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Animal legacies lost and found in river ecosystems

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E-mail: therese.frauendorf@yale.edu**Keywords:** animal legacy, ecosystem engineering, freshwater, invasive species, livestock, species decline**Abstract**

Animals can impact freshwater ecosystem structure and function in ways that persist well beyond the animal's active presence. These legacy effects can last for months, even decades, and often increase spatial and temporal heterogeneity within a system. Herein, we review examples of structural, biogeochemical, and trophic legacies from animals in stream and river ecosystems with a focus on large vertebrates. We examine how the decline or disappearance of many native animal populations has led to the loss of their legacy effects. We also demonstrate how anthropogenically altered animal populations, such as livestock and invasive species, provide new legacy effects that may partially replace lost animal legacies. However, these new effects often have important functional differences, including stronger, more widespread and homogenizing effects. Understanding the influence of animal legacy effects is particularly important as native animal populations continue to decline and disappear from many ecosystems, because they illustrate the long-term and often unanticipated consequences of biodiversity loss. We encourage the conservation and restoration of native species to ensure that both animal populations and their legacy effects continue to support the structure and function of river ecosystems.

1. Introduction

Animals can strongly impact their environment through direct and indirect effects on abiotic and biotic processes (Schmitz *et al* 2018). Streams and rivers are particularly impacted by animals since they host aquatic and semi-aquatic species and act as a point of attraction for terrestrial species. Beavers build dams and lodges that shape the geomorphology and hydrology of river systems (Wohl 2021). Migratory fishes bring energy and nutrients from the ocean that fundamentally alter nutrient cycling and production in streams and rivers (Moore 2006). Ungulates shape riparian zones through trampling and grazing in ways that alter both the vegetation communities and the timing, magnitude and chemistry of inflows (Naiman and Rogers 1997). Many of these impacts can persist beyond an animal's living presence in the

system and shape system properties and dynamics for years to centuries.

Legacy effects are ecological impacts that persist after a species has disappeared from the system or ceased its activity (Hastings *et al* 2007, Cuddington 2011). Much use of the term *legacy effect* has focused on long-lasting human-related impacts, such as agricultural nutrient inputs and land use changes (e.g. Martin *et al* 2021). However, other animal taxa can have similar large and long-lasting ecological effects, and these may have been even more important before the decline and loss of many animal species due to anthropogenic drivers (Lyons *et al* 2004). What constitutes a legacy effect in terms of magnitude and persistence is highly variable in the literature, ranging from ephemeral impacts that last for days to fundamental changes in system structure that persist for centuries (Monger *et al* 2015). For example, caddisfly

cases can persist at least 60 d on stream beds after the larvae are gone, providing habitat structure and altering benthic velocity at small spatial and short temporal scales (Tumolo *et al* 2019, Maguire *et al* 2020). On the other end of the spectrum, beaver dams can turn streams into wetlands that persist for centuries after the beavers cease activity (Johnston 2015).

The full extent of animal legacy impacts on river ecosystems may be difficult to perceive or measure because they persist after the drivers are no longer active. Furthermore, current declines in both freshwater and terrestrial biodiversity are accompanied by the loss of multiple and interacting ecological roles those animals play in aquatic ecosystems. Loss of animal legacy effects could impact ecosystems for years or decades in ways that are difficult to predict given our current understanding of these processes. Concurrent with declines in native large animal populations, the widespread raising of livestock and introductions of invasive species have led to the rise of modern analogues of animal legacies that have replaced native animals, yet with potentially substantial functional differences. As such, we cannot understand rivers without understanding the legacies of past animal activity and the new legacies associated with modern animals. In the context of conservation, freshwater ecology is well advised to embrace animals as important drivers of geomorphology, biogeochemistry and hydrology.

In this paper, we explore what determines the importance of animal legacies, how legacy effects change when humans add/remove species and alter animal populations, and how our current understanding of animal legacies can shape conservation efforts for freshwater systems. We focus on the influence of larger-sized animals that produce legacy effects in streams and rivers over long time scales, but we invite readers to apply our ideas and discussion to smaller-bodied animals, shorter time scales, and other aquatic ecosystems.

2. Types of animal legacy effects in river ecosystems

Animals can create three general types of legacy effects across different temporal scales: structural, biogeochemical, and trophic (figure 1).

