Influences of beaver (*Castor canadensis*) activity on ecology and fish assemblages of dryland streams

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Abstract

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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. However, despite growing interest in reintroduction programs, surprisingly little is known about the ecology of beaver in dryland streams, and science to guide management decisions is often fragmented and incomplete. In my first chapter I systematically reviewed 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. 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 lack empirical evidence, especially from dryland streams. One of the most important areas of uncertainty identified by this review is the influence of beaver activity on the proliferation and success of non-native species. Streams of the American Southwest support a highly endangered native fish fauna and abundant non-native fishes, and in my second chapter I investigated the hypothesis that beaver ponds in this region may lead to fish assemblages dominated by non-native species. I sampled fish assemblages within beaver ponds and within unimpounded stream reaches in the free-flowing upper Verde River basin, central Arizona. I found that although non-native fishes consistently outnumbered native species, this dominance was greater in pond than in stream assemblages. Multivariate analysis indicated that fish assemblages in beaver ponds were distinct from those in stream reaches, in both mainstem and tributary locations. Few native species were recorded within ponds, while some non-natives, notably green sunfish (*Lepomis cyanellus*) and western mosquitofish (*Gambusia affinis*) were abundant within ponds. Overall, this study provides evidence that, relative to unimpounded stream habitat, beaver ponds in the Verde River basin support abundant small-bodied non-native fishes, which could have negative impacts on co-occurring native fish populations.

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CHAPTER 1

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 programs, 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 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, we urge managers and conservation organizations to implement monitoring programs and consider the full range of possible ecological effects and trade-offs.

Keywords

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 (*C. fiber*) have rebounded to inhabit much of their former geographic range. Hunting restrictions 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 cause 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 (e.g., 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, due 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 (Fig. 1.1). 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 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 comparable species diversity to upland areas (Knopf *et al.*, 1988). Water demand to support growing urban centers 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 streamflow for the desert Southwest (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 anthropogenic 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). Beaver 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) synthesize published research related to the ecology and management of beaver in drylands; (2) highlight the ways in which beaver ecological function may differ between arid and semi-arid ('dryland') and humid ('temperate') regions; and (3) 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) in order 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, paleontology, epidemiology, or providing no information beyond beaver presence, were excluded); (3) study was conducted in a dryland region (see Fig. 1.1); 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 systematically locate all such sources. 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, in order 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. Finally, a similar opportunistic search for density reports from temperate streams provided a comparison to 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 allowed for 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 (see Fig. 1.1). Survey segment length and beaver dam density were compared between dryland and temperate streams using Student's *t* test. The analysis was restricted to only 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 nineteenth 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 Southwest 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 nineteenth 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 twentieth 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 twentieth century (Johnson, 2011). Around the same time, likely 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 Southwest (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). Ongoing 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 (Fig. 1.1). Establishing whether beaver were historically present in a region can play an important role in decisions about beaver management (e.g., 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; Fig. 1.1) 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 (e.g., 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.*, 2012); 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). Additionally, 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 (e.g., Hoffmeister, 1986; Demmer and Beschta, 2008). Development of canal networks in arid regions like 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 (USGS) broadly estimates range-wide potential beaver habitat within the southwestern 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 likely 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 (e.g., 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 due 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 anthropogenic 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 via increased availability of stable riparian habitat (Hoffmeister, 1986). Additionally, 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 likely 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 favorable 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 (via controlled floods; Fig. 1.2) 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.*, 2012). Because of its ecological importance, this review focuses primarily on beaver dam-building in streams. However, not all beaver construct dams: along lakes and large rivers, for example, beaver dig bank dens and make use of the existing deep water (Mortenson *et al.*, 2008). A relatively large proportion of dryland beaver are bank-dwellers rather than dam-builders (e.g., 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 watersheds 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 (Fig. 1.1). 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 beaver 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 in order 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, beaver 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.

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 (Fig. 1.3a). 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; n = 44) and temperate stream (1.50 dams/km; n = 329) segments (Student's *t*-test, *p* = 0.117, df = 62; Fig. 1.3b), despite a significantly greater mean survey length for dryland (16.2 km) than for temperate (9.0 km) steam 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) relative to a more homogenous distribution in temperate streams (Johnston and Naiman, 1990). Additional research on beaver dam abundance in dryland streams is needed to better describe 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; additionally, 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 Wyoming, for example, most beaver dams were found to be between 5-19 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 discharge and dam failure, Andersen and Shafroth (2010) found that flood pulses of about 60 m^3/s (relative to base flow of ~1 m^3/s) 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 flood pulse – but ‘significant’ damage to beaver dams was observed at discharge as low as 5 m^3/s, 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.*, 2012).

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 like 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 function 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 streamflow 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 (Seager *et al.*, 2007) is a primary conservation concern for many dryland streams (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 little data is 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 is available to evaluate downstream effects on discharge. Additionally, 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 (e.g., DeVries *et al.*, 2012). However, in many dryland river systems, large peak flows are important to 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 due 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 southeast Oregon stream were consistently slightly warmer within beaver ponds than in neighboring 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. Interestingly, 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 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 (e.g., 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); additionally, 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 (e.g., 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 percent willow cover, and they suggest 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, relative to 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 a set of 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. Additionally, 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 (e.g., 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 (e.g., Mortenson *et al.*, 2008). There is some evidence that beaver herbivory can promote the spread of non-native plants like 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 find 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 for 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 even greater within dryland streams, where reduced water table due to 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 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 favorable for willow establishment (e.g., Cooper *et al.*, 2006). Several authors have observed that, following the return of beaver to semi-arid streams, mud bars deposited behind dams or 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 likely 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 Southwest, 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 suggest that otter reintroduction efforts should focus on locations where beaver are present. Frey and Malaney (2009) suggest that beaver ponds likely provide ideal riparian habitat for the rare meadow jumping mouse (*Zapas 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 adjacent unimpounded stream.

Birds

Dryland cottonwood-willow riparian forests support a famously 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 Southwest is focused on the federally endangered southwestern 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 relations 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*) (e.g., Call, 1970). Ultimately the conservation value of beaver ponds for native trout will depend on the tradeoff 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 (*Rana chiricahua*), native to Arizona and New Mexico, requires perennial water for successful reproduction. However, creation of rare perennial wetland habitat likely also benefits the invasive bullfrog (*Lithobates catesbeianus*), which is widespread throughout the desert Southwest. Bullfrogs are associated with significant impacts to 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 provide ideal habitat. Additionally, beaver ponds are believed to pose a threat to federally endangered arroyo toad (*Bufo californicus)* populations in California because the ponds inundate favorable 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 employing beaver in stream conservation plans has outpaced research on the consequences and effectiveness of this approach in dryland streams. Our 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 behavior is less likely in dryland than in temperate streams, and stream hydrology likely plays a large 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. Additionally, we hope that good science will be available to guide decisions about 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 anthropogenic 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 is scarce (e.g., Shafroth *et al.*, 2010). An example of this quantitative approach is provided by Macfarlane and Wheaton's (2013) model to estimate the potential density of beaver dams across a landscape. 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 behavior in warm desert streams remains largely unknown. Third, in 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 scientist and managers to work together to develop clear hypotheses, define robust controls (i.e., Before-After-Control-Impact designs), and implement monitoring programs where hydrologic, physical and ecological responses are tracked over time. This approach has been implemented in ongoing 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, and 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.

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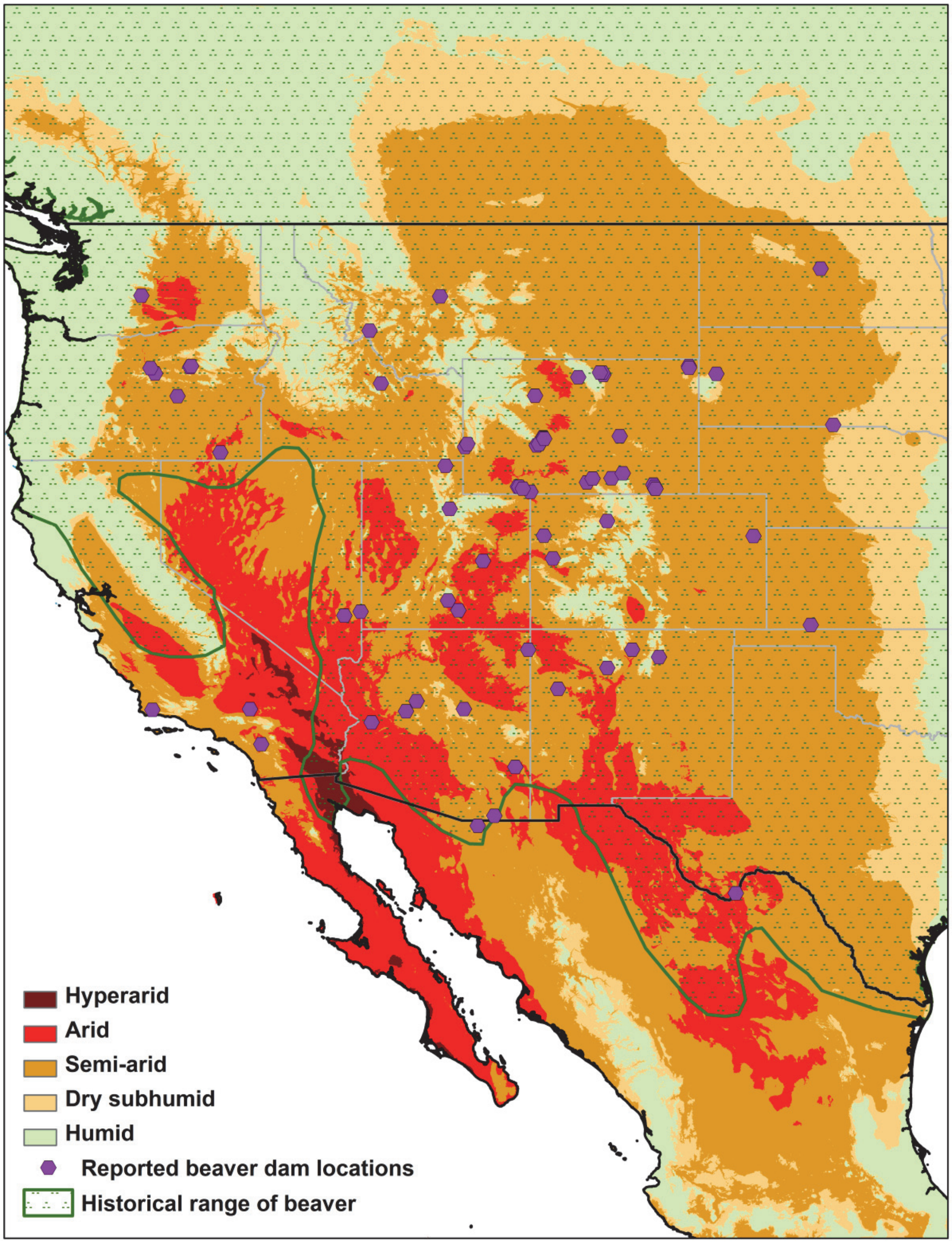

Figure 1.1

Approximate historical range of North American beaver (shaded area) in western North America and reported locations of beaver dams (triangles) 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).

Figure 1.2

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

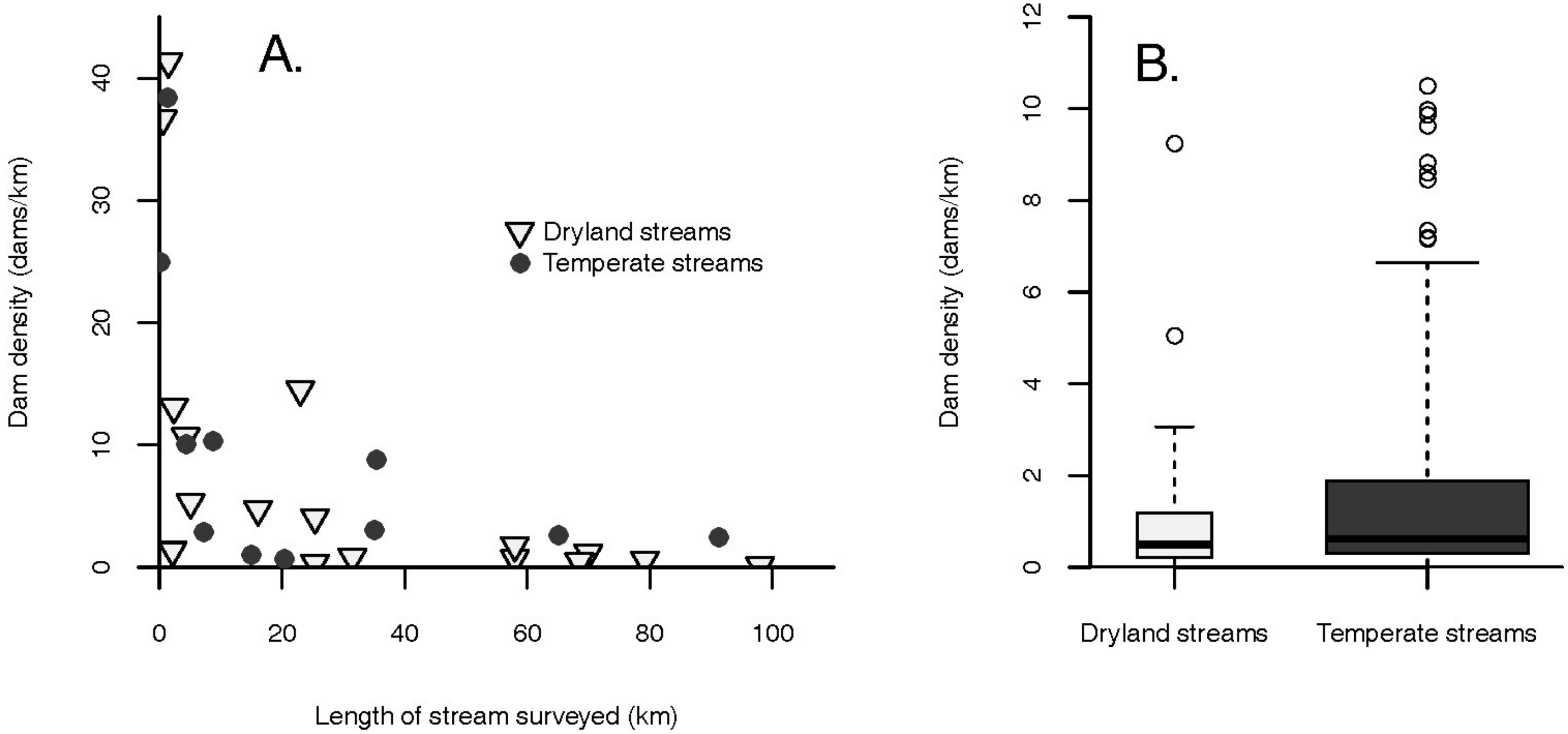

Figure 1.3

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. Open triangles indicate densities from dryland streams and dark circles represent temperate streams. Not shown is an extreme dryland value of 25.6 dams/km 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).

