Chapter 12
Invertebrates in Beaver-Created Wetlands and Ponds

Bryana M. Bush and Scott A. Wissinger

Introduction

Eurasian (*Castor fiber*) and North American (*Castor canadensis*) beavers are semi-aquatic mammals that modify the hydrology of streams and other water bodies by constructing dams. The modified aquatic habitats associated with beaver activities were once a ubiquitous feature of the post-Pleistocene landscape throughout the temperate and boreal zones of North America and Europe. By the end of the nineteenth century, trapping and hunting by humans had extirpated beavers across much of their former range (e.g., Johnson and Chance 1974; Danilov et al. 2011). Since then, the recovery and/or reintroduction of populations in North America and Europe (Naiman et al. 1988a, b; Hartman 1994, 1995; Nolet and Rosell 1998; Bluzma 2003; Halley et al. 2012; Law et al. 2014) have led to (1) dramatic changes in the structure and function of headwater and middle orders streams and adjacent riparian zones (Naiman et al. 1988b; Rosell et al. 2005) and (2) the creation and maintenance of wetland habitats within and beyond the boundaries of stream valleys (McCall et al. 1996; Syphard and Garcia 2001).

Research on invertebrate communities in aquatic habitats associated with beaver activities can be divided into general groups of studies: (1) those with a distinctly "running water perspective" that focus on how beaver dams change stream invertebrate communities at multiple scales (reach, stream segment, stream system; Allan 2004) and (2) those with a distinctly wetlands/pond perspective on the plant and animal life that inhabit the many types of shallow lentic habitats outside of stream channels. We first briefly summarize the major themes from the large literature focused on how beavers affect stream invertebrate communities, and then turn to focus on the distinctly lentic invertebrate communities that occur in non-channel wetlands created by beavers.

Stream Ecology Perspective on Beaver Dam Invertebrates

Beaver Reestablishment in Native Range and Changing Streamscapes

Robert Naiman and colleagues established the general paradigm for the effects of beaver activity on stream invertebrates by describing how the presence of beaver dams in stream channels modifies nearly every aspect of the physicochemical (water chemistry, carbon budgets, nutrient spiraling, flow regimes, physical substrates, retention/turnover of organic matter, etc.) and biological (hetero- and auto-trophic microbial assemblages, community metabolism, plants, invertebrates, fish, waterfowl) environment in stream channels and adjacent riparian habitats (Naiman and Melillo 1984; Naiman et al. 1986, 1988a, b; also see Rosell et al. 2005). From the perspective of stream ecologists, hydrologists, and fluvial geomorphologists, the recovery of beaver populations in North America and Eurasia during the past 100 years has prompted a reevaluation of the structure and function of headwater and middle-order streams as compared to when and where beavers had (have) been extirpated (Naiman et al. 1986, 1988b; Cirmo and Driscoll 1993; Devito and Dillon 1993; Hammerson 1994; Pollock et al. 1995; Klotz 1998; Snodgrass and Meffe 1998; Collen and Gibson 2001; Butler and Malanson 2005; Pollock et al. 2007; Burchsted and Daniels 2014; Curran and Cannatelli 2014). The hydrology of beaver ponds in this context is dominated by stream flow inputs and outputs, and the dams can reduce peak channel discharge by temporarily storing water and shunting it to the adjacent riparian zone/floodplain (Fig. 12.1a). This is one of three potential losses of water between channel inflow and outflow in beaver dams. A second is through evapotranspiration because of the increased surface area and residence times, especially in arid environments (Andersen et al. 2011), and a third is through downwelling into the shallow ground water that moves down vallies through unconsolidated sediments. In arid land streams, groundwater recharge from beaver ponds and wetlands can enhance shallow groundwater storage, which later supplements channel flow during low-flow conditions, potentially converting intermittent to perennial streams (Fig. 12.1b, Gibson and Olden 2014).

In steep gradient headwater and middle-order streams, beaver activity in North America and Eurasia leads to the replacement of erosional (riffle) assemblages of invertebrates typical of high-oxygen, turbulent-flow, hard-substrate habitats (e.g., stoneflies, mayflies, riffle beetles, net-spinning caddisflies) with communities that are more typical of depositional environments (pools, runs) that have relatively slow, laminar flow, relatively low oxygen, and a predominance of soft substrates (e.g., chironomids and other dipterans, odonates, dytiscid beetles, hemipterans, annelids, epibenthic crustaceans). At the reach scale, invertebrate biomass is much higher (1.3–11.1 g m^{-2}) in pools behind beaver dams than in adjacent riffles (0.01–0.6 g m^{-2}), but taxonomic diversity between the habitats is similar (McDowell and Naiman 1986; Naiman et al. 1986). However, at the stream-segment or beta
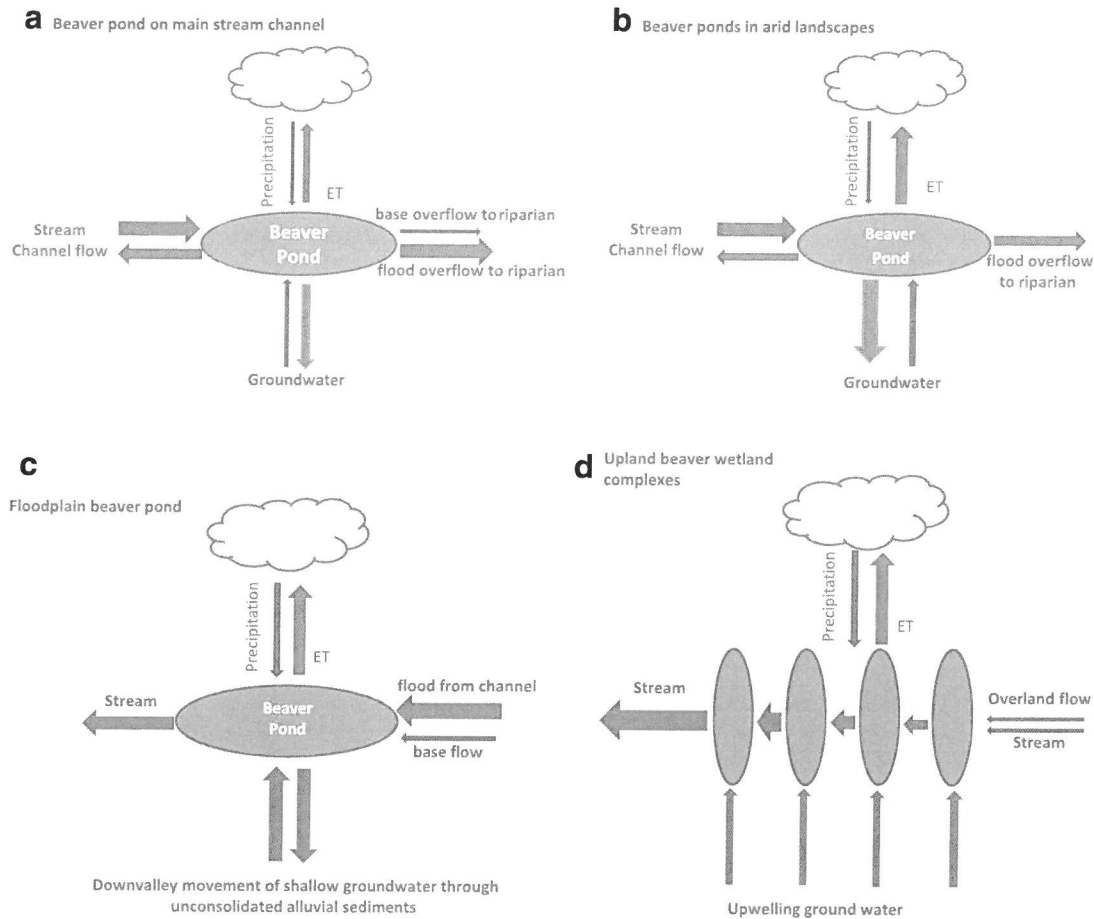
a Beaver pond on main stream channel

b Beaver ponds in arid landscapes

c Floodplain beaver pond

d Upland beaver wetland complexes

Fig. 12.1 The hydrology of ponds and wetlands associated with beaver activity. (**a**) The hydrology of beaver ponds in main channels will be dominated by stream flow inputs and outputs, and hence be temporally dynamic. Channel flow can be greater than outflow because of (1) bank overflow to the adjacent riparian zone, (2) enhanced evapotranspiration, and/or (3) hyporheic loss with the downstream return flow path dependent on the geomorphologic context (Rosell et al. 2005). (**b**) In arid landscapes, the three losses between stream input and output will be exaggerated because of enhanced evaporation and lateral and vertical losses to shallow groundwater. The temporary storage in that shallow groundwater can be especially important for ameliorating downstream low-flow conditions (Gibson and Olden 2014). (**c**) In beaver ponds and wetlands situated in floodplains away from the main stream channel, the hydrologic budget will be strongly influenced by shallow ground water and lateral hyporheic flow moving down valley through unconsolidated sediments. Proximity to the main channel will determine the frequency and duration of inputs from floods (see Fig. 12.3b). (**d**) Beaver dam wetland complexes in relatively upland landscapes (perched water tables, along valley margins) receive much of their hydrologic input from springs and upwelling groundwater discharge that then leaves the wetland complex as the channel flow of headwater streams. This hydrology model fits beaver meadow complexes in Northeastern North America and those on valley margins in Western North America (see text)

diversity scale (Allan 2004), the longitudinal sequences of these alternating habitat types results in an increase in the overall taxonomic and trophic (functional-feeding-group) diversity as compared to streams lacking beaver dams (e.g., Sprules 1940 [Ontario]; McDowell and Naiman 1986 [Quebec]; Harthun 1999 [Hesse, Germany]; Smith et al. 1991 [New York]; Margolis et al. 2001 [Pennsylvania]; Pliūraitė and Kesminas 2012 [Lithuania]).

The patches of large woody debris associated with dams (Fig. 12.2) and huts can harbor unique assemblages of invertebrate species dominated by grazers and filter feeders (e.g., simuliid larvae; Clifford et al. 1993; Adler and Mason 1997). Rolauffs et al. (2001) found higher invertebrate diversity and higher secondary productivity on coarse woody substrates of dams than in either riffles or the pools created by the dams, perhaps as a result of some combination of the (1) extensive surface area of these complex structures, (2) availability of organic materials (wood substrate with biofilm and flow-through suspended particulates), (3) high organic turnover rate, and (4) aerobic conditions at the water–air interface.

Several studies have compared stream invertebrate communities between comparable habitats above and below beaver dams. In a small, low gradient stream in northeastern North America (New York state), Smith et al. (1991) found that stream invertebrate assemblages below dams are less diverse and have lower densities of Plecoptera, Trichoptera, and filter feeders (taxa not specified). In contrast, Fuller and Peckarsky (2011a) found no systematic differences among functional feeding groups (FFGs) above and below ponds and no differences driven by dam morphology among FFG with the exception of suspension feeders. The abundance of suspension feeders, and especially simuliids, increases below beaver ponds with high hydraulic head dams, which is also typical downstream of man-made reservoirs due to high seston pulses (Mackay and Waters 1986; Richardson and Mackay 1991). However, suspension feeders decrease below ponds with a low hydraulic head dam, and the difference between high- and low-head dams is not driven by algae spillover from dams. Fuller and Peckarsky (2011a) hypothesize that higher abundance of suspension feeders below high head dams could be related to a higher availability of bacterial seston or increased scour downstream of high head dams, but not below low head dams, both of which are favorable for simuliids. Invertebrates were not influenced by any differences in nutrients, algal biomass, and benthic organic matter among stream reaches above and below ponds related to dam morphology.

In a related study, Fuller and Peckarsky (2011b) studied the impact beaver pond morphology had on mayfly life history (Fig. 12.2). They evaluated downstream effects of beaver pond morphology on *Baetis bicaudatus* size and timing of emergence. Reaches downstream of high head, low surface area ponds produced larger females than low head ponds with larger surface area, and females found below the pond were larger than those found above. Male size differences followed similar patterns but were not significantly different. Because large female *B. bicaudatus* are more fecund than small females, Fuller and Peckarsky hypothesize that the next generation could vary in size by +11 to −12 % depending on pond morphology. Larger female size downstream of high head ponds corresponds with colder water temperatures in these areas. Outflow water is colder than pond water, probably as a result of groundwater upwelling below the high hydraulic head dams. Despite temperature differences, pond morphology did not predict timing of emergence of mayflies downstream of dams. In general, where groundwater lost through the hyporheic in beaver ponds resurfaces as channel

Fig. 12.2 Beaver dams on a high gradient stream (West Brush Creek) in the Elk Mountains of Colorado (see Fuller and Peckarsky 2011a, b; photo courtesy of Matt Fuller)

flow (see Fig. 12.1a, b) should have important consequences for how beaver dams affect downstream invertebrate communities.

