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Why so sceptical? The role of animals in fluvial geomorphology

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ABSTRACT

Despite acknowledgement of zoogeomorphological impacts and a positive trajectory for biogeomorphology, the cumulative geomorphic significance of animals remains largely unknown across geomorphic scales. We do not know the proportion of erosion, transport and deposition that is mediated by animal activity in different environments and cannot answer questions like how changing animal distributions under climate change will affect sediment fluxes and landscapes? This partly reflects a healthy scepticism about the net significance of biological energy and zoogeomorphic processes when set against the orthodox assumption that geophysical energy dominates. Zoogeomorphology is regarded as a 'niche' interest, or worse, as inconsequential. Drawing on examples from fluvial geomorphology, this essay challenges that scepticism with the aim of encouraging greater consideration of the relevance of coupled biomorphodynamic systems. Five assumptions that belittle the role of animals are considered: that the number of species acting as geomorphic agents is small and their abundance limited; that limited geographical extent and periods of activity preclude widespread effects; and that impacts on sediment fluxes and morphological change are insignificant. In the hope that some scepticism is overcome, four interrelated challenges for future research are outlined: empirical investigation of zoogeomorphic processes, scaling-up process understanding, embracing new technologies and approaches, and developing suitably integrated modelling tools. Such advances, alongside a willingness to recognise coupled biomorphodynamic interactions as the norm, rather than the exception, can improve our ability to understand both geomorphological and ecological phenomena and transform our understanding of how landscapes interact with the animals that live on, and in, them.

Caption: Challenges key points of scepticism about the role of animals in fluvial geomorphology, advocating for zoogeomorphology's importance in coupled biomorphodynamic systems that are the norm, not the exception.

1. INTRODUCTION

Many animals that live in and around rivers interact with river-bed and floodplain sediments in ways that can affect the size distribution, stability, mobility, transport and organisation of those sediments. Laboratory and field research are revealing the mechanisms involved and quantifying the impact of aquatic insects, crustaceans, fish and mammals on fluvial sediment fluxes and morphology. Several reviews of zoogeomorphic effects in rivers are available (Moore, 2006; Statzner, 2012; Rice et al., 2012; Albertson & Allen, 2015; Bylak & Kakula, 2020) building on earlier foundational work in biogeomorphology (Viles, 1988; Naylor et al., 2002), zoogeomorphology (Butler, 1995) and ecosystem engineering (Jones et al. 1994, 2012. In addition, intellectual curiosity surrounding biota's role in the co-evolution of life, landscapes and sedimentary stratigraphy continues (Corenblit et al., 2007; Phillips, 2016; Davies et al., 2020) and new interdisciplinary avenues are opening including notable technical (Larsen et al., 2018), theoretical (Allen et al., 2014; Stallins & Corenblit, 2018), modelling (Murray et al., 2008; Albertson et al., 2014a; Fremier et al., 2018) and applied (Polvi & Sarneel 2018; Johnson et al., 2020) advances.

Despite these developments, recent appraisals that highlight the buoyancy of biogeomorphological research (Viles, 2019; Larsen et al., 2021) and a clear case that biotic-abiotic interactions are “ubiquitous” on Earth (Allen et al., 2014; Phillips, 2016, p16), there is greater focus on plant life than animal life in biogeomorphology, key processes, like burrowing, remain under-investigated (Harvey et al., 2019), and the aggregate geomorphic significance of animals remains largely unknown across all scales. Zoogeomorphological impacts are evident in all geomorphological realms, but the focus here is on fluvial geomorphology where the absence of zoogeomorphology is a potential constraint on our understanding of fluvial sediment dynamics, fluvial depositional systems and therefore landscape evolution over large portions of the Earth’s surface, now and throughout Earth history. For example, we know very little about: how river morphology is affected by the animals that live in and around rivers; what contribution animals make to the flux of sediment into depositional basins; or how climate-driven range-shift, the spread of invasive species or the reintroduction of keystone animals might affect river behaviour and fluvial hazards including, for example, flood risk (cf. Orlandini et al., 2015). In part, our inability to answer these questions reflects a healthy scepticism about the net importance of zoogeomorphic effects driven by metabolic energy, relative to more familiar geophysical forcing mechanisms that remain the predominant explanation for geomorphological phenomena - our geophysical orthodoxy, even though there is good initial evidence that the role of biological energy is significant in geomorphic systems (Phillips, 2009).