CHAPTER 2

BEAVER DAMS SHIFT DESERT FISH ASSEMBLAGES TOWARD DOMINANCE BY NON-NATIVE SPECIES (VERDE RIVER, ARIZONA, USA)

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Abstract

The reintroduction of beaver (*Castor canadensis*) into arid and semi-arid rivers is receiving increasing management and conservation attention in recent years, yet very little is known about native vs. non-native fish occupancy in beaver pond habitats. Streams of the American Southwest support a highly endemic, highly endangered native fish fauna and abundant non-native fishes, and here we investigated the hypothesis that beaver ponds in this region may lead to fish assemblages dominated by non-native species. We sampled fish assemblages within beaver ponds and within unimpounded lotic stream reaches in the mainstem and in tributaries of the free-flowing upper Verde River, central Arizona. Non-native fishes consistently outnumbered native species, and this dominance was greater in pond than in stream assemblages. Few native species were recorded within ponds. Multivariate analysis indicated that fish assemblages in beaver ponds were distinct from those in stream reaches, in both mainstem and tributary locations. Individual species driving this distinction included abundant non-native green sunfish (*Lepomis cyanellus*) and western mosquitofish (*Gambusia affinis*) in pond sites, and native desert sucker (*Catostomus clarkii)* in streams. Overall, this study provides the first evidence that, relative to unimpounded stream habitat, beaver ponds in the Verde River basin support abundant small-bodied non-native fishes, which could have negative impacts on co-occurring native fish populations.

Keywords

Castor canadensis; non-native species; desert fishes; assemblage structure; impoundments; microhabitat use.

Introduction

Management of freshwater ecosystems takes place at the intersection of numerous ecological and social trends, which can create novel challenges for natural resource conservation and policy. Recent decades have witnessed growing interest in employing or mimicking the remarkable engineering power of beaver (*Castor canadensis* and *C. fiber*) in stream restoration efforts (Pollock et al. 2007; DeVries et al. 2012). After widespread extirpations of North American beaver during several centuries of intense fur trade, hunting restrictions combined with deliberate reintroductions contributed to successful beaver recovery (Pollock et al. 2003). However, restoration of beaver populations also raises new questions for ecosystem management, especially within arid and semi-arid environments (Gibson and Olden, in press): for example, the introduction and continuing spread of invasive fishes pose a substantial threat to freshwater ecosystems (Cucherousset & Olden 2011), and it is unclear how native and non-native fish species are using beaver pond habitat, and thus how contemporary fish assemblages might respond to changes in the abundance of beaver ponds as beaver return to more of their historical range.

Beaver are widely recognized as ecosystem engineers with major influence on the structure of aquatic ecosystems. Beaver dams create distinct lentic habitat patches within the lotic stream corridor; these beaver ponds promote landscape heterogeneity and alter stream hydrology, sediment dynamics, nutrient cycling, and aquatic and riparian biotic communities (Rosell et al. 2005). Previous research has shown that beaver pond habitats can have substantial consequences for stream fish populations: individual species, especially salmonids, have shown higher growth, survival, or abundance within beaver ponds relative to unimpounded stream habitat (Murphy et al. 1989), and some species preferentially select beaver pond habitats during certain life stages or environmental conditions (e.g., Schlosser 1995). In addition to upstream pond habitat, high velocity habitat downstream of dams may favor fluvial specialists (Smith & Mather 2013). Beaver ponds can influence composition of fish assemblages at scales ranging from individual ponds (Snodgrass & Meffe 1999) to entire drainages (Schlosser & Kallemeyn 2000).

Results demonstrating benefits of beaver dams for salmonid fishes (e.g., Pollock et al. 2004) tend to lead to the assumption that beaver dams will improve habitat for native fish. However, this remains an untested hypothesis for many systems (Kemp et al. 2012), especially in the context of invasion by non-native fish. In southern Chile, where both beaver and rainbow trout (*Oncorhynchus mykiss*) are non-native, the density of native puye (*Galaxias maculatus*) was found to be substantially higher in stream reaches with beaver dams, regardless of whether trout were present (Moorman et al. 2009). Habitat heterogeneity created by beaver dams and backwater habitat along the Provo River (Utah) supported several species of native fish in a system otherwise dominated by non-native brown trout (*Salmo trutta*) (Billman et al. 2012). Rates of beaver dam passage also differed between native and non-native trouts in a Utah stream (Lokteff et al. 2013). These studies reveal that beaver dams can have complex effects on native and non-native fish, but their influence on the overall structure of contemporary fish assemblages containing both native and non-native species is unknown.

Community dynamics between native and non-native fishes are particularly relevant to conservation of native aquatic communities in the American desert Southwest. The native fish fauna of the lower Colorado River Basin (CRB) is both highly endemic and highly endangered: three-quarters of the native species pool in Arizona, for example, are federally listed under the US Endangered Species Act (Minckley & Deacon 1968; Turner & List 2007). Non-native fishes pose a primary threat to the persistence of the native fish fauna. Numerous species have been introduced to the CRB, and spread of non-native fish has been accompanied by dramatic declines of native fish populations (Olden & Poff 2005; Rinne & Miller 2006). Predation by non-native fish on native species, accompanied by competition and indirect effects of predation risk, is considered the primary mechanism for the widespread replacement of native fish (Minckley et al. 2003). Numerous studies have documented direct predation, agonistic interactions, and shifts in resource use by native fishes in response to non-natives, including both large-bodied predators and abundant small insectivores (Cucherousset & Olden 2011). Non-native crayfishes (primarily *Orconectes virilis* and *Procambarus clarkii*) have also been introduced and spread throughout the CRB, although historically crayfish were entirely absent from the basin (Martinez 2012). Effective management for conservation of native fish requires understanding how habitat and environmental features can influence their coexistence with non-native fish and crayfish.

Very little is known of the influence of beaver dams on fish assemblages in the CRB (Gibson and Olden, in press). Historically beaver dams were abundant in parts of the CRB (Carrillo et al. 2009), one piece of the mosaic of aquatic habitats available to and presumably exploited by native fishes. Current reintroductions of extirpated beaver populations are usually motivated by growing recognition of the potential value of beaver engineering for achieving conservation goals (e.g., Fredlake 1997). However, within the contemporary landscape, promotion of beaver dams may also have unexpected consequences: natural history and previous studies suggest that the habitat conditions created by beaver ponds are likely to benefit some non-native fishes in the CRB. Many of the common non-native species are associated with pool habitats and deep, slow-moving water (Olden et al. 2006; Rinne & Miller 2006). In a long-term study of fish assemblage in the Gila River basin (New Mexico), higher densities of non-native fish were associated with low flows and greater abundance of pools (Propst et al. 2008). Rinne and Miller (2006) conclude that deep (>2m) pools provide optimum habitat for non-native predatory fishes such as bass and catfishes, while lack of pools reduces their abundance. Additionally, beaver ponds may affect success of non-native fishes by mitigating the effects of extreme high and low flows. Deep pools behind beaver dams may promote survival – especially of large-bodied species – through harsh drought conditions, while the physical beaver dam structure could provide immediate refuge from floods. Although these hydrological effects of beaver dams would apply to native and non-native fishes alike, non-native fishes lack an evolutionary history with the region's highly variable streamflow (Olden et al. 2006), and thus non-native species might benefit disproportionately from mitigation of these hydrological disturbances.

The strong impacts of non-native fishes on native populations and the potential for beaver ponds to promote non-native species suggest the general hypothesis that beaver dams in the CRB may lead to fish assemblages dominated by non-native species, with potential negative effects on native fishes. In this study we investigate how beaver ponds influence the structure of mixed native and non-native fish assemblages in the Verde River basin in Arizona. Specifically, we address the following questions: (1) does fish assemblage structure differ between beaver pond and stream habitat types? How do native and non-native species differentially occupy these habitats? (2) Do fish assemblage structure and the influence of beaver ponds differ between the mainstem river and its tributary streams?

Methods

Study Area

The Verde River watershed, a semi-arid tributary of the Lower Colorado River basin, drains 17,212 km^2 of central Arizona (Fig. 2.1). The perennial mainstem river runs approximately 300 km from its headwaters in the Big Chino Wash (elevation = 1,325 m) to its confluence with the Salt River north of Phoenix, AZ (elevation = 402 m), while numerous perennial tributaries contribute runoff from the southwestern edge of the Colorado Plateau (Bonar et al. 2004). The study region included stream reaches in the upper Verde River mainstem and in five major tributaries (Fig. 2.1). Unusually for perennial rivers in the desert Southwest, the upper Verde River is largely free-flowing, although several diversion dams and small impoundments are present in the upper watershed, primarily on tributaries (Medina & Neary 2012). Hydrology in the upper Verde River mainstem is characterized by relatively steady, spring-fed base flow, with high flow events that vary in magnitude and timing among years in response to storm runoff. Mean annual streamflow in the upper mainstem is 1.2 m^3/s; streamflow in the four perennial and one ephemeral (Dry Beaver Creek) tributaries examined in this study ranges from 0.9 – 2.3 m^3/s and includes more snowmelt runoff. Development is limited within the basin, and primary anthropogenic disturbances are livestock grazing and reduction in base flows as a result of groundwater withdrawals (Blasch et al. 2006). Beaver are common throughout the watershed, but beaver dam-building activity is more limited (J. Agyagos, pers. comm.; P. Gibson, unpublished data).

The Verde River watershed, especially the headwaters of the mainstem, is an important site for conservation of native fish in Arizona (Turner & List 2007; Pool et al. 2013). At least twelve fish species are native to the basin, but the fish assemblage is changing rapidly, and currently only five native species are present (Medina & Neary 2012). Many of the species historically present in the Verde have been absent for decades, but federally endangered spikedace (*Meda fulgida*) was last documented in the basin in 1997, and its current status in the basin is uncertain. Two other small-bodied native species, longfin dace (*Agosia chrysogaster*) and speckled dace *(Rhinicthys osculus*) have become rare in the Verde River mainstem, and native roundtail chub (*Gila robusta*) has been proposed for federal listing. Numerous non-native fishes are present in the basin, including several species of centrarchids, ictalurid catfishes, and minnows (Rinne 2012; Table 2.1). Fish community composition of the Verde River varies widely among years, but non-native fish have generally outnumbered natives for the past two decades. Management goals for fish assemblages of the upper Verde River include maintenance of current native populations and reintroduction of extirpated species, including spikedace (Rinne 2012).

Site selection

We surveyed fish assemblages in two different habitat types within the Verde River mainstem and five tributaries: 1) beaver ponds formed by dams across the main stream channel (representing the most common position of dams in this system); and 2) stream reaches unmodified by beaver dams. Focusing on stream segments with a high probability of beaver dam presence (as suggested by regional managers), continuous longitudinal census of beaver dams on Verde watershed streams in April 2012 located 37 functional (i.e., impounding water) beaver dams on the mainstem and tributaries (data available at http://dx.doi.org/10.6084/m9.figshare.867703). The highest density of beaver dams and the largest and most complex ponds were located on the mainstem (23 dams in 24.0 km of stream), while dams on the tributaries were less common and usually smaller (14 dams in 40.4 km). Pond sampling sites (mainstem n = 6; each tributary n = 0-3) were designated proportionally to their abundance within a given stream; fish sampling occurred in the first 100 m upstream of each dam (all ponds extended beyond 100 m, with the exception of a single 90 m pond site). Stream sampling sites (mainstem n = 10; each tributary n = 3-4) were distributed throughout the stream segments that had been surveyed for beaver dams, at distances ranging from 1 – 2,650 m from the nearest dam (where dams were present). At each stream site, we designated a sampling reach approximately 100 m long (range = 80 – 115 m) which contained representative segments of pool, riffle, and run macrohabitat, as available.