Structural legacy effects are physical changes to the abiotic environment, which can include geomorphological changes, construction of habitat features, and provision of structural elements. Animals can have a range of geomorphological effects in streams. For example, salmon dig nests during spawning that decrease the amount of fine sediments in streams even after the salmon have left (Moore *et al* 2004). Trampling by large animals such as wildebeests, elk, or hippos can create relatively permanent paths within river channels that alter the riparian and river bottom topography (Naiman and Rogers 1997), while bison

can widen stream channels by up to 20% at crossings (Fritz *et al* 1999). In tropical and subtropical rivers, animals like crocodiles, elephants, and baboons create large holes that provide dry-season refuge for many aquatic organisms (Naiman and Rogers 1997, Somaweera *et al* 2020). Animals also can construct habitat features out of sediment or vegetation. Perhaps one of the best known examples of habitat construction are beaver dams (Wohl 2021), which significantly transform the aquatic environment for its inhabitants (Gable *et al* 2020). Other animals like crocodiles build mound nests out of vegetation on riparian edges or islands of floating vegetation, which can provide nesting sites for other reptiles and invertebrates (Somaweera *et al* 2020). Finally, animals can leave structural elements in river systems, such as bones and dung, that decompose for long periods after animals die. For example, wildebeest bones in the tropical Mara River decompose over 80 years (Subalusky *et al* 2020), while hippo dung decomposes over 80 d (Subalusky *et al* 2018). All of these examples change river morphology and often create more complex habitats, increasing species diversity and abundance (Torres-Pulliza *et al* 2020).

Biogeochemical legacy effects are lasting impacts on biogeochemistry caused by animal excretion and egestion, carcass decomposition, and bioturbation. For example, hippo dung can change oxygen and nutrient conditions in river pools to the point that they are detrimental to fish unless the system becomes flushed (Dutton *et al* 2021). Bones and shells from dead animals in rivers slowly release nitrogen and phosphorus over several decades, providing a small but consistent nutrient supply to rivers through time (Wenger *et al* 2019, Subalusky *et al* 2020). Animal movements can also increase sediment and nutrient fluxes in aquatic systems. Permanent pathways on river banks created by terrestrial animals can facilitate runoff of water and sediments into rivers (Naiman and Rogers 1997). Bioturbation increases when terrestrial animals (e.g. bison, moose) enter an aquatic system or when freshwater animals excavate the bottom (e.g. fish redds). This increase in disturbance elevates total suspended solids and releases limiting nutrients (e.g. N and P) from sediments that can alter primary productivity and freshwater community structure (Holtgrieve and Schindler 2011, Larson *et al* 2013, Bump *et al* 2017).

Trophic legacies are lasting effects that emerge from consumption of primary and secondary production in aquatic and riparian food webs. Grazing by large mammals has been described as one of the earliest recognized examples of animal legacy effects in terrestrial ecosystems (Cuddington 2011), and herbivory is just as impactful in freshwaters. Semiaquatic (e.g. beavers) or terrestrial (e.g. moose) herbivores can decrease vegetation biomass and species richness in riverine ponds (Bergman and Bump 2015). Herbivores remove on average 40%–48% of plant biomass

