Pollock *et al*. (2007) observed relatively cooler water temperature immediately below beaver dams in central Oregon, presumably an effect of groundwater upwelling. In addition to beaver dams creating thermal effects, beaver foraging may also influence water temperature by reducing riparian canopy shade (Rosell *et al*., 2005), a potential effect that has not been examined.

Several studies have shown effects of beaver dams on input and retention of organic matter and nutrients in dryland streams that are largely consistent with results from temperate streams. Harper (2001) confirmed that benthic sediments from beaver ponds in an arid Nevada stream contained higher levels of particulate organic matter than did sediments from unimpounded reaches. Based on this study it seems probable that beaver ponds increase net ecosystem retention of nitrogen and, thus, overall productivity of ponds and downstream waters (Coleman and Dahm, 1990). Altered nutrient retention has conservation implications for water quality in dryland streams: concentrations of nutrients and suspended solids decreased in a Wyoming stream after passing through several beaver ponds, indicating that promotion of beaver dams in tributaries may be an effective strategy to reduce downstream nutrient export (Maret *et al*., 1987). Beaver dams can also affect nutrient retention through increased hyporheic exchange (Lautz *et al*., 2006); this may be particularly important where channel incision and livestock grazing add pollution or limit ecosystem uptake of nutrients.

BIOTIC EFFECTS

Riparian vegetation

Considerable management effort has been devoted to conservation and restoration of riparian plant communities in dryland environments, especially the globally endangered cottonwood–willow forest type (Stromberg, 2001), and there is clear evidence that beaver activity alters the riparian community both directly through herbivory and indirectly through dam construction. Beaver are unique in their ability to cut mature trees and thus alter the riparian canopy cover (Baker and Hill, 2003); in addition, beaver foraging activity is concentrated along the water's edge (McGinley and Whitham, 1985). Unlike a majority of the ecosystem effects associated with beaver activity, herbivory will occur wherever beaver are present, not limited to dam-building sites. Managers are frequently concerned that beaver foraging will damage desired riparian vegetation (Mortenson *et al*., 2008), and numerous studies have sought to assess the net effects of beaver foraging on dryland riparian communities.

Effects of herbivory on native plants

Feeding trials and field observations indicate that willow (*Salix* spp.) and cottonwood (*Populus* spp.) are preferred woody forage plants for dryland beaver (Harper, 2001; Kimball and Perry, 2008). Several studies have documented a close association between beaver presence and distribution of willow (Mortenson *et al*., 2008; Tallent *et al*., 2011), but there is little evidence for a negative population-level response of willow to beaver foraging. For example, despite concern that beaver foraging may contribute to observed declines of now-rare Goodding's willow (*S. gooddingii*) stands in Grand Canyon National Park, findings from a survey of the spatial distribution of beaver and willow did not support this hypothesis (Mortenson *et al*., 2008). Along the shores of Lake Mojave, Tallent *et al*. (2011) showed a significant positive association between beaver herbivory and percentage willow cover, and they suggested that beaver foraging promoted willow 'coppicing' and regrowth into dense stands, thus increasing total willow cover. Kindschy (1985) found that stems of red willow (*S. lasiandra*) grew faster after being cut by beaver, compared with growth in unbrowsed plants. At a small scale, however, beaver may consume most readily available willow plants within reach of a beaver colony (Hall, 2005).

Like willow, cottonwood browsed by beaver can sometimes resprout from stumps or roots, typically producing a 'shrubbier' (short, more branches) growth form, with unknown consequences for reproductive success (McGinley and Whitham, 1985). However, unlike willow, substantial negative population-level effects of beaver herbivory on cottonwood have been documented. In combination with flow regulation, beaver herbivory may effectively prevent establishment and therefore persistence of cottonwood (Lesica and Miles, 1999). In studies on the Green and Yampa Rivers (Utah and Colorado), Breck *et al.* (2001) showed that flow regulation promoted growth of willow close to the wetted channel, which allowed beaver populations to increase. In addition, where cottonwood abundance and density was lower (i.e. along the regulated Green River), the probability of beaver damage to any individual plant was much higher, and therefore beaver herbivory had a greater overall impact on the cottonwood population (Breck *et al.*, 2003). In general these results suggest that cottonwood populations already stressed by river regulation or dewatering are more vulnerable to beaver herbivory. Restoration strategies such as modifying dam releases on regulated rivers to promote cottonwood establishment may increase the resilience of cottonwood populations to beaver herbivory. Alternatively, more direct management interventions such as protecting vulnerable young trees with wire, or even trapping and removal of beaver, may be necessary where promotion of vulnerable riparian cottonwood populations is a priority (Crawford and Umbreit, 1999) or where restoration projects attempt to plant new cottonwood stands (Nolte *et al.*, 2003).