So, despite the advances that are being made, why are we not doing more to challenge that orthodoxy? What constrains interest in the role of fauna in fluvial geomorphology and the development of a deeper understanding of how their metabolic energy works with geophysical energy in fluvial and other systems? The slow uptake of biology into mainstream geomorphology is part of the issue (Johnson, 2002). However, there appears to be substantially less scepticism about the role of plants in geomorphology, with a greater proportion of biogeomorphological work focused on plants rather than animals. This may reflect long-term interest in the effects of vegetation on hydrology, sediment transfers and flood hydraulics, especially in the context of managing water resources, soil erosion and flow resistance. Relatively less attention has historically been given to the impacts of animals on water and soil resources and it is certainly true that animals that do geomorphology are less immediately evident in the landscape than the vegetation that blankets large swathes of the continents. It is possible that some straightforward facts about the scale and scope of zoogeomorphic activity in rivers remain hidden from mainstream geomorphology and contribute to scepticism about the aggregate role of animals. With the aim of helping to unlock greater interest and exploration of the role of zoogeomorphology, ultimately to address the types of question exemplified above, this essay: (1) challenges five perspectives on animals in rivers that belittle their role in geomorphology; and (2) briefly outlines four goals for future research in this arena. The five challenges are those that I return to myself and which may therefore be common.

2. CHALLENGING FIVE SOURCES OF INDIFFERENCE ABOUT ZOOGEOMORPHOLOGY

2.1 (Not) many species do geomorphology

Literature summaries presented by Statzner (2012) and Albertson and Allen (2015) document the fluvial geomorphic impacts of species of freshwater insect larvae (14), molluscs (4), crustaceans (26), fish (16) and mammals (1). The geomorphological consequences of these organisms can be direct, including displacement of gravels during redd building (Hassan et al., 2008) and entrainment of fine sediment by bioturbation (Harvey al., 2011), or indirect, including destruction of stabilising bed-material structures (Pledger et al., 2017) and biostabilisation via organic constructions (Statzner et al., 1999). The species involved are not rare, or unusual; in these examples, sockeye salmon (*Oncorhynchus nerka*), signal crayfish (*Pacifastacus leniusculus*), common barbel and chub (*Barbus barbus*, *Squalius cephalus*), and the caddisfly *Hydropsyche siltalai*, respectively. Importantly, the number of species that have been shown to affect fluvial sediments in laboratory and field studies like these is only a small proportion of the number that have the potential to affect fluvial processes because of common activities and behavioural and physiological traits.

For example, research that explicitly addresses crayfish bioturbation and burrowing in river channels has examined ten species (e.g. Guan, 1994 *Pacifastacus leniusculus*; Barbaresi et al., 2004 *Procambarus clarkii*; Statzner & Peltret, 2006 *Orconectes rusticus*; Albertson & Daniels, 2018 *Faxonius limosus*; Parkyn et al., 1997 *Parenophrops planifrons*; Creed and Reed, 2004 *Cambarus bartoni*; Helms & Creed, 2005 *Faxonius cristavarius*, *Cambarus chasmodactylus*; Ludlam & Magoulik, 2009 *Orconectes meeki;* Willis-Jones Tambo, 2018 *Astacus leptodactylus*) and Butler (2002) documented the pedological influence of crayfish burrowing on floodplains in the Roanoke River, N. Carolina, where up to nine crayfish species are known. In comparison to these 19 species, there are approximately 670 known species of crayfish (Crandall & De Grave, 2017) which share many of the same physiological and behavioural traits as the studied species. Notwithstanding the importance of trait variations for fully understanding ecogeomorphic and ecohydraulic processes (Allen et al., 2014), it is entirely reasonable to assume that all crayfish species are potential zoogeomorphic agents. Indeed, a large body of ecological research documents burrowing behaviour in many species (Hobbs, 1981; Horwitz & Richardson, 1986), to the extent that Berrill and Chenoweth (1982) suggest that some crayfish burrow as a matter of course and all species will burrow when they need to, for example to establish a moist shelter or to find cover. Recent work has emphasised the importance of burrowing animals, including crayfish for river bank stability, bank erosion and sediment delivery to rivers (Harvey et al., 2019; Sanders et al., 2021). This example highlights the fact that we have only investigated the tip of the iceberg when it comes to identifying zoogeomorphic species, which are more common than is generally appreciated.