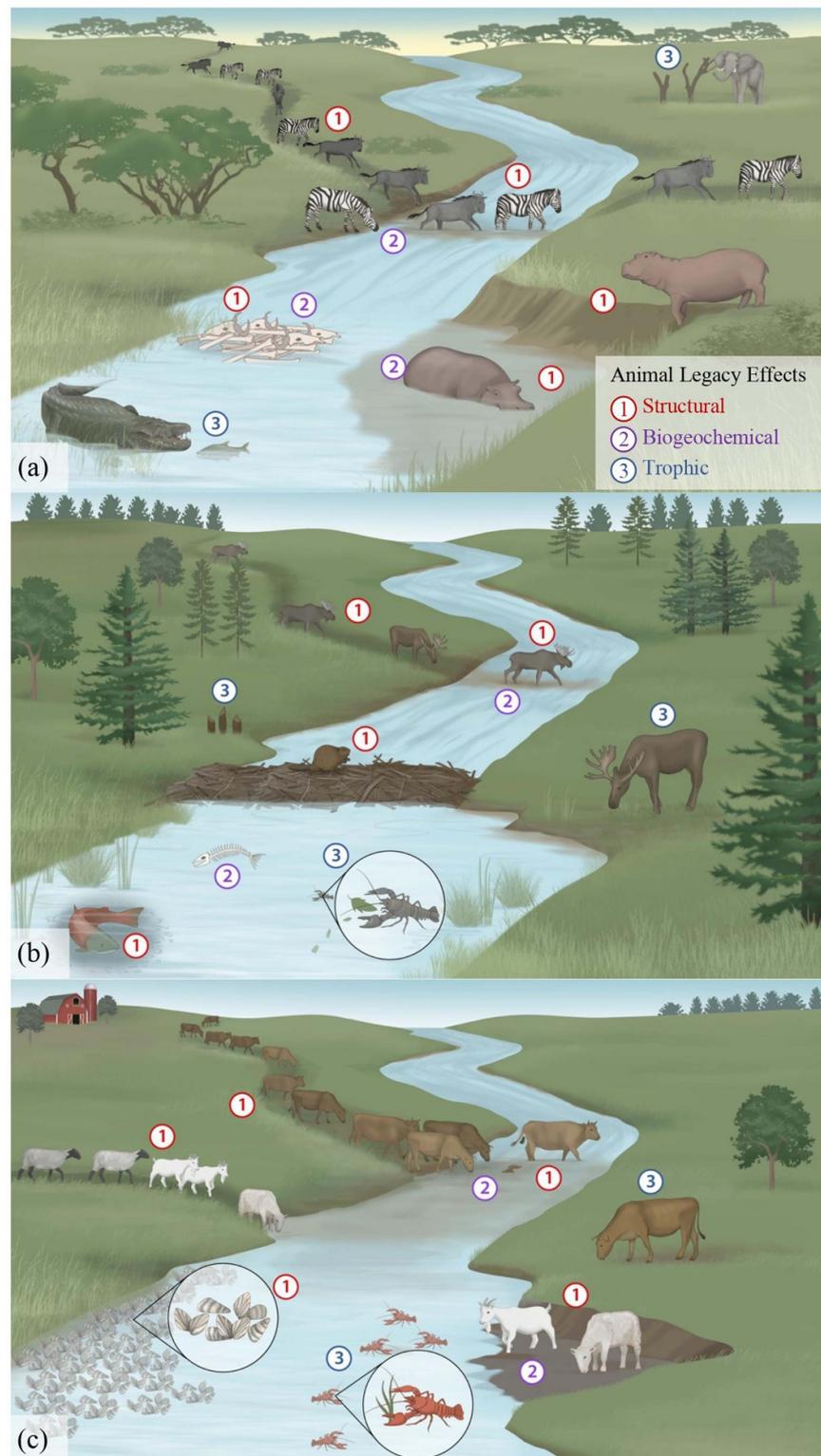


Figure 1. Examples of structural [1], biogeochemical [2], and trophic [3] animal legacy effects on freshwater ecosystems. (a) In East Africa, wildebeest and zebra crossings create animal trails [1] and release nutrients during bioturbation [2], while elephants feeding in the riparian zone alter tree density around the waterbody [3]. Bones from animal drownings provide structure [1] and slowly leach phosphorus [2]. Hippos also alter the geomorphology through trampling [1] and their egestion can influence biogeochemistry [2] and trophic ecology [3]. Crocodiles can shape food webs through predation [3]. (b) In northwest North America, moose crossings create paths in and around the water [1], increase bioturbation [2], and modify riparian vegetation through herbivory [3]. Beavers build dams [1] by removing riparian trees [3]. Salmon build redds [1] and their carcasses release nutrients [2]. (c) Modern analogues of animal legacies such as livestock alter the geomorphology in and around the waterbody [1], increase bioturbation and nutrients [2] during watering events, and graze down vegetation in riparian areas [3]. Invasive mussels can alter benthic structure [1] and water nutrients [2], and invasive crayfish can reduce litter decay rates through predation on invertebrate shredders [3]. Animal legacy effects of modern analogues are often more intense, widespread, and homogeneous compared to traditional animal legacies in freshwater systems.

from aquatic ecosystems (compared to 4%–5% in terrestrial), providing strong direct and indirect effects on aquatic ecosystem function (Bakker *et al* 2016). Herbivory in riparian zones can also impact aquatic ecosystems. For example, in Nova Scotia (Canada), moose prevented the regeneration of riparian forest after a budworm outbreak, which increased stream temperatures, nutrients, and suspended solids in streams (MacSween *et al* 2019). Elephants in Botswana reduce tree density and alter tree species composition in riparian zones (Rutina and Moe 2014), which can leave abiotic (e.g. increased light and water temperature) and biotic (e.g. increased algae and invertebrate biomass) legacies within a river. Large animals also may act as predators in aquatic systems, which can influence food web structure and function (Power 1990) and lead to indirect effects on species phenotype and behavior (Reznick *et al* 1997, Dalton and Flecker 2014). However, this may not always be the case; while crocodilians have been described as keystone predators, it is uncertain if their predation has long-term effects (Somaweera *et al* 2020).