Sampling methods

We sampled 26 stream and 12 pond sites during late spring (May - June) 2012. We isolated the ~100 m stream reaches with block nets (4mm bar mesh) and sampled with double-pass removal backpack electrofishing (Smith-Root Model L-24*,* 180-320 V, 30 Hz*),* where 90% of fish and 100% of species were caught after two passes relative to three-pass removal of selected sites*.* A standard effort level of 1200 total seconds (st. dev. = 162 sec.) was adjusted as needed to account for length and variable habitat complexity within the reach. All fish captured were identified, enumerated, and released alive after electrofishing was complete. In rare instances, fish observed but not captured (i.e., misses or large schools of small fish) were included when the fish could be confidently identified. Pond sites were typically too large, deep, and complex to be effectively sampled with backpacking electrofishing, and too remote for use of boat electrofishing; instead, we followed previous studies (e.g., Smith & Mather 2013) in using a standardized combination of baited minnow traps (12 minnow traps and 12 crayfish traps set for 12 h at 0.2 – 1.5 m depth), trammel nets (3 nets, 9.1 x 1.8 m, 0.3 m wall size, 51 mm mesh size, set for 3 h), seine hauls (4 mm mesh, 5 hauls sampling approximately 60 m^2 total), and snorkel survey (1 person snorkeled full pond perimeter plus one transect down pond center line; visibility was generally excellent in tributary sites but limited in mainstem sites), in order to achieve an accurate representation of species occurrence and relative abundance.

Crayfish were also surveyed at all sites. In pond sites, all crayfish captured in seine hauls, minnow traps, and crayfish traps were counted; we calculated crayfish CPUE for each gear type, as well as the sum total of crayfish caught across all gears at each site. In stream sites, we used timed D-net (0.5

mm mesh) sweeps to sample crayfish density along with other benthic macroinvertebrates. The crayfish sample for each stream site consisted of 10 point samples, covering a total surface area of 4 m^2 and total sampling effort time of 150 seconds, in standardized microhabitats from both the upstream and downstream ends of the sampling reach. All crayfish with carapace length ≥ 3 mm and ≤ 30 mm (larger crayfish were not sampled effectively with this methodology) were sorted from the sample and counted.

Statistical analysis

Sampling effort was constant among all pond sites and among all stream sites, and thus species abundance for each site (i.e., CPUE) was calculated as the total number of individuals of that species captured at the site across all gear types. Raw abundances were log-transformed to reduce the influence of highly abundant species and then standardized to relative abundance at each site. Using relative rather than raw abundances allowed us to make comparisons between pond and stream sampling sites despite different sampling methods. To examine differences in relative abundance of individual species between pond and stream sites, we calculated the mean of pond-stream pairwise differences in relative abundance for each species (separately for mainstem and tributary sites). Within pond sites and within stream sites we also tested for correlations between abundance of crayfish and abundance of smallmouth bass (*Micropterus dolomieu*) and of all non-native fishes combined (abundances log-transformed).

Patterns in multivariate fish assemblage structure were examined using principal coordinate analysis (PCoA; Legendre & Legendre 1998) of species relative abundances at each site. Notably, ordinations using presence-absence data produced qualitatively similar results. PCoA is similar to principal component analysis (PCA), but generalized to allow the use of any ecologically relevant dissimilarity measure. For this analysis we used Bray-Curtis distance (which excludes double absences and which is widely used for community abundance data) and corrected for negative eigenvalues. Rare species (present in ≤ 2 sites), which can have a disproportionate effect on multivariate results (Gauch 1982), were removed from this analysis. Statistical significance of the PCoA axes was determined according to the broken stick rule ($P < 0.05$; Legendre & Legendre 1998). Raw species correlations with the axes were overlaid as vectors on the ordination plots in order to examine the contribution of individual species to observed patterns in community data.

We formally assessed differences between pond and stream fish assemblage using permutational multivariate analysis of variance (perMANOVA; Anderson 2001). This approach identifies differences in group mean (i.e., location in PCoA ordination space) or differences in group variability (i.e., spread in ordination space), or a combination of the two; therefore, we also tested for homogeneity of multivariate dispersion between groups (Anderson 2006), a multivariate analogue to the univariate Leven's test, in order to locate the source of any significant differences identified by the perMANOVA. This dispersion test computes an *F*-statistic to compare the average distance from an individual sample to the group centroid defined in the PCoA space of a chosen dissimilarity measure (in our case, Bray–Curtis dissimilarity). Both of these multivariate tests estimate statistical significance (*P* value) by permuting the appropriate least-squares residuals. All analyses were performed using R version 2.13.1 (R Development Core Team 2011), using the *vegan* package 2.0-2 for multivariate community analysis (Oksanen et al. 2011).

Results

Species occurrence and abundance

During our study we recorded >12,500 individual fish from 4 native and 9 non-native species (Table 2.1). Smallmouth bass was the most frequent and abundant non-native fish, followed by green sunfish (*Lepomis cyanellus*), western mosquitofish (*Gambusia affinis*), and red shiner (*Cyprinella lutrensis*); the most frequent native species, desert sucker (*Catostomus clarkii*) was found in 45% of sites (Table 2.1). Species richness per site varied from 1 to 8 species, with a considerably larger species pool in the Verde River mainstem (mean spp. richness ± SE = 5.9 ± 0.39, range 4-8) than in tributaries (2.7 ± 0.20, range 1-4). Species found only in the mainstem include roundtail chub, western mosquitofish, fathead minnow (*Pimephales promelas*), Sonora sucker (*Catostomus insignis*), and red shiner (with the exception that

Sonora sucker and red shiner were also present in one tributary). Additionally several species (desert sucker, speckled dace, and rock bass, *Ambloplites rupestris*) were present only in stream samples, while fathead minnow was only in pond sites. Only one (Sonora sucker) of the four native species was frequently found in ponds. Speckled dace and rock bass were found only in two sites; these species were considered rare and excluded from multivariate analyses.

Almost without exception, non-native fishes outnumbered natives in samples (mean = 85% non-native; range = 35 – 100%), and the non-native fraction of the assemblage was consistently greater in pond than in stream sites, in both the mainstem and tributaries (Fig. 2.2). These differences primarily reflect large numbers of small non-native fish in most pond samples. The increased dominance of non-native fish in ponds was also apparent across individual species, with the non-native species displaying generally higher relative abundances in ponds, whereas native species were relatively more abundant in stream sites (Fig. 2.3). The difference in abundance between habitat types was especially strong for desert sucker and green sunfish in tributaries. Smallmouth bass and, to a lesser extent, yellow bullhead (*Ameirus natalis*) were the only non-native species whose mean relative abundance was greater in stream sites at both mainstem and tributary locations.

Northern crayfish (*Orconectes virilis*) were present at all sites, although density varied widely among both stream sites (0.3 – 28.3 individuals/m^2) and pond sites (0 – 37 individuals/minnow trap) (Table 2.2). Within pond sites there was a marginally significant positive relationship between abundance of crayfish (total number of individuals sampled across all gears within each site) and abundance of smallmouth bass ($r = 0.55$, $P = 0.07$), but not between crayfish and all non-native fish combined ($r = 0.14$, $P = 0.66$). By contrast, in stream sites there was no evidence of a relationship between abundance of crayfish and either smallmouth bass ($r = -0.01$, $P = 0.94$) or all non-native fish combined ($r = -0.20$, $P = 0.32$).

Fish assemblages

Multivariate ordination revealed strong differences in fish assemblage structure between mainstem and tributary sites (Fig. 2.4A), reflecting the different species pools in the two locations. The first three principal component axes were statistically significant, and collectively explained 52% the total variation in fish assemblage. A two-way perMANOVA analysis indicated that fish assemblage differed significantly by both location (mainstem vs. tributary) and habitat type (pond vs. stream), although location contributed the greater component of variation (Table 2.3). There was no evidence of an interaction effect, nor of any differences in within-group variability. In order to focus on differences between habitat types, subsequent analyses were conducted separately for mainstem and for tributary sites.

An ordination of mainstem sites showed modest differentiation between pond and stream habitat types (Fig. 2.4B); perMANOVA confirmed a significant difference in fish assemblage by habitat type, although there was no difference in variability (Table 2.3). In the ordination, the first two principal coordinate axes explained 57% of the total variation; only the first two axes were statistically significant. Axis 1 appeared to describe a separation of fish assemblages along a gradient from pond sites on the left-hand side of the plot to stream sites on the right. Western mosquitofish (GAAF) and green sunfish (LECY) were strongly correlated with each other and with Axis 1, indicating that pond sites on the left-hand site of the plot were associated with abundant mosquitofish and sunfish, while stream sites to the right were more associated with relatively abundant desert sucker (CACL). By contrast, other species, including common smallmouth bass (MIDO) showed a stronger correlation with Axis 2, and no strong tendency toward either pond or stream sites. Axis 2 described a general gradient from sites dominated by small-bodied red shiner (CYLU) and mosquitofish (GAAF) on the bottom to sites dominated by larger-bodied smallmouth bass (MIDO) and Sonora sucker (CAIN) on the top, a gradient present in both pond and stream sites.

Within tributary sites only, fish assemblage again differed significantly between pond and stream habitat types (Table 2.3). An ordination of tributary sites showed, again, some clustering of pond sites, although pond and stream sites appear less differentiated than in the mainstem ordination. Additionally, patterns in habitat associations of individual species were similar to the patterns seen for mainstem sites (Fig. 2.4C). The first two principal coordinates explained 62% of the total variation; only the first two axes were statistically significant. Pond sites were clustered together in the lower-right quadrant of the plot, but within ordination space also occupied by stream sites. Although stream sites occupied a greater area in the ordination space than did pond sites, there was no evidence for a difference in group variability (Table 2.3). Green sunfish (LECY) again showed a strong correlation with Axis 1, and again the ordination plot suggested a gradient between pond sites with abundant sunfish to the lower-right and stream sites with relatively abundant desert sucker (CACL) to the upper-left. Finally, the smallmouth bass (MIDO) vector was again perpendicular to the sunfish-desert sucker gradient, and again lacked a strong tendency toward either pond or stream sites. Axis 2 partially described a gradient from sites almost entirely dominated by smallmouth bass at the bottom, moving to sites with more desert sucker (for streams) and relatively fewer bass at the top. This tributary ordination plot was strongly influenced by the two pond and three stream sites (mostly clustered on the far right-hand side of the plot) from one tributary stream (Dry Beaver Creek), which was smaller, ephemeral, and supported a different fish species pool than the other sampled tributaries. Red shiner (CYLU) were found only in this tributary, and there only within pond sites, resulting in the strong horizontal vector for this species in the ordination plot.

Discussion

In this study, we assessed the influence of beaver pond habitats in structuring the composition of mixed native and non-native fish assemblages in a free-flowing desert river. To our knowledge, this is the first study to address the effect of beaver ponds on non-native fishes at the community level. Our analyses showed that in both the upper Verde River mainstem and in its tributaries, there were significant differences in fish assemblage composition between lentic beaver pond and lotic stream habitat. Non-native species dominated the fish assemblage to a greater extent within ponds than within streams: non-native fish (both small-bodied fishes and juveniles of larger species) were often highly abundant in pond samples, while native species were rarely documented within ponds. These results are generally consistent with the hypothesis that beaver ponds could lead to fish assemblages dominated by non-native species.

Our results are also consistent with studies of fish assemblage in relation to manmade dams. Impoundments behind small, low head dams are the closest analog to beaver pond habitat: Beatty et al. (2009) found abundant non-native fish (primarily fathead minnow and white sucker, *Catostomus commersonii*) within and downstream of an artificial wetland created by a small dam on an upper CRB stream (Wyoming), while native fishes were restricted to upstream of the wetland and to tributaries without impoundments. Dominance of non-native fishes within large reservoirs of the CRB is well-established (Minckley & Marsh 2009), and reservoirs can promote proliferation of non-native species downstream, even without major changes to downstream flow or thermal regimes (Martinez et al. 1994). However, beaver dams are typically smaller, more permeable, and much less permanent than artificial analogs, which may affect the direction or mechanism of influences on fish.

Responses of individual species

We found that responses to beaver pond habitat varied by species. Here we focus on four of the most common non-native species – smallmouth bass, green sunfish, western mosquitofish, and crayfish – and on the native fishes.

Non-native smallmouth bass, the most common species in our study region, were frequently present and often the most abundant large-bodied species in both stream and pond habitat types. In stream samples, especially, bass often dominated the total fish assemblage. The high numbers of bass found in both habitat types in our study confirms the habitat flexibility of this species. From a conservation perspective, smallmouth bass are of particular interest because this widespread species is often as identified as a substantial threat to native fishes in the CRB: a bioenergetics model of non-native fishes the Yampa River, Colorado, found that because of their abundance, total potential piscivory of smallmouth bass exceeded that of two larger non-native predators (northern pike, *Esox lucius*, and channel catfish, *Ictalurus punctatus*) (Johnson et al. 2008). In the upper Verde River, a bioenergetics model identified smallmouth bass as the greatest source of potential piscivory and suggested that non-native control efforts should target this species (Bonar et al. 2004).