2.2 Relevant animals are (not) abundant

In a meta-analysis that quantified the effect of aquatic biota on sediment stabilisation and destabilisation, Albertson and Allen (2015) found that studies which manipulated organism density recorded significantly larger geomorphic effects (66% greater) when organism density was high (n=44 studies). This suggests that abundance is a strong control on zoogeomorphic effects. Species abundance is highly variable depending on the reproductive success, recruitment, maturation, dispersal, and vital rates of organisms as affected by a host of ecosystem factors, including environmental factors that sustain these biological processes. A comprehensive evaluation of such complexity is beyond the scope of this essay. However, it is possible to ask whether those species that we know to be zoogeomorphic agents in rivers are rare or naturally abundant. The answer is that many highly effective animals can occur at high abundances.

For example, there are over 16,000 species of caddis flies (Morse et al, 2019), all of which spin silk that is used to build cases, retreats or filter-feeding nets on river beds during the larval phase. Of the net-spinning caddis, the Hydropsychidae family is the largest group, consisting of approximately 1980 species (Morse et al., 2019). Their retreats and nets have been shown to stabilise bed materials, increase the shear stress required for particle entrainment and have long-lasting impacts on near-bed hydraulics (Statzner et al. 1999; Cardinale et al., 2004; Johnson et al., 2009; Albertson et al., 2014b; Albertson et al., 2019; Maguire et al. 2020). Hydopsychidae is often the numerically dominant caddisfly family, for example constituting approximately 80% of all caddis individuals in large North American rivers (Wallace & Merrit, 1980). Typical stream densities in the cited geomorphological studies are in the range $10^2 – 10^3$ m^{-2}, but Statzner *et al.* (1999) and Miller (1984) point to densities exceeding $1 – 7 \times 10^4$ m^{-2} in some rivers. The density of filter feeders can be so high, partly because they catch food from upstream, so their abundance is not restricted by local food production. Even at typical densities, this abundance can produce large amounts of bed-stabilising silk. For example, based on estimates of caddisfly biomass production rates (Parker & Voshell, 1983) and average values of caddis silk density and dimensions, Statzner et al. (1999) calculated that caddis in unregulated rivers may produce silk at a rate exceeding 900 km m^{-2} yr^{-1} and in regulated rivers, where biomass production is higher, over 6600 km m^{-2} yr^{-1}.

While Hydropsychid caddis may represent a particularly abundant species and it is clear that not all zoogeomorphic species are as profuse, it would be unreasonable to argue that zoogeomorphic agents in rivers are numerically rare.