Animals often create more than one type of legacy in lotic ecosystems (figure 1). For example, beavers leave trophic (herbivory) and structural legacies (beaver dam), while wildebeest leave structural (trampling paths, bones from mass drownings) and biogeochemical legacies (phosphorus leaching from bones). These various legacies may interact with one another and with environmental context.

3. Drivers of animal legacy effects

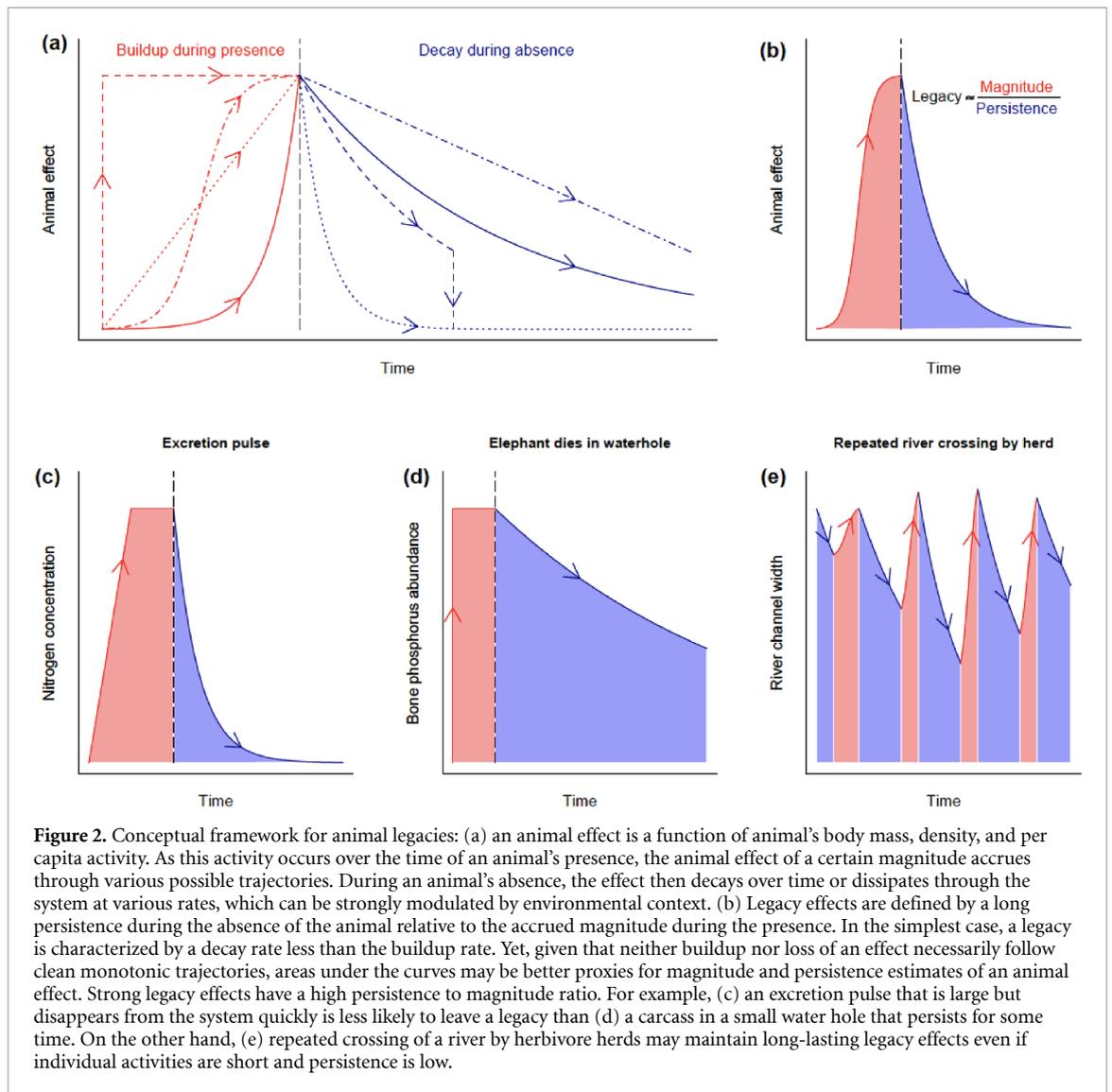
We propose that the degree to which an animal effect becomes a legacy is related to the magnitude and persistence of the effect (Moore 2006, Cuddington 2011, Monger *et al* 2015). The *magnitude* of an animal effect is a function of animal size, density, per capita activity, and duration of animal presence. Larger-bodied animals (e.g. hippos, moose) and animals that aggregate in high densities (e.g. salmon, wildebeest) are more likely to create legacy effects (Moore 2006, Subalusky and Post 2019). Larger activities (e.g. beaver dams) or activities with high repetition (e.g. repeated river crossings) are also likely to create stronger legacies. The *persistence* of animal effects is a function of how quickly an effect decays or dissipates over time. Causal effects that remain longer in the system are more likely to become legacies (e.g. bones versus soft tissue from carcasses). Therefore, what defines a legacy is the rate at which an effect dissipates or decays during the absence of an animal relative to the magnitude of the effect built up during the living presence of the animal (figure 2). Thus, even small-bodied animals can create ecological legacies if the magnitude of the effect is large, the decay rate is slow, and/or the effect is repeated over time. In this context, extremely slow decay rates could make it difficult to detect a legacy effect, as it may appear to be a