Green sunfish were frequently present in both stream and pond habitats, but in streams they were usually present only at low numbers, whereas in ponds they were often highly abundant. This pattern was true for both mainstem and tributary sites. The association of green sunfish with pond habitats is consistent with other studies which report that species of the genus *Lepomis* were common in beaver pond fish assemblages (Snodgrass & Meffe 1999; Pollock et al. 2003), and with the species' known habitat preference for slow current velocity (Dudley & Matter 2000; Olden et al. 2006). Presence of green sunfish has been implicated in steep declines of native fish populations (e.g., Clarkson et al. 2010). Although gut content analysis of green sunfish from the Verde River found a very low incidence of piscivory (mean 0.61% of stomach content by volume, n = 754; Bonar et al. 2004), laboratory and field evidence shows that this species can be an effective predator of larval and juvenile native fishes in the CRB (Dudley & Matter 2000; Carpenter & Mueller 2008). Elevated $\delta^{15}N$ isotope signatures from green sunfish relative to native fishes in another Arizona river system also demonstrate a strong propensity towards piscivory (Pilger et al. 2010). Additionally, highly aggressive behavior by green sunfish and congeners indicates a probable advantage over native fishes in competition for space or food (Karp & Tyus 1990; Marchetti 1999). These lines of evidence suggest that there is potential for green sunfish to have substantial impacts on native fishes in the Verde River basin, especially given the high sunfish densities that we observed in beaver ponds in addition to high frequency across all sites.

Western mosquitofish showed a strong association with beaver pond habitat, although high abundances were also observed in some mainstem stream locations. Consistent with our results, preferred mosquitofish habitat features include shallow water, slow current, and dense vegetation (Pyke 2008), all typical features of beaver ponds (Rosell et al. 2005). Mosquitofish have been widely introduced worldwide (Pyke 2008), and, in the CRB, spread of mosquitofish is closely associated with declines of the ecologically similar native Gila topminnow (*Poeciliopsis occidentalis*) (Meffe 1985). Laboratory and field studies have demonstrated that agonistic interactions with aggressive mosquitofish can lead to injury, changes in behaviour, and reduced growth for native fishes (particularly small-bodied species), and mosquitofish also prey directly on eggs and larvae (Meffe 1985; Mills et al. 2004; Ayala et al. 2007). In isolated backwater habitats otherwise free of non-native fish, presence of mosquitofish is believed to be responsible for failed recruitment by stocked native razorback suckers (*Xyrauchen texanus*) (Ley et al. 2012); abundant mosquitofish may similarly impede attempts to restore populations of spikedace in the Verde River.

In addition to non-native fishes, we observed high densities of non-native northern crayfish within both stream and beaver pond habitats of the Verde River basin. This study is one of the first to report abundance metrics for crayfish in Arizona. In a tributary stream of the Gila River drainage (Arizona), Carpenter (1999) found a mean density of 1.83 large individuals (> 25 mm carapace length [CL]) / $m^{2;}$, relative to our densities of 9.3 and 7.4 small individuals (mean CL = 8.4 mm) / m^2 in mainstem and tributary sites, respectively. Crayfish density was even higher (10.9 individuals / m2 in 2005; mean CL = 16.1 mm) in the Yampa River (Colorado), where Martinez (2012) estimated that total river-wide crayfish biomass exceeded that of all fish and other invertebrates combined. Invasive crayfish can have strong impacts on multiple levels of aquatic food webs (Twardochleb et al. 2013), and laboratory and field evidence indicate that crayfish can compete with and prey on native CRB fishes directly (Carpenter 1999). Many non-native fishes consume crayfish (Bonar et al. 2004), while the native fishes sampled in this study are more exclusively invertivores/herbivores (Olden et al. 2006; Pilger et al. 2010), more likely to compete with crayfish than to prey on them (Carpenter 2005; Arena et al. 2012). The greatest impact of crayfish on native fishes may be indirect, via apparent competition. In the Yampa River, Martinez (2012) documented simultaneous large increases in smallmouth bass and northern crayfish populations (along with steep declines in small-bodied native fish): abundant crayfish may provide an alternative prey source when small fish have been depleted, thus stabilizing large populations of smallmouth bass. Our finding of a positive relationship between crayfish and bass abundances in ponds is consistent with this hypothesis. By creating relatively stable hydrology and deep pools, beaver ponds may provide favorable habitat for crayfish (e.g., Light 2003); the influence of beaver ponds on crayfish populations in the CRB requires additional investigation.

Native fishes in general showed a tendency toward higher abundance in stream habitats: all four of the native species recorded in this study were found in stream sites, but only two species (Sonora sucker and roundtail chub) were present in ponds. The two native suckers in our species pool differ in modes of feeding and use of habitat. Desert sucker is herbivorous and inhabits predominantly swift-flowing streams with hard-bottom substrate, whereas Sonora sucker feeds on invertebrates and detritus and is abundant in deep pools with restricted flow and fine substrate (Minckley & Marsh 2009). These differences were reflected in findings of our study. Desert sucker showed a strong association with stream habitat: it was frequently present and often relatively abundant in stream sites, but never found within ponds. Sonora sucker, by contrast, was present and occasionally abundant in both habitat types. Native roundtail chub, much like Sonora sucker, is an omnivorous feeder associated with deep pool habitat. However, we rarely found this species in ponds. It is possible that roundtail chub presence or abundance was underestimated in ponds due to size-selectivity of sampling methodology: size frequency data from pond samples (unpublished data) suggests that mid-sized fish (approximately 150-300 mm total length) may have been consistently under-sampled in ponds. Species most likely to have been underestimated in this way are roundtail chub, desert sucker, and, to a lesser extent, smallmouth bass. Alternatively, the rarity of roundtail chub in beaver ponds could reflect unfavorable habitat conditions for these fish, whether due to unique abiotic properties of beaver ponds or to the high density of non-native fish.

The three small-bodied native fishes present in the upper Verde River within recent decades (not recorded in our study, except for speckled dace in tributaries) are generally associated with riffle habitat

(Minckley & Marsh 2009). Therefore it is unlikely that adults of those species would directly utilize beaver pond habitat, although they might occupy fast tailwaters downstream of dams (Smith & Mather 2013). Extensive conversion of lotic habitat to lentic beaver ponds, as has been documented on the regulated Bill Williams River, Arizona (Shafroth et al. 2010), could limit the potential for restoration of these native riffle specialists. This situation occurred on Bonita Creek, AZ, where extensive beaver dam activity has resulted in the cessation of stocking efforts for native loach minnow (*Tiaroga cobitis*) and spikedace, due in part to a lack of lotic habitat and an increase in abundance of green sunfish (H. Blausius, pers. comm.).

However, the greatest importance of beaver ponds for fish communities in the Verde River may be their function as spawning or rearing habitat for juvenile fish. Previous studies have found ontogenetic shifts in fish use of beaver pond habitat, with some species moving into ponds to spawn (Schlosser 1998; Snodgrass & Meffe 1999). Schlosser (1995; 1998) further suggests that beaver ponds may function as reproductive "sources" for some species, while adjacent stream reaches are "sinks" with little successful recruitment. Beaver ponds often include extensive shallow, vegetated areas with slow current, many of the same features that characterize typical rearing habitat for juvenile CRB native fishes (Childs et al. 1998). Backwaters and other off-channel rearing habitats have been the target of restoration activities (Minckley et al. 2003), and given the importance of backwaters for successful recruitment of native fish, the possibility that beaver ponds could provide equivalent rearing habitat conditions is worthy of investigation. However, the abundant non-native fish that we documented within margins and backwaters of beaver ponds may make these areas unsuitable for juvenile native fish (Minckley et al. 2003; Carpenter & Mueller 2008). Size-selectivity of different sampling gears prevents formal analysis of differences in habitat use by life stage in our data. However, we did record young-of-the-year (YOY) individuals of several species (native Sonora sucker and non-native smallmouth bass, green sunfish, common carp [*Cyprinus carpio*], and yellow bullhead) within ponds, suggesting that these species may sometimes utilize beaver ponds for rearing habitat.

Variation over time

This study provides a snapshot view of fish assemblage at a single point in time, focusing on the distinction between pond and stream habitat types. Long term studies of fish assemblage in the Verde River and similar systems document substantial interannual variation in absolute and relative abundance of native fishes, especially in response to stream discharge (e.g., Propst et al. 2008; Rinne 2012). Similarly, the response of fish assemblage to beaver pond habitats is likely to vary with time and discharge, and therefore caution should be used in extrapolating results of the present study to different environmental conditions. Sampling for this study occurred during May and June, typically the driest months of the year (Blasch et al. 2006), and during a drought year; the upper Verde River mainstem had not experienced a significant high-flow event since 2010 (USGS 2013). Low flow conditions are of particular importance from the perspective of native fish conservation. Numerous studies have found strong positive correlations between discharge level and native fish abundance: native fishes as a group tend to increase in absolute and relative abundance following large peak flows or years with elevated discharge; conversely, during dry years non-native species are more likely to become established and to dominate assemblages (Gido et al. 2013), and drought conditions are associated with extirpations of native species (Propst et al. 2008). Therefore drought and low discharge likely represent critical periods for persistence of native fishes, and the most important time to understand the influence of beaver dams and other habitat features on native and non-native assemblage structure.

Contrasting mainstem and tributary habitats

Our finding of a strong distinction between fish assemblages of the upper Verde River mainstem and its tributaries is consistent with other observed differences between the two locations, including differences in species pool, habitat features, and distribution of beaver dams. We found that beaver dams were generally more abundant and larger in the upper mainstem than in the tributaries, and mainstem ponds appeared older and more complex. This may reflect the more stable hydrology in the upper mainstem relative to the tributaries: beaver dams in the upper mainstem tend to increase steadily during periods of moderate discharge, although occasional large floods can eliminate most or all dams (D. Campbell, pers. comm.). In Verde River tributaries, by contrast, dams are more likely to wash out annually in snowmelt or monsoon floods (K. Schonek, pers. comm.), thus preventing enlargement and succession of the beaver pond habitat over multiple years. It seems likely that longevity of beaver ponds may affect their ecological function, and several studies have demonstrated that fish assemblage in beaver pond habitats varies with pond age (Snodgrass & Meffe 1998; Schlosser & Kallemeyn 2000). However, despite differences in hydrology and pond stability, we observed some consistent patterns in individual species' response to pond habitat in both the mainstem and tributaries.

Net effects of beaver ponds on fish communities

In this study we documented patterns of presence and abundance for native and non-native fish within beaver ponds as compared to unimpounded stream reaches. Our results point to further questions about the consequences of these patterns: what will be the net effect of beaver dams on fish populations in the Verde River basin and similar desert rivers? Beaver dams modify numerous different aspects of aquatic ecosystems, which influence fish in different ways. In Table 2.4 we suggest how specific ecosystem effects of beaver dams may affect native and non-native fishes in the CRB, and we hypothesize potential net outcomes for native fish.

At the scale of individual beaver ponds, a better understanding is needed of how fish use of pond habitat varies with season, environmental conditions, and life stage; identifying which species may be employing beaver ponds for spawning or rearing habitat would be particularly valuable. However, the net effect of utilizing beaver pond habitat will depend on the degree of biotic interactions occurring in these habitats, and whether beaver ponds tend to increase or decrease negative interactions between native and non-native species. Beaver ponds generally increase habitat complexity relative to unimpounded stream, in terms of both channel morphology (e.g., secondary channels, overbank flooding; Kemp et al. 2012; Smith & Mather 2013) and habitat structure (e.g., large wood; Pollock et al. 2003). Habitat complexity may provide refuge from predation and increase spatial segregation between native and non-native fishes, thus reducing negative interactions (Crowder & Cooper 1982; Meffe 1985; Billman et al. 2012). However, if beaver pond habitats also support significantly higher densities of non-native fish than unmodified stream reaches, then this could override any advantages of habitat structure for native fish. In particular, use of beaver pond margins as rearing habitat could increase predation on vulnerable native larvae when, as in our results, these areas also support abundant small non-native fishes.

The influence of beaver dams on fish assemblages can also extend beyond the pond itself to the rest of the stream network. Fish from beaver pond assemblages may spill over into neighboring stream reaches (Schlosser 1998; Snodgrass & Meffe 1999). Beaver ponds can provide source habitat for some species, as discussed earlier. In general, beaver ponds promote fish species richness at the drainage level by supporting species that otherwise might not persist in unmodified habitat (e.g., Hanson & Campbell 1963; Snodgrass & Meffe 1998; Smith & Mather 2013), but this effect may be undesirable if it is the richness of non-native species that is increased. Beatty *et al*. (2009) suggest that an artificial impoundment provided source habitat for non-native fishes in an upper CRB stream (Wyoming), while tributary streams lacking any impoundments (i.e., source habitat for non-natives) were dominated by native fishes. The abundant green sunfish and western mosquitofish recorded within ponds in our study suggest that beaver ponds could provide source habitat for these small lentic fishes in the Verde River basin. However, we found no evidence for a correlation between distance from a pond and abundance of these or any other species (unpublished results); additionally, thriving populations of non-native species in similar streams without beaver activity (e.g., Fossil Creek, Arizona; M. O’Neill, pers. obs.; Marks et al 2009) indicate that beaver pond habitats are not essential to their life history. Nonetheless, beaver ponds could promote higher abundances of these fish or increase their resistance or resilience to disturbance.

Within desert river systems like the Verde, the influence of beaver ponds on fish assemblage response to large-scale disturbance by drought and floods is of particular interest. Previous studies have suggested that beaver ponds can provide refuge habitat for fish during drought and seasonal low flows (Hanson & Campbell 1963; Magoulick & Kobza 2003; White & Rahel 2008). This function may be particularly important in intermittent tributary streams, especially with projected decreases in perennial surface flow due to water withdrawals and climate change (Marshall et al. 2010). In ephemeral Dry Beaver Creek in our study, we observed large native Sonora suckers within deep pools that had been expanded by beaver dams. However, concentrating fish within small refuge habitats typically increases the intensity of biotic interactions (Magoulick & Kobza 2003): enforced habitat overlap between non-native predators and vulnerable native fishes within ponds could lead to extensive predation and other negative interactions, such that native fishes would derive no net benefit from the refuge habitat. Beaver dams may also provide fish some protection from floods or peak flows (Kemp et al. 2012), potentially speeding recolonization of a drainage by non-native species following the flood. Future research should address the ability of beaver ponds to provide refuge from these disturbances, and the relative impact of that refuge on native and non-native fishes.

