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The missing dead: The lost role of animal remains in nutrient cycling in North American Rivers

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ABSTRACT

While leaf litter, wood, and other plant remnants are known to play a central role in lotic ecosystems, animal remains (carcasses, bones, shells) have received less attention. We propose a simple classification scheme for animal remains in rivers based on origin (authochthonous vs. allochthonous) and frequency (pulsed vs continuous). We then present case studies in which we estimate the former biomass of several taxonomic groups that are now diminished in abundance to determine whether their remains could have historically constituted a significant flux of nutrients in rivers of North America. We focus on bones and shells, which decompose slowly and could provide long-term reservoirs of nutrients. We find that carcasses of alligator snapping turtles, once abundant in southeastern rivers, could have provided an amount of phosphorus equivalent to about 1% of total phosphorus (TP) load at median flow, and more at low flows. Mussel shells could have contributed a similar amount (0.8% of TP) but the contribution of beaver carcasses, even at former abundances, was likely small. In contrast, a single documented mass drowning of bison in the Assiniboine River could have contributed half the annual TP load for that river. Such drownings could have been a common occurrence prior to the loss of most wild terrestrial megafauna in North America. We conclude that animal remnants, particularly allochthonous remains from terrestrial animals, formerly played a substantial role in nutrient cycling. Existing models of ecosystem function under reference conditions are incomplete without consideration of these lost animal legacies.

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1. Introduction

Ecologists have long recognized the fundamental role of dead plant matter in freshwater ecosystems. Headwater streams, limited in their autotrophic production by shading, are fueled by the allochthonous carbon and nutrients from senesced leaves and wood (Vannote et al., 1980; Wallace et al., 1997), while both streams and rivers are physically structured in part by deposited large wood (Gurnell et al., 2002). The anthropogenic reduction of leaves and wood is a well-known stressor to freshwater ecosystems (Collins et al., 2002; Wallace et al., 1997). In contrast, the role of dead animal matter and the effect of anthropogenic reduction in the supply of animal carcasses have received comparatively scant attention (see Subalusky and Post, 2018, for a review of this literature in the context of the broader topic of animal spatial resource subsidies). This imbalance in research attention was identified >25 years ago (Parmenter and Lamarra, 1991), but relatively little work has been done since then to rectify the deficit.

Studies of Pacific salmon (*Oncorhynchus* spp.) constitute a major exception. Anadromous salmon carcasses have been shown to constitute a substantial transfer of carbon and nutrients from marine to freshwater systems, increasing ecosystem productivity and fish growth rates (Cederholm et al., 1999; Gende et al., 2002; Wipfli et al., 2003). The drastic decline in salmon populations due to dam construction, overharvest and habitat degradation (Montgomery, 2003) has prompted extensive research to understand the role that carcasses play in ecosystems. Gresh et al. (2000) estimated that marine-derived phosphorus and nitrogen have declined by >93% in parts of the Pacific Northwest as a result of salmon declines, and the low nutrient state of spawning and rearing habitats may inhibit salmon recovery. While salmon spawning runs represent dramatic pulsed carcass deposition events, they are not the only sources of aquatic animal carcasses in rivers. Presumably, the steady supply of dead non-migratory aquatic animals, including fish, also constitutes a substantial nutrient flux when carcasses remain in the aquatic system (Parmenter and Lamarra, 1991).

The carcasses of terrestrial animals can also provide important subsidies to freshwater, but populations of many wild terrestrial animals have been reduced as much or more than salmon stocks; the current global biomass of wild land mammals is perhaps one seventh of its level prior to the Quaternary megafauna extinctions (although the

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biomass of humans and domestic animals has increased by an even larger amount; Bar-On et al., 2018). Formerly, terrestrial mammals may have contributed large numbers of carcasses to freshwater systems partly by gravity (dead animals, like dead plants, will gradually be moved towards the low places of the landscape) and in part via mass mortality events during migrations across treacherous rivers. Subalusky et al. (2017) reported that the annual migration of >1 million Serengeti wildebeest (*Connochaetes taurinus*) results in an annual mean of 6250 carcasses entering the Mara River, providing a substantial portion of fish diet and representing a long-term source of nutrients via slow-decomposing bone. They also observed that such migrations and drownings were formerly documented in North America and other regions, and that the lost input of resources from mass drownings may have dramatically altered the way these river ecosystems function (Subalusky et al., 2017).