2.3 Relevant animals are (not) geographically widespread

Some individual species capable of zoogeomorphic work may be limited to a small endemic range; for example, some of the 670 known crayfish species are limited to a relatively few river networks. However, many zoogeomorphic agents including crayfish, have successfully evolved over millennia with phylogeny and geographical spread reflecting the impacts of continental drift and the widespread establishment of new species. Since their evolution, probably in the Late Permian, and the establishment of Laurasian and Gondwanan superfamilies at the break-up of Pangea, crayfish have been present on all continents at one time or another, including Antarctica (Duris & Petrusek, 2015). Extant crayfish occupy rivers in parts of Central and South America, most of Europe and western Asia, small parts of the Far East of Asia, and the whole of Madagascar, with particularly high richness in North America and Australasia (Duris, 2015). There are also large areas currently devoid of crayfish (most of Asia, most of South America and continental Africa) but the proportion of the total continental landmass where crayfish are present is approximately 25% and in North America, Europe and Australasia a majority of rivers contain crayfish. The potential for zoogeomorphic work by crayfish is therefore uneven, but one could not argue that it is of limited geographical extent. Similar arguments for uneven but geographically extensive presence can be made for several orders and families of benthic insect larvae and fish that are known geomorphic actors. For example, caddisflies are currently present in all ecozones except Antarctica, with the greatest richness in the Neotropical and Indomalayan realms (de Moor & Ivanov, 2008) and wild, redd-building salmonids spawn in rivers draining in to both sides of the northern Pacific and Atlantic oceans, and the Arctic ocean and have been introduced to Patagonia and New Zealand.

At smaller scales, species distributions are partly determined by the availability of suitable physical habitat and, for those reliant on dispersal via the channel network, by disconnections including dams and weirs. Although this may lead to patchy distributions of individual species, at network scales multiple species with common ways of interacting with sediment may occupy different parts of the catchment and collectively create widespread potential for zoogeomorphic activity. Rice et al. (2019) examined the spatial distribution of benthivorous fish in the Trent catchment, UK (10,495 km^2) using Environment Agency fish sampling data collected from 176 widely distributed sites between 2013 and 2015. Both obligate bed feeders (e.g. barbel, *Barbus, barbus*) and those that opportunistically feed on organisms in the bed (e.g. chub, *Squalius cephalus*) are known to change bed material grain-size distributions and undo water-worked structures as they feed, and so alter bed material transport rates (Statzner et al., 2003; Pledger et al. 2016, 2017). Of 30 species present, 13 were obligate (52.6% 32,118 fish) and 12 were opportunistic (46.2% 28,185 fish) benthivores, although approximately 50% of the individuals were regarded as too small to affect coarse bed materials. Their distributions varied considerably: for example, barbel abundance was low (23 fish) and restricted to 4% of sampling locations in the lower Trent and one of its larger tributaries; whereas Chub (985 fish) were found at 38% of sites across the whole catchment excepting the steeper, northern headwaters; and bullhead (*Cottus gobio*; 21,800 fish) were found at 84% of sites, mainly in the headwaters and seldom in the main stem Trent. Collectively, the distribution of benthivorous fish covered the whole catchment, raising the possibility of widespread zoogeomorphic effects unconstrained by habitat patchiness and disconnectivity.

It therefore is unreasonable to assume that zoogeomorphic actors are limited to a few locations such that the propensity for zoogeomorphic work is geographically limited.

2.4 Relevant activities are (not) time limited

Many animal behaviours are driven by seasonal variations in climate and light, by daily temperature and light cycles, or occur episodically in response to particular environmental cues. Such time-dependent behaviour may constrain periods of zoogeomorphic activity, making impacts time limited. Nocturnalism is common but of little concern because it affects geomorphic work only on the shortest of timescales, but seasonal patterns of activity have the potential to limit zoogeomorphic impacts.

Signal crayfish activity is strongly seasonal, driven primarily by water temperature (and to a lesser extent, water depth), with the activity levels highest in summer and least in winter (Bubb et al., 2002; Johnson et al., 2013). Burrowing crayfish, like signals, are therefore most likely to do geomorphic work during the summer rather than the winter, and measurements of seasonal variations in crayfish zoogeomorphology support that: crayfish bioturbation of fine sediments was seasonal on the Brampton Branch of the River Nene, UK where crayfish bioturbation contributed a minimum of 569 kg month^{-1} to suspended sediment fluxes in summer months but only 199 kg month^{-1} in winter (Rice et al., 2016). However, despite the seasonal cycle, some work was still done in the winter months, confirming that activity was reduced rather than entirely absent. This seasonal variability is true of other organisms. For example, benthivorous fish feed less in winter as a function of metabolic requirements driven by temperature, but they still eat throughout the year. In so doing, they disturb bed sediments all year around, albeit that we should expect greater disturbance when they are feeding most, in warmer months.