Ultimately, the consequences of beaver dam-building activity for native fish populations depend on the extent to which a dam’s influence extends beyond the pond: if beaver ponds support a high density of non-native fish only within the pond itself, then the net impact on native fish populations at the drainage level may be negligible. However, if abundant non-native fish spill over into adjacent stream reaches, or if beaver ponds promote reproduction and maintain source populations of non-native species, then beaver dams could have far-reaching consequences for the overall composition of the fish assemblage.

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Table 2.1. Our study recorded 4 native fish species, 9 non-native fish species, and 1 non-native crayfish species in the upper Verde River mainstem and tributaries.

				Proportion of sites where species is present		
Family	**Species**	**Common name**	**Code**[a]	**All sites** *n = 38*	**Pond sites** *n = 12*	**Lotic Sites** *n = 26*
NATIVE						
Catostomidae	*Catostomus clarkii*	desert sucker	CACL	0.45	0.00	0.65
	Catostomus insignis	Sonora sucker	CAIN	0.39	0.50	0.35
Cyprinidae	*Gila robusta*	roundtail chub	GIRO	0.24	0.08	0.31
	Rhinicthys osculus	speckled dace	RHOS	0.05	0.00	0.08
NON-NATIVE						
Centrarchidae	*Micropterus dolomieu*	smallmouth bass	MIDO	0.87	0.83	0.88
	Lepomis cyanellus	green sunfish	LECY	0.61	0.83	0.50
	Ambloplites rupestris	rock bass	AMRU	0.05	0.00	0.08
Cyprinidae	*Cyprinella lutrensis*	red shiner	CYLU	0.37	0.42	0.35
	Cyprinus carpio	common carp	CYCA	0.16	0.33	0.08
	Pimephales promelas	fathead minnow	PIPR	0.08	0.25	0.00
Ictaluridae	*Ameirus natalis*	yellow bullhead	AMNA	0.29	0.25	0.31
Poeciliidae	*Gambusia affinis*	western mosquitofish	GAAF	0.37	0.50	0.31
Salmonidae	*Oncorhynchus mykiss*	rainbow trout	ONMY	0.11	0.08	0.12
NON-NATIVE CRAYFISH						
Cambaridae	*Orconectes virilis*	Northern crayfish	ORVI	1.00	1.00	1.00

[a] Combination of first two letters of genus and first two letters of species. Used to indicate species on ordination plots.

Table 2.2. Density and catch per unit effort (CPUE) of non-native northern crayfish in pond and stream habitats.

		Mainstem Sites			Tributary Sites			Estimated crayfish CL (mm)[a]
Habitat type	**Abundance metric**	***n***	***mean***	***range***	***n***	***mean***	***range***	***range***
Stream sites, *density*	individuals/m^2	10 sites	9	0.3 - 28.3	16 sites	7.3	1.5 - 22.3	3 - 30 (mean = 8.4)
Pond sites, *CPUE*	Crayfish traps (individuals/trap)	72 traps	3.0	0.0 - 9.0	71 traps	1.8	0.0 - 10.0	20 - 60
	Minnow traps (individuals/trap)	72 traps	5.0	0.0 - 37.0	71 traps	1.1	0.0 - 12.0	20 - 50
	Seine hauls (individuals/m^2 seined)	33 hauls	4.1	0.0 - 21.0	32 hauls	0.5	0.0 - 4.3	10 - 70

[a] Size range of crayfish caught in each gear type. Sizes indicate carapace length [CL] in mm. Except for lotic densities (top row), crayfish were not measured and size ranges are estimates.

Table 2.3. Results of perMANOVA and multivariate dispersion tests examining effects of location (mainstem vs. tributary) and habitat type (pond vs. stream) on fish assemblages within all sites and within mainstem and tributary sites only.

			perMANOVA		**Homogeneity of dispersion**	
Sites	**Factor**	**n**	**pseudo *F***	***P***	**pseudo *F***	***P***
All sites	Habitat type x Location	38				
Location			18.91	<0.001	1.31	0.227
Habitat type			5.65	0.003	0.62	0.450
*Location*Habitat type*			1.60	0.158	*na*	*na*
Mainstem sites	Habitat type	16	3.61	0.009	0.38	0.550
Tributary sites	Habitat type	22	3.85	0.014	0.37	0.551

Table 2.4. Hypothesized effects of various types of ecosystem change resulting from construction of beaver dams on native and non-native fishes in the CRB, as well as possible outcomes of each change for native fish in a mixed native-non-native assemblage. Arrows indicate whether the effect on fish is expected to be positive (↑) or negative (↓). Beaver dams and ponds are highly variable, and not all effects will apply to all beaver ponds.

Category	Effect of beaver dam[a]	Consequence for native fishes[b]	Consequence for non-native fishes	Potential outcomes[c]
Direct habitat effects	Pooled water, reduced current velocity.	↑ Deep pools provide habitat for larger or pool-dwelling fish, potentially including "big river" native fish. ↑ Shallow lentic water in pond margins and backwaters provides habitat for lentic/marsh habitat specialists . ↓ Decreased habitat availability to fluvial specialists due to conversion of lotic to lentic habitat in beaver ponds.	↑ Deep pools provide habitat for larger or pool-dwelling fish, including carp, catfishes, and some sunfishes. ↑ Shallow lentic habitat provides habitat for lentic/marsh habitat specialists. ↑ Relative stability of beaver pond habitat resembles typical habitat in the native range of many non-native species.	↑ Reduced intensity of biotic interactions due to habitat segregation; *or* ↓ Increased competition and predation due to high densities of non-native fishes in ponds.
	Increased habitat complexity, including channel morphology (side channels, backwaters) and habitat structure (large wood, macrophytes).	↑ Spawning/rearing habitat for numerous species in shallow, vegetated, backwater-type habitats. ↑ Habitat structure provides cover and refuge from predation.	↑ Spawning/rearing habitat for numerous species in shallow, vegetated, backwater-type habitats. ↑ Habitat structure provides cover for predators, increases predation success; *or* ↓ Habitat structure provides cover for prey, reduces predation success.	↑ Reduced predation due to availability of cover and refuge habitats. ↑ Complexity promotes habitat segregation and reduces intensity of biotic interactions; *or* ↓ Abundant small non-native fish present in potential native fish rearing habitat increase rates of predation and competition with native larval fish.
	Retention of sediment, *reduced turbidity*.	↑ Reduce sedimentation downstream of ponds. ↓ Fine sediment within ponds unfavorable for species that prefer coarser substrate. ↓ Loss of visual cover due to decreased turbidity.	↑ Reduce sedimentation downstream of ponds. ↓ Fine sediment within ponds unfavorable for species that prefer coarser substrate. ↑ Increase success of visual predators due to decreased turbidity.	↑ Improved downstream habitat quality for some species due to altered sediment flows. ↓ Increased predation due to visibility.
	Increased fluvial habitat (fast water, coarse substrate) downstream of beaver dams.	↑ Provide habitat for small fluvial specialists.	↑ Provide habitat for small fluvial specialists.	↑↓ Change in quality or quantity of habitat available to fluvial specialists.
	Altered water quality, including temperature regime and dissolved oxygen (DO).	↑ Reduce thermal stress due to temperature-buffering effect of ponds; *or* ↓ Increase thermal stress due to higher temperatures in ponds.	↑ Reduce thermal stress due to temperature-buffering effect of ponds; *or* ↓ Increase thermal stress due to higher temperatures in ponds.	↓ Increased competitive advantage for non-native fishes due to thermal stress.
Indirect effects	Increased rate of primary productivity and standing stock of organic matter.	↑ Increase food availability for herbivores and detritivores.	↑ Increase food availability for herbivores and detritivores.	↑ Reduced competition due to greater availabilty of resources; *or* ↓ Increased competition and predation due to higher densities of non-native fish.
	Increased biomass and altered community structure of benthic invertebrates.	↑ Increase food availability for invertivores. ↓ Reduce relative abudance of lotic invertebrate taxa preferred by some species.	↑ Increase food availability for crayfish-consuming species. ↓ Reduce relative abudance of lotic invertebrate taxa preferred by some species.	↑ Reduced competition due to greater availabilty of resources; *or* ↓ Increased competition and predation due to higher densities of non-native fish.

Table 2.4, cont.

Category	Effect of beaver dam[a]	Consequence for native fishes[b]	Consequence for non-native fishes	Potential outcomes[c]
Drainage-level effects	*Flow stabilization: dampened peak flows.*	↑ Provide slack water refuge during peak flows, particularly for vulnerable larval or juvenile fish. ↓ Reduce recruitment success dependent on peak flow events. ↓ Reduce power of peak flows to move sediment and rejuvenate spawning and rearing habitats.	↑ Provide slack water refuge during peak flows: may be especially important for non-native species that lack adaptations for surviving flood conditions	↓ Reduction in the ability of native fishes to benefit from peak flow events. ↓ Increased survival of non-native fish through peak flow events and/or increased speed of recolonization following disturbance.
	Flow stabilization: maintenance of surface water within beaver pond and/or downstream of dam.	↑ Provide refuge habitat during drought and low flows.	↑ Provide refuge habitat during drought and low flows: may be particularly important for non-native species that lack adaptations for surviving drought conditions.	↑ Increased ability of native fishes to persist through combined stressors of drought and non-native fish; *or* ↓ Increased negative biotic interactions due to concentration of native and non-native species within small refuge habitats . ↓ Increased survival of non-native fish through drought events and/or increased speed of recolonization following disturbance.
	Barriers to fish movement.	↓ Reduce habitat connectivity, fish dispersal between populations.	↓ Reduce habitat connecitivity, fish dispersal between populations. ↓ Slow rate of spread up new drainages and tributary systems.	↑ Potential for dams to create habitat patches that are temporarily isolated from non-native fish. ↓ Dams limit ability to move between habitats in response to drought or other environmental conditions.
	Unique lentic habitat patches within lotic habitat corridors.	↑ Provide reproductive source habitat for some species. ↑ Promote persistence of lentic/marsh habitat specialists within a drainage. ↑ Potentially increase the upstream extent of suitable habitat for "big river" fishes in smaller river or tributary systems.	↑ Provide reproductive source habitat for some species. ↑ Promote persistence of lentic/marsh habitat specialists within a drainage. ↑ Potentially increase the upstream extent of suitable habitat for large piscivores such as catfishes in smaller river or tributary systems.	↑ Higher species richness of native fishes within a drainage. ↓ Higher species richness of non-native fishes within a drainage. ↓ Spillover from pond habitat increases abundance of non-native fish throughout a drainage.
	Reduced channelization and increased abundance of marshy and cienega habitats.	↑ Diversity of aquatic habitats promotes regional species richness.	↑ Diversity of aquatic habitats promotes regional species richness.	↑↓ Different habitat supports a different assemblage of native and non-native fishes.

a Well-established effects of beaver dams are in plain text, while hypothesized or uncertain effects are indicated in italics.

b Response of native fish, *independent of* or *in the absence of* non-native fish.

c Hypothesized outcomes of the beaver dam effect for *native fish* , when non-native fish are present. In some cases mutually exclusive alternatives are presented.

Sources informing development of this table include: Schlosser 1995, 1998; Snodgrass & Meffe 1998, 1999; Pollock et al. 2003; Rosell et al. 2005; Propst & Gido 2008; Minckley & Marsh 2009; Stefferud et al. 2009; Kemp et al. 2011; Smith & Mather 2013; Gibson & Olden in press.