Here we explore the role that animal remains may have once played in nutrient cycling in North American rivers and streams. Our focus is on the more persistent components of the remains—bones and shells—as these provide long-term nutrient reservoirs after the initial pulse of nutrients from soft tissues. Bone is a composite material consisting of a mineral phase (calcium phosphate primarily in the form of hydroxylapatite), an organic phase (collagen, non-collagenous proteins, and lipids), and water (Currey, 2002). Phosphorus comprises a large proportion of bone material, and while the ratio of nitrogen (N) to phosphorus (P) in vertebrate soft tissue ranges from 10 to 100:1, in bones it is <1:1 (Elser et al., 1996; Subalusky et al., 2017). In their study of wildebeest carcasses, Subalusky et al. (2017) found that bones accounted for 44% of the dry mass of the carcass and 95% of the P. Shells from bivalves have lower nutrient content than bone but may nevertheless be significant due to the high abundances and densities they achieve. In the succeeding sections we introduce a simple framework for classifying animal remains, and then examine several case studies from different taxonomic groups that were formerly abundant in North America to answer the question: did animal remains formerly constitute a substantial nutrient flux in North American flowing waters?

2. A taxonomy of animal remains in lotic ecosystems

We classify the different types of animal remains in flowing waters based on their origin and the timing of their input (Table 1). At the most general level we can identify animal remains as either autochthonous or allochthonous. Autochthonous remains are those of freshwater or riparian animals that lived and died within the stream ecosystem itself; their decomposition is a form of internal nutrient cycling, provided the animals obtained most of their food from within the aquatic system. Autochthonous remains either can be *continuous* – death occurs at a fairly steady rate – or *pulsed*, when animals die en masse. Examples of the latter are fish kills due to hypoxia (e.g., Dutton et al., 2018) and mussel die-offs due to drought conditions (Gagnon et al., 2004). Pulsed authochthonous inputs can be important nutrient contributions when they occur, and they are likely becoming more common occurrences due to changing hydrological regimes (Vaughn et al., 2016).

Allochthonous remains are those resulting from animals that primarily lived outside of the stream ecosystem, and thus their death and decomposition represent a transfer of nutrients and carbon into the system. Like autochthonous inputs, we can divide these remains into *pulsed* inputs (generally seasonal inputs by migratory animals) and *continuous* inputs (distributed throughout the year by non-migratory animals). Migratory animals likely to contribute pulsed allochthonous inputs include terrestrial animals that cross hazardous large rivers during seasonal movements (Subalusky et al., 2017) and anadromous fishes such as salmon and shad (*Alosa* spp.; Twining et al., 2017). In this category we also include insects such as cicadas (*Magicicada* sp.) that experience periodic booms that deliver pulses of dead individuals to rivers and streams (Menninger et al., 2008; Nowlin et al., 2007). These pulsed inputs can be caused or compounded by seasonal environmental fluctuations such as flood and drought, both of which may increase mortality in and near rivers (Subalusky and Post, 2018). Continuous allochthonous inputs are likely to come from non-migratory animals either that feed in terrestrial ecosystems but tend to die in or near aquatic ecosystems, such as beaver (*Castor* spp.), or that feed and die in terrestrial ecosystems and whose remains are delivered from the watershed to aquatic ecosystems during rain events. The latter form of inputs can include a wide range of species, and these inputs have long been studied by paleontologists interested in interpreting the origin of fluvial bonebeds (e.g., Behrensmeyer, 2007). The degree of importance of any of these input routes likely varies by river and season and depends on aquatic versus terrestrial animal abundance, watershed size, and distinct regional characteristics, among other factors.

In the following sections, we examine case studies of both autochthonous and allochthonous animal remains, focusing on taxa that were once abundant in North American streams and rivers and have now declined.