Effects of herbivory on non-native plants

The spread of non-native riparian plants, especially salt cedar ('tamarisk'; *Tamarix* spp.), and replacement of native plant communities represents a major challenge for dryland riparian management (Mortenson *et al.*, 2008). There is some evidence that beaver herbivory can promote the spread of non-native plants such as tamarisk at the expense of native communities. Food choice experiments indicate that high tannin and salt levels physiologically limit beaver consumption of tamarisk (Kimball and Perry, 2008), and observational studies have found that beaver rarely forage on tamarisk (Lesica and Miles, 2004; Mortenson *et al.*, 2008; Tallent *et al.*, 2011), although they may cut tamarisk shoots for use in dam construction (Harper, 2001). In semi-arid eastern Montana, Lesica and Miles (2004) found that tamarisk and non-native Russian olive (*Elaeagnus angustifolia)* both grew significantly faster under an open canopy created by beaver foraging than under the shade of intact cottonwood forest. In the Grand Canyon, a positive association between beaver presence and tamarisk cover was consistent with the hypothesis that beaver herbivory promotes tamarisk dominance (Mortenson *et al.*, 2008). These results suggest that under some circumstances, especially river regulation, the arrival of beaver in streams at risk of invasion by tamarisk or other non-native plants may compromise conservation efforts for native plant communities.

Indirect effects on vegetation

Beaver dams raise and stabilize the surrounding water table, which creates ideal conditions for some riparian plants. The strong interdependence between beaver dams, groundwater elevation, and willow has been extensively studied in temperate Yellowstone National Park, where restoration of tall riparian willow communities was dependent on restoration of the hydrologic conditions created by beaver dams (Marshall *et al.*, 2013). Beaver populations, in turn, cannot persist without abundant willow, thus preventing re-establishment of beaver once they have been lost (Baker *et al.*, 2005). Management interventions designed to break this positive feedback cycle include constructing imitation beaver dams in order to encourage willow growth (Marshall *et al.*, 2013), or planting or importing vegetation to provide an initial food supply for beaver until ponds are re-established (Albert and Trimble, 2000).

The importance of these hydrological effects for vegetation is likely to be even greater within dryland streams, where lowered water tables caused by water diversion and groundwater extraction is considered a serious threat to cottonwood–willow forest (Stromberg *et al*., 1996). Cooke and Zack (2008) found a positive association between beaver dam density and width of riparian vegetation cover in semi-arid Wyoming, and several studies anecdotally report a general increase in abundance of willow and other vegetation over time following the return of beaver dams to semi-arid streams (Apple *et al*., 1985; Demmer and Beschta, 2008), although in each case these results are confounded by concurrent exclusion of livestock grazing. Reductions in non-native tamarisk due to flooding behind beaver dams have also been reported anecdotally (Albert and Trimble, 2000; Baker and Hill, 2003; Longcore *et al*., 2007), and in contrast to the more positive effects of beaver herbivory (see 'Effects of herbivory on non-native plants' above). On small streams, promoting beaver dams may be an effective strategy for increasing riparian vegetation cover.

Beaver dam modifications to channel shape and sediment dynamics also have consequences for riparian vegetation. Landforms associated with beaver dams (secondary channels, breached beaver ponds) are known to be favourable for willow establishment (Cooper *et al*., 2006). Several authors have observed that, following the return of beaver to semi-arid streams, mud bars deposited behind dams and newly exposed sediments of drained ponds were densely colonized by riparian vegetation (Apple *et al*., 1985; Demmer and Beschta, 2008). Construction of beaver ponds also promotes growth of aquatic macrophytes, rushes, and sedges, which may increase the habitat value for other wildlife or even produce desirable forage for livestock (Call, 1970; Hall, 2005). However, in addition to willow germination, bare soils of breached beaver ponds probably also promote colonization by opportunistic, 'weedy' non-native plants (Zedler and Kercher, 2004). A dynamic cycle of pond creation, abandonment, and breaching may be the most effective regime to promote establishment and persistence of a native riparian vegetation community.