permanent part of the system, rather than something that could eventually be lost with time after the causal animal driver ceases (Gutiérrez *et al* 2003).

Environmental context is an important modulator of animal legacies, influencing how and which magnitude may be achieved, and determining the rate and trajectory of a legacy effect disappearing from a system (Subalusky and Post 2019). The large degree of environmental variability inherent in freshwater ecosystems makes them an interesting place to consider the role of legacy effects. Hydrology is perhaps one of the most important environmental factors for freshwaters (Moore 2006) and high flow variability may mitigate in-stream animal legacies. For example, Dutton *et al* (2021) show that water residence time was the most important driver of the influence of hippo inputs on pool biogeochemistry. Substratum type and availability are also important abiotic factors influencing legacies. Moose crossing a stream with an alluvial riverbed may leave both a geomorphological legacy by compacting a trail, and a biogeochemical legacy by releasing phosphorus from disturbed sediments; however, a moose crossing a bedrock stream may leave neither (Bump *et al* 2017). Lastly, some animal legacies create habitat complexity by changing the abiotic environment through structural effects (e.g. elephant drinking holes), which often lead to increased species diversity and abundance (Torres-Pulliza *et al* 2020). The increased spatial heterogeneity associated with legacy effects of animals are likely to be more consequential where aquatic habitats have lower initial habitat complexity.

4. The lost animal legacies from river ecosystems

The reduction in abundance or extirpation of terrestrial and aquatic fauna and their associated legacy effects has had significant influences on freshwater ecosystem processes. Rates of biodiversity loss and decline have been greatest in freshwater ecosystems, with an 83% decline in monitored populations between 1970 and 2014 (World Wide Fund for Nature 2018). Freshwater megafauna (>30 kg) exhibit even larger declines (–88%) as a result of bigger and more complex habitat requirements, slow life cycles, and overexploitation (He *et al* 2019). For some of these animals, like freshwater dolphins, we are just beginning to understand their ecology, and we have little idea about their potential legacy effects. Many of the large terrestrial animal migrations that formerly crossed water courses have disappeared or are in steep decline (Wilcove and Wikelski 2008). In North America, an estimated 30–60 million bison historically roamed the Great Plains, likely shaping the rivers they crossed in myriad ways, with legacy effects that gradually disappeared over the decades after their populations were decimated (Wenger *et al* 2019).



Several studies have shown that declines in animal legacies reshape freshwater ecosystems. For example, the loss of the structural legacies associated with beaver dams reduces sediment storage, nutrient uptake, primary production, and habitat diversity (reviewed by Wohl 2021). Only 6%–7% of the original marine-derived nutrients from salmon carcasses now reach stream systems in western North America, resulting in lower algal and invertebrate production which in turn leads to smaller sized juvenile salmon (Gresh *et al* 2000, Oke *et al* 2020). The same is true in eastern North America, where diadromous alewife carcasses and excretion once supplied the majority of nitrogen and phosphorus to coastal lakes, but now supply only 6%–7% of the historic marine-derived nutrients where runs remain (Twining *et al* 2013). In Neotropical streams the loss of herbivorous tadpoles doubled algal biomass, reduced nitrogen uptake by half, and changed invertebrate functional structure (Colón-Gaud *et al* 2009, Whiles *et al* 2013). The widespread anthropogenic extirpation of top predators, such as crocodilians and large piscivorous fishes,

has caused the simplification of food webs, which in turn has severe impacts on ecological processes and functioning through trophic cascades that may take years to reach new equilibria (He *et al* 2019). Most of these studies indicate that there is no functional redundancy when these animals are lost (e.g. Whiles *et al* 2013), suggesting that these kinds of animal legacy effects cannot be easily replaced.