3. Alligator snapping turtle (autochthonous, continuous)

We start with a large, once-common autochthonous vertebrate: the alligator snapping turtle (*Macrochelys temminckii*), which is native to the southern US and can attain masses of 90 kg or more. It is one of over 250 species of turtles that inhabit freshwaters around the world (Buhlmann et al., 2009; Moll and Moll, 2004), including several other giant species such as the South American river turtle (*Podocnemis expansa*), and the giant softshell turtles of Asia (*Rafetus swinhoei, Pelochelys* spp.). Although population numbers are difficult to estimate (e.g., studies typically report catch per unit sampling effort, which is difficult to convert to a population estimate), historical accounts indicate that many riverine turtle taxa were once highly abundant. For example, 18th and 19th century explorers estimated populations of 400,000 or more adult South American river turtles in the Orinoco and Amazon rivers, based only on the amount of oil harvested annually from eggs taken from nesting beaches (Mittermeier, 1978). River turtles are still harvested in Amazonia, although populations have been diminished by centuries of exploitation (Mittermeier, 1978; Moll and Moll, 2004; Miorando et al., 2013). In fact, freshwater turtle abundances are depressed globally (Gibbons et al., 2000), potentially resulting in losses

Table 1
Four types of animal remains in rivers, classified by origin and timing, with examples used in this article. See text for methods of calculation of phosphorus (P) loading and the proportion of annual P loading in the reference river systems.

Origin of remains	Timing	Drivers	Example	P input from bones (kg P yr^{-1})	% of annual P load (Reference)
Autochthonous	Continuous	Annual mortality from aquatic animals	Alligator snapping turtle Freshwater mussels	52 40	1.1% (Kinchafoonee Cr, US) 0.8% (Kinchafoonee Cr, US)
Autochthonous	Pulsed	Mass mortality of aquatic animals due to environmental conditions	[Not addressed here]		
Allochthonous	Continuous	Annual mortality from terrestrial or semi-aquatic animals	Beaver	0.15	<0.01% (Kinchafoonee Cr, US)
Allocthhonous	Pulsed	Seasonal mortality from migratory animals	Bison	42,810	50% (Assiniboine River, CAN)

to freshwater ecosystem function. Ecologists have explored the effects of turtle excretion and feeding activities on water quality and nutrient dynamics in freshwater systems (Lindsay et al., 2013; Sterrett et al., 2015), but not the role of dead turtle bones and shells.

Alligator snapping turtles were extensively harvested in the 1960s–1980s for turtle soup. Although incompletely documented, records include an estimated seasonal catch from one southeastern US river system of 3–4 tons (or ~3175 kg) a day over several years, with a single trapper reportedly taking ~450 kg a day and a total of 4000 to 5000 individuals from one river in that system (Pritchard, 1989). Extrapolating from this single trapper (daily take of 450 kg/3175 kg, or 14% of harvest), we estimate a total of approximately 31,500 (i.e., 4500/0.14) alligator snapping turtles harvested from perhaps 300–500 stream km, and thus a pre-harvest density on the order of 100 individuals per km. This estimate may be low, given that some turtles likely escaped harvest. Nonetheless, recent catch rates of alligator snapping turtles in this system remain >90% lower than rates during commercial trapping (King et al., 2016), suggesting a large portion of the population was harvested.

Natural mortality of aquatic turtles could provide a substantial input of rapidly decomposing carrion and more slowly decomposing bone and shell to freshwater ecosystems. Given our approximate pre-harvest estimate of alligator snapping turtle density and an average wet mass exceeding 30 kg (based on harvest sizes in the 1970s (Jensen and Birkhead, 2003), even a low annual mortality of 2% (Reed et al., 2002) would introduce >60 kg of turtle carrion (wet mass) per km annually. Body composition data from other turtles (Sterrett et al., 2015) indicates that this includes about 1.4 kg of P, of which 1.3 kg is in the shell and skeleton. At equilibrium the decay rate is equal to the input rate, which means that prior to harvest, decomposing alligator snapping turtle skeletons and shells would have supplied about 1.3 kg of P km^{-1} y^{-1} to the rivers in which they occurred. At equilibrium the standing stock would have been about 60 kg dry mass of shell and bone, assuming a decomposition rate of 0.001 d^{-1} (Subalusky et al., 2017).