Salmonid spawning provides a further example of how zoogeomorphic behaviours may wax and wane but seldom turn off completely. Spawning occurs during relatively short time windows of 2-8 weeks driven primarily by temperature variations and the optimal timing of fry emergence. It is therefore possible that the changes to bed sediment characteristics, bed mobility and morphology caused by spawning (e.g. DeVries, 2012), may be short lived and inconsequential over the longer term. However, the timing of spawning varies between species within individual catchments and intraspecific phenotype variation between populations can be associated with several spawning events per year that are related to spatial differences in water temperature (Webb & Mclay, 1996; Lisi et al., 2013). Therefore, in rivers supporting multiple intraspecific populations or multiple lithophilic spawners, the collective occurrence of redd construction and geomorphic responses may extend over longer periods. In general, activities that are inherently time-limited, may collectively be more frequent where the common zoogeomorphic behaviour is shared by a larger group, partly because individual taxa have evolved and adapted to avoid concurrent timing of resource-intensive activities.

These examples suggest that geomorphic behaviours are not generally time-limited, which is not to deny that periods of complete inactivity may be present amongst some zoogeomorphic organisms, but rather suggests that restricted durations of activity are not a substantive reason to reject zoogeomorphology's importance.

Two final points to consider here. First that the timing, not just duration, of time-limited activities may be important for geomorphic processes. In the signal crayfish example, zoogeomorphic activity is greatest during periods of low flow so that the contribution of crayfish bioturbation to sediment fluxes is relatively high at times when hydraulic drivers are weak. On the Brampton Branch, the *minimum* proportion of total suspended sediment driven by bioturbation was 0.1% in the winter months but averaged 9% from March to November (Rice et al., 2016). This means that a substantial amount of sediment was entrained by biotic energy during periods of low flow when it otherwise could not be entrained.

Second, even where zoogeomorphic work is time limited, the geomorphic effectiveness of that work may be persistent, especially if repetition reinforces the effect. A good example of this is the work done by hippopotamuses (*Hippopotamus amphibius*) to create incised channels (up to 1 m deep and 2 m wide) in the Okavango delta, which are associated with various processes including distributary channel maintenance, lake-infilling, and channel generation (McCarthy et al., 1998). The erosion is caused by regular (daily) movements of the animals from deep-water sites where they spend the day, to night-time feeding grounds along the same network of partially submerged paths. Even though the time spent on these paths represents a small proportion of total time, it is sufficient to suppress vegetation and promote erosion of the sandy substrate to create and maintain the channels.

2.5 Impacts on sediment fluxes and morphology are (not) small

The volumes of sediment mobilised or stabilised by individuals may be small, but the cumulative, aggregate effect of animal populations can be substantial. Darwin (1881) measured the impact of casting by individual earthworms on soil displacement, estimating that the combined effect of myriad small displacements was a downslope soil movement of 0.057 t km^{-1} a^{-1} in southern England, smoothing topography and contributing to continental denudation. Wilkinson's (2009) review of a broad range of soil bioturbators (earthworms, ants, termites and others) concludes that despite the small impact of individuals and even colonies, their maximum combined impact on soil displacement is equivalent to maximum rates of tectonic uplift; on the order of 5 m Ma^{-1}. There has not been an equivalent study for river environments, but it is possible that such an effect is there and unrecognised for want of careful investigation. Like Darwin's worms, smaller aquatic animals (for example, insect larvae) tend to affect the mobility of small amounts of sediment, with Albertson and Allen's 2015 meta-analysis finding a significant, if noisy, relation between individual biomass and the geomorphic effect size of individuals. However, small animals are generally more abundant and moreover, Albertson and Allen (2015) found that smaller riverine animals (like insect larvae) had significantly greater absolute impacts on sediment stability per unit biomass than large animals. It is therefore feasible that, like Darwin's worms on hillslopes, the combination of many small, highly effective individual events by largely unseen small animals could have significant cumulative impacts on sediment fluxes in river systems.