Wildlife

Mammals

Research indicates that dryland beaver activity can enhance habitat for aquatic and riparian-associated mammals, including some species of conservation concern. River otter (*Lontra canadensis*), which have suffered particularly steep population declines in the desert South-west, are known to make use of beaver ponds and dens; within the upper Colorado Basin, Depue and Ben-David (2010) documented an association between beaver sign and otter presence, and they suggested that otter reintroduction efforts should focus on locations where beaver are present. Frey and Malaney (2009) proposed that beaver ponds are likely to provide ideal riparian habitat for the rare meadow jumping mouse (*Zapus hudsonius luteus*) in New Mexico. More generally, Medin and Clary (1991) found that a semi-arid Idaho beaver pond supported a greater abundance and a different assemblage of riparian small mammals than an adjacent unimpounded stream.

Birds

Dryland cottonwood–willow riparian forests support a high richness and density of breeding songbirds (Knopf *et al*., 1988; Johnson, 2011), which highlights the conservation importance of beaver impacts to these forests. Considerable research in temperate regions has found that the wetland habitat and altered riparian vegetation structure surrounding beaver ponds promotes species richness and abundance of birds (reviewed in Rosell *et al*., 2005); similar patterns appear in the more limited studies from dryland streams. Density, biomass, and species richness of riparian birds were all higher surrounding a beaver pond than along an unimpounded reach of a semi-arid Wyoming stream (Medin and Clary, 1990). Cooke and Zack (2008) further showed that riparian bird abundance and diversity in similar Wyoming streams were positively related to the density of beaver dams in a stream reach. Following reintroduction of beaver to the San Pedro River (see 'History and status' above), Johnson (2011) found that abundance and species richness of obligate riparian birds were correlated with presence and age of beaver dams even after controlling for covariates such as presence of surface water and density of riparian vegetation. Waterfowl presence in dryland streams is also strongly associated with beaver ponds (Brown *et al.*, 1996; McKinstry *et al.*, 2001). Collectively these studies indicate strong and positive relationships between presence of dryland beaver ponds and the overall abundance and species richness of riparian-associated bird communities.

Considerable conservation attention in the desert South-west is focused on the federally endangered south-western willow flycatcher (*Empidonax traillii extimus*). The flycatcher breeds in dense riparian vegetation, including willow and cottonwood (Finch and Stoleson, 2000). Managers speculate that beaver dam-building activity may benefit flycatcher populations by creating desirable backwater habitat, and beaver reintroduction has been proposed as a restoration technique for flycatcher conservation plans (USFWS, 2002). However, there is also concern that beavers 'damage habitat by removing vegetation' and thus beaver activity may be detrimental to flycatchers (Finch and Stoleson, 2000). This concern has even prompted active beaver removal efforts (Longcore *et al.*, 2007), although no published studies have addressed the issue empirically. Further research is needed to clarify the relationships between beaver activity and habitat for flycatchers and other riparian bird species of concern.

Fish

The effects of beaver dam-building activity on fish populations have received extensive study in temperate streams (Pollock *et al.*, 2003). Within dryland streams, most research addressing beaver–fish relationships has focused on trout species; these studies generally conclude that, consistent with temperate stream findings, trout populations benefit from beaver ponds (Jakober *et al.*, 1998; Talabere, 2002). For example, White and Rahel (2008) showed that beaver ponds could provide important refuge habitat for native cutthroat trout (*Oncorhynchus clarkii utah*) during extended drought conditions. However, beaver ponds also provide excellent conditions for non-native brook trout (*Salvelinus fontinalis*) (Call, 1970). Ultimately the conservation value of beaver ponds for native trout will depend on the trade-off between benefits in habitat for native fish and costs in promotion of undesired non-native species.

Surprisingly little information is available to describe associations between beaver activity and non-salmonid fishes in dryland streams. From a conservation perspective, native fishes of the Colorado River basin are of particular interest: this fish community is both highly endemic and highly endangered, due in part to widespread introductions of predatory non-native fishes. Many of these non-native fishes prefer pool habitats and deep, slow-moving water, and increased abundance of pool habitats has been associated with greater density of non-natives (Rinne and Miller, 2006). This suggests that construction of beaver ponds may enhance the success of non-native fishes, to the detriment of native fish communities.