Impounded reaches of channels in low gradient streams are likely to have an enhanced wetted area of overhanging vegetation and snag habitats along flooded shoreline margins (Johnston and Naiman 1987). The importance of channel-margin overhanging vegetation as substrate for aquatic invertebrates is well described in other stream contexts (e.g., coastal plain rivers—Benke et al. 1985). The secondary production of aquatic invertebrates on these substrates can dwarf that on channel substrates and can be the most important source of production for fisheries in slow-moving, soft-sediment channels (as in Benke et al. 1984). Indeed, literature reviews and meta-analyses of the positive effects of beavers on stream fish cite the high invertebrate productivity in stream habitats associated with beaver activity (pools, wetted margins, dams, huts) as an important positive effect on stream fish abundance, growth, and productivity (reviews by Collen and Gibson 2001; Kemp et al. 2012). Other positive effects of beavers on fish are related to the effects of habitat heterogeneity in the streamscape on overwintering success, juvenile refugia, recruitment, and connectivity between juvenile and adult habitats; whereas barriers to fish movement and increased temperatures (and decreased oxygen) towards upper tolerance thresholds are cited as negative effects in those

same reviews. The degree to which beavers have a positive or negative effect on native brook trout, the top predator in high gradient, headwater streams in northeastern North America, appears to vary across locations and geomorphological context (White and Rahel 2008; Niles et al. 2013). From the perspective of our focus here on invertebrates, we did not find any studies that consider how the changes in fish communities associated with beaver activity feed back on invertebrate communities.

There is also a large literature on the positive effects of beaver activity on the growth, survival, and diversity of waterbirds that is attributed to the creation of structurally favorable habitats for breeding and survival (e.g., Brown et al. 1996; McKinstry et al. 2001), and to the high primary and secondary productivity in beaver-created wetlands, including invertebrate production (e.g., Nummi and Hahtola 2008; Nummi and Holopainen 2014). However, it is not clear how increased density, diversity, and production of waterbirds in turn affect beaver pond invertebrate communities.

In relatively flat landscape settings, it appears that the invertebrate communities in the pools that develop upstream of dams are comparable to those typical in standing water habitats. For example, in low gradient streams in Hesse, Germany, the macroinvertebrate communities in beaver ponds are distinctly different from those in unimpounded reaches with high diversity of taxonomic groups (e.g., 11–18 odonates, 11–22 caddisflies including many limnephilids that are typically lentic; Harthun 1999). In contrast, in the Bigoray River in Alberta, Canada, Clifford et al. (1993) found that, although the percent composition varied between habitats, there were seven taxa that were common to both unimpounded and impounded reaches of this slow moving 3rd order stream. For example, Simuliidae represented more than 80 % of the most abundant taxa in the fast water associated with the dams, but less than 3 % in unimpounded sites. Chironomidae made up less than 12 % of the most abundant taxa in dams; however, it comprised more than 48 % in unimpounded reaches of the same streams. In addition, unimpounded sites contained taxa frequently associated with slower reaches (*Pisidium* spp., *Leptophlebia cupida*, *Caenis* spp.) and both cluster and principal component analysis separated dam sites and stream sites. Thus, it appears that in some hydrologic and geomorphic contexts, beaver dams can be important refuge for lotic taxa in slow moving streams, and in others, are more likely to reduce the available habitat for those taxa. It is possible that in relatively small streams with confined valleys, beaver activities may overwhelm the capacity and competence of low stream discharge to create truly lentic-like habitats, whereas in the context of higher flows and unconfined channels, the redistribution and artificially cascaded nature of channel flows across multiple distributaries may actually enhance the lateral presence of erosional (riffle) and depositional (pool) habitats.

In unconfined geomorphological settings (e.g., broad valleys), the in-channel invertebrate diversity at the stream-segment scale should be complemented by the creation of lateral habitats that support other types of invertebrate assemblages on adjacent shoreline margins (see Johnston and Naiman 1987), and out-of-channel

riparian habitats including paleochannels with active and abandoned beaver dams. For example, in relatively flat stream segments in the U-shaped valleys created by mountain glaciers in western North America (Fig. 12.3a), single, meandering channels can be transformed by beavers into valley wide systems of distributaries, each with a complex longitudinal and lateral sequence of habitat types associated with beaver activities including open ponds, systems of channels connecting those ponds, and extensive willow (*Salix* sp.) and sedge (*Carex* sp.) meadow wetland habitats (Fig. 12.3b). The hydrology of floodplain beaver ponds outside of the main channel will vary depending on proximity to the main channel. The hydrology of ponds close to the main channel will be more affected by changes in stream flow conditions than those isolated laterally from the channel. The hydrology of the latter will be dominated by inputs and outputs dominated by the down valley movements of shallow groundwater and lateral hyporheic losses from the main channel (Figs. 12.1c and 12.3b). In this geomorphologic setting, there is likely to

Fig. 12.3 Beaver pond wetlands in the lower East River Valley in the Elk Mountains of central Colorado below the Rocky Mountain Biological Laboratory. (**a**) Overview of meandering river in a glacially widened montane valley in spring (photo by Scott Wissinger). (**b**) *Arrow* indicates location of zoom to floodplain complex of beaver ponds (note beaver hut in pond on *lower left*) and difference in water color between channel (spring runoff) and beaver-created riparian wetlands which include open ponds, channels connecting ponds, and extensive willow-thicket and sedge-meadow wetlands that cover most of the valley bottom (photo by Susan Washko)

be a continuum of invertebrate communities ranging from those dominated by taxa typical of pools in stream channels to those dominated by lentic taxa typical of non-riparian wetlands and ponds (see discussion below of Western Beaver Wetlands; Appendix).

Beaver Impacts Outside of Native Range

Finally, given the transformative effects that beavers can have on nearly every aspect of running water systems, it is not surprising that they are having profound impacts as invasive species on stream ecosystems outside of their native range. In streams of south-temperate South America, Anderson and colleagues studied the impacts of invasive beavers on stream ecosystem structure and function, including the effects on stream invertebrate diversity, community composition, and productivity (Anderson and Rosemond 2007, 2010; Anderson et al. 2009). In a comprehensive review of the impacts of beavers on the physical and biological environments of stream systems in south temperate South America, they concluded that the impacts of beavers as exotic invasive species was of similar magnitude and direction as that observed in studies in the native range of beavers (Anderson et al. 2009). In South America, they compared unimpacted reaches to reaches with beaver ponds to reaches below beaver ponds and found lower taxonomic and FFG diversity in the pools associated with dams than in either upstream or downstream reaches, which did not differ from unimpacted reaches (Anderson and Rosemond 2007). They attributed this difference to the relatively homogenous microhabitat in the soft sediments of the pools, although they did not appear to include other types of habitats (wetted margins, dams, hut). Examining other beaver-associated habitats could be important in obtaining a full picture of invertebrate diversity as these other connected habitats increase habitat heterogeneity, which has increased diversity in beaver-influenced habitats elsewhere. They also found invertebrate abundance, biomass, and secondary production were higher in the pools associated with dams as compared to above or below undammed reaches (Anderson and Rosemond 2007), which was consistent with the literature from North America and Eurasia (Anderson et al. 2009). They tested the hypothesis that this higher productivity was associated with increased production and input of allochthonous detritus using stable isotopes and found a slight increase in reaches with vs. without beaver dams (Anderson and Rosemond 2010). Anderson and colleagues argued that because the in-stream productivity and metabolism in these forested catchments is naturally driven primarily by allochthonous subsidies, beaver impacts are small. They predict that in streams where autochthonous production contributes a larger fraction of the overall energy budget, beavers will have a bigger impact on shifting the metabolism of a stream reach towards autochthonous production (as in Naiman et al. 1986, 1988b).

Lentic Invertebrate Communities in Beaver Wetlands

Beaver-Meadow Wetland Complexes in Northeastern North America

In relatively flat-lying landscapes, beaver activities beyond the main channels of streams can create extensive and persistent wetland complexes that are distinctly lentic in character (Fig. 12.4a). These habitats are variably described as "beaver-pond wetlands," "beaver meadow wetlands," or "valley beaver impoundments" (Burchsted et al. 2010; Polvi and Wohl 2012). As a result of the recolonization of beavers over the past 100 years, these wetland complexes have become a ubiquitous feature of the landscape in northeastern North America (from west to east— Minnesota, Wisconsin, Michigan, Ontario, Ohio, Pennsylvania, New York, New England, Quebec, New Brunswick, and non-urbanized areas of the coastal Atlantic states). Along the northern tier of this region (i.e., southern Canada and border states of the USA), beaver dams that occur beyond the margins of stream courses can transform vast tracts of saturated-soil peatlands into complexes of open ponds, marshes, and shrub swamps that are interconnected by beaver-constructed standing-water canals (Naiman et al. 1986, 1988b; Rebertus 1986; Johnston and Naiman 1990; Woo and Waddington 1990; McCall et al. 1996; Donkor and Fryxell 2000; Ray et al. 2004). Beaver wetland complexes that are not part of peatlands are also common further to the south in glaciated and unglaciated landscapes of Ohio, Pennsylvania, Ontario, and New York, often at the boundary between upland and lowland terrain (Johnston and Naiman 1987; Grover and Baldassarre 1995; Wissinger and Gallagher 1999). The hydrologic budget of beaver wetland complexes is often tied to upwelling areas of groundwater discharge with the outflows below the complexes forming perennial headwater streams (Fig. 12.1d). These wetland complexes are distinctly different from the pools created by beaver dams in large stream channels (Hodkinson 1975a, b; Ray et al. 2001; Burchsted et al. 2010).

Compared to the many detailed studies of how beaver dams change stream invertebrate communities at the streamscape level (see above), there are relatively few studies that describe the invertebrate communities in beaver-meadow wetland complexes. These complexes are ubiquitous in the hummocky glaciated terrain of northwestern Pennsylvania (Fig. 12.4), and the complexes are long-lived, especially where beaver colonies are protected (e.g., PA State Game Lands, Erie National Wildlife Refuge). Wissinger and Gallagher (1999) studied the invertebrate communities in two such complexes (Robinson-South Marsh Complex; and Church-Kiser Marsh Complex in Allegheny College's Environmental Research Reserve). The beaver dams at these sites are located on terraces along the edges of the valley and impound groundwater discharge as it resurfaces at the base of the slopes of uplands. The complex of habitats created in the relatively flat-lying terrain include:
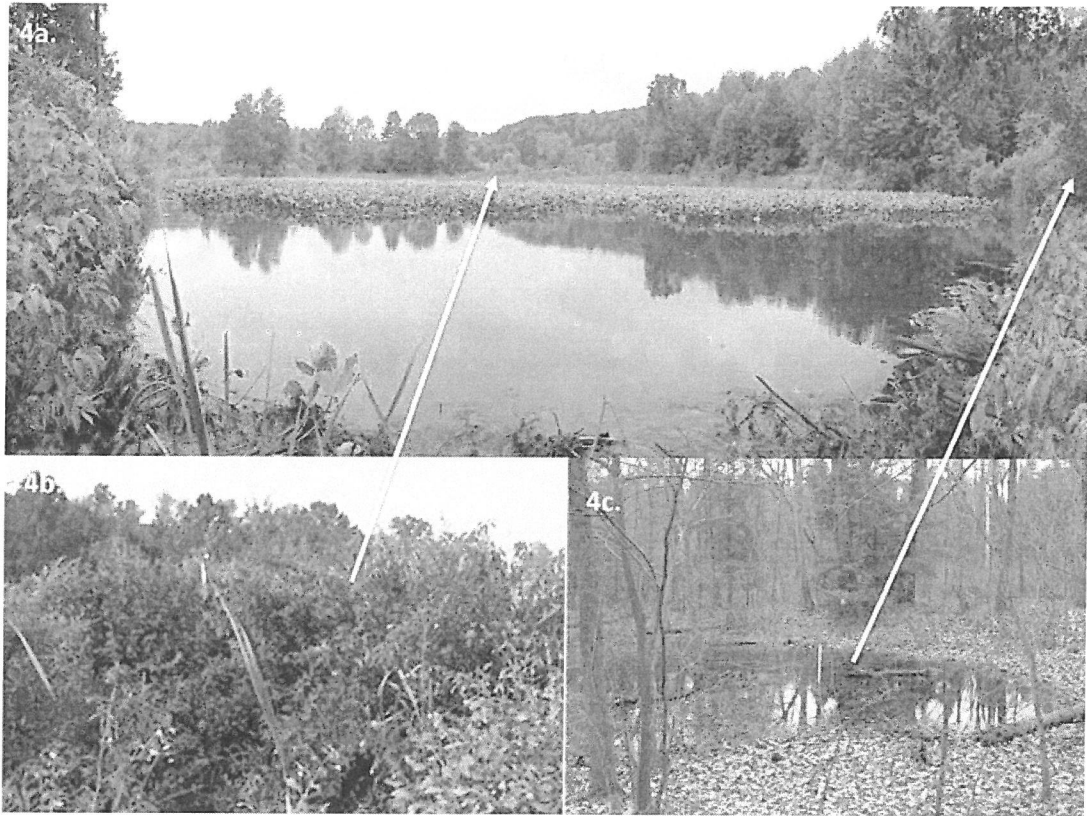
Fig. 12.4 Habitats associated with beaver meadow wetland complex in northwestern Pennsylvania, USA. (**a**) Active beaver pond embedded in a series of ponds and other beaver-affected wetland habitats on Allegheny College's Environmental Research Reserve. Habitats include open water zone in the foreground, lily pad zone, and shrub swamp (plant species given in text) at the forest edge in the background (photo by Ben Plohr). (**b**) Mixed species shrub swamp on the upslope edge of pond, and (**c**) vernal pool in adjacent woodland enhanced by locally raised water table (photo by Scott Wissinger)

1. **Relatively deep (>1 m) ponds** immediately behind the dam structure that have complex plant zonation ranging from an open-water zone of floating pads of spatterdock (*Nuphar variegata*) and submergent vegetation (e.g., *Potamogeton* spp., *Ceratophyllum*) towards shoreline vegetation with deep (e.g., *Typha angustifolia* and *T. latifolia*) and shallow water emergents (e.g., *Scirpus cyperinus* and *Sparganium eurycarpum*) (Fig. 12.4a).