Many of our conceptual frameworks for understanding aquatic ecosystems do not account for potential animal legacies (Moss 2015). This may be because many of the aquatic ecosystems that shaped our conceptual frameworks have already lost the animals that would create strong legacies. For example, the River Continuum Concept attributes headwater streams as the location for the majority of allochthonous inputs in river systems (Vannote *et al* 1980). However, this framework was developed in North America, where the majority of megafauna disappeared over 10 000 years ago, with further declines in the 19th century (e.g. bison) (Lyons *et al* 2004). In East Africa, where many megafauna remain,

large wildlife have pronounced geomorphological and biogeochemical impacts on river ecosystems, including the substantial transport of allochthonous inputs in the middle and lower river reaches (Masese *et al* 2015, Subalusky *et al* 2018). Furthermore, many modern conceptions of rivers assume a largely unidirectional transport of materials from upper watersheds down gravitational flow paths into oceans. However, Doughty (2017) proposed that a system of marine mammals, seabirds, anadromous fishes, and large terrestrial vertebrates historically provided a biotic pump that moved materials in the reverse direction; its current capacity was estimated at <10% of historical values.

5. The new animal legacies of the anthropocene

As many native animal populations and their legacies have declined or disappeared in freshwater ecosystems, others have emerged. These animals include many farmed and invasive or introduced species, which may have their own structural, biogeochemical, and trophic legacy effects (figures 1(c) and 3). Livestock, including cattle, sheep, and goats, have largely replaced native animal biomass in many landscapes (Hempson *et al* 2017). Livestock can have pronounced ecological effects on aquatic ecosystems. For example, in northern Australia, feral water buffalo that roamed from the 1960s until the mid 1980s contributed to seawater intrusion into freshwater wetlands by deepening connecting channels, which amplified effects of sea level rise (Bowman *et al* 2010). During watering and crossings at water bodies, livestock increase bioturbation and nutrients through egestion and excretion (Iteba *et al* 2021), which can increase primary and microbial production (Masese *et al* 2020). Livestock may also have legacy effects on aquatic ecosystems when heavily grazed landscapes are subject to increased erosion and sediment delivery to water bodies, which can persist long after the livestock are no longer present (Dutton *et al* 2018).

Aquaculture is globally more widespread in freshwater than in marine ecosystems (Barrett *et al* 2019). Many of these farms release inorganic and organic nutrients that build up over time, often leading to hyper-eutrophication, a state that has been shown to exist for more than 60 years in a Philippine lake (Legaspi *et al* 2015, Barrett *et al* 2019). To our knowledge legacy effects of aquaculture have not been studied since many aquaculture sites continue to be used. However, it can reasonably be assumed that if a fish farm in a lake or reservoir ceases, the resulting biogeochemical impacts can last for decades to centuries, at least for phosphorus (Hamilton 2012). Fish farming and restocking also have trophic effects that can alter diets and seasonal foraging behavior of consumers like otters (Ludwig *et al* 2002). Studies show that farming and restocking often create population

sinks for many species that will last beyond several generations of fish (reviewed by Barrett *et al* 2019). A number of fish species are farmed or restocked in their native habitat (e.g. rainbow trout in North America and common carp in Europe), but many are farmed and stocked in non-native ranges (e.g. Nile tilapia), which commonly results in escape and species invasions (Nobile *et al* 2020).

The degree to which introduced animal legacy effects play the same ecological roles as in their native range varies (reviewed by Emery-Butcher *et al* 2020). In some cases, modern analogues seem to have similar legacy effects on aquatic ecosystems to those of native animals. The introduced signal crayfish in France can replace the trophic legacy of the lost native noble crayfish (Lagrue *et al* 2014), while the seasonal crossing of cattle in the prairies may replace some of the geomorphological legacy effects that bison had on streams (Grudzinski and Daniels 2018). Nevertheless, the impacts from the majority of modern analogues, even when the form of the legacy is similar, can be fundamentally different. This has been demonstrated for structural (e.g. Faller *et al* 2016), biogeochemical (e.g. Masese *et al* 2020, Shurin *et al* 2020), and trophic (e.g. Rodríguez-Pérez *et al* 2016) animal legacy effects (figure 3).