Other taxa

For several aquatic and riparian animal taxa, including amphibians and invertebrates, searches found no published studies addressing the influence of dryland beaver activity. Available natural history information suggests potential relationships between these groups and beaver pond habitats, but relationships are speculative only. In all cases, particularly the effects of beaver activity on populations of undesired non-native species, research is needed to investigate these relationships empirically.

Amphibians. By constructing perennial wetlands in stream channels that might otherwise go dry – especially as climate change and water withdrawals increase the threat of stream drying – beaver dam-building activity could provide valuable habitat for dryland amphibians. For example, the federally threatened Chiricahua leopard frog (*Lithobates chiricahuensis*), native to Arizona and New Mexico, requires perennial water for successful reproduction. However, creation of rare perennial wetland habitat may also benefit the invasive bullfrog (*Lithobates catesbeianus*), which is widespread throughout the desert South-west.

Bullfrogs are associated with significant impacts on native aquatic communities, including native frogs and fishes; bullfrogs also require perennial water for breeding, and they are generally associated with lentic rather than lotic habitats (Maret *et al.*, 2006), suggesting that beaver ponds could provide ideal habitat. Beaver ponds are believed also to pose a threat to federally endangered arroyo toad (*Anaxyrus californicus)* populations in California because the ponds inundate favourable breeding habitat and support non-native crayfish, African clawed frogs (*Xenopus laevis*), and bullfrogs, all of which prey on the toads (USFWS, 2009).

Invertebrates. Very little is known about relationships between beaver activity and dryland invertebrate communities. Perhaps the most urgent research need is for studies of how beaver ponds may influence crayfish populations. Historically no crayfish were present in the Colorado River basin, but several non-native species (notably *Orconectes virilis* and *Procambarus clarkii*) are now well-established, and continuing spread of these and other species poses an immediate threat to native aquatic communities (Moody and Taylor, 2012).

CONCLUSIONS

Growing interest in using beaver in stream conservation plans has outpaced research on the consequences and effectiveness of this approach in dryland streams. This systematic review of the literature revealed that a majority of studies are small-scale and observational, and in many cases lack the replication needed to draw strong inferences. Many hypotheses are supported only by anecdote or speculation. Despite these limitations, work completed to date indicates that (1) in general, dam-building behaviour is less likely in dryland than in temperate streams, and stream hydrology probably plays an important role. (2) Beaver activity, including both herbivory and dam-building, can be a powerful force in structuring the riparian vegetation community. In some cases beaver herbivory may inhibit regeneration of vulnerable cottonwood populations and/or promote spread of non-native plants. (3) Beaver dams have strong effects on local geomorphology, promoting diverse and perennial wetland habitat; it has been demonstrated that promotion of beaver dams can be an effective technique for restoration of incised stream channels. (4) Beaver ponds have been implicated in promoting the spread of a variety of problematic non-native animal species, but this hypothesis has not been tested.

Better knowledge of the role of beaver in dryland streams and wetlands will improve understanding of the function of these ecosystems and how they are likely to respond to change. In addition, we hope that good science will be available to guide decisions on when management interventions in beaver populations will be most effective, appropriate, and ethical. This review highlights that ecological effects of beaver are wide-ranging and complex, especially in the context of varying management goals and human alteration of dryland riparian ecosystems. As indicated by feedback relationships between beaver activity and environmental conditions, the contemporary ecological landscape does not necessarily represent the full range of potential effects of beaver. Rather than attempting to classify beaver activity as ‘good’ or ‘bad’, from a management perspective the role of this iconic species in the conservation of dryland stream ecosystems could best be viewed as a series of trade-offs involving both challenges and opportunities for conservation.