For context, we compare this P supply rate to the P load of Kinchafoonee Creek, a small river in Southwest Georgia with a drainage area of 1365 km^2 that supported an intensive harvest of alligator snappers in the 1970s (Pritchard, 1989). We estimate that this river includes about 40 km of habitat suitable for alligator snapping turtles at an average density, which means that carcasses of the species could have supplied 40 $*$ 1.3 or 52 kg P y^{-1} or 142 g P d^{-1}. We extracted 25 measured concentrations of total phosphorus (TP) from the National Water Information System (https://nwis.waterdata.usgs.gov/ga/nwis/qwdata/) for Kinchafoonee Creek (1992–2000; USGS site 02350900) and calculated their median to be 0.02 mg L^{-1}. At median discharge of 7698 L s^{-1} this sums to 13.3 kg P d^{-1}, which means that decomposing shells and bones of Alligator Snapping Turtles in the system could have contributed about 1.1% of P at a typical flow. At high flow the contribution would have been negligible, but at low flows it's possible that the equivalent of 10% of water column P could have been derived just from alligator snapping turtle shell and bone.

4. Mussels (autochthonous, continuous)

Freshwater pearly mussels (bivalves in the families Unionidae, Margaritaferidae and Hyriidae) are globally distributed and often highly abundant, although many taxa have experienced substantial declines over the course of the past century. North America exemplifies this pattern, with the highest mussel diversity in the world (Haag, 2010) and the greatest number of imperiled taxa (Haag and Williams, 2014; Williams et al., 1993). Contributors to imperilment have included habitat loss, water quality declines, loss of host fish, and direct harvest (Strayer, 2008). Many populations likely never have recovered from the massive harvests for the button industry in the early 1900s, when the shell removals in the Mississippi Basin frequently exceeded 20 million kg per year (Claassen, 1994).

Mussels can form highly dense aggregations, and mussel beds can be hotspots of nutrient recycling (Atkinson and Vaughn, 2015). Whether dead mussels also contribute (or formerly contributed) substantially to nutrient fluxes is not obvious, as mussel biomass is largely in the shell, which is composed mainly of nutrient-poor calcium carbonate crystals (primarily in the form of aragonite). This implies that after the soft material of a mussel has decomposed, the spent shells may not serve as a long-term nutrient reservoir the way that bones and turtle carapaces do. However, Unionids and Margaritaferids have a layer of complex proteins called conchiolins that separate the outer shell from the nacre (Kat, 1983), and the nacre itself (primarily aragonite) has been shown to have a complex composition, including small amounts of phosphorus (Soldati et al., 2008).

Actual studies of shell nutrient content are few. Atkinson and Vaughn (2015) measured the body chemistry of 138 individuals of multiple Unionid species from mussel beds in the Kiamichi River and reported that on the average, 91% of mussel P and 86% of mussel N was in the shell rather than the soft tissue. However, they did not report actual chemical composition. Hoellein et al. (2017) reported P composition of 0.1% to 0.2% for soft body tissue for *Lasmigona complanata* and *Pyganodon grandis*, respectively, and much lower percent composition for the shell, but shell P was nevertheless substantial due to the large total mass relative to soft body tissue. For L. *complanata* the majority of P was in the shell, whereas for *P. grandis* the majority was in the soft tissue. At the stream reach scale, the mussels accounted for more standing stock of P than was in the sediment (71% vs. 29%).

We conducted a series of calculations similar to those described above for Alligator Snapping Turtles to estimate the potential role of spent mussel shells in nutrient cycling. We assumed that P content of mussel shells was 0.05%. We took the mid-range of mussel shell production values used by Strayer and Malcom (2007) in their estimates of shell standing stocks, which was 100 g m^{-2} y^{-1}. The size of standing stocks can vary over orders of magnitude depending on water hardness and other factors (Strayer and Malcom, 2007); however, we assumed that populations were at equilibrium and that dissolution was equal to production. Therefore, we estimate P release from mussel shells to be 0.05 g m^{-2} y^{-1}. If we assume this level of nutrient release across the same reference river described above (Kinchafoonee Creek), we calculate total P loading from decaying mussel shells at 40 kg P y^{-1} or 110 g d^{-1}. This constitutes 0.8% of the total estimated P loading at median flow, a bit less than what we estimated for Alligator Snapping Turtle carapaces, but nevertheless potentially substantial during low flow periods.