High densities and spatial and temporal homogenization are two main reasons why the majority of modern analogues differ functionally from native animal legacies in freshwater systems. Livestock, aquaculture, and invasive species densities are often higher than the density of a native animal species with a legacy effect. For example, the per capita dung input by cattle into a Kenyan river is 1% that of hippos, but can comprise >50% of total inputs due to their very high densities (Masese *et al* 2020, Iteba *et al* 2021). Secondly, modern analogues are often spatially and temporally homogeneous. For example, common herding practices include letting livestock drink at the same spot along the water body, often more than once a day, while wild terrestrial herd mammals have larger home ranges or migrate (e.g. bison, wildebeest). Invasive species also create spatial homogeneity by dominating the non-native niche space (e.g. invasive mussels, Ilarri *et al* 2018). Both homogenization and high animal densities lead to the intensification of a legacy effect, which commonly has negative implications for the receiving water body. Furthermore, both livestock and invasive species are widespread and may be introduced into ecosystems where no native analogue existed.

6. Conservation and restoration of animal legacies

The legacy effects of native animal communities can be conserved and restored on the landscape through three main approaches: (a) conservation and restoration of native species, (b) replacement of the

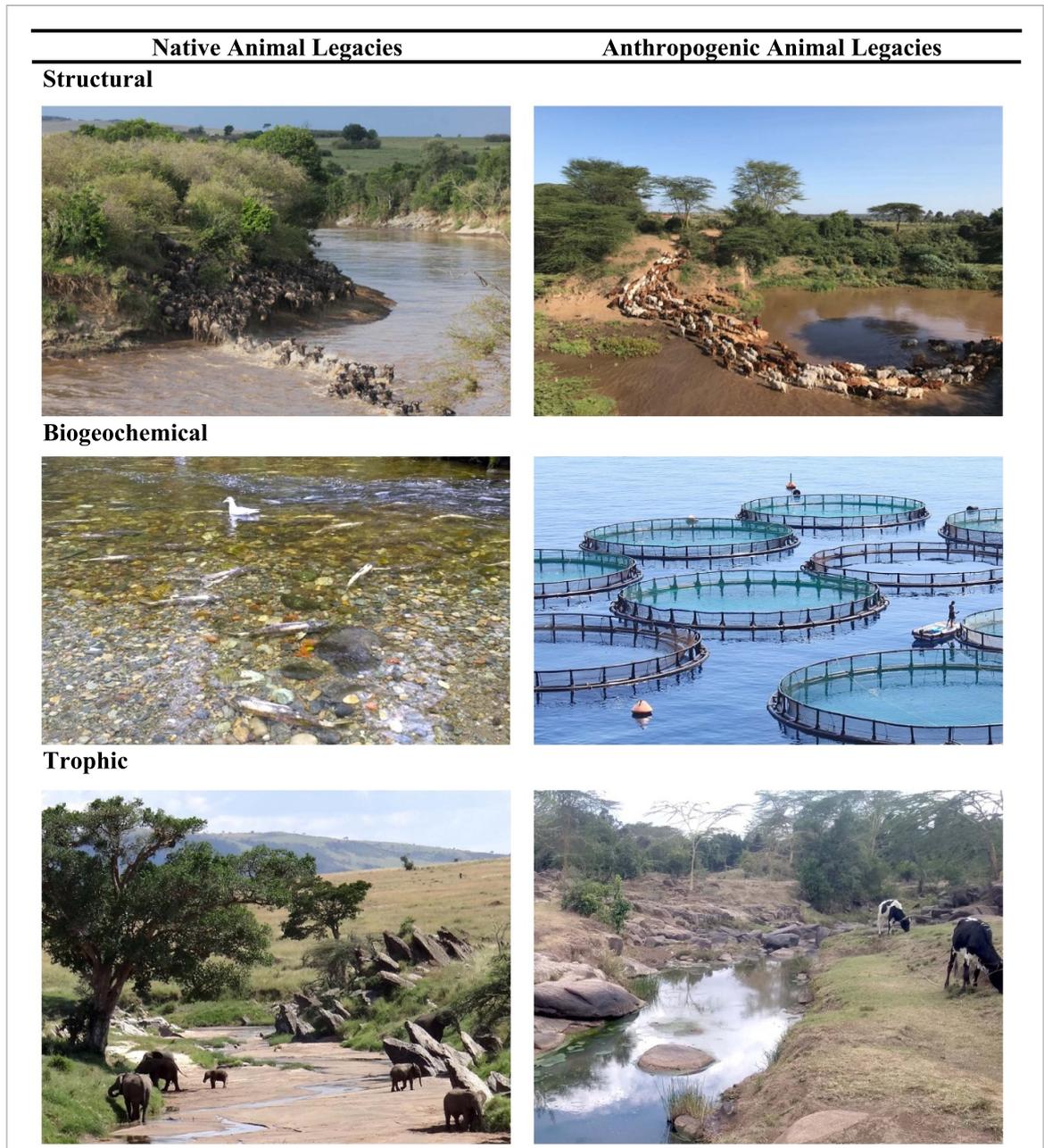


Figure 3. The functional roles of native animal legacies often differ from those of modern analogues. *Structural legacies* such as trails caused by wildebeest river crossings (Photo credit: A Subalusky) often result in less bank erosion and compaction than frequently used cattle watering points and river crossings (Photo credit: E Rosi). *Biogeochemical legacies* such as nutrient excretion and carcasses from anadromous salmon runs (Photo credit: T Frauendorf) contribute resources that differ in quantity and quality from nutrient inputs from aquaculture facilities (Photo credit: This file is licensed under the Creative Commons Attribution-Share Alike 4.0 International license). *Trophic legacies* from elephants grazing in riparian woodlands (Photo credit: C Dutton) are of different magnitude and spatial extent compared to livestock grazing in riparian zones (Photo credit: F Masese). This Fish-farm-hero.jpg image has been obtained by the author(s) from the Wikimedia website where it was made available by Asc1733 under a [CC BY-SA 4.0](https://creativecommons.org/licenses/by-sa/4.0/) licence. It is included within this article on that basis. It is attributed to Asc1733.

ecological effects of lost species, and (c) managing the effects of modern analogues. First, native species whose populations have declined or been extirpated can be restored in freshwater ecosystems and surrounding landscapes. For example, the reintroduction of beavers on the landscape has increased spatial heterogeneity and biodiversity of freshwater ecosystems (Kemp *et al* 2012, Law *et al* 2019). Second, where restoration of the species is impossible or impractical, the ecological effects of native species