RESEARCH AGENDA

Results of this systematic review of the literature suggests several research topics that are most in need of further study in dryland streams and wetlands. First, where possible, researchers should seek to quantify the ecological effects of beaver activity. The literature is replete with anecdotal reports of ecological patterns observed in relation to beaver ponds, yet the quantitative data needed for cost-benefit analyses in complicated management decisions are scarce (Shafroth *et al.*, 2010). An example of this quantitative approach is provided by the model to estimate the potential density of beaver dams across a landscape (Macfarlane and Wheaton, 2013). Second, the majority of dryland beaver research has been conducted in high elevation, semi-arid rangeland systems; more study is needed within lowland, arid desert landscapes. In particular, the distribution and density of dam-building behaviour in warm desert streams remains largely unknown. Third, in the face of challenges from increasing drought and demand for water in dryland environments, empirical study of the influence of beaver activity on stream hydrology (including surface water, groundwater, evaporation, and total stream water budget) and hence its potential as a climate adaptation strategy is needed (Wild, 2011). Fourth, the spread of many non-native species poses a significant threat to conservation of dryland stream ecosystems, and research is needed to assess the effects of beaver ponds on populations of non-native fishes, bullfrogs, and crayfishes.

Ongoing beaver reintroductions represent large-scale ecological experiments and provide an unparalleled opportunity to advance scientific knowledge of beaver ecology in dryland streams while concurrently informing on-the-ground restoration practices. We urge scientists and managers to work together to develop clear hypotheses, define robust controls (i.e. Before-After-Control-Impact designs), and implement monitoring programmes where hydrologic, physical and ecological responses are tracked over time. This approach has been implemented in continuing research on the effects of beaver dam structures at Bridge Creek, Oregon, where data collection includes monitoring of stream discharge, groundwater level, channel morphology (gradient, sinuosity, and lateral connectivity), water temperature, abundance of riparian vegetation, and abundance of steelhead trout (*Oncorhynchus mykiss*), associated with numbers and locations of beaver dams over time (Pollock *et al.*, 2012). We cite the need for long-term monitoring of ecosystem responses in order to understand the broader or longer-term success of beaver reintroductions as a restoration strategy.

ACKNOWLEDGEMENTS

Funding for PPG was provided by a University of Washington Top Scholar Graduate Fellowship and by the H. Mason Keeler Endowment for Excellence through the School of Aquatic and Fishery Sciences. JDO was supported in part by an H. Mason Keeler Endowed Professorship and by the Department of Defense - Strategic Environmental Research and Development Program (RC-1724). M. Pollock and two anonymous reviewers provided valuable comments that improved the manuscript. We also thank W. Anderson for enlightening discussion and H. Cooke, P. Gurche, G. Johnson, J. Smith, A. Talabere, and S. White for generously sharing their data.

REFERENCES

Albert S, Trimble T. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. *Ecological Restoration* **18**: 87–92.

Andersen DC, Shafroth PB. 2010. Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology* **3**: 325–338.

Andersen DC, Shafroth PB, Pritekel CM, O'Neill MW. 2011. Managed flood effects on beaver pond habitat in a desert riverine ecosystem, Bill Williams River, Arizona USA. *Wetlands* **31**: 195–206.

Apple LL, Smith SB, Dunder DJ, Baker BB. 1985. The use of beavers for riparian–aquatic habitat restoration of cold desert gully-cut stream systems in southwestern Wyoming USA. In *Investigations on Beavers*, Pilleri G (ed.). Brain Anatomy Institute: Berne, Switzerland; 123–130.

Bailey V. 1931. Mammals of New Mexico. United States Dept. of Agriculture, Bureau of Biological Survey.

Baker BW, Hill EP. 2003. Beaver (*Castor canadensis*). In *Wild Mammals of North America: Biology, Management, and Conservation*, Feldhamer GA, Thompson BC, Chapman JA (eds). John Hopkins University Press: Baltimore, MD; 288–310.

Baker BW, Ducharme HC, Mitchell DC, Stanley TR, Peinetti HR. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological Applications* **15**: 110–118.

Billman EJ, Kreitzer JD, Creighton JC, Habit E, McMillan B, Belk MC. 2013. Habitat enhancement and native fish conservation: can enhancement of channel complexity promote the coexistence of native and introduced fishes? *Environmental Biology of Fishes* **96**: 555–566.

Breck SW, Wilson KR, Andersen DC. 2001. The demographic response of bank-dwelling beavers to flow regulation: a comparison on the Green and Yampa rivers. *Canadian Journal of Zoology* **79**: 1957–1964.

Breck SW, Wilson KR, Andersen DC. 2003. Beaver herbivory and its effect on cottonwood trees: influence of flooding along matched regulated and unregulated rivers. *River Research and Applications* **19**: 43–58.