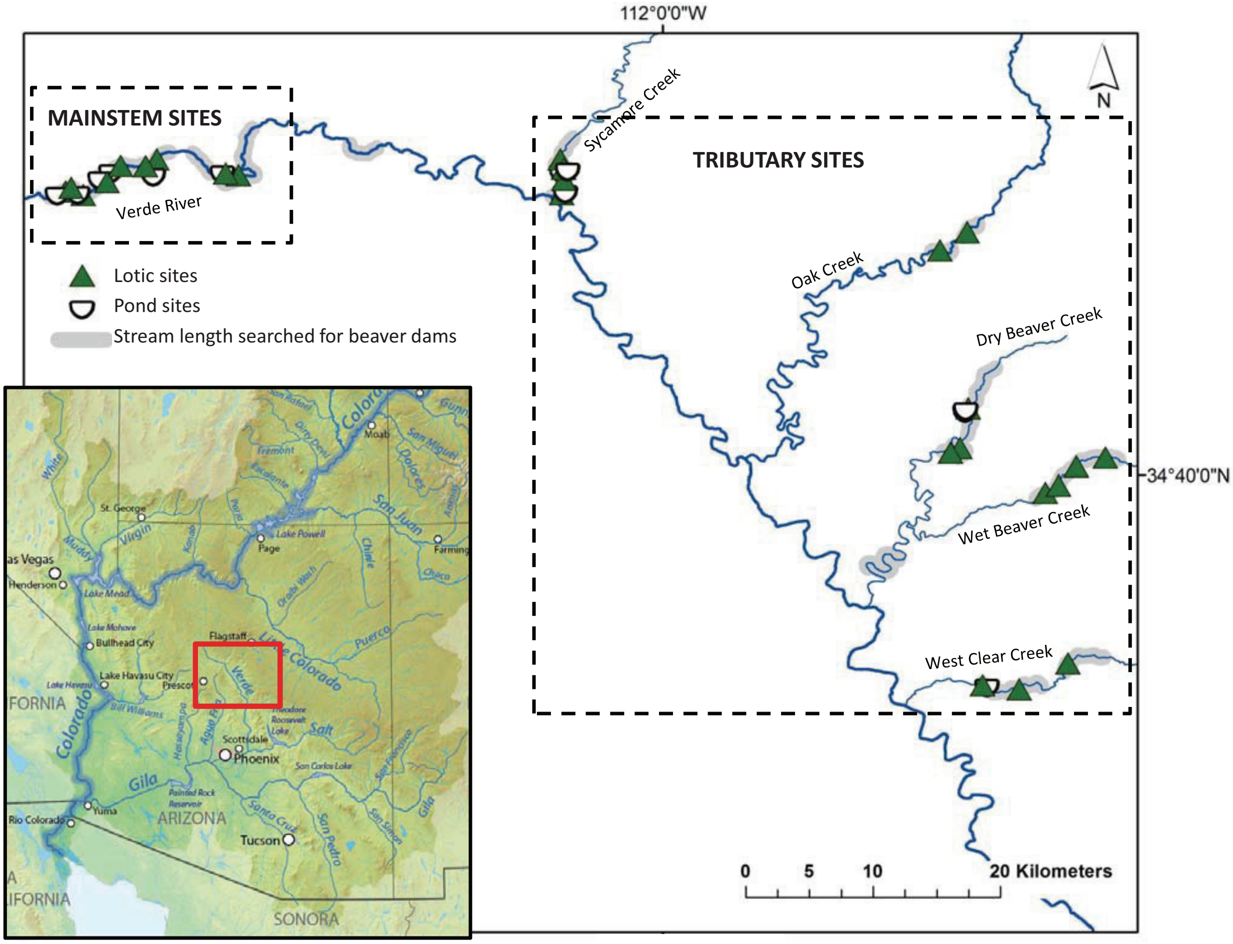

Figure 2.1.
Map of the study area in the Verde River basin and fish sampling sites, distributed among the mainstem and five tributaries. Gray shading indicates stream segments surveyed for beaver dams.

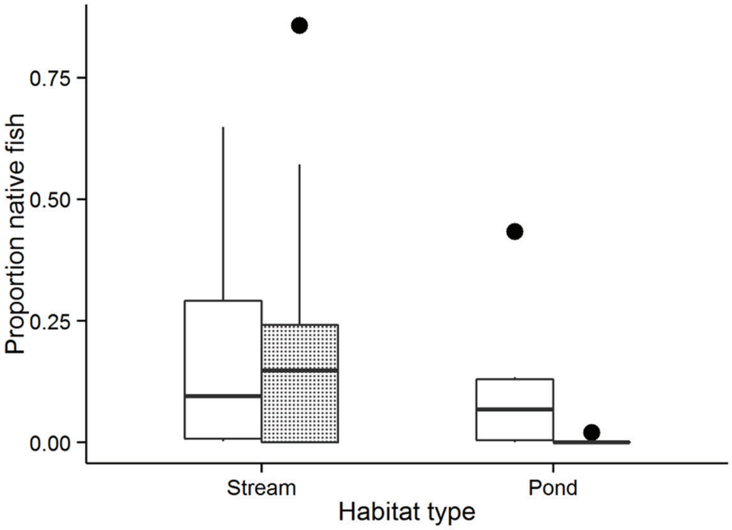

Figure 2.2.
Boxplots showing the distributions of the proportion native fish across all pond sites and all stream sites. Distributions are calculated separately for mainstem sites (white boxes) and tributary sites (hatched grey boxes).

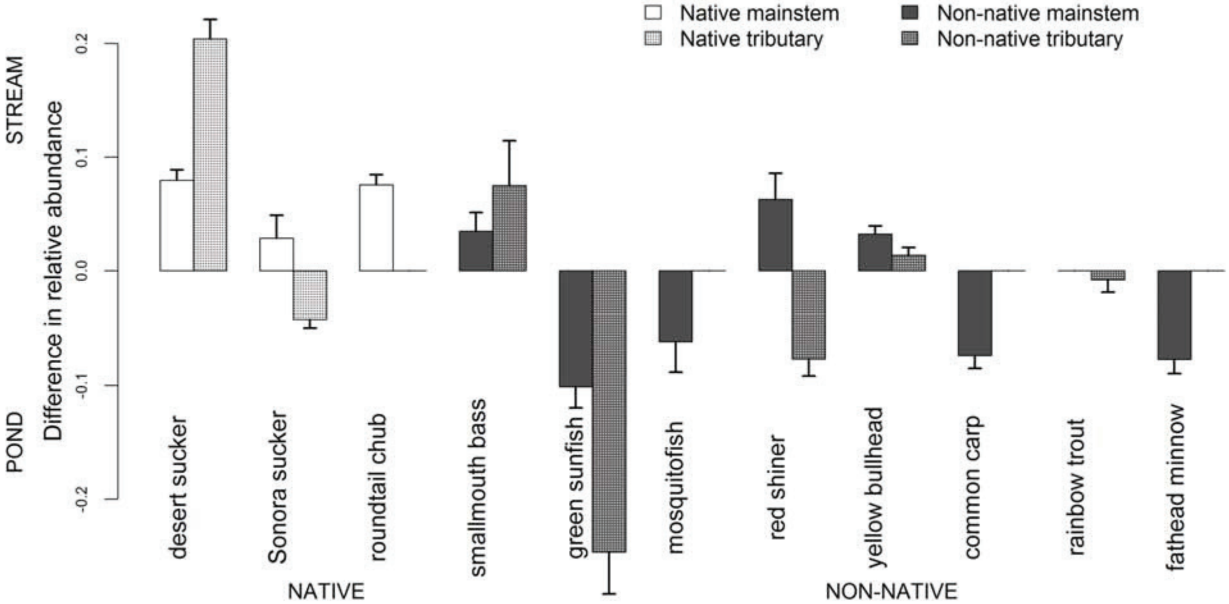

Figure 2.3.
Mean difference in relative abundance between stream and pond sites (averaged for all pond site-stream site pairwise comparisons, within mainstem sites and within tributary sites), for each species recorded in this study. Positive values (i.e., bars above the midline) indicate higher relative abundance in stream sites than in pond sites, while negative values indicate higher relative abundance in pond sites. Error bars show standard error of the mean.

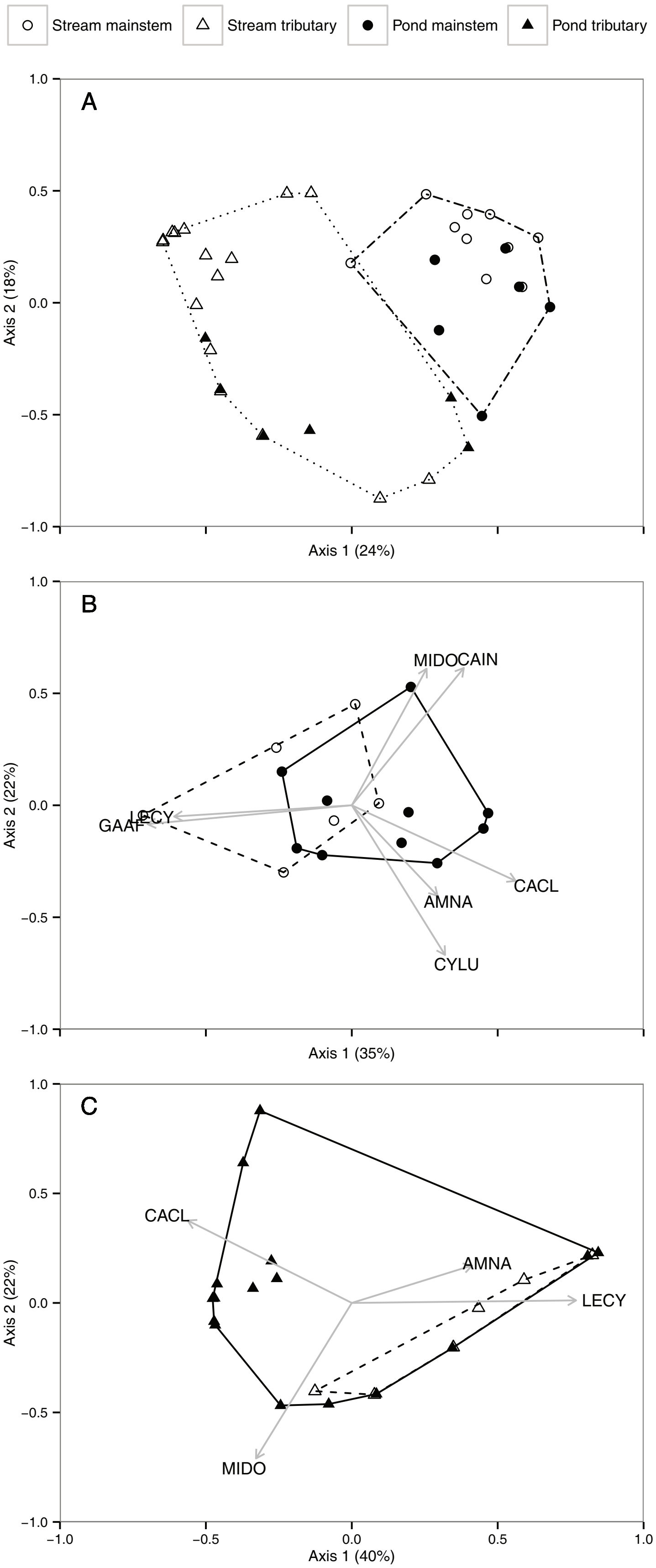

Figure 2.4.
PCoA ordination plots of fish assemblage data for all sites (A); mainstem sites only (B); and tributary sites only (C). Hulls are drawn around tributary vs. mainstem sites in panel (A) and around pond vs. stream sites in panels (B) and (C). Only significant ($P < 0.05$) vectors are displayed.

SUPPLEMENTARY MATERIAL

Appendix 1. Distribution and status of Eurasian beaver in dryland streams

The Eurasian beaver, *Castor fiber,* has only a limited presence dryland streams. Estimates of the historical range of Eurasian beaver include dryland areas in Spain, Turkey, Iraq, Iran, southern Russia, northern Kazakhstan, China, and Mongolia, but in many of these areas beaver were apparently extirpated centuries ago (Nolet and Rosell 1998). The full extent of historical *C. fiber* presence in dryland Eurasia is uncertain and has received little research attention. Currently beaver are widespread through most of northern Europe, but they remain absent or rare from much their former Asian range (Nolet and Rosell 1998). The only extant Eurasian beaver in drylands are found in the Ulungur watershed of Mongolia and China, where the small and isolated population is considered vulnerable and in need of further protection (Chu and Jiang 2009). However, as Eurasian beaver continue to spread through or beyond their historical range, there is potential for increased presence of beaver in Eurasian drylands in the future.

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Appendix 2. Comparing extent of research effort for beaver ecology in drylands versus temperate regions

We performed standardized keyword searches in ISI Web of Knowledge in order to roughly estimate the extent of research related to beaver in drylands vs. temperate regions (search date: 05 February 2013). Methods for keyword searches are described below in sections A.1-A.2. Results of the searches are displayed in Supplementary Material, Table S1.

A.1 Keywords

(a) Beaver keywords (all searches):

Topic = ("castor canadensis" OR "castor fiber")

(b) Subtopic keywords:

AND Topic= [terms listed in Table S1 "Search terms" column]

(c) Dryland limiting keywords:

AND Topic=(desert* OR *arid* OR washington OR oregon OR california OR idaho OR nevada OR utah OR arizona OR "new mexico" OR montana OR colorado OR wyoming OR texas OR "north dakota" OR "south dakota" OR nebraska OR kansas OR mojave OR mohave OR sonora* OR chihuahua* OR mexic* OR "great basin")

NOT Topic= (*alpine OR tidal OR "western Washington" OR "western Oregon" OR "Coast Range" OR "Sierra Nevada" OR "Rocky Mountain National Park" OR "Glacier National Park" OR Yellowstone OR "Mount Desert Island" OR "Tierra del Fuego")

(This search limitation was conservative, i.e., hits included many studies that would not formally qualify as dryland locations.)

A.2 Methods

To calculate numbers of dryland papers [Table S1 column "Number of studies from drylands"], we performed searches with all keywords (a+b+c) for each subtopic. Numbers of hits were recorded directly, with no further manual screening.

To calculate numbers of temperate papers [Table S1 column “Number of studies from temperate regions”], we performed searches for each subtopic using only beaver keywords and subtopic keywords (a+b), and any paper not qualifying as a dryland paper was assumed to be a temperate paper (i.e., the two categories were mutually exclusive). For example: for the ‘Geomorphology’ subtopic, first a search was performed using only (a) beaver keywords + (b) subtopic keywords:

a) Topic = ("castor canadensis" OR "castor fiber")
b) AND Topic = (geomorph* OR sediment* OR erosion* OR incis* OR entrench* OR aggrad* OR "channel morphology")

The resulting number of papers was the ‘Total hits’.