In contrast, and like the hippopotamuses noted above, the cumulative effects of some riverine species are immediately visible in the morphology and evolution of fluvial landscapes. Beavers (*Castor sp.*) are a good example (Gurnell, 1998; Brazier et al., 2020); their ponds and wetlands retain large amounts of sediment (millions to billions of cubic metres in North America, for example) and can therefore have a significant impact on reach, catchment and continent-scale sediment storage and delivery (Butler & Malanson, 2005; de Visscher et al., 2014; Puttock et al., 2018). Widespread removal of beavers from western North America following European colonisation dramatically affected river form, and the geomorphic work of recovering beaver populations can dominate floodplain processes (Westbrook et al., 2011; Polvi and Wohl, 2012). Other drastic changes in animal numbers associated with human settlement; for example, the catastrophic decline in Bison (*Bison bison*) numbers on the North American grasslands during the eighteenth and nineteenth centuries, are thought to have had significant effects on regional runoff and sediment yield (Butler, 2006). In addition to the impacts of changing populations of wild and rewilded animals, domesticated stock, particularly cattle (*Bos taurus*), can have a substantial cumulative effect on fluvial systems (Trimble & Mendel 1995; Magilligan & McDowell, 1997). A recent modelling study from Queensland, Australia has suggested that riparian bank and trail erosion caused by cattle is responsible for 30% of the sediment delivered to the Great Barrier Reef lagoon from the Fitzroy River, estimated to be 419,000 t a^{-1} (Packett, 2020). Cumulative effects such as these must affect landscape evolution on the largest time and space scales but attempts to isolate those effects are rare. A notable exception is Fremier et al.'s (2018) demonstration of the feasibility that salmon spawning impacts on river-bed gravel mobility affect longitudinal river profile development and thence the nature and pattern of watershed erosion in mountain belts.

We may be entering a period when large-scale zoogeomorphic effects will increase in intensity and extent. Range-shift associated with climate change and increasing instances of deliberate or inadvertent translocation of animals by human action means that animal invasion is increasing (Bellard et al., 2018; Pysek et al., 2020). Non-native species are prone to be significant zoogeomorphic agents because they encounter landscapes that have not co-evolved to be resilient to them (Crooks, 2002; Harvey et al., 2011; Fei et al., 2014). While rewilding projects that reintroduce keystone species, like beaver, may partially manage the adjustment of landscapes to new animals, it is also possible that effective ecosystem engineers can overwhelm geomorphic resilience and realise landscape metamorphosis (Butler, 2006; Butler et al., 2019). For example, the introduction of beaver to Patagonia (20 individuals in 1946, growing to an estimated population of 170,000 by 2015) has had a profound effect on the regions hydrogeomorphology and vegetation (Westbrook et al., 2016).

There is, therefore, an abundance of evidence that the cumulative impact of zoogeomorphic activity can be substantial for both sediment dynamics and landscape development.

3. KEY CHALLENGES FOR FUTURE RESEARCH

Zoogeomorphic impacts are not limited to a few species, occurring in small numbers in a few places. Animal impacts on sediment fluxes and morphology are not small, nor are they likely to become smaller in the future. Animal impacts on Earth history have been profound and animal activity in the 'critical zone' is substantial (National Research Council, 2010; Atkinson et al., 2017). The risks (e.g. Orlandini et al., 2015) and landscape management opportunities presented by zoogeomorphic activity are increasingly apparent. Hopeful that these considerations make it easier to embrace the potential significance of zoogeomorphology, what are the priorities for future research? I think these revolve around four interrelated key challenges.