Brown DJ, Hubert WA, Anderson SH. 1996. Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. *Wetlands* **16**: 127–133.

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.

Call MW. 1970. Beaver pond ecology and beaver–trout relationships in southeastern Wyoming. PhD thesis, University of Wyoming, WY.

Carrillo C, Bergman D, Taylor J, Nolte D, Viehoever P, Disney M. 2009. *An overview of historical beaver management in Arizona*. USDA National Wildlife Research Center – Staff Publications, Fort Collins, CO.

CEC (Commission for Environmental Cooperation). 1997. Ecological regions of North America. Commission for Environmental Cooperation, Montreal, Quebec.

Cluer B, Thorne C. 2012. A stream evolution model integrating habitat and ecosystem benefits. *River Research and Applications*. DOI: 10.1002/rra.2631.

Coleman RL, Dahm CN. 1990. Stream geomorphology: effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society* **9**: 293–302.

Cooke HA, Zack S. 2008. Influence of beaver dam density on riparian areas and riparian birds in shrubsteppe of Wyoming. *Western North American Naturalist* **68**: 365–373.

Cooper DJ, Dickens J, Hobbs NT, Christensen L, Landrum L. 2006. Hydrologic, geomorphic and climatic processes controlling willow establishment in a montane ecosystem. *Hydrological Processes* **20**: 1845–1864.

Crawford CS, Umbreit NE. 1999. Restoration and monitoring in the Middle Rio Grande Bosque: current status of flood pulse related efforts. In *Rio Grande Ecosystems: Linking Land, Water, and People*, Finch DM, Whitney JC, Kelly JF, Loftin SR (eds). USDA Forest Service: Albuquerque, NM; 151–163.

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

Depue JE, Ben-David M. 2010. River otter latrine site selection in arid habitats of western Colorado, USA. *Journal of Wildlife Management* **74**: 1763–1767.

DeVries P, Fetherston KL, Vitale A, Madsen S. 2012. Emulating riverine landscape controls of beaver in stream restoration. *Fisheries* **37**: 246–255.

Ffolliott PF, Clary WP, Larson FR. 1976. Observations of beaver activity in an extreme environment. *The Southwestern Naturalist* **21**: 131–133.

Finch DM, Stoleson SH. 2000. Status, ecology, and conservation of the southwestern willow flycatcher. USDA Forest Service, Rocky Mountain Research Station, Odgen, UT.

Fredlake M. 1997. Re-establishment of North American beaver (*Castor canadensis*) into the San Pedro Riparian National Conservation Area. US Bureau of Land Management, Environmental Assessment EA no. AZ-060–97-004, Tucson, AZ.

Frey JK, Malaney JL. 2009. Decline of the meadow jumping mouse (*Zapus hudsonius luteus*) in two mountain ranges in New Mexico. *The Southwestern Naturalist* **54**: 31–44.

Gallo-Reynoso J-P, Suárez-Gracida G, Cabrera-Santiago H, Coria-Galindo E, Egido-Villarreal J, Ortiz LC. 2002. Status of beavers (*Castor canadensis frondator*) in Rio Bavispe, Sonora, Mexico. *The Southwestern Naturalist* **47**: 501–504.

Gangloff MM. 2013. Taxonomic and ecological tradeoffs associated with small dam removals: Editorial. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 475–480.

Hall F. 2005. Emigrant Creek cattle allotment: lessons from 30 years of photomonitoring. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Harper BJ. 2001. The ecological role of beavers (*Castor canadensis*) in a Southwestern desert stream. MS thesis, University of Nevada, NV.

Hoffmeister DF. 1986. *Mammals of Arizona*. University of Arizona: Tucson, AZ.

Jakober MJ, McMahon TE, Thurow RF, Clancy CG. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. *Transactions of the American Fisheries Society* **127**: 223–235.

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

Johnson G. 2011. Bird abundance and richness in a desert riparian area following beaver re-introduction. PhD thesis, University of Arizona, AZ.

Johnston CA, Naiman RJ. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* **171**: 1617–1621.

Kimball BA, Perry KR. 2008. Manipulating beaver (*Castor canadensis*) feeding responses to invasive tamarisk (*Tamarix* spp.). *Journal of Chemical Ecology* **34**: 1050–1056.