5. Beaver (allochthonous, continuous)

Annual mortality from semi-aquatic mammals such as beaver also must contribute a regular input of carcasses to aquatic ecosystems, as these animals spend most of their lives in river and riparian systems. However, because the animals primarily feed on terrestrial vegetation, their carcasses provide allochthonous inputs to aquatic ecosystems. Keenan et al. (2018) estimated that the current population of 9 million beaver, with an estimated annual mortality rate of 6%, could lead to the introduction of 0.05 kg nitrogen (N) and 0.29 kg carbon (C) km^{-2} yr^{-1} over their current native range of 8.7 million km^2. They did not include an estimate for the amount of phosphorus contributed by beavers, but using the allometric relationship between skeletal mass and body mass (Prange et al., 1979) and the stoichiometry of wildebeest bones (Subalusky et al., 2017), we can estimate that beavers contribute 0.01 kg P km^{-2} yr^{-1}, 91% of which would be in the form of slowly decomposing bones. These inputs are relatively small, particularly in comparison to anthropogenic nutrient levels; however, these inputs may have been much more substantial for historical beaver populations that were much larger and more widespread.

Before the arrival of Europeans in North America and the subsequent trapping and removal of beavers, an estimated 60–400 million beaver were distributed over 15 million km^2 (Naiman et al., 1988). Using the same calculations as above, we can estimate historical beaver populations may have contributed 1.1–7.4 kg C, 0.2–1.3 kg N and 0.04–0.30 kg P km^{-2} yr^{-1}. Again, 0.04–0.27 kg P km^{-2} yr^{-1} would be in the form of bones, which decay over years and slowly leach phosphorus into the system. If we assume a similar decomposition rate as wildebeest bones (0.001 d^{-1}), the standing stock of beaver bones at equilibrium would have equaled 1.5–9.7 kg bones (dry mass) km^{-2}. To assess whether these bones could have provided a significant amount of P to streams, we considered the same reference river as above (Kinchafoonee Creek) and assumed a mean density of 2.5 beaver dams km^{-1} with a mean colony size of 4–8 beavers, yielding an average of one carcass km^{-1} yr^{-1} (Naiman et al., 1988). This input would provide 2 kg bones and 150 g P km^{-1} yr^{-1}, which is about the same contribution as we estimated from alligator snapping turtles *per day*. Thus, even at historical densities, beaver bones probably were not a major component of nutrient cycling in rivers and streams. However, historical populations of other semi-aquatic mammals, including mink, muskrat and river otter, were also similarly large (Raesly, 2001), and these species often live sympatrically, so total contributions from semi-aquatic mammals could be several times that estimated for beavers.

6. Bison and Caribou (allochthonous, pulsed)

Allochthonous, pulsed remains from anadromous fishes have already been discussed above and covered widely in the literature. Less well recognized is the potential input from migratory terrestrial animals into aquatic ecosystems. Most large ungulate migrations have disappeared in North America due to declining populations and fragmented landscapes (Berger et al., 2014; Harris et al., 2009; Wilcove and Wikelski, 2008). However, historical estimates suggest there were 30–60 million bison roaming the Great Plains of the western US until the late 1700s. Early explorers provided multiple accounts of mass drownings of bison, particularly when they would cross rivers in early spring and the thin ice would break. Saindon (2003) suggested that, given the number of accounts of mass drownings and the number of large rivers in the Great Plains, it is reasonable to suppose that several hundred thousand bison drowned annually during the spring break-up of river ice. We get a similar estimate if we assume that the same proportion of bison drowned annually as that observed in the intact Serengeti wildebeest migration (0.48% of the herd): approximately 144,000 to 288,000 bison might have drowned annually in rivers of the Great Plains.

Bison have a mean mass of 588 kg, so these drownings could have translated to an annual input of 85,000–169,000 metric tons of biomass (wet weight). Using the allometric relationship between skeletal mass and body mass (Prange et al., 1979) and the stoichiometry of wildebeest soft tissue and bones (Subalusky et al., 2017), these drownings would have translated to an annual input of 8300–16,600 tons C, 1900–3900 tons N, and 900–1800 tons P. Bones account for 40% of the dry mass of bison, and assuming a similar stoichiometry as wildebeest bones, they would comprise 800–1700 tons of the P introduced. Assuming a similar decay rate as measured for wildebeest bones, this annual input would yield a standing stock of 30,000–60,000 tons of bones (dry mass) in rivers of the Great Plains. Bone decomposition rate is likely much slower compared to tropical rivers due to lower temperatures, so standing stocks may actually have been much larger.