Next, we calculated the number of hits for the subtopic when limited to dryland streams by performing a search with (a) beaver keywords + (b) subtopic keywords + (c) dryland limiting keywords:

a) Topic = ("castor canadensis" OR "castor fiber")

b) AND Topic = (geomorph* OR sediment* OR erosion* OR incis* OR entrench* OR aggrad* OR "channel morphology")

c) AND Topic = (desert* OR *arid* OR washington OR oregon OR california OR idaho OR nevada OR utah OR arizona OR “new mexico” OR montana OR colorado OR wyoming OR texas OR “north dakota” OR “south dakota” OR nebraska OR kansas OR mojave OR mohave OR sonora* OR chihuahua* OR mexic* OR “great basin”)

   NOT Topic = (*alpine OR tidal OR "western Washington" OR "western Oregon" OR "Coast Range" OR "Sierra Nevada" OR "Rocky Mountain National Park" OR "Glacier National Park" OR Yellowstone OR "Mount Desert Island" OR "Tierra del Fuego")

The resulting number of papers was the ‘Dryland hits’ [Table S1 column “Number of studies from drylands”].

Finally, ‘Dryland hits’ was subtracted from ‘Total hits’ to produce the number of ‘Temperate hits’ for each subtopic [“Number of studies from temperate regions”].

Column C [“Number of studies from drylands, *manual screening”*] is not based solely on keyword searches but, instead, is derived from the formal list of sources (Supplementary Material, Table S3) that meet all the screening criteria for this review. Column C indicates the number of sources from this manually screened list that address each subtopic.

For all searches (including the manual screening), subtopics were not mutually exclusive: a single paper could count toward multiple subtopics.

Appendix Tables

Table S1. Comparison of numbers of published papers addressing beaver ecology in drylands vs. temperate regions, by subtopic. Based on a standardized keyword search in ISI Web of Knowledge. Methods and keywords for searches are described in Supplementary Material, Appendix 2.

Topic	Number of studies from temperate regions	Number of studies from drylands	Number of studies from drylands, *manual screening*[a]	Search terms
status and distribution	503	61	*28*	status OR distribution OR density OR occupancy OR extirp*
geomorphology	94	13	*9*	geomorph* OR sediment* OR erosion* OR incis* OR entrench* OR aggrad* OR "channel morphology"
hydrology	81	14	*15*	hydrolog* OR perennial OR ephemeral OR intermittent OR discharge OR "surface water" OR groundwater OR hyporheic OR "water table" OR evaporat* OR aquifer* OR velocity
water quality and chemistry	133	9	*12*	"water quality" OR chemistry OR "water temperature" OR "dissolved oxygen" OR nutrient* OR eutroph* OR autotroph* OR "organic matter" OR pollut* OR nitrogen OR phosphorus
riparian vegetation	121	31	*22*	"riparian vegetation" OR willow* OR salix OR cottonwood* OR aspen* OR populus OR tamarix OR "riparian trees" OR "riparian plant*" OR herbivory
other mammals			*6*	*no standardized keyword search*
birds	98	11	*6*	*bird* OR waterfowl OR duck*
amphibians and reptiles	46	6	*0*	amphib* OR reptil* OR *frog* OR *toad* OR salamander* OR newt* OR turtle* OR tortoise* OR *snake* OR *lizard*
fish	167	15	*9*	*fish*
invertebrates	102	14	*0*	*invertebrate* OR crayfish* OR mollusc* OR *snail* OR *insect* OR arthropod*; NOT parasit* OR disease* OR bacteria
stream restoration	206	21	*9*	restor* OR *introduc*
ALL PAPERS	**1200**	**118**	***76***	**[none]**

[a] Number of papers from the official list of sources (Table S3), manually screened according to the criteria described in Chapter 1 *Methods*, that address each subtopic.

Table S2. Literature search terms and results. Date of search: 04 January 2013.

Source	Search terms	Number of hits	Number of hits meeting selection criteria[a]
ISI Web of Knowledge (Databases=ALL, Timespan=1900-2012)	Topic=(beaver* OR castor*) AND Topic=(desert* OR *arid* OR washington OR oregon OR california OR idaho OR nevada OR utah OR arizona OR “new mexico” OR montana OR colorado OR wyoming OR texas OR “north dakota” OR “south dakota” OR nebraska OR kansas OR mojave OR mohave OR sonora* OR chihuahua* OR mexic* OR “great basin” OR southwest*) NOT Topic=(ricinus or "castor oil")	820	57
Google Scholar (only first 300 results were screened)	("castor canadensis" OR "castor fiber") AND (desert OR arid OR semiarid OR semi-arid)	2990 (first 300 results were screened)	25

[a] Sources meeting screening criteria are listed in Table S3.

Table S3. All sources, identified during literature searches, that meet the screening criteria described in *Methods*; table lists subtopic(s) addressed by each study and location where the study was conducted.

Reference	Subject[a]	Location[b]	Source[c]
Albert S, Trimble T. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. *Ecological Restoration* **18:** 87-92.	G, H, B, R	NM	Reference lists
Andersen DC, Cooper DJ. 2000. Plant-herbivore-hydroperiod interactions: effects of native mammals on floodplain tree recruitment. *Ecological Applications* **10**: 1384–1399.	V	CO, UT	ISI
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.	D, H	AZ	ISI, GS
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.	G, H, W	AZ	ISI, GS
Apple, 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.	G, H, V, R	WY	ISI
Arp CD, Cooper DJ. 2004. Analysis of sediment retention in western riverine wetlands: the Yampa River watershed, Colorado, USA. *Environmental Management* **33:** 318-330**.**	G	CO	ISI
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.	V	CO	ISI
Basey JM, Jenkins SH, Busher PE. 1988. Optimal central-place foraging by beavers: tree-size selection in relation to defensive chemicals of quaking aspen. *Oecologia* **76**: 278–282.	V	NV	Reference lists
Billman EJ, Kreitzer JD, Creighton JC, Habit E, McMillan B, Belk MC. 2012. 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.	F	UT	ISI
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.	D, V	CO, UT	ISI, GS
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.	V	CO, UT	ISI
Breck SW, Wilson KR, Andersen DC. 2003. Beaver herbivory of willow under two flow regimes: a comparative study on the Green and Yampa Rivers. *Western North American Naturalist* **63:** 463-471.	V	CO, UT	ISI
Breck SW, Goldstein MI, Pyare S. 2012. Site-occupancy monitoring of an ecosystem indicator: linking characteristics of riparian vegetation to beaver occurrence. *Western North American Naturalist* **72**: 432–441.	D, V	AZ	Reference lists

Reference	Subject[a]	Location[b]	Source[c]
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:** DOI: 10.1029/2011WR011227.	H	WY	ISI
Brown DJ, Hubert WA, Anderson SH. 1996. Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. *Wetlands* **16**: 127–133.	B	WY	ISI
Call MW. 1970. Beaver pond ecology and beaver-trout relationships in southeastern Wyoming. PhD thesis, University of Wyoming, WY.	F	WY	ISI
Chu H, Jiang Z. 2009. Distribution and conservation of the Sino-Mongolian beaver *Castor fiber birulai* in China. *Oryx* **43:** 197-202.	D	China, Mongolia	GS
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.	W	NM	ISI
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.	D, V, B	WY	ISI, GS
Dalquest WW, Stangl Jr FB, Kocurko MJ. 1990. Zoogeographic implications of Holocene mammal remains from ancient beaver ponds in Oklahoma and New Mexico. *The Southwestern Naturalist* **35**: 105–110.	D	NM, OK	ISI
Demmer R, Beschta RL. 2008. Recent history (1988–2004) of beaver dams along Bridge Creek in central Oregon. *Northwest Science* **82**: 309–318.	D, G, H, V	OR	ISI, GS
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.	M	CO	ISI, GS
DeVries P, Fetherston KL, Vitale A, Madsen S. 2012. Emulating riverine landscape controls of beaver in stream restoration. *Fisheries* **37**: 246–255.	G, H, R	ID	ISI, GS
Dixon J. 1922. Rodents and reclamation in the Imperial Valley. *Journal of Mammalogy* **3**: 136–146.	D	CA	GS
Easter-Pilcher A. 1990. Cache size as an index to beaver colony size in northwestern Montana. *Wildlife Society Bulletin* **18**: 110–113.	D	MT	ISI
Fanelli RM, Lautz LK. 2008. Patterns of water, heat, and solute flux through streambeds around small dams. *Ground Water* **46**: 671–687.	H, W	WY	Reference lists
Ffolliott PF, Clary WP, Larson FR. 1976. Observations of beaver activity in an extreme environment. *The Southwestern Naturalist* **21**: 131–133.	D	AZ	ISI, GS

Reference	Subject[a]	Location[b]	Source[c]
Fischer JW, Joos RE, Neubaum MA, Taylor JD, Bergman DL, Nolte DL, Piaggio AJ. 2010. Lactating North American beavers (*Castor canadensis)* sharing dens in the southwestern United States. *The Southwestern Naturalist* **55**: 273–277.	D	AZ	ISI, GS
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.	G	MT	Reference lists
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.	D	Sonora, Mexico	ISI
Harper BJ. 2001. The ecological role of beavers (*Castor canadensis*) in a Southwestern desert stream. MS thesis, University of Nevada, NV.	D, W, V	NV	GS
Hubbard KA, Lautz LK, Mitchell MJ, Mayer B, Hotchkiss ER. 2010. Evaluating nitrate uptake in a Rocky Mountain stream using labelled 15N and ambient nitrate chemistry. *Hydrological Processes* **24**: 3322–3336.	H, W	WY	ISI
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.	F	MT	ISI
Jin L, Siegel DI, Lautz LK, Otz MH. 2009. Transient storage and downstream solute transport in nested stream reaches affected by beaver dams. *Hydrological Processes* **23**: 2438–2449.	H, W	WY	ISI
Johnson DR, Chance DH. 1974. Presettlement overharvest of upper Columbia River beaver populations. *Canadian Journal of Zoology* **52**: 1519–1521.	D	AB, ID, OR, WA	Reference lists
Johnson G. 2011. Bird abundance and richness in a desert riparian area following beaver re-introduction. MS thesis, University of Arizona, AZ.	D, G, B, R	AZ	Reference lists
Johnson SL, Rahel FJ, Hubert WA. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. *North American Journal of Fisheries Management* **12**: 118–124.	F	WY	ISI
Kelsch SW. 1994. Lotic fish-community structure following transition from severe drought to high discharge. *Journal of Freshwater Ecology* **9**: 331–341.	F	ND	ISI
Kimball BA, Perry KR. 2008. Manipulating beaver (C*astor canadensis*) feeding responses to invasive tamarisk (*Tamarix* spp.). *Journal of Chemical Ecology* **34**: 1050–1056.	V	none	GS
Kindschy RR. 1985. Response of red willow to beaver use in southeastern Oregon. *The Journal of Wildlife Management* **49**: 26–28.	V	OR	ISI, GS
Kindschy RR. 1989. Regrowth of willow following simulated beaver cutting. *Wildlife Society Bulletin* **17:** 290-294.	V	OR	Reference lists

Reference	Subject[a]	Location[b]	Source[c]
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.	D	CA	ISI
Lautz LK, Siegel DI, Bauer RL. 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. *Hydrological Processes* **20**: 183–196.	H, W	WY	ISI
Lautz LK, Kranes NT, Siegel DI. 2010. Heat tracing of heterogeneous hyporheic exchange adjacent to in-stream geomorphic features. *Hydrological Processes* **24**: 3074–3086.	H, W	WY	Reference lists
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.	V	MT	ISI
Lesica P, Miles S. 2001. Natural history and invasion of Russian olive along eastern Montana rivers. *Western North American Naturalist* **61**: 1–10.	V	MT	ISI
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.	V	MT	ISI, GS
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.	D	WA	GS
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.	V, B, R	CA	ISI, GS
Lowry MM. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. MS thesis, Oregon State University, OR.	H, W	OR	GS
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.	W	WY	ISI, GS
McComb WC, Sedell JR, Buchholz TD. 1990. Dam-site selection by beavers in an eastern Oregon basin. *Western North American Naturalist* **50**: 273–281.	D	OR	ISI, GS
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.	V	UT	Reference lists
McKinstry MC, Anderson SH. 1999. Attitudes of private-and public-land managers in Wyoming, USA, toward beaver. *Environmental Management* **23**: 95–101.	M	WY	ISI
McKinstry MC, Anderson SH. 2002. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. *Canadian Field-Naturalist* **116**: 60–68.	D, R	WY	ISI