Kindschy RR. 1985. Response of red willow to beaver use in southeastern Oregon. *The Journal of Wildlife Management* **49**: 26–28.

Knopf FL, Johnson RR, Rich T, Samson FB, Szaro RC. 1988. Conservation of riparian ecosystems in the United States. *The Wilson Bulletin* **100**: 272–284.

Lanman RB, Perryman H, Dolman B, James CD, Osborn S. 2012. The historical range of beaver in the Sierra Nevada: a review of the evidence. *California Fish and Game* **98**: 65–80.

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

Lesica P, Miles S. 1999. Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Canadian Journal of Botany* **77**: 1077–1083.

Lesica P, Miles S. 2004. Beavers indirectly enhance the growth of Russian olive and tamarisk along eastern Montana rivers. *Western North American Naturalist* **64**: 93–100.

Levick LR, Goodrich DC, Hernandez M, Fonseca J, Semmens DJ, Stromberg JC, Tluczek M, Leidy RA, Scianni M, Guertin DP. 2008. The ecological and hydrological significance of ephemeral and intermittent streams in the arid and semi-arid American southwest. US Environmental Protection Agency, Office of Research and Development and USDA/ARS Southwest Watershed Research Center.

Lind JM. 2002. A habitat suitability model for beavers (*Castor canadensis*) in an arid environment using Geographic Information Systems (GIS). MS thesis, Central Washington University, WA.

Longcore T, Rich C, Müller-Schwarze D. 2007. Management by assertion: beavers and songbirds at Lake Skinner (Riverside County, California). *Environmental Management* **39**: 460–471.

Lowry MM. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. MS thesis, Oregon State University, OR.

MacFarlane WW, Wheaton JM. 2013. Modeling the capacity of riverscapes to support dam-building beaver – case study:

Escalante River Watershed. Ecogeomorphology and Topographic Analysis Lab, Utah State University, Logan, UT.

Maret TJ, Parker M, Fannin TE. 1987. The effect of beaver ponds on the nonpoint source water-quality of a stream in southwestern Wyoming. *Water Research* **21**: 263–268.

Maret TJ, Snyder JD, Collins JP. 2006. Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biological Conservation* **127**: 129–138.

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

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

McGinley MA, Whitham TG. 1985. Central place foraging by beavers (*Castor canadensis*) – a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). *Oecologia* **66**: 558–562.

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

McKinstry MC, Caffrey P, Anderson SH. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of American Water Resources Association* **37**: 1571–1577.

MEA (Millennium Ecosystem Assessment). 2005. Dryland systems. In *Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment*, Hassan RM, Scholes RJ, Ash N (eds). Island Press: Washington, DC; 623–662.

Medin DE, Clary WP. 1990. Bird populations in and adjacent to a beaver pond ecosystem in Idaho. USDA Forest Service, Ogden, UT.

Medin DE, Clary WP. 1991. Small mammals of a beaver pond ecosystem and adjacent riparian habitat in Idaho. USDA Forest Service, Ogden, UT.

Mellink E, Luévano J. 1998. Status of beavers (*Castor canadensis*) in Valle de Mexicali, Mexico. *Bulletin Southern California Academy of Sciences* **97**: 115–120.

Moody EK, Taylor CA. 2012. Red swamp crayfish (*Procambarus clarkii*) discovered in the San Pedro River, Arizona: a new invader in a threatened ecosystem. *Southwestern Naturalist* **57**: 339–340.

Mortenson SG, Weisberg PJ, Ralston BE. 2008. Do beavers promote the invasion of non-native *Tamarix* in the Grand Canyon riparian zone? *Wetlands* **28**: 666–675.

Naiman RJ, Melillo JM, Hobbie JE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* **67**: 1254–1269.

Nolet BA, Rosell F. 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biological Conservation* **83**: 165–173.

Nolte DL, Lutman MW, Bergman DL, Arjo WM, Perry KR. 2003. Feasibility of non-lethal approaches to protect riparian plants from foraging beavers in North America. USDA National Wildlife Research Center, Fort Collins, CO.

ODFW (Oregon Department of Fish and Wildlife). 1997. ODFW Aquatic Inventories Project stream habitat distribution coverages. Oregon Department of Fish and Wildlife, Corvallis, OR.