2. **Shallow marshes of emergent vegetation that grade into moist-soil herbaceous communities** that develop on flooded fields adjacent to active dams, and then invade pond basins when dams are abandoned. In addition to the emergent vegetation surrounding the ponds per se (see above), seasonally inundated wet meadow plant assemblages are dominated by rushes and sedges (e.g., *Juncus effusus*, *Carex hystericina*, and *C. lurida*) and herbaceous plants (e.g., *Eupatorium maculatum* and *Verbena hastata*).

3. **Shrub-swamps** along margins of active or abandoned ponds that are dominated by alder (*Alnus rugosa*), wetland dogwoods (*Cornus amomum* and *C. stolonifera*), willows (*Salix* spp.), and buttonbush (*Cephalanthus occidentalis*); and wet meadow shrubby species including meadowsweet (*Spirea alba*) and sweet gale (*Myrica gale*) (Fig. 12.4b).

4. **Back-flooded forests** with dead snags of trees that are intolerant of anaerobic soil conditions soils (e.g., *Prunus serotina*, *Fagus grandifolia*, and *Quercus* spp.).

5. **Living red-maple/hemlock moist-soil swamps with vernal woodland pools** that develop in the depressional micro-topography from the raised water table in back-flooded forests (Figure 15.1 in Wissinger and Gallagher 1999; Fig. 12.4c). Despite the apparent remoteness of these woodland pools to beaver activity, the hydrologic dependence becomes apparent when beaver dams are abandoned, and the adjacent water table falls.

Across all of these subhabitats in these beaver-pond wetland complexes, there is a remarkable diversity of wetland plants (Wissinger et al. 2001) and animals (amphibians, reptiles, fishes, invertebrates) (Wissinger and Gallagher 1999). Wissinger and Gallagher studied the resiliency of the invertebrate communities to short-term drought in the main pond communities by monitoring the multiple pathways by which species recolonized after drought, and experimentally by rehydrating soil cores that were extracted from dried basin sediments. They found that (1) the invertebrate assemblages in semi-permanent basins (abandoned beaver ponds and marginal wetland habitats) were more resilient after drought than those in the permanent basins, (2) the overall rapid recovery of the invertebrate diversity prior to drought (>90 % after 18 months in semi-permanent basins) was attributable to a variety of recolonization modes (e.g., use of micro-refuges in dried basins (see Strachan et al. 2014), desiccation tolerance of eggs, larvae, adults, flexible life history traits, and seasonally timed emergence), and (3) high dispersal rates among habitats with different hydroperiods lead to metapopulation and metacommunity dynamics that stabilize beta diversity across the complex of habitats (Wissinger and Gallagher 1999).

Combining the species identified in the original surveys (see taxonomic list in Wissinger and Gallagher 1999) with subsequent annual surveys (2000–2009; S. Wissinger unpublished data) reveals the presence of >250 invertebrate taxa including 40+ species of odonates, 16 species of caddisflies, 30+ species of beetles, 18 species of water bugs, 50+ dipteran taxa, 11+ molluscs, and 20+ crustaceans (see Appendix for list of families). The taxonomic resolution attainable for odonates and caddisflies (species-level identification of adults and larvae, respectively in the field) provides insight into two levels of habitat heterogeneity that underlie this diversity. First, there is considerable habitat heterogeneity *within* types of subhabitats in the complexes. For example, different species of anisopteran and zygopteran dragonfly larvae are encountered at different depths and in different vegetation zones within main beaver ponds (Table 12.1). This type of spatial niche segregation within ponds (also see Crowley and Johnson 1982; Wissinger 1988; Van de Meutter et al. 2008) is

Table 12.1 Distribution of odonates in different subhabitats within a beaver-meadow wetland complex in northwestern Pennsylvania

Active beaver ponds 1–3 m depth and permanent (pumpkinseed, bluegill, grass pickerel, bass)			Abandoned pond, marsh, shrub swamp <1 m depth, semi-permanent (mudminnow, stickleback, salamander larvae)		Temporary <0.5 m depth (salamanders)
Benthic open basin	Submergent vegetation	Shoreline with emergent vegetation	Marshes—emergent and submergent vegetation	Shrub swamps	Woodland pools/margins
Libellula lydia	*Libellula luctuosa*	*Libellula luctuosa*	*Libellula pulchella*	*Libellula pulchella*	*Aeshna umbrosa*
Libellula julia	*Libellula incesta*	*Libellula incesta*	*Libellula luctuosa*	*Libellula luctuosa*	
Gomphus exilis	*Erythemis simplicicollis*	*Erythemis simplicicollis*	*Libellula quadrimaculata*	*Aeshna constricta*	
Gomphus spicatus	*Sympetrum vicinum*	*Sympetrum vicinum*	*Anax junius*	*Aeshna canadensis*	
Arigomphus furcifer	*Leucorrhinia intacta*	*Leucorrhinia intacta*	*Sympetrum vicinum*	*Sympetrum ambiguum*	
Perithemis tenera	*Pachydiplax longipennis*	*Pachydiplax longipennis*	*Sympetrum semicinctum*		
Epitheca cynosura	*Celithemis elisa*	*Celithemis elisa*	*Sympetrum obtrusum*		
Epitheca canis	*Celithemis eponina*	*Celithemis eponina*	*Aeshna tuberculifera*		
	Argia fumipennis	*Ischnura verticalis*	*Tramea lacerata*		
	Ischnura verticalis	*Ischnura posita*	*Tramea carolina*		
	Ischnura posita	*Enallagma civile*	*Pantala flavescens*		
	Enallagma signatum	*Enallagma signatum*	*Ischnura verticalis*		
		Enallagma vesperum	*Ischnura posita*		
		Nehalennia irene	*Enallagma civile*		
		Lestes vigilax	*Enallagma boreale*		
			Enallagma aspersum		
			Nehalennia irene		
			Lestes disjunctus		
			Lestes eurinus		
			Lestes congener		

Top vertebrate predators in parentheses (salamanders=*Ambystoma maculatum* and *Notophthalmus viridescens*). Larval occurrences based on Wissinger and Gallagher (1999) and subsequent D-net and aerial surveys taken during May–October between 2000 and 2009. Data are cumulative; i.e., not all species were collected in a given year. Larvae of all species are encountered along shorelines during their emergence periods

not limited to dragonflies—in general, plant zonation is a well-described axis of niche segregation for invertebrates in many types of wetlands (Batzer and Wissinger 1996; Wissinger 1999; De Szalay and Resh 2000; Batzer 2013). Thus, the high diversity of habitat types and distinct plant communities associated with beaver-meadow wetland complexes (Grover and Baldassarre 1995; Wright et al. 2002, 2003) translates into a diverse invertebrate fauna (Hood and Larson 2014). Other microhabitats that create hotspots of diversity within beaver ponds include those associated with the structural complexity of beaver huts and dams (France 1997).

A second scale of heterogeneity in beaver-meadow wetland complexes is related to variation *between* different types of wetland habitats. Although specific patterns are difficult to predict across wetland types (Batzer 2013), for wetlands and ponds of similar size, species richness decreases along a gradient from permanent to temporary habitats, with species in temporary habitats often being a nested subset of those in the permanent habitats. In addition to nestedness patterns in ponds (see review by Batzer and Ruhí 2013), invertebrate community composition can also shift from permanent, relatively deep-water (1–2 m depth) ponds that typically have large-gaped predatory fish that prey on invertebrates (bass, sunfish, pickerel), to semi-permanent marshes and shrub-swamps habitats with small-gaped fish (stickle-back, mudminnows) and/or salamander predators, to temporary habitats in which salamander larvae and invertebrates are the top predators (Batzer and Wissinger 1996; Wellborn et al. 1996). In the beaver-wetland complex studied by Wissinger and Gallagher (1999), all of these types of habitats are present and odonates and caddisflies provide evidence for shifts in species composition along predator-permanence gradients. Although there are generalists that occur across habitat types, some species tend to occur mainly at one end (permanent) or the other (temporary) of this gradient (Tables 12.1 and 12.2). Similar differences are observed for beetle assemblages in temporary habitats vs. permanent ponds including beaver ponds beyond stream channels (Fairchild et al. 2000, 2003). Such shifts in species composition are expected for nearly every invertebrate taxon (beetles, bugs, odo-nates, caddisflies, true flies, crustaceans, molluscs, etc.) associated with wetland habitats; i.e., different combinations of species within genera and different genera within families will be present in different types of basins as a result of differential dispersal and colonization rates combined with the different biological and physico-chemical filters that affect establishment and survival (Batzer and Wissinger 1996; Wellborn et al. 1996; McCauley 2008). The mechanisms that underlie species replacements across permanence gradients (as in Tables 12.1 and 12.2) are well described for odonates and caddisflies, and typically involve tradeoffs between physiological, behavioral, and morphological traits that facilitate coexistence with different types of predators, or tradeoffs between traits that facilitate coexistence with predators and those that expedite the completion of life cycles in temporary habitats (e.g., Stoks and McPeek 2003, 2006; Wissinger et al. 2006; McCauley 2008; McCauley et al. 2010). Patterns of species replacements across habitat types in beaver wetland complexes may be confounded by cycles of dam building and abandonment that lead to legacy effects associated with shifts in permanence and in the presence/absence of large-gaped predatory fish. This temporal variability may be even more likely for beaver ponds and wetlands in the floodplains of major

Table 12.2 Distribution of cased caddisflies (Limnephilidae and Phryganeidae) across subhabitats in two beaver-meadow wetland complexes in northwestern Pennsylvania

Permanent ponds	Semi-perm marshes and shrub swamps	Temporary woodland pools	Seeps and rivulets
Banksiola crotchii	*Nemotaulius hostilis*	*Ptilostomus ocellifera*	*Ironoquia punctatissima*
Platycentropus radiatus	*Limnephilus indivisus*	*Ptilostomus postica*	
Pycnopsyche subfasciata	*Limnephilus submonilifer*	*Ironoquia parvula*	
Agrypnia vestita	*Limnephilus moestus*		
Anabolia consocia	*Banksiola doussaria*		
Fabria inornata	*Bansiola crotchii*		
	Anabolia bimaculata		
	Ptilostomus occellifera		
	Phryganea sp. *(sayi?)*		

Larval occurrences based on Wissinger and Gallagher (1999) and subsequent D-net samples taken during October–November, and April–May from 2000 to 2009. Top predators in (a) permanent ponds (active beaver ponds) are large-gaped fishes (sunfish, bass, grass pickerel); (b) in semi-permanent marshes (herbaceous emergent) and shrubswamps are mudminnows, brook stickleback, and newts; and (c) backflooded temporary habitats and woodland pools are *Ambystoma* salamander predators. Seeps and rivulets are small flowing water habitats between various standing water habitats in the beaver meadow complexes (see Fig. 15.1 Wissinger and Gallagher 1999)

streams because of the stochastic arrival of fishes and unpredictable filling and drying events associated with floods (e.g., Kohler et al. 1999).