An anecdotal observation of a bison mass drowning event on the Assiniboine River in 1795, during which a trapper counted all 7360 carcasses along the river bank, suggests these inputs were locally important. Performing the same suite of calculations as described above, this drowning would have resulted in the input of 4300 tons of biomass (wet weight) and 700 tons of bones (wet weight), the latter of which would have contributed 43 tons of phosphorus. To compare this input to baseline P levels in the river, we can use the median estimate of baseline P in rivers of the Great Plains, which is 0.06 mg L^{-1} (Smith et al., 2003), multiplied by the average discharge on the Assiniboine River, which is 45 m^3 sec^{-1}, to estimate P flux as 233 kg P d^{-1} or 85,147 kg P yr^{-1}. Thus, the total input of P from bones from this bison drowning is equivalent to 50% of the annual load. Since pre-development levels of P could have been much lower, these carcass inputs could have been a major driver of P cycling in Great Plains rivers.

Mass drownings also have been documented for caribou migrations. In 1984, a mass drowning happened in the George River herd, which was once the world's largest caribou herd (Hummel and Ray, 2008). Estimates are that 10,000–22,000 individuals drowned in a crossing of the Caniapiscau River near Calcaire Falls during high flows. Given the herd size at that time, this drowning accounted for ~2% of the herd. Caribou have an average mass of 135 kg per individual; thus, this drowning resulted in 1400–3000 tons of biomass (wet mass) entering the river. Using the allometric relationship between skeletal mass and body mass (Prange et al., 1979) and the stoichiometry of wildebeest soft tissue and bones (Subalusky et al., 2017), this input would include 190–410 tons of bones (wet mass), which would comprise 12–26 tons of P.

There are other accounts of small, annual drownings happening in the George River herd. If we assume that annual mass drownings happened historically at the same rate as documented for the wildebeest migration, then at the peak herd size of ~750,000 in the 1980s, which had recovered since the first counts in the 1940s so possibly resembled pre-European levels, we would estimate 3600 individuals drowned annually. This annual input would equal 490 tons of biomass (wet mass) every year, of which 68 tons (wet mass) would be bones providing 4.2 tons of P. Assuming the same decomposition rate as measured for wildebeest bones, this annual input would yield a standing stock of 151 tons of bones (dry mass) in the river.

7. Discussion

Our calculations suggest that carcasses from aquatic animals formerly contributed a modest but non-trivial amount of nutrients on a regular basis to North American rivers, while terrestrial animal carcasses from migratory animals were periodically deposited in large quantities. Although the phosphorus contributions of dead turtles, mussels and beaver were probably individually modest, these constitute just a few of the taxa that would have contributed carcasses. We did not attempt to quantify the biomass of the dominant form of animal biomass in most river systems—fish. However, research has shown that fish bones are large reservoirs of P, and that carcass bones and scales can be relatively recalcitrant (Parmenter and Lamarra, 1991; Vanni et al., 2013). Other taxa, such as waterfowl and the American alligator (*Alligator mississippiensis*), could be regionally important. When combined with terrestrial animal bones, the mass of these slow-decomposing animal remnants may have once constituted a substantial portion of overall nutrient fluxes, especially at low flows.

Understanding the scale of these historical inputs is significant because our idea of what rivers ought to be—the pre-development state that is often the explicit or implicit model for restoration—is colored by past losses (Moss, 2015). Even rivers that are not obviously impacted by land use, dams or contamination may be missing autochthonous animals due to past extirpations, and we assume that nearly all North American rivers have fewer bones from migratory terrestrial animals than in the past. Certainly missing are the many megafauna species that went extinct at the end of the Pleistocene. North America alone lost 65 species with a mean weight of 846 kg (Doughty et al., 2013), with consequences for terrestrial biogeochemistry, vegetation community composition, and terrestrial trophic structure (Davis, 2017; Malhi et al., 2016). We presume the loss of the majority of large mammal species also had consequences for freshwater ecosystems (Moss, 2015).