can be replaced. For example, addition of nutrient pellets to streams as proxies for salmon carcasses increases primary production in streams where salmon runs have declined, although to a lesser extent than real carcasses (Wipfli *et al* 2010). In addition, artificial beaver dams have been installed to mimic the effects of lost beaver populations (e.g. Weber *et al* 2017). However, many animal species have multifaceted impacts on an ecosystem, which can make it difficult to fully replace them with a single proxy.

Third, livestock and other anthropogenically driven animal legacies can be managed to have ecological effects that more closely resemble those of native animal legacies. For example, grazing cattle that were moved around seasonally mimicked the geomorphological legacy effects of bison (Grudzinski and Daniels 2018). This illustrates that modern analogues can and should be managed with the target to recreate a lost legacy including its positive effect on the spatial and temporal heterogeneity on the landscape. Understanding legacy effects thus helps to identify ecologically informed conservation targets instead of merely aiming to reduce heavily concentrated impacts of anthropogenic animal legacies.

Current conservation of freshwater ecosystems is often guided by a 'reference state' approach, which strives to conserve based upon a perceived natural state prior to a set time in the past, often before observed anthropogenic impact (Moss 2015). This approach primarily follows a bottom-up tactic where provisioning of adequate habitat is thought to maintain animal and plant communities. If the roles of animals in shaping historical freshwater ecosystems are not fully appreciated, then important drivers of ecosystem state, integrity, and function may be ignored. There is a growing body of research demonstrating the influence of both aquatic and terrestrial animals on aquatic ecosystem function; however, there is still much research needed on the duration of their ecological effects and consequences of their loss.

The animal legacy effects we describe here are specific to freshwater ecosystems, but the general concepts likely apply to terrestrial and marine ecosystems as well. Understanding the influence of animal legacy effects is particularly important as animal populations continue to decline and disappear from ecosystems, yet the full ecological impact of their loss may not be apparent for some time. The replacement of animal legacy effects by modern analogues can help to mitigate this loss in some ecosystems, although these analogues are unlikely to play fully equivalent functional roles and may entail unintended consequences. Conserving and restoring native animal species is likely the best and most cost-effective way to maintain animal legacies on the landscape.

Data availability statement

No new data were created or analysed in this study.

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