In summary, the habitat heterogeneity observed within and between the different types of basins in beaver-meadow wetland complexes combined with the potential for diversity-enhancing metacommunity dynamics associated with dispersal and high connectivity among basins should lead to an overall higher diversity of plants and animals as compared to in structurally simple and isolated wetland basins (Wissinger and Gallagher 1999; Wright et al. 2002, 2003; Caudill 2005; McCauley et al. 2010). Moreover, because the combinations of habitats in beaver-meadow complexes that are part of the cyclic and multi-successional pathways associated with beaver activity (see Naiman et al. 1988b; McMaster and McMaster 2001) are constantly changing, understanding the degree to which assemblage structure and composition at a given point in time at a given location is a result of extant vs. legacy conditions will require long-term and wetlandscape-level study.

Beaver Dam Wetlands in Western North America

Wetland habitats associated with beaver activity in western North America occur in a variety of geomorphological contexts including (1) northern peatlands (e.g., Hood and Bayley 2008a, b, 2009); (2) on rivers of the "High Plains" to the east of the

Rocky Mountains and in arid intermountain basins among the major North American Cordilleran ranges where created ponds and wetlands expand the riparian ecotone of stream systems and create perennial wetland habitats in arid landscapes (e.g., Andersen and Shafroth 2010; Gibson and Olden 2014); (3) on relatively small tributaries in the foothills of mountain ranges (e.g., Hodkinson 1975a, b; Clifford et al. 1993; Morrison et al. 2015); (4) in the riparian zone of montane and subalpine rivers that flow through the U-shaped valleys carved by mountain glaciers in the Rocky and Sierra mountain ranges (Malanson and Butler 1990; Butler and Malanson 1995; Fuller and Peckarsky 2011a, b; Polvi and Wohl 2012; Levine and Meyer 2014) (Figs. 12.3 and 12.5); and (5) on streams flowing on terraces and other valley-side and headwater habitats in montane and alpine valleys (Caudill 2002; Fig. 12.5b).

Beaver Activity Enhances Habitat Heterogeneity in Northern Peatlands

As described for northeastern North America above, beaver activity in the peatlands of western Canada and Alaska enhances existing habitat heterogeneity in these wetland landscapes. In Miquelon Lake Provincial Park, Alberta, Canada, beavers alter existing shallow isolated wetlands via channel digging (Hood and Larson 2014,
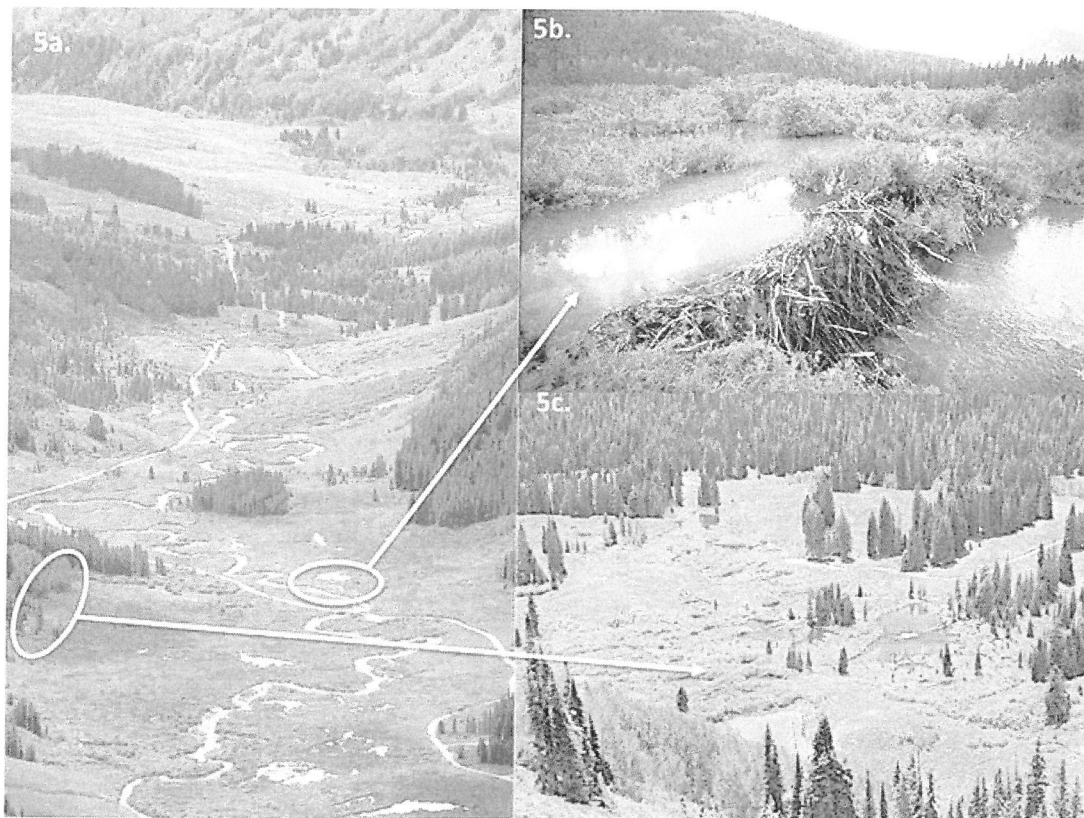

Fig. 12.5 (**a**) Overview of geomorphological settings of beaver dam wetlands in the upper East River Valley in the Elk Mountains of central Colorado (photo by Scott Wissinger), (**b**) valley bottom riparian beaver pond (photo by Chris Caudill), and (**c**) upland beaver wetland complex on valley margin terrace (photo by Susan Washko)

2015). Beavers dig long, deep channels perpendicularly from the wetland edge outward that connect to other wetlands or upland areas, thereby increasing habitat heterogeneity (Hood and Larson 2014) and wetland connectivity (Hood and Larson 2015). Hood and Larson (2014) found that beaver activity increased the amount of vegetated-edge habitat, which had higher species richness, diversity, and evenness than open water and beaver channels. Invertebrate richness, diversity, abundance, and density varied by year and yearly differences were driven by precipitation. Drought resulted in higher densities while higher water levels resulted in more diversity. *Daphnia* spp. were the most abundant taxon regardless of hydrologic conditions. Invertebrates were compared between active and inactive beaver wetlands and between different types of habitats (open water, beaver channels, and vegetated edges) within each category (active, inactive). Predators were the most species-rich group in both active and inactive wetlands, and Chaoboridae larvae were numerically dominant, especially in active beaver channels. Gerridae and Gyrinidae were unique to active channels despite low numbers of individuals. Tabanidae were unique to inactive channels and Culicidae were associated with all three subhabitats in inactive wetlands. Amphipoda were associated with active vegetative edges and Hood and Lawson posit that amphipods are influenced by an increase of organic material brought in by beaver and that beaver maintain deeper water, which may reduce habitat for mosquito larvae. The strongest differences were seen at the within-wetland level with beaver channels and vegetated edges having more functional feeding groups than open water.

Abandoned Beaver Pond Invertebrate Communities

Beaver ponds are notorious sinks for mineral and organic sediments and patterns of accumulation of these various types of sediments should have multiple consequences for the development of benthic invertebrate communities. In general, the sediments at old dam sites contain higher amounts of organic material than those at relatively young sites (Butler and Malanson 1995). Hodkinson (1975a, b) studied the aquatic invertebrates in abandoned beaver ponds in forested landscapes in the foothills of the Rocky Mountains in Alberta, Canada, with a particular focus on understanding patterns of distribution and abundance of dipteran larvae, which were the dominant taxa in the organic-rich sediments in these habitats. Although the invertebrate communities in these abandoned beaver ponds included surface-dwelling Ephemeroptera, Plecoptera, Megaloptera, and Trichoptera, the great majority of taxa listed (67/83 species) were dipterans living in the soft organic-laden sediments in these basins. Tipulid larvae were particularly diverse (26 species), and Hodkinson determined that their distribution and abundance varied among substrate types. Coarse-grained, lotic-like gravel substrates in stream courses were dominated by non-tipulid lotic taxa. The abundance and species composition of the dipteran assemblages in the organic-laden, soft-sediments of the abandoned ponds varied along a gradient that varied in (1) particle size; (2) degree of compaction (flocculent

to firm); and (3) amount (mostly organic to mostly mineral) and type (herbaceous, woody deciduous leaves, conifer needles) of detrital plant material. Invertebrate biomass was higher in loose, flocculent, detrital substrates than in relatively compacted, mainly mineral substrates. Dietary analyses by Hodkinson combined with those in previous studies by Pritchard and Hall (1971) and Pritchard and Leischner (1973) revealed that (1) allochthonous vascular plant detritus dominated the diets of most species in these wetlands and (2) habitat partitioning led to dietary partitioning in terms of the type of vascular plant detritus ingested.

Succession in Riverine Floodplains

Beaver dams are frequently breached, rebuilt, relocated, or abandoned in relatively large streamscapes. Malison et al. (2014) studied invertebrates in different successional stages on a large river floodplain in Alaska, USA. Invertebrate communities in beaver ponds differed from flood-channel spring brooks but were similar among early-, mid-, and late-successional ponds despite the fact that early-successional ponds had a greater degree of connectivity to the main channel.

The return of beavers to large river systems in arid landscapes is an area of intensive study because of the potential effects on conservation efforts—both on the positive side of the reestablishment of natural flora and fauna, and on the negative side as an interactor with invasive species (Gibson and Olden 2014). While there is evidence for how beaver reestablishment and subsequent cyclical changes associated with damming and abandonment can influence successional changes in vegetation, there are few data on changes to invertebrate communities (Gibson and Olden 2014).

Metapopulation Dynamics in Montane Beaver Wetland Complexes

Beaver activity on small streams in montane settings often creates step-like complexes of multiple ponds and wetlands that cascade along the relatively flat terrain of mountainside terraces and along the sides of montane valleys (Fig. 12.5b). The lateral development of these complexes creates multi-basin clusters of active and abandoned ponds with hydrologic budgets akin to those described above for the wetland complexes in northeastern North America; i.e., inputs are often dominated by first order streams, springs, and/or groundwater upwellings at valley margins (Fig. 12.1d). The proximity of multiple habitats makes it likely that aquatic insects with even moderate dispersal abilities can move between ponds. In a series of related studies Caudill (2003a, b, 2005) evaluated the dynamics of a mayfly (*Callibaetis ferrugineus hageni*) metapopulation in beaver ponds of the upper East River Valley of Colorado, USA, with and without trout (Fig. 12.5b, c). Caudill found that late instar larval mayflies densities are significantly higher and adult emergence nearly an order of magnitude greater in troutless ponds than in those with trout. Surprisingly, trout ponds with few or no emerging adults subsequently

have similar larval recruitment to ponds with high emergence rates (Caudill 2003a). Isotope labeled adult females move between trout and troutless ponds and there is no relationship between oviposition and trout (Caudill 2003b). A comparison of adult emergence compared to larval recruitment rates point to a source–sink population dynamic among beaver ponds, and models based on these empirical data predict that this mayfly cannot persist in ponds with trout in the absence of adult dispersal from neighboring troutless habitats (Caudill 2005).