Even terrestrial animals that are non-migratory can affect streams and rivers when they die. The position of aquatic ecosystems in the landscape makes them receiving systems for a lot of resource inputs that wash off uplands (Leroux and Loreau, 2008), and these watershed inputs can include whole or partial carcasses (Behrensmeyer, 1982). The carcasses of terrestrial animals often decompose in place, leading to long-term biogeochemical hotspots in terrestrial systems (Bump et al., 2009). However, the skeletal stage can persist for months to years (Keenan et al., 2018), which could allow bones to be washed off the landscape into receiving rivers during rains (Behrensmeyer, 1982). For example, in the East Fork River, WY, 66 bones were recorded in 3.9 km of channel, and they came from deer, antelope, cow, horse, elk, beaver, badger, coyote, rabbit, rodent and various birds and fishes (Behrensmeyer, 1982). Carcass inputs from the landscape would largely be a function of terrestrial animal abundance, but (excluding domestic animals) present-day levels are a fraction of what once existed in North America.

Bones and shells decompose slowly, which influences their role in ecosystem function. Subalusky et al. (2017) reported bone decomposition rates of 0.001 d^{-1}, which translates to about 31% loss in the first year. However, the decomposition rate likely is influenced by sediment dynamics, as material can be buried and rendered inaccessible over short or long time periods. Kitchell et al. (1975) calculated that only 50% of fish carrion P would be available for decomposition and nutrient cycling due to burial. Other studies have shown that up to 15% of fish bone and scale P is subject to long-term burial, suggesting animal remnants may act as a long-term P store that becomes slowly available over time (Schenau and De Lange, 2000; Vallentyne, 1960; Vanni et al., 2013). Burial and resurfacing of bones can influence P dynamics on long time scales, as evidenced by the 2018 re-surfacing of a skull from a now extinct species of bison in Clear Lake, Iowa (*http://www.kimt.com/content/news/Bison-skull-found-in-Clear-Lake-483656871.html*).

Even when present in moderate amounts, animal remnants are likely to be locally important as hot spots of metabolic activity. Like rocks, bones can serve as substrate for biofilms, but unlike rocks, bones are also rich in available nutrients—much like nutrient diffusing substrates used for ecosystem ecology experiments (Tank et al., 2017). We suspect that bone biofilms have their own communities that specialize on this substrate, just as there are epizoic algae that colonize the shells of living turtles (Edgren et al., 1953; Garbary et al., 2007; Wu and Bergey, 2017). However, to our knowledge, this area of research is unexplored.

If animal carcasses are an important component of stream ecosystems, could they also be a component of restoration? This is not a new idea for salmon managers, who for the last two decades have used fish carcasses and fertilizer pellets to try to jump-start the production of oligotrophic streams with depleted salmon runs. Studies have shown that fertilizer pellets are less effective than actual salmon carcasses at stimulating production, which may have to do with the complexity of resource availability in carcasses (Wipfli et al., 2010) and the other functions played by spawning fish prior to death (Collins et al., 2015). It seems likely that the addition of ungulate carcasses would replicate the pre-Columbian nutrient dynamics of North American rivers better than the current widespread addition of dissolved nutrients in runoff from fertilized agricultural fields and discharges from wastewater treatment plants. Of course, there are practical and aesthetic considerations to introducing large animal carcasses to rivers, as anyone who has conducted field collections in the vicinity of recently deceased large mammals can attest.

Our research revealed quite a few knowledge gaps that make it hard to fully assess the role of animal remains in freshwater ecosystems. We found a lack of direct measurements of nutrient content for the shells and bones of many taxa of interest. Estimates of historical and prehistorical animal abundances were uncertain and based on few sources, though we suspect there is more information waiting to be discovered in historical accounts. Most importantly, there have been very few empirical studies of animal carcass decomposition and its effects on ecosystems. Consequently, it is unclear the extent to which nutrient release from animal carcasses can augment aquatic productivity, particularly during periods of low flows and diminished watershed inputs. It is also untested whether bone and shell colonization by biofilms and associated consumers support unique food web pathways. Better quantifying the functional importance of long-lasting animal remains in freshwaters could reveal otherwise unappreciated benefits of wildlife restoration and lead to novel management techniques that recognize the importance of the missing dead.

Conflict of interest

The authors have no conflicts to report with respect to their submission of this manuscript.

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