Ogden PS. 1971. *Peter Skene Ogden's Snake Country Journals, 1827–28 and 1828–29*, Vol **28**. Hudson's Bay Record Society: London.

Patterson BD, Ceballos G, Sechrest W, Tognelli MF, Brooks T, Luna L, Ortega P, Salazar I, Young BE. 2007. Digital distribution maps of the mammals of the Western Hemisphere, version 3.0. NatureServe, Arlington, VA.

Pattie JO. 1905. *The personal narrative of James O. Pattie of Kentucky*. The Arthur H. Clark Company: Cleveland, OH.

Pollock MM, Heim M, Werner D. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. In *The Ecology and Management of Wood in World Rivers*, Gregory SV, Boyer K, Gurnell A (eds). American Fisheries Society: Bethesda, MD; 213–233.

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, Wheaton JM, Bouwes N, Volk C, Weber N, Jordan CE. 2012. Working with beaver to restore salmon habitat in the Bridge Creek Intensively Monitored Watershed: design rationale and hypotheses. National Oceanic and Atmospheric Administration, Seattle, WA.

Pool TK, Olden JD, Whittier JB, Paukert CP. 2010. Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 1791–1807.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rinne JN, Miller D. 2006. Hydrology, geomorphology and management: implications for sustainability of native southwestern fishes. *Reviews in Fisheries Science* **14**: 91–110.

Rosell F, Bozser O, Collen P, Parker H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* **35**: 248–276.

Sabo JL, Sinha T, Bowling LC, Schoups GH, Wallender WW, Campana ME, Cherkauer KA, Fuller PL, Graf WL, Hopmans JW. 2010. Reclaiming freshwater sustainability in the Cadillac Desert. *Proceedings of the National Academy of Sciences* **107**: 21263–21269.

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, *et al*. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* **316**: 1181–1184.

Shafroth PB, Wilcox AC, Lytle DA, Hickey JT, Andersen DC, Beauchamp VB, Hautzinger A, McMullen LE, Warner A. 2010. Ecosystem effects of environmental flows: modelling and experimental floods in a dryland river. *Freshwater Biology* **55**: 68–85.

Stromberg JC. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments* **49**: 17–34.

Stromberg JC, Tiller R, Richter B. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: The San Pedro, Arizona. *Ecological Applications* **6**: 113–131.

Talabere AG. 2002. Influence of water temperature and beaver ponds on Lahontan cutthroat trout in a high-desert stream, southeastern Oregon. MS thesis, Oregon State University, OR.

Tallent N, Nash M, Cross CL, Walker LR. 2011. Patterns in shoreline vegetation and soils around Lake Mohave, Nevada and Arizona: implications for management. *Western North American Naturalist* **71**: 374–387.

Tappe DT. 1942. The status of beavers in California. State of California, Department of Natural Resources, Division of Fish and Game, Sacramento, CA.

Trabucco A, Zomer RJ. 2009. Global aridity index (Global-Aridity) and global potential evapo-transpiration (Global-PET) geospatial database. CIGAR Consortium for Spatial Information. http://csi.cgiar.org/aridity/index.asp/ [23 October 2012]

USFWS (US Fish and Wildlife Service). 2002. Southwestern willow flycatcher recovery plan. US Fish and Wildlife Service, Albuquerque, NM.

USFWS (US Fish and Wildlife Service). 2009. Arroyo toad (*Bufo californicus*), 5-year review: summary and evaluation. US Fish and Wildlife Service, Ventura, CA.

USGS National Gap Analysis Program. 2007. Digital animal-habitat models for the Southwestern United States. New Mexico Cooperative Fish and Wildlife Research Unit, New Mexico State University, Las Cruces, NM.

Webb RH, Leake SA. 2006. Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States. *Journal of Hydrology* **320**: 302–323.

Weber DJ. 1971. *The Taos Trappers: the Fur Trade in the Far Southwest, 1540–1846*. University of Oklahoma Press: Norman, OK.

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

White SM, Rahel FJ. 2008. Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. *Transactions of the American Fisheries Society* **137**: 881–894.

Wild C. 2011. Beaver as a climate change adaptation tool: concepts and priority sites in New Mexico. Seventh Generation Institute, Santa Fe, NM.

Zedler JB, Kercher S. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Criticial Reviews in Plant Science* **23**: 431–452.

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