Beaver-Pond vs. Non-beaver Pond Montane Invertebrate Assemblages

Caudill's beaver-pond study sites are located in the Elk Mountains of Colorado, USA, where Wissinger and colleagues have surveyed the invertebrate community composition of both beaver and non-beaver ponds for the past 25 years (Wissinger et al. 2003; Wissinger, unpublished data). The spatial configurations of the different types of montane wetland and pond habitats in the Elk Mountains are characteristic of many glaciated mountain valleys throughout the central Rocky Mountains—i.e., beavers dam the main stem of the East River as it meanders through a U-shape glacial valley creating wetland complexes with some ponds highly connected to main channel flow (as in Fuller and Peckarsky 2011a, b; Malison et al. 2014), and others that are less directly connected (see Figs. 12.3 and 12.5). Beavers also dam headwater side tributaries where they traverse glacier-formed terraces on valley walls (as in Caudill; Fig. 12.5c). Kettle ponds and other non-beaver dam wetland habitats associated with the glacial landscape also occur in these valleys. A comparison of the invertebrate communities in these various wetland habitats within the same valley reveals several patterns (Table 12.3). First, assemblages in main-stem and valley-floor complexes have a higher number of running-water invertebrates including stream-dwelling mayflies, stoneflies, and caddisflies than those on valley terraces. Inlet and outlet areas of ponds at the upper and lower extent of beaver-pond complexes include some of these stream-dwelling EPTs that, in addition to a distinctly lentic group of organisms (see taxa lists in Appendix; Table 12.3), create a much higher total diversity than in communities in valley-floor complexes. There is considerable overlap in the dominant taxa in upland beaver pond complexes and those in non-beaver kettle ponds, with the former often as a nested subset of the species of the caddisflies, odonates, water bugs, and beetles that dominate (in terms of biomass) the large-bodied invertebrate fauna in non-beaver wetlands (Table 12.3; Fig. 12.6). There are several large-bodied taxa that characteristically dominate the biomass in upland beaver ponds but are rare or absent in non-beaver ponds including (1) *Callibaetis* mayflies (Fig. 12.6b); (2) tipulid flies (6–8 species (Fig. 12.6e)); (3) dixid flies; and (4) amphipod crustaceans. There are also subtle, species-level differences that are consistently observed between beaver- and non-beaver upland wetlands. For example, the water boatman *Callicorixa audeni* and *Cenocorixa bifida* are common in montane kettle ponds, whereas several species of *Hesperocorixa* (a relatively lotic genus) dominate in nearby beaver wetlands (Caudill 2002). Many

Table 12.3 Number of species in relatively lentic vs. lotic aquatic insect groups in ponds and wetlands in the upper East River Valley in the Elk Mountains of Colorado near the Rocky Mountain Biological Laboratory

Order	Family	Valley beaver	Upland beaver	Non-beaver
Ephemeroptera	Total taxa	7	3	2
	Baetidae	1	2	1
	Caenidae		1	1
	Ephemerellidae	1		
	Heptageniidae	3		
	Leptophlebiidae	1		
	Siphlonuridae	1		
Plecoptera	Total taxa	7	2	
	Chloroperlidae	2	1	
	Nemouridae	2	1	
	Perlidae	2		
Odonata	Total taxa	1	11	18
	Aeshnidae	1	3	3
	Coenagrionidae		3	4
	Corduliidae		1	2
	Lestidae		2	3
	Libellulidae		2	6
Coleoptera	Total taxa	7	16	22
	Chrysomelidae		1	1
	Dytiscidae	4	10	15
	Gyrinidae	1	1	1
	Haliplidae	1	1	2
	Helophoridae	1	1	1
	Hydrophilidae		2	2
Hemiptera	Total taxa	3	8	11
	Corixidae	1	2	3
	Gerridae	1	2	3
	Mesoveliidae		1	1
	Notonectidae		1	1
	Saldidae	1	1	2
	Veliidae		1	1
Trichoptera	Total taxa	8	8	10
	Hydropsychidae	1		
	Leptoceridae		1	1
	Limnephilidae	5	6	8
	Phryganeidae		1	1
	Polycentropodidae	2		
	Rhyacophilidae	1		

(1) Valley beaver=ponds with hydrologic connections to the East River (Fig. 12.5b); (2) upland beaver=beaver ponds on small tributaries along the valley sides (Fig. 12.5c); and (3) non-beaver=kettle ponds in mid-valley moraines. Data combined from Caudill (2002), B. Peckarsky (unpub. data), and S. Wissinger (unpub. data)
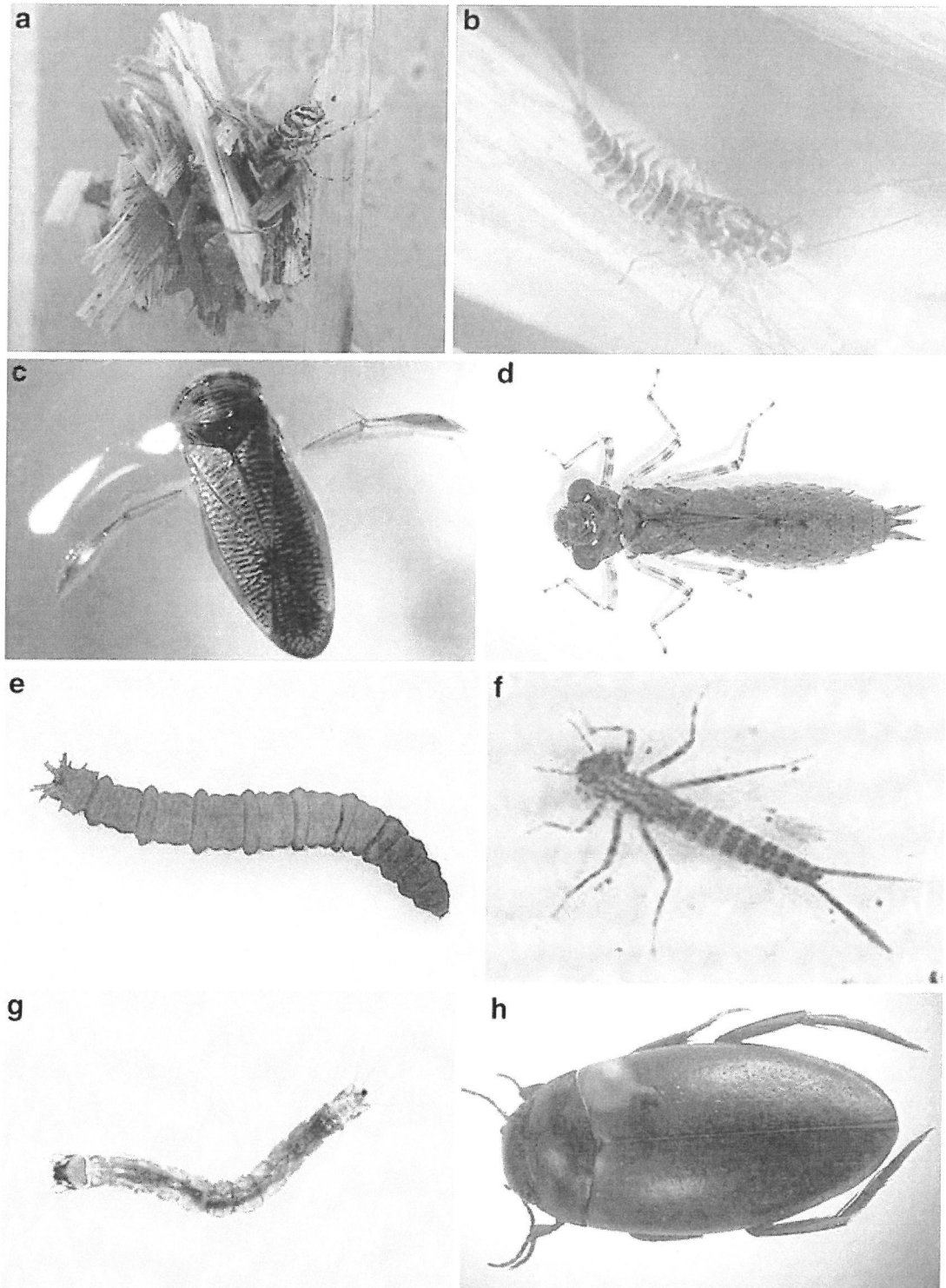
Fig. 12.6 Frequently encountered abundant invertebrates in upland beaver wetlands in the East River Valley in the Elk Mountains of central Colorado studied by Caudill (2002) and Wissinger (unpublished data): (**a**) larva of the caddisfly, *Limnephilus externus* (photo by Nixie Boddy); (**b**) larva of the mayfly, *Callibaetis ferrugineus hageni* (photo by Chris Caudill); (**c**) adult water boatman, *Hesperocorixa* (photo by Timothy Loh); (**d**) larva of the dragonfly, *Aeshna palmata* (photo by Jim Johnson); (**e**) tipulid fly larva (photo by John Meyer); (**f**) larva of the damselfly, *Coenagrion resolutum* (photo by Susan Washko); (**g**) larva of the meniscus midge *Dixella* (photo by Stephen Luk); and (**h**) adult dytiscid diving beetle, *Agabus tristus* (photo by Susan Washko)

of the dominant taxa in temporary non-beaver ponds are rare or absent in beaver ponds (Wissinger unpublished data). Whether the presence of trout in valley bottom beaver pond complexes explains the rarity of many of the larger bodied lentic taxa (odonates, beetles, water bugs, cased caddisflies; Table 12.3) found in upland habitats (beaver and non-beaver) bears further study.

Finally, beaver dam wetlands have the potential to play a stabilizing role in maintaining beta and regional diversity in wetland habitats in the face of climate change. Wetlands, ponds, and other shallow, temporary basins are considered to be the most vulnerable aquatic habitats to changes in temperature and precipitation regimes, especially at relatively high latitudes and elevations (Barnett et al. 2005; Corcoran et al. 2009; Tuytens et al. 2014). Ponds and other wetland habitats associated with beaver activity are typically permanent because of their hydrological connection to stream courses or their proximity to points of groundwater discharge (Fig. 12.1d). This permanence has the potential for creating refuges for species in habitats that are becoming increasingly temporary (see Smol and Douglass 2007). For example, in the East River Valley, the cased caddisfly, *Limnephilus externus* (Fig. 12.6a), is ubiquitous in beaver and non-beaver ponds and wetlands (also see Hodkinson 1975a, b). The local habitat range of this species is limited by pond drying because of the extended time spent in the final instar during late summer (Wissinger et al. 2003). Censuses of the presence and abundance of this species throughout the valley for 25 years reveal that during the past decade (2005–2015), early pond drying has resulted in complete cohort failures not observed in the previous 15 years (Wissinger, unpublished data). For example, in 2009 and 2012, a combination of a light snow pack, early snow melt, and a dry early summer, led to the disappearance of over 30 populations of this species in temporary wetland habitats in the East River Valley. The only populations of this species that survived to pupate and emerge in the valley in both years were associated with beaver dam wetlands (both main-valley and terrace complexes; see Figs. 12.3 and 12.5), which remained permanent as a result of their landscape position in stream courses. Spatial patterns of recolonization in non-beaver pond basins after these drought events suggest that beaver-pond populations provide a regional haven for this species in drought years and source of colonists for the reestablishment of populations in non-beaver habitats (Wissinger unpublished data).

Beaver Wetlands of the Southeastern USA

Southeastern USA beaver wetlands are typically unstable transitory systems due to regional weather and a history of extreme sedimentation. The Southeastern USA receives more annual precipitation (1300+ mm per year) than most other areas with beaver-created wetlands and is subject to intense tropical and winter storms that create large stream pulses. These pulses can breach many beaver dams, and at least temporarily drain beaver wetlands. In addition, river and stream beds in the

Southeast, particularly the Piedmont region, are unstable (Mukundan et al. 2011) due to poor cotton-era farming practices in the late 1800s and early 1900s that eroded 10–30 cm of topsoil into streams and floodplains (Trimble 1974). At current export rates, Jackson et al. (2005) estimate that 6–10 millennia will be required to export sediment mobilized during the cotton-era from a Georgia Piedmont watershed. The precipitation patterns in the Southeast combined with unstable, sand and silt substrates limit vegetation growth in and around beaver wetlands to relatively simple communities (e.g., *Panicum* grasses) adapted to shifting hydrologic conditions. Exceptions include ponds built to incorporate old roadbeds or those isolated from main channel flows. Overall, however, most beaver wetlands in the Southeast are small, unstable habitats.

Succession in Invertebrate Communities in Southeastern Beaver Wetlands

Beaver wetlands in the Southeastern USA are typically formed from damming small streams that then flood adjacent riparian forest (Fig. 12.1a). In early-stage beaver wetlands, many upland trees persist. The wetlands overall are rather shallow other than the area immediately adjacent to the dam, and in the original stream channel. As beaver wetlands persist, terrestrial vegetation dies under stress from flooding, creating open pond-like wetlands with emergent and submergent vegetation. However, because dams often breach due to frequent and intense storms, these wetlands are frequently abandoned by beaver, and subsequently drain. Abandoned ponds can develop complex braided drainage networks, as the original channel becomes sediment filled and numerous secondary channels develop. Abandoned beaver wetlands usually fill with some seasonal standing water, and upland tree species are slow to reinvade. Typically, abandoned ponds are large open meadow-like wetlands with aquatic, semiaquatic, and terrestrial subhabitats. A few studies have examined invertebrate communities in abandoned wetlands in other regions (Hodkinson 1975a, b; Wissinger and Gallagher 1999; Hood and Larson 2014), but not in southeastern North America.