While we still need to (1) pursue the careful experimental investigations necessary to understand and quantify zoogeomorphic mechanisms, it is also imperative to (2) scale up process understanding to elucidate the impact of populations and ecosystems for geomorphological processes and outcomes at larger scales. This involves a move from controlled laboratory, mesocosm and small-scale field studies to larger scale plot, catchment and longitudinal studies, and a greater understanding of how local ecology and geomorphology mediate animal impacts on sediment fluxes (when animals have an effect, where they have an effect, how affects vary with life stage, abundance and other ecological factors). This much has been said before by others (e.g. Larsen et al., 2021) but remains a significant challenge because of the effort and resources required to obtain useful measurements at larger scales across longer periods, and the methodological challenges of isolating zoogeomorphic impacts in a noisy, uncontrolled environment.

A third key challenge is therefore to (3) embrace new technological and methodological advances that can help to unlock some of these difficulties, not least by developing meaningful collaborative work with ecologists who can bring new theoretical and methodological perspectives and tools (Allen et al., 2014). Technological advances that help to identify the presence and abundance of organisms without the need for extensive physical sampling are valuable and may include the use of eDNA (Larsen et al., 2018), remote sensing technologies and advances in numerical modelling.

Indeed, numerical modelling is essential for unlocking many of the longer-term, larger scale questions about how zoogeomorphology affects landscape change and evolution (e.g. Fremier et al., 2018) but also for unravelling the two-way interactive feedbacks between habitat, organisms and zoogeomorphology emphasised by Murray et al. (2008) in the term biomorphodynamics. Systematic investigation of zoogeomorphic effects across time and space is precluded by the lack of suitable modelling tools. It is therefore important that we (4) build coupled ecological-geomorphological models (Murray et al., 2008) that can simulate the dynamic interplay between the spatial population dynamics of an animal and geomorphological landscape change, including feedbacks from morphology to habitat suitability. This would transform our ability to investigate how landscapes interact with the animals that live on, and in, them, both in terms of the fundamental science but also the risks (Orlandini et al., 2015) and restorative opportunities zoogeomorphology presents (Johnson et al., 2020). As climate change affects the distribution of suitable habitats and resources, and the distribution and intensity of geomorphic processes, the nature of zoogeomorphic interactions will change (Butler, 2012) and numerical models that incorporate climatic drivers of both spatial population dynamics and geomorphology, may be the only reasonable means for predicting complex and non-linear climate impacts on biomorphodynamics. While numerical modelling of plant-geomorphology interactions is developing (Kleinhans et al., 2018; Lera et al., 2019), modelling animal interactions lags behind. Advances in this area will require innovative means of incorporating zoogeomorphic effects into sediment transport and other process formulations, which are currently rare (e.g., Albertson et al., 2014a), and will depend on continued empirical work to provide parameterisation and validation data sets.

4. CONCLUSION

The benefits and challenges of establishing effective and fruitful interactions at the interface of geomorphology and biology are widely discussed elsewhere. Johnson (2002) argues that the exclusion of biology from mainstream geomorphology almost certainly reflects a complex of reasons including historic accident, propinquity, the personalities of key gatekeepers, inadequate integrative language and theory, and the inertia of siloed disciplinary thought. Challenging such inertia is what W.M. Davis had in mind when he delivered his “outrageous hypotheses” talk at Berkeley in 1925 (Baker, 1996). He espoused the value of doing violence to established principles, “…as a means of encouraging the contemplation of other possible behaviours…” (Davis, 1926, 467-468). Zoogeomorphic agency is acknowledged and increasingly investigated, so cannot be compared with the challenges to orthodoxy in the transformative projects of Agassiz, Wegener or Bretz that Davis had in mind. However, biological energy and the activity of animals is a more important factor in exogenic geomorphology than is widely recognised and, while healthy scepticism remains important, full understanding of the Earth’s surface requires better integration of coupled geophysical and ecological processes. In this case, it is appropriate to recognise that zoogeomorphic actors in rivers are common, abundant, widespread, active and cumulatively effective in doing geomorphological work, such that biomorphodynamic coupling between ecology and geomorphology should be regarded as the norm, not the exception.

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