Reference	Subject[a]	Location[b]	Source[c]
McKinstry MC, Caffrey P, Anderson SH. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association* **37**: 1571–1577.	D, B, R	WY	ISI, GS
McKinstry MC, Karhu RR, Anderson SH. 1997. Use of active beaver, *Castor canadensis*, lodges by muskrats, *Ondatra zibethicu*s, in Wyoming. *Canadian Field-Naturalist* **111:** 310-311.	M, R	WY	ISI
Mellink E, Luevano J. 1998. Status of beavers (*Castor canadensis)* in Valle de Mexicali, Mexico. *Bulletin Southern California Academy of Sciences* **97:** 115-120.	D	Mexico	ISI
Milholland MT, Shumate JP, Simpson TR, Manning RW. 2010. Nutria (*Myocastor coypus)* in Big Bend National Park: a non-native species in desert wetlands. *Texas Journal of Science* **62:** 205-222.	F, M	TX	ISI
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.	V	AZ	ISI
Osmundson CL, Buskirk SW. 1993. Size of food caches as a predictor of beaver colony size. *Wildlife Society Bulletin* **21**: 64–69.	D	WY	ISI
Pinkowski B. 1983. Foraging behavior of beavers (*Castor canadensis)* in North Dakota. *Journal of Mammalogy* **64**: 312–314.	V	ND	ISI
Platt SG, Fast Horse Z, Rainwater TR, Miller SM. 2009. Distribution records and comments on mammals in western South Dakota. *Western North American Naturalist* **69**: 329–334.	D	SD	ISI
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.	G, H, R	OR	ISI, GS
Robel RJ, Fox LB. 1993. Comparison of aerial and ground survey techniques to determine beaver colony densities in Kansas. *The Southwestern Naturalist* **38:** 357–361.	D	KS	ISI, GS
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.	D	AZ	ISI
Sharps DE. 1996. Spatial and temporal characteristics of groundwater levels adjacent to beaver ponds in Oregon. MS thesis, Oregon State University, OR.	H	OR	Reference lists
Skinner QD, Speck Jr JE, Smith M, Adams JC. 1984. Stream water quality as influenced by beaver within grazing systems in Wyoming. *Journal of Range Management* **37:** 142–146.	D, W	WY	ISI
Swenson JE, Knapp SJ, Martin PR, Hinz TC. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. *The Journal of Wildlife Management* **47:** 697–703.	D	MT	ISI

Reference	Subject[a]	Location[b]	Source[c]
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.	F, W	OR	GS
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.	V	AZ, NV	ISI, GS
Thompson DJ, Fecske DM, Jenks JA, Jarding AR. 2009. Food habits of recolonizing cougars in the Dakotas: prey obtained from prairie and agricultural habitats. *The American Midland Naturalist* **161**: 69–75.	M	ND, SD	ISI
Weintraub JD. 1986. Coyote diets, five years later, at Cuyamaca Rancho State Park. *Bulletin-Southern California Academy of Sciences* **85:** 152:157.	M	CA	ISI
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.	F	WY	ISI
Winkle PL, Hubert WA, Rahel FJ. 1990. Relations between brook trout standing stocks and habitat features in beaver ponds in southeastern Wyoming. *North American Journal of Fisheries Management* **10**: 72–79.	F	WY	ISI
Wolff SW, Wesche TA, Hubert WA. 1989. Stream channel and habitat changes due to flow augmentation. *Regulated Rivers: Research & Management* **4**: 225–233.	D	WY	ISI

[a] Subtopic(s) addressed by source: D = Distribution and status; G = Geomorphology; H = Hydrology; W = Water quality and chemistry; V = Riparian vegetation; M = Mammals; B = Birds; F = Fish; R = Restoration.

[b] Location of study site. Abbreviations indicate USA states or Canadian provinces.

[c] Method by which source was located: ISI = ISI Web of Science; GS = Google Scholar; additional sources were identified via Reference lists.

Table S4. Sources for density values displayed in Fig. 1.3. Unless otherwise indicated, density values are based on ground surveys for beaver dams, and dam numbers include all functional beaver dams (i.e., both active and inactive).

Reference	Stream length surveyed (km)	Num. dams	Dam density (dams/km)	Location	Stream[a]	Num. streams[b]	Aridity[c]	Comments
DAM DENSITY IN TEMPERATE STREAMS								
Butler DR, Malanson GP. 1994. Beaver landforms. *The Canadian Geographer* **38**: 76–79.	0.2	5	25.0	Montana	unspecified	1	humid	Not a formal survey. Authors report upper end of range of dam densities observed in Glacier National Park area.
Flynn NJ. 2006. Spatial associations of beaver ponds and culverts in boreal headwater streams. MS thesis, University of Alberta, AB.	153.0	172	1.1	Alberta	numerous within north-central Alberta	numerous	humid	Numerous 2km survey segments centered around road crossings. 1st-3rd order streams only.
Kotak, BG, Selinger A, Johnston B. 2005. Influence of watershed features and disturbance history on water quality in boreal shield streams and rivers of eastern Manitoba. Black River First Nation Manitoba Model Forest Report 04-2-63.	512.0	193	0.4	Manitoba	numerous within Manitoba Model Forest area	12	humid	Aerial survey. Survey includes several tributaries in addition to 12 primary streams.
Leidholt-Bruner K, Hibbs DE, McComb WC. 1992. Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. *Northwest Science* **66**: 218–223.	15.0	16	1.1	Oregon	Cummins Creek and Cape Creek	2	humid	Stream length is estimated to nearest km.
Loates BM, Hvenegaard GT. 2008. The density of beaver, *Castor canadensis*, activities along Camrose Creek, AB, within differing habitats and management intensity levels. *The Canadian Field-Naturalist* **122**: 299–302.	35.0	107	3.1	Alberta	Camrose Creek	1	dry sub-humid	
McCullough MC, Eisenhauer DE, Dosskey MG, Admiral DM. 2006. Hydraulic characteristics and dynamics of beaver dams in a midwestern us agricultural watershed. *World Environmental and World Resources Conference*.	7.3	21	2.9	Nebraska	Little Muddy Creek	1	humid	Dam numbers are conservative (count excludes damaged dams, even if the dam is still impounding water). 1st-3rd order streams only.
MidCoast Watersheds Council. 2008. Annual report. MidCoast Watersheds Council, Newport, OR.	91.2	229	2.5	Oregon	Yaquina River basin	numerous	humid	Survey prompted by concern that beaver numbers had declined sharply in this river basin over the past decade.

Reference	Stream length surveyed (km)	Num. dams	Dam density (dams/km)	Location	Stream[a]	Num. streams[b]	Aridity[c]	Comments
Naiman RJ, Melillo JM, Hobbie JE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* ***67***: 1254–1269.	4.3	43	10.1	Quebec	Matamek and Moisie River basins	4	humid	Nearly pristine area.
Smith AE. 1950. Effects of water runoff and gradient on beaver in mountain streams. MS thesis, University of Michigan, MI.	8.7	90	10.3	Colorado	Slate Creek	1	dry sub-humid	Dam count may include non-functional dams.
Smith JM, Mather ME. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology* **58**: 1523–1538.	20.4	14	0.7	Massachusetts	Fish Brook	1	humid	Only mainstem Fish Brook (no tributaries) is included in density value.
Stevens C, Paszkowski C, Foote A. 2007. Beaver (*Castor canadensis)* as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation* **134**: 1–13.	325.6	590	1.8	Alberta	North Saskatchewan River and Pembina River basins	numerous	humid	Beaver ponds located using aerial photography.
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.	65.0	170	2.6	Oregon	Drift Creek basin	11	humid	1st-5th order streams.
USDA Forest Service. 2004. Strawberry Watershed restoration report. Uinta National Forest, Heber City, UT.	35.4	311	8.8	Utah	Strawberry River basin	16	dry sub-humid	
Warren ER. 1926. Notes on the beaver colonies in the Longs Peak region of Estes Park. Roosevelt *Wildlife Annals* **1:**2.	1.3	50	38.5	Colorado	Roaring Fork	1	humid	Dam count and stream length are approximate. Survey documents the density of beaver dams within a single large colony. Author reports "an enormous amount of beaver work" in this area.

Reference	Stream length surveyed (km)	Num. dams	Dam density (dams/km)	Location	Stream[a]	Num. streams[b]	Aridity[c]	Comments
DAM DENSITY IN DRYLAND STREAMS								
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.	58.0	42	0.7	Arizona	Bill Williams River	1	arid	Combination of ground survey and aerial photographs. 0.72 dams/km was the minimum dam density reported over three years of beaver dam survey. Most of the dams counted in this year's survey were concentrated within a single valley.
Andersen and Shafroth, 2010 [maximum density]	58.0	104	1.8	Arizona	Bill Williams River	1	arid	Combination of ground survey and aerial photographs. 1.79 dams/km was the maximum dam density reported over three years of beaver dam survey.
Baker B, Cade B. 1995. Predicting biomass of beaver food from willow stem diameters. *Journal of Range Management* **48**: 322–326.	23.0	334	14.5	Colorado	Douglas Creek	1	semi-arid	Highly eroded drainage; dam density at time of survey (1990) had increased following ten years of watershed restoration effort (e.g., increased willow cover, wider floodplains).
Call MW. 1970. Beaver pond ecology and beaver-trout relationships in southeastern Wyoming. PhD thesis, University of Wyoming, WY.	144.8	4280	29.6	Wyoming	several within Pole Mountain Recreation Area	12	borderline semi-arid/dry sub-humid	Survey includes several tributaries in addition to 12 primary streams.
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.	1.5	62	41.3	Wyoming	unspecified	1	semi-arid	This dam density is an overestimate: reported survey length is in straight-line distance rather than river distance. Additionally, this dam density represents the maximum density obseved, from a pool of 11 surveyed stream segments located throughout Wyoming.
Demmer R, Beschta RL. 2008. Recent history (1988–2004) of beaver dams along Bridge Creek in central Oregon. *Northwest Science* **82**: 309–318.	25.4	9	0.4	Oregon	Bridge Creek	1	semi-arid	0.35 dams/km was the minimum dam density reported over seventeen years of semiannual beaver dam survey.
Demmer and Beschta, 2008 [maximum density]	25.4	103	4.1	Oregon	Bridge Creek	1	semi-arid	4.06 dams/km was the maximum dam density reported over seventeen years of semiannual beaver dam survey.

Reference	Stream length surveyed (km)	Num. dams	Dam density (dams/km)	Location	Stream[a]	Num. streams[b]	Aridity[c]	Comments
Gibson, unpublished data	79.2	48	0.6	Arizona	Verde River basin	7	semi-arid	Survey includes segments of mainstem and six tributaries. Dam densities vary widely among and within tributaries.
Gurche P. 2011. In search of desert beaver: an assessment of *Castor canadensis* in the lower Escalante River watershed. Grand Canyon Trust.	70.0	82	1.2	Utah	lower Escalante River basin	8	arid/semi-arid	Density varies widely among individual tributaries.
Harper BJ. 2001. The ecological role of beavers (*Castor canadensis*) in a Southwestern desert stream. MS thesis, University of Nevada, NV.	31.5	26	0.8	Nevada	Meadow Valley Wash	1	arid/semi-arid	
Hubbard KA, Lautz LK, Mitchell MJ, Mayer B, Hotchkiss ER. 2010. Evaluating nitrate uptake in a Rocky Mountain stream using labelled 15N and ambient nitrate chemistry. *Hydrological Processes* **24**: 3322–3336.	2.2	3	1.4	Wyoming	Red Canyon Creek	1	semi-arid	Management has "encouraged" beaver occupancy of this area.
Jin L, Siegel DI, Lautz LK, Otz MH. 2009. Transient storage and downstream solute transport in nested stream reaches affected by beaver dams. *Hydrological Processes* **23**: 2438–2449.	2.4	31	13.1	Wyoming	Cherry Creek	1	semi-arid	Area selected for relatively high beaver dam density. Dam density varies widely within survey reach.
Johnson G. 2011. Bird abundance and richness in a desert riparian area following beaver re-introduction. MS thesis, University of Arizona, AZ.	68.5	32	0.5	Arizona	San Pedro River	1	semi-arid	Beaver dam activity appeared to be increasing at the time of this survey (2006), just six years after reintroduction of beaver to the San Pedro River.
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.	16.1	76	4.7	Washington	Umtanum Creek	1	semi-arid	Density value based on perennial stream length only, not including intermittent stream length.
Lokteff RL, Roper BB, Wheaton JM. 2013. Do beaver dams impede the movement of trout? *Transactions of the American Fisheries Society* **142**: 1114–1125.	5.1	27	5.3	Utah	Temple Fork and Spawn Creek	2	semi-arid	
McComb WC, Sedell JR, Buchholz TD. 1990. Dam-site selection by beavers in an eastern Oregon basin. *Western North American Naturalist* **50**: 273–281.	98.0	14	0.1	Oregon	Long Creek basin	4	semi-arid	Survey by air.

Reference	Stream length surveyed (km)	Num. dams	Dam density (dams/km)	Location	Stream[a]	Num. streams[b]	Aridity[c]	Comments
Robinson AT, Carter C, Ward D, Blasius H. 2009. Bonita Creek native fish restoration: native aquatic species salvage, chemical renovation, and repatriation of native aquatic species. Arizona Game and Fish Department, Phoenix, AZ.	4.3	46	10.7	Arizona	Bonita Creek	1	arid / semi-arid	46 beaver dams removed as part of a native fish salvage effort.
Scheffer PM. 1938. The beaver as an upstream engineer. *Soil Conservation* **3:** 178-181.	0.6	22	36.7	Washington	East Branch Mission Creek	1	semi-arid	Survey documents the density of beaver dams within a single large colony.
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.	28.1	260	9.3	Oregon	Willow Creek	1	semi-arid	
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.	12.2	48	3.9	Wyoming	Water Canyon, Huff Creek	2	semi-arid	2 streams surveyed, but functional beaver dams found only on Water Canyon (Water Canyon only = 4.9km survey length, density = 9.8 dams/km).

[a] Name of stream or watershed where dam survey was conducted.

[b] Number of separate streams included in the density value (e.g., 1 mainstem + 5 tributaries = 6 streams). Sources providing densities for multiple tributaries from one watershed were combined into a single aggregate value.

[c] Aridity zone of the location where the survey was conducted. Aridity zones based on Trabucco and Zomer (2009) (see Fig. 1).