To compare invertebrate communities of beaver wetlands among three basic stages of habitat succession, invertebrates were sampled in newly formed (created within 2 years; $n=4$), mature (established for >15 years; $n=4$), and abandoned wetlands (breached dams; $n=3$) in October 2013 and May 2014 in Oconee National Forest in Georgia, USA (Bush and Batzer, unpublished data). There were a relatively high number of taxa (>60 families; Appendix) in each wetland type, with strong seasonal variation in invertebrate communities (Fig. 12.7). In October, invertebrate communities differed among all successional stages, while in May only the mature beaver wetland communities differed from newly formed or abandoned ponds (Fig. 12.7). Ostracoda, Copepoda, Branchiopoda (mainly daphniids), Chironomidae, and Ceratopogonidae collectively accounted for 89–95 % of total invertebrates, regardless of condition, with ostracods alone accounting for 49–76 % of all individuals (Fig. 12.8). Ostracods can be particularly abundant in systems with
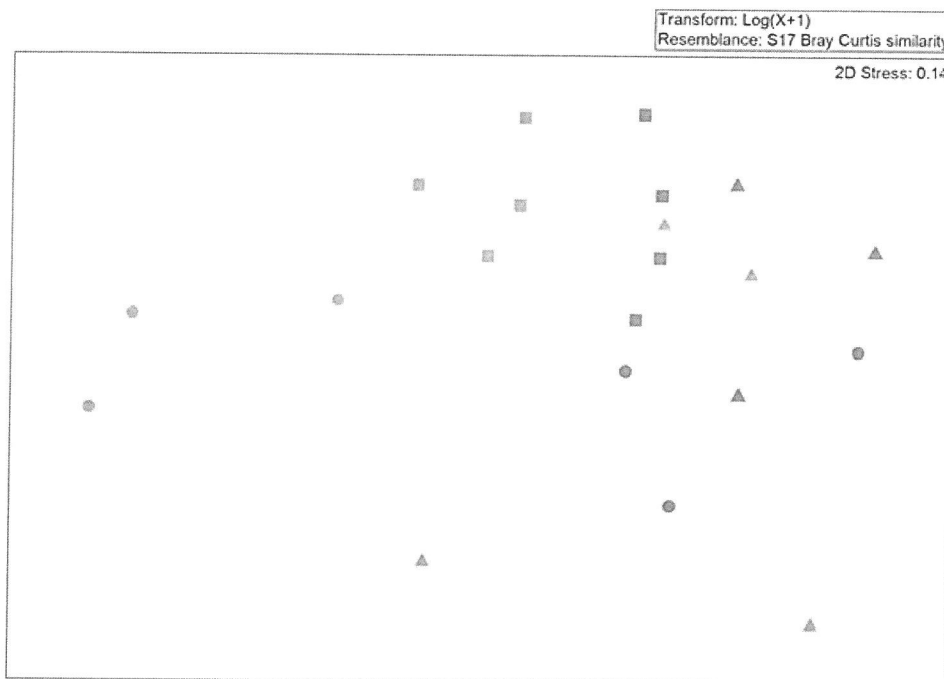
Fig. 12.7 Nonmetric multidimensional scaling plot showing patterns among newly created (*filled triangle*), mature (*filled square*), and abandoned (*filled circle*) beaver wetland invertebrate communities (Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts) in October 2013 (*orange fill*; new vs. mature $R = 0.344$, $P = 0.029$; new vs. abandoned $R = 0.704$, $P = 0.029$; mature vs. abandoned $R = 0.741$, $P = 0.029$) and May 2014 (*blue fill*; new vs. mature $R = 0.685$, $P = 0.029$; new vs. abandoned $R = 0.630$, $P = 0.1$; mature vs. abandoned $R = 0.556$, $P = 0.029$)

copious benthic organic detritus combined with relatively shallow, warm water, which is typical in Southeastern beaver wetlands (Smith and Delorme 2010). This preponderance of small, benthic taxa suggests that fish predation is important in these wetlands (Wellborn et al. 1996), and most beaver wetlands of the Southeastern USA support large populations of *Gambusia* mosquitofish (Poecilidae). Given that all three successional types were dominated by the same five small-bodied taxa, the differences among successional states (Fig. 12.7) are likely driven by rarer, larger-bodied invertebrate taxa.

The greatest differences among successional states were observed in October when terrestrial and semi-aquatic taxa such as springtails (Entomobryidae), scale bugs (Coccoidea), and spiders (Araneae) were among the most abundant macroinvertebrates in abandoned wetlands (Table 12.4). Macroinvertebrates in newly formed and mature beaver wetlands were dominated by common lentic taxa (e.g., Coenagrionidae, Libellulidae, Baetidae, Caenidae), and differences between communities were more likely driven by variation in relative abundance than community composition, per se.

In May, invertebrate communities were similar among successional states, with only the stable mature wetlands exhibiting a unique community structure (Fig. 12.7). This seasonal difference suggests that both seasonal change and
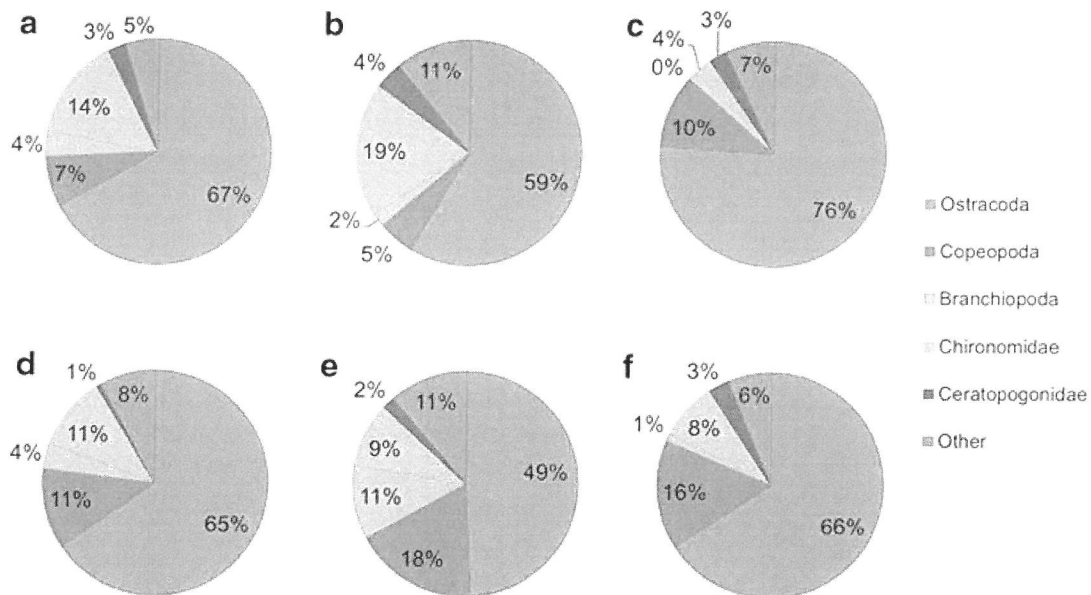
Fig. 12.8 Relative abundance of most dominant taxonomic groups in (**a**) October newly created, (**b**) October mature, (**c**) October abandoned, (**d**) May newly created, (**e**) May mature, and (**f**) May abandoned beaver wetlands of Georgia

Table 12.4 Ten most abundant large-bodied taxa (excluding Ostracoda, Branchiopoda, Copepoda, Chironomidae, and Ceratopogonidae) in new, mature, and abandoned beaver wetlands of Georgia, in October 2013

Newly created	Mature	Abandoned
Oligochaeta	Caenidae	*Entomobryidae*
Dogielinotidae	Dogielinotidae	*Coccoidea*
Coenagrionidae	Coenagrionidae	Oligochaeta
Non-oribatid Acarina	Non-oribatid Acarina	Non-oribatid Acarina
Libellulidae	Libellulidae	*Araneae*
Sphaeriidae	Sphaeriidae	Coenagrionidae
Caenidae	Baetidae	Sphaeriidae
Baetidae	Veliidae	Oribatidae
Dytiscidae	Oribatidae	Corethrellidae
Araneae	Scirtidae	*Delphacidae*

Italicized taxa represent exclusively terrestrial taxa

longer-term succession strongly control invertebrate community structures in these beaver wetlands.

While one might expect a linear successional pattern as a stream changes into a pond and then into a wet meadow (see Naiman et al. 1988b), the succession we observed appears more stochastic. In the Southeastern USA, beaver wetlands are frequently changing from one stage to another, and back again. Dams in new beaver wetlands are frequently breached and abandoned before the wetland ever becomes mature. In our study ponds, two of the newly formed wetlands were abandoned due to dam breaches soon after we sampled, and two newly formed wetlands

had been recreated from formerly abandoned sites. Thus, invertebrates in these wetlands have to be able to adapt to constantly changing conditions or be highly mobile colonizers. Where mature beaver wetlands persist, pond-like communities of lentic invertebrates develop that are able to take advantage of both permanent water and high habitat heterogeneity, and can tolerate high fish predation rates (e.g., Benke et al. 1999). Invertebrate communities in abandoned ponds may be (1) former residents of mature wetlands that are able to take advantage of residual channels and seasonal filling, (2) migrants from nearby newly created or mature wetlands in the complex (Hodkinson 1975a; Wissinger and Gallagher 1999), or (3) semi-aquatic or terrestrial residents taking advantage of damp soil conditions or lush vegetation (as in abandoned pond in Hodkinson 1975a, tussock zone of Benke et al. 1999, marsh habitat in Wissinger and Gallagher 1999, and vegetative edges in Hood and Larson 2014).

Zonation and Habitat Heterogeneity Within Beaver Wetlands

As in Northeastern North America (see above), mature beaver wetlands in southeastern North America can be complex heterogeneous habitats with a variety of semi-aquatic, emergent, and submergent vegetation, as well an abundance of woody debris (Benke et al. 1999). Benke and colleagues examined the distribution of invertebrate communities in different habitat zones in a mature beaver wetland in Talladega National Forest, Alabama, USA. This wetland is the largest in a series of beaver-created wetlands on a low gradient small stream in the coastal plain of Alabama, and is sub-divided into three distinct vegetative zones each containing several subhabitats. These zones consist of (1) a small, deep unvegetated area of open water adjacent to the beaver dam, with a thin benthic layer; (2) a moderately shallow area in the middle of the pond dominated by floating white water lily (*Nymphaea odorata*), with a thicker benthic layer and extensive woody debris; and (3) a shallow semi-aquatic region at the edge of the pond dominated by emergent rush (*Juncus effuses*), which had two distinct subhabitats: rivulets and *Juncus* tussocks.

The taxon richness of the invertebrate community in the Talladega beaver pond is tightly coupled with increasing habitat heterogeneity from the open water zone to the *Nymphaea* zone to the *Juncus* zone. The open water has the simplest invertebrate community (Hood and Larson 2014). Copepods are common to both open water and the benthic substrate, while cladocerans dominate the open water. The benthic layer here is dominated by Chironomidae larvae (as was the case for the *Nymphaea* and *Juncus* zones; and like ponds in other regions - e.g. McDowell and Naiman 1986; Clifford et al. 1993; Margolis et al. 2001; Hood and Larson 2014), oligochaetes, and microcrustaceans. Ceratopogonidae larvae are also common (similar to Georgia wetlands above) in all three zones, and are the most important predator by relative abundance in the benthos of the open water zone.

Taxon richness is highest in the structurally complex *Nymphaea* habitat. There is a higher species richness of microcrustaceans in the *Nymphaea* zone compared to open water. Chironomids are the dominant insect in all three sub-habitats (vegetation, woody debris, and benthos) of this zone. *Hyalella azteca* is the most common non-insect invertebrate. Overall community structure is similar between the benthos and woody debris, and consisted of many typical lentic taxa. Caenids and baetids were the most abundant mayfly taxa, and dytiscid beetles were the dominant coleopterans. Hydroptilidae and Phryganeidae caddisfly larvae are observed, but in low numbers. The most important predators are Odonata larvae (Coenagrionidae and Libellulidae). The invertebrates on vegetation of the *Nymphaea* zone are similar to woody debris and benthos (although less abundant) with two exceptions: Chrysomelidae beetle larvae (*Donacia* spp.) and Pyralidae moth larvae which are both specifically associated with *Nymphaea* leaves.

The *Juncus* zone has the highest overall taxon richness of all three zones (>100 taxa), which reflects the presence of both aquatic and semi-aquatic sub-habitats. The second most abundant taxa (after Chironomidae) are semiaquatic/terrestrial collembolans in both tussocks and rivulets (similar to the abandoned Georgia wetlands). Semiaquatic/terrestrial Carabidae and Staphylinidae beetles, and Lycosidae spiders, along with aquatic Dytiscidae beetles, are the most common predators. Mites are another common predator in the *Juncus* zone, especially in the tussocks. Sciaridae larvae are only found in the *Juncus* zone and are only abundant in the tussocks. While insects are more taxonomically diverse in the *Juncus* zone than in the other zones, there are fewer microcrustacea taxa than in the *Nymphaea* zone, and those present are dominated by copepods and ostracods rather than copepods and cladocerans (as in the *Nymphaea* and open water zones). Curiously, the preponderance of Ostracoda seen in the Georgia beaver wetlands described above (Bush and Batzer, unpublished data) does not develop in the Talladega beaver pond studied by Benke et al. (1999).

Benke et al. (1999) and Stagliano et al. (1998) also studied insect emergence in all three zones of the Talladega beaver pond. Insects emerge in every month of the year, and chironomids are the most frequently collected insects in emergence traps, and the only group collected in the open water zone. Chironomid emergence is highest in the *Nymphaea* zone, which was several times higher than the open water zone even at its lowest point and is annually twice that of the *Juncus* zone. Insect emergence year-round coupled with continuously high chironomid larval abundance likely means that growth continues year round in this warm water wetland. While chironomid emergence is lower in the *Juncus* zone than the *Nymphaea* zone, ceratopogonid emergence is highest in the *Juncus* zone. Sciaridae, Cecidomyiidae, and Lepidoptera also emerge in high numbers from the *Juncus* zone. The majority of emerging insects from the *Juncus* zone are semi-aquatic or terrestrial.

Conclusions

Beaver wetlands have high invertebrate taxon richness. A recent analysis of macro-invertebrate family richness and composition from 447 individual wetlands by Batzer and Ruhí (2013) included five beaver wetlands (four from Wissinger and Gallagher 1999 and one from Benke et al. 1999). These beaver wetlands ranked first, third, fourth, sixth, and ninth overall as supporting the most families out of the 447 sites, not including the semi-terrestrial invertebrate families that are discussed above as being prevalent in abandoned beaver ponds (e.g., beaver complexes in the Southeastern USA; see Table 12.4 and Appendix). Our review suggests that beaver wetlands support high taxon richness primarily due to high habitat heterogeneity (e.g., Benke et al. 1999; Wissinger and Gallagher 1999; Hood and Larson 2014), which has several components:

- Beaver wetlands have a variety of subhabitats including open water, emergent and submergent vegetation, varying water depths, wetted semi-aquatic edges, mud substrates, highly organic benthic layers of varying complexity, and woody debris, which can each support unique organisms (e.g., Benke et al. 1999; Wissinger and Gallagher 1999).
- Beavers increase habitat heterogeneity of existing wetlands by digging long, deep channels that increase connectivity to other wetlands (e.g., Hood and Larson 2014).
- Beavers create complex woody debris structures including lodges (France 1997) and dams the support unique invertebrate assemblages (e.g., Clifford et al. 1993; Rolauffs et al. 2001).
- Beaver activities (damming of streams, building of channels, etc.) create a mosaic of lentic and lotic hydrology that provides habitat for both stream and pond invertebrates (e.g., Table 12.3; Appendix).
- Beaver wetland environments are constantly changing through time, which creates dynamic, frequently nonlinear, multidimensional succession in habitat conditions and invertebrate community structure (Naiman et al. 1988b; Fig. 12.7).
- Beaver dam complexes often include multiple basins that are hydrologically connected and within dispersal distances that foster metapopulation dynamics that enhance alpha and beta diversity (e.g., Caudill 2005).
- Wetted edges, shallow regions, and abandoned beaver wetlands create refuge for many terrestrial and semi-terrestrial taxa (see discussions in Western and Southeastern North America vignettes).
- A variety of predators of invertebrates (other invertebrates, amphibians, fishes, and birds) exploit beaver wetlands, and because predation pressure changes spatially across and temporally within beaver wetlands, heterogeneity should be enhanced. Few studies have considered these potential feedbacks on invertebrate communities in beaver wetlands.
- At the continental scale, conservation efforts to recover and reintroduce beaver populations in their native range (North America and Europe) have been

successful and beaver now have healthy populations that create wetlands across a wide variety of geomorphological, hydrological, and climactic conditions (e.g., Gibson and Olden 2014).

Our review further identifies important ecological values and services to our society that emanate from beaver activities and associated invertebrate communities including:

- Creation and maintenance of new wetlands (e.g., Fustec et al. 2001; Syphard and Garcia 2001; Cunningham et al. 2006; Nummi and Holopainen 2014; Morrison et al. 2015), in the face of ongoing wetland loss in Europe and North America (Zedler and Kercher 2005; Dahl 2011).
- Enhancement of existing wetlands, which aids in increasing wetland density important to conserving wetland dependent organisms as human populations increase (Gibbs 2000).
- Restoration of water quality and quantity in arid lands that has important consequences for regional water management issues and for conservation of plants and animals in those regions (Maret et al. 1987; Gibson and Olden 2014).
- Maintenance of natural flows (Wild 2011) during drought and flood buffering against extreme precipitation events, both of which are likely to become more frequent and severe in the face of climate change (IPCC 2014).
- Creation of refuges for invertebrates during drought, which are then able to recolonize other wetlands post-drought, stabilizing regional diversity (e.g., Wissinger and Gallagher 1999).
- Maintenance of abundant and rich aquatic invertebrate communities that provide important ecosystem services such as the processing of organic matter (e.g., Klemmer et al. 2012; Prather et al. 2013) and linking primary energy sources to wetland fish and waterfowl (Kemp et al. 2012; Nummi and Holopainen 2014).

Beavers and beaver wetlands will likely become especially crucial management partners and resources as climate change and population growth continue to threaten wetlands overall (Wild 2011).

Appendix

Invertebrates recorded (*) in beaver-associated ponds and wetlands in Georgia (Bush and Batzer unpublished), Pennsylvania (Wissinger and Gallagher 1999; Wissinger unpublished), and Colorado, USA (Caudill 2002; B. Peckarsky, unpublished data; S. Wissinger unpublished data).

	Family	SE NA beaver dam wetlands			NE NA beaver pond complexes	Central Colorado Montane beaver dam ponds and wetlands	
		New	Mature	Abandoned	All basins	Valley terrace pond complexes	Stream channel/riparian distributary
Turbellaria			*		*	*	*
Gastropoda	Lymnaeidae	*	*	*	*	*	*
	Physidae	*	*	*	*	*	*
	Planorbidae	*	*	*	*	*	*
Bivalvia	Sphaeriidae	*	*	*	*	*	*
Oligochaeta		*	*	*	*	*	*
Hirudinea		*	*	*	*	*	*
Araneae		*	*	*	*	*	*
Acari		*	*	*	*	*	*
Pseudoscorpiones		*					
Ostracoda		*	*	*	*	*	
Cladocera	Bosminidae	*	*	*	*	*	*
	Chydoridae				*	*	
	Daphniidae				*	*	
Copepoda	Calanoida	*	*	*	*	*	*
	Cyclopoida					*	
Decapoda	Cambaridae	*	*		*		
Isopoda	Asellidae	*	*		*		
Amphipoda	Crangonyctidae	*	*	*	*	*	*
	Dogielinotidae	*	*	*	*	*	*

(continued)

(continued)

	Family	SE NA beaver dam wetlands			NE NA beaver pond complexes	Central Colorado Montane beaver dam	
		New	Mature	Abandoned	All basins	Valley terrace pond complexes	Stream channel/riparian distributary
Collembola	Entomobryidae	*	*	*	*		
	Hypogastruridae	*		*	*		
	Isotomidae	*	*	*			
	Poduridae			*	*	*	*
	Sminthuridae		*	*			
Ephemeroptera	Baetidae	*	*	*	*	*	
	Caenidae	*	*	*	*	*	*
	Ephemeridae		*				
	Ephemerellidae						*
	Heptageniidae						*
	Leptophlebiidae						*
	Siphlonuridae						*
Odonata	Aeshnidae	*		*	*	*	*
	Coenagrionidae	*	*	*	*	*	*
	Gomphidae	*			*	*	*
	Lestidae		*		*	*	*
	Libellulidae	*	*	*	*	*	*
Plecoptera	Chloroperlidae					*	*
	Nemouridae					*	*
	Perlidae						*

Order	Family						
Orthoptera	Gryllidae				*		
	Tettigoniidae				*		
Psocoptera							
Thysanoptera	Terebrantia				*		
Hemiptera	Aphidae				*	*	*
	Belostomatidae			*	*	*	*
	Cercopidae				*		
	Cicadellidae				*	*	*
	Coccoidea				*	*	*
	Corixidae	*	*	*	*	*	*
	Delphacidae				*	*	*
	Gelastocoridae			*			
	Gerridae	*	*	*		*	
	Hebridae		*	*	*		
	Hydrometridae			*	*		
	Mesoveliidae		*	*	*	*	*
	Miridae				*		*
	Nepidae						
	Reduviidae			*		*	*
	Veliidae		*	*	*	*	*
Neuroptera	Corydalidae			*	*	*	*
	Sialidae			*	*		

(continued)

(continued)

| | SE NA beaver dam wetlands | | | NE NA beaver pond complexes | Central Colorado Montane beaver dam ponds and wetlands | |
| | | | | | | |
Family	New	Mature	Abandoned	All basins	Valley terrace pond complexes	Stream channel/ riparian distributary
Coleoptera						
Anthicidae		*				
Carabidae		*	*	*	*	
Chrysomelidae			*	*	*	
Coccinellidae	*	*	*			
Curculionidae		*	*	*		
Dytiscidae	*	*	*	*	*	*
Elateridae			*			
Elmidae	*		*			*
Gyrinidae			*	*	*	
Haliplidae		*	*	*	*	
Hydraenidae			*	*		
Hydrophilidae	*	*	*	*	*	
Lampyridae		*	*			
Latridiidae			*			
Noteridae		*	*	*		
Phalacridae			*			
Ptilodactylidae		*	*			
Scirtidae		*	*	*		
Silvanidae			*			
Staphylinidae			*	*	*	

Trichoptera	Hydroptilidae	*	*	*			
	Hydropsychidae	*		*			
	Leptoceridae	*			*	*	
	Limnephilidae				*	*	*
	Phryganeidae				*	*	
	Polycentropodidae	*					*
	Rhyacophilidae	*					*
Lepidoptera	Crambidae	*					
	Noctuidae	*	*	*			
	Tineidae	*	*				
Diptera	Ceratopogonidae	*	*	*	*	*	*
	Chaoboridae				*	*	
	Chironomidae	*	*	*	*	*	*
	Corethrellidae	*	*	*	*		
	Culicidae	*	*	*	*	*	*
	Dixidae				*	*	*
	Dolichopodidae				*		
	Empididae	*	*		*		
	Ephydridae		*		*		
	Psychodidae			*	*		
	Ptychopteridae	*	*	*	*		
	Simuliidae			*	*		
	Stratiomyidae	*	*	*	*	*	*
	Tabanidae	*	*	*	*	*	
	Tipulidae	*	*	*	*	*	*
Hymenoptera	Formicidae	*	*	*			
	Chalcidoidea			*			
	Mymaridae	*					
	Platygastroidea	*	*	*			

References

Adler PH, Mason PG (1997) Black flies (Diptera: Simuliidae) of East-Central Saskatchewan, with description of a new species and implications for pest management. Can Entomol 129:81–91

Allan JD (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu Rev Ecol Evol System 35:257–284

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

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

Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologia 154:141–153

Anderson CB, Rosemond AD (2010) Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. Hydrobiologia 652:349–361

Anderson CB, Pastur GM et al (2009) Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. Mammal Rev 39:33–52

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309

Batzer DP (2013) The seemingly intractable ecological responses of invertebrates in North American wetlands: a review. Wetlands 33:1–15

Batzer DP, Ruhí A (2013) Is there a core set of organisms that structure macroinvertebrate assemblages in freshwater wetlands? Freshw Biol 58:1647–1659

Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annu Rev Entomol 41:75–100

Benke AC, Arsdall TCV, Gillespie DM, Parrish FK (1984) Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol Monogr 54:25–63

Benke A, Henry R, Gillespie D, Hunter R (1985) Importance of snag habitat for animal production in southeastern streams. Fisheries 10:8–13

Benke A, Ward G, Richardson T (1999) Beaver impounded wetlands of the southeastern coastal plain. In: Batzer D, Rader R, Wissinger S (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 217–245

Bluzma P (2003) Beaver abundance and beaver site use in a hilly landscape (Eastern Lithuania). Acta Zool Lituanica 13:8–14

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

Burchsted D, Daniels MD (2014) Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A. Geomorphology 205:36–50

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

Butler DR, Malanson GP (1995) Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13:255–269

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

Caudill CC (2002) Metapopulation biology of the mayfly *Callibaetis ferrugineus hageni* in high-elevation beaver ponds. Ph.D. Dissertation, Cornell University, Ithaca, NY

Caudill CC (2003a) Empirical evidence for nonselective recruitment and a source-sink dynamic in a mayfly metapopulation. Ecology 84:2119–2132

Caudill CC (2003b) Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation. Oikos 101:624–630

Caudill CC (2005) Trout predators and demographic sources and sinks in a mayfly metapopulation. Ecology 86:935–946

Cirmo CP, Driscoll CT (1993) Beaver pond biogeochemistry: acid neutralizing capacity generation in a headwater wetland. Wetlands 13:277–292

Clifford HF, Wiley GM, Casey RJ (1993) Macroinvertebrates of a beaver altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. Can J Zool 71:1439–1447

Collen P, Gibson RJ (2001) The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. Rev Fish Biol Fish 10:439–461

Corcoran RM, Lovvorn JR, Heglund PJ (2009) Long-term change in limnology and invertebrates in Alaskan boreal wetlands. Hydrobiologia 620:77–89

Crowley PH, Johnson DM (1982) Habitat and seasonality as niche axes in an odonate community. Ecology 63:1064–1077

Cunningham JM, Calhoun AJK, Glanz WE (2006) Patterns of beaver colonization and wetland change in Acadia National Park. NE Natural 13:583–596

Curran JC, Cannatelli KM (2014) The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. Earth Surf Process Landf 39:1236–1244

Dahl TE (2011) Status and trends of wetlands in the conterminous United States 2004 to 2009. US Department of the Interior, Fish and Wildlife Service, Washington, DC

Danilov P, Kanshiev V, Fyodorov F (2011) Characteristics of North American and Eurasian beaver ecology in Karelia. In: Sjöberg G, Ball JP (eds) Restoring the European beaver: 50 years of experience. Pensoft, Sofia, pp 55–72

De Szalay FA, Resh VH (2000) Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. Freshw Biol 45:295–308

Devito KJ, Dillon PJ (1993) Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. Can J Fish Aquat Sci 50:2222–2234

Donkor NT, Fryxell JM (2000) Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (Castor canadensis) foraging and edaphic factors. Plant Ecol 148:1–12

Fairchild GW, Faulds AM, Matta JF (2000) Beetle assemblages in ponds: effects of habitat and site age. Freshw Biol 44:523–534

Fairchild GW, Jason C et al (2003) Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. J North Am Benthol Soc 22:224–240

France RL (1997) The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. Can J Zool 75:1009–1013

Fuller MR, Peckarsky BL (2011a) Does the morphology of beaver ponds alter downstream ecosystems? Hydrobiologia 668:35–48

Fuller MR, Peckarsky BL (2011b) Ecosystem engineering by beavers affects mayfly life histories. Freshw Biol 56:969–979

Fustec J, Lode T, Le Jacques D, Cormier JP (2001) Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. Freshw Biol 46:1361–1371

Gibbs JP (2000) Wetland loss and biodiversity conservation. Conserv Biol 14:314–317

Gibson PP, Olden JD (2014) Ecology, management, and conservation implications of North American beaver (Castor canadensis) in dryland streams. Aquat Conserv Mar Freshw Ecosys 24:391–409

Grover AM, Baldassarre GA (1995) Bird species richness within beaver ponds in south-central New York. Wetlands 15:108–118

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

Hammerson GA (1994) Beaver (*Castor canadensis*) ecosystem alterations, management, and monitoring. Nat Areas J 14:44–57

Harthun M (1999) The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of brooks in Hesse (Germany). Limnologica 29:449–464

Hartman G (1994) Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. Conserv Biol 8:713–717

Hartman G (1995) Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. Wildl Biol 1:97–103

Hodkinson ID (1975a) A community analysis of the benthic insect fauna of an abandoned beaver pond. J Anim Ecol 44:533–551

Hodkinson ID (1975b) Energy flow and organic matter decomposition in an abandoned beaver pond ecosystem. Oecologia 21:131–139

Hood GA, Bayley SE (2008a) Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biol Conserv 141:556–567

Hood GA, Bayley SE (2008b) The effects of high ungulate densities on foraging choices by beaver (*Castor canadensis*) in the mixed-wood boreal forest. Can J Zool 86:484–496

Hood GA, Bayley SE (2009) A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. For Ecol Manage 258:1979–1989

Hood GA, Larson DG (2014) Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. Wetlands 34:19–29

Hood GA, Larson DG (2015) Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. Freshw Biol 60:198–208

IPCC (2014) Climate change 2014: synthesis report. In: Pachauri RK, Meyer LA (eds) Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. IPCC, Geneva, Switzerland

Jackson CR, Martin JK, Leigh DS, West LT (2005) A southeastern Piedmont watershed sediment budget: evidence for a multi-millennial agricultural legacy. J Soil Water Conserv 60:298–310

Johnson DR, Chance DH (1974) Presettlement overharvest of Upper Columbia River beaver populations. Can J Zool 52:1519–1521

Johnston CA, Naiman RJ (1987) Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecol 1:47–57

Johnston CA, Naiman RJ (1990) Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621

Kemp PS, Worthington TA et al (2012) Qualitative and quantitative effects of reintroduced beavers on stream fish. Fish Fisher 13:158–181

Klemmer AJ, Wissinger SA, Greig HS, Ostrofsky ML (2012) Nonlinear effects of consumer density on multiple ecosystem processes. J Anim Ecol 81:770–780

Klotz RL (1998) Influence of beaver ponds on the phosphorus concentration of stream water. Can J Fish Aquat Sci 55:1228–1235

Kohler SL, Corti D, Slamecka MC, Schneider DW (1999) Prairie floodplain ponds—mechanisms affecting invertebrate community structure. In: Batzer DP, Rader RD, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America. Wiley, New York, pp 711–730

Law A, Jones KC, Willby NJ (2014) Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. Aquat Bot 116:27–34

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

Mackay RJ, Waters TF (1986) Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67:1680–1686

Malanson GP, Butler DR (1990) Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, U.S.A. Arctic Alpine Res 22:183–194

Malison RL, Lorang MS, Whited DC, Stanford JA (2014) Beavers (*Castor canadensis*) influence habitat for juvenile salmon in a large Alaskan river floodplain. Freshw Biol 59:1229–1246

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 Res 21:263–268

Margolis BE, Raesly RL, Shumway DL (2001) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. Wetlands 21:554–563

McCall TC, Hodgman TP, Diefenbach DR, Owen RB (1996) Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. Wetlands 16:163–172

McCauley SJ (2008) Slow, fast and in between: habitat distribution and behaviour of larvae in nine species of libellulid dragonfly. Freshw Biol 53:253–263

McCauley SJ, Brodin T, Hammond J (2010) Foraging rates of larval dragonfly colonists are positively related to habitat isolation: results from a landscape-level experiment. Am Nat 175(3):E66–E73

McDowell DM, Naiman RJ (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (Castor canadensis). Oecologia 68:481–489

McKinstry MC, Caffrey P, Anderson SH (2001) The importance of beaver to wetland habitats and waterfowl in Wyoming. J Am Water Resour Assoc 37:1571–1577

McMaster RT, McMaster ND (2001) Composition, structure, and dynamics of vegetation in fifteen beaver-impacted wetlands in western Massachusetts. Rhodora 103(915):293–320

Morrison A, Westbrook CJ, Bedard-Haughn A (2015) Distribution of Canadian Rocky Mountain wetlands impacted by beaver. Wetlands 35:95–104

Mukundan R, Radcliffe DE, Ritchie JC (2011) Channel stability and sediment source assessment in streams draining a Piedmont watershed in Georgia, USA. Hydrol Process 25:1243–1253

Naiman RJ, Melillo JM (1984) Nitrogen budget of a subarctic stream altered by beaver (Castor canadensis). Oecologia 62:150–155

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

Naiman RJ, Décamps H, Pastor J, Johnston CA (1988a) The potential importance of boundaries of fluvial ecosystems. J North Am Benthol Soc 7:289–306

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

Niles JM, Hartman KJ, Keyser P (2013) Short-term effects of beaver dam removal on brook trout in an Appalachian headwater stream. NE Nat 20:540–551

Nolet BA, Rosell F (1998) Comeback of the beaver Castor fiber: an overview of old and new conservation problems. Biol Conserv 83:165–173

Nummi P, Hahtola A (2008) The beaver as an ecosystem engineer facilitates teal breeding. Ecography 31:519–524

Nummi P, Holopainen S (2014) Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. Aquat Conserv Mar Freshw Ecosys 24:623–633

Pliūraitė V, Kesminas V (2012) Ecological impact of Eurasian beaver (Castor fiber) activity on macroinvertebrate communities in Lithuanian trout streams. Cent Eur J Biol 7:101–114

Pollock MM, Naiman RJ et al (1995) Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. In: Jones CG, Lawton JH (eds) Linking species & ecosystems. Springer, New York, pp 117–126

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 Surf Process Landf 32:1174–1185

Polvi LE, Wohl E (2012) The beaver meadow complex revisited—the role of beavers in post-glacial floodplain development. Earth Surface Process Landform 37:332–346

Prather CM, Pelini SL et al (2013) Invertebrates, ecosystem services and climate change. Biol Rev 88:327–348

Pritchard G, Hall HA (1971) An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of Tipula sacra Alexander (Diptera; Tipulidae). Can J Zool 49:467–482

Pritchard G, Leischner TG (1973) The life history and feeding habits of Sialis cornuta Ross in a series of abandoned beaver ponds (Insecta; Megaloptera). Can J Zool 51:121–131

Ray AM, Rebertus AJ, Ray HL (2001) Macrophyte succession in Minnesota beaver ponds. Can J Bot 79:487–499

Ray HL, Ray AM, Rebertus AJ (2004) Rapid establishment of fish in isolated peatland beaver ponds. Wetlands 24:399–405

Rebertus AJ (1986) Bogs as beaver habitat in north-central Minnesota. Am Midl Nat 116: 240–245

Richardson JS, Mackay RJ (1991) Lake outlets and the distribution of filter feeders: an assessment of hypotheses. Oikos 62:370–380

Rolauffs P, Hering D, Lohse S (2001) Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. Hydrobiologia 459:201–212

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

Smith AJ, Delorme LD (2010) Ostracoda. In: Covich JH, Thorp AP (eds) Ecology and classification of North American freshwater invertebrates, 3rd edn. Academic, San Diego, CA, pp 725–771

Smith ME, Driscoll CT et al (1991) Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack mountains, New York. Can J Zool 69:55–61

Smol JP, Douglas MSV (2007) Crossing the final ecological threshold in high Arctic ponds. Proc Natl Acad Sci U S A 104:12395–12397

Snodgrass JW, Meffe GK (1998) Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928–942

Sprules WM (1940) The effect of a beaver dam on the insect fauna of a trout stream. Trans Am Fish Soc 70:236–248

Stagliano DM, Benke AC, Anderson DH (1998) Emergence of aquatic insects from two habitats in a small wetland of the southeastern USA: temporal patterns of numbers and biomass. J North Am Benthol Soc 17:37–53

Stoks R, McPeek MA (2003) Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. Ecology 84:1576–1587

Stoks R, McPeek MA (2006) A tale of two diversifications: reciprocal habitat shifts to fill ecological space along the pond permanence gradient. Am Nat 168(S6):S50–S72

Strachan SR, Chester ET, Robson BJ (2014) Microrefuges from drying for invertebrates in a seasonal wetland. Freshw Biol 59:2528–2538

Syphard AD, Garcia MW (2001) Human- and beaver-induced wetland changes in the Chickahominy River watershed from 1953 to 1994. Wetlands 21:342–353

Trimble SW (1974) Man-induced soil erosion on the southern piedmont. Soil Conservation Society of America, Ankeny, pp 1700–1970

Tuytens K, Vanschoenwinkel B, Waterkeyn A, Brendonck L (2014) Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. Freshw Biol 59:955–968

Van de Meutter F, Cottenie K, De Meester L (2008) Exploring differences in macroinvertebrate communities from emergent, floating-leaved and submersed vegetation in shallow ponds. Fund Appl Limnol 173:47–57

Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Annu Rev Ecol System 27:337–363

White SM, Rahel FJ (2008) Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. Trans Am Fish Soc 137:881–894

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

Wissinger SA (1988) Life history and size structure of larval dragonfly populations. J North Am Benthol Soc 7:13–28

Wissinger SA (1999) Ecology of wetland invertebrates: synthesis and applications for conservation and management. In: Batzer DP, Rader RD, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 1043–1086

Wissinger SA, Gallagher LJ (1999) Beaver pond wetlands in northwestern Pennsylvania. Modes of colonization and succession after drought. In: Batzer D, Rader R, Wissinger S (eds)

Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 333–362

Wissinger SA, Ingmire S, Bogo J (2001) Invertebrate and plant communities in restored wetlands in Pennsylvania. IN: R.R. Rader, D.P. Batzer, and S.A. Wissinger (eds.) Biomonitoring and Management of North American Wetlands. John Wiley & Sons, NY

Wissinger SA, Brown WS, Jannot JE (2003) Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.). Freshw Biol 48:255–270

Wissinger SA, Whissel JC, Eldermire C, Brown WS (2006) Predator defense along a permanence gradient: roles of case structure, behavior, and developmental phenology in caddisflies. Oecologia 147:667–678

Woo M-K, Waddington JM (1990) Effects of beaver dams on subarctic wetland hydrology. Arctic 43:223–230

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

Wright JP, Flecker AS, Jones CG (2003) Local vs landscape controls on plant species richness in beaver meadows. Ecology 84:3162–3173

Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Annu Rev Environ Resour 30:39–74