Opinion piece /Commentary

Biotic drivers of river and floodplain geomorphology – new molecular methods for assessing present-day and past biota

Annegret Larsen, Université de Lausanne, 1015 Lausanne, Switzerland

Nadir Alvarez, Université de Lausanne, 1015 Lausanne, Switzerland

Christoph Sperisen, Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, 8903 Birmensdorf, Schweiz

Stuart N. Lane, Université de Lausanne, 1015 Lausanne, Switzerland

Abstract

Geomorphology has increasingly considered the role of biotic factors as controls upon geomorphic processes across a wide range of spatial and temporal scales. Where timescales are long (centennial and longer), it has been possible to quantify relationships between geomorphic processes and vegetation using, for example, the pollen record. However, where the biotic agents are fauna, longer term reconstruction of the impacts of biological activity upon geomorphic processes is more challenging. Here, we review the prospect of using environmental DNA as a molecular proxy to decipher the presence and nature of faunal influences on geomorphic processes in both present and ancient deposits. When used appropriately, this method has the potential to improve our understanding of biotic drivers of geomorphic processes, notably fauna, over long timescales and so to reconstruct how such drivers might explain the landscape as we see it today.

Biotic drivers of river and floodplain geomorphology

Geomorphology has long considered the role of abiotic factors in geomorphic processes, including tectonics, geology, climate and relief, as well as humans impact upon them. Biotic factors are increasingly recognized as governing geomorphic processes on many spatial and temporal scales (Corenblit, et al., 2011, Gurnell, 2014, Osterkamp, et al., 2012). For geomorphologists, plants are without doubt an influential “ecosystem” engineer (Jones, et al., 1996), or more specifically a “geomorphological” engineer (Corenblit, et al., 2011). In the deep past (250 Ma years), the emergence of terrestrial plants has been argued to have altered fundamentally the geological record produced by surface processes (Gibling, et al., 2012). Modern-day feedbacks between plants and morphodynamics have been studied in marshy, coastal environments, where marsh vegetation grows on higher surfaces created by physical processes, and then exerts primary control on erosion, transport and sediment deposition processes (Murray, et al., 2008). On hillslopes, vegetation roots and litter stabilize surfaces and prevent incision, however bioturbation of roots also causes downhill sediment transport (Roering, et al., 2002). In river corridors, plants modify surface flow, retain sediments and stabilize new fluvial deposits (Gurnell, 2014). Enhanced bank stability through root binding of vegetation can cause a river planform to change from multi-thread braiding systems to single-thread meandering (Tal, et al., 2007), even in systems where vegetation growth rate is limited by groundwater access (Bätz, et al., 2016). Woody debris changes river-floodplain connectivity and

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/esp.4238

enhances flow complexity (Wohl, et al., 2014, Wohl, et al., 2010). However, recent studies have indicated that the control of vegetation might be part of a longer-term cycle, in which the dominance of biotic and abiotic processes not only switch, but depend on each other (Lane, et al., 2016, Larsen, et al., 2016). Biota and abiotic processes may have co-evolved over both longer and shorter timescales (Corenblit, et al., 2011).

However, the ecosystem engineers of river corridors are not only plants but can include bacteria and protists, biofilms, fungi, insects, invertebrates, and animals (Odling-Smee, et al., 2003). These have been much less studied by geomorphologists although, as Butler (1992) showed, the geomorphic impacts of animal activity may be much greater than thought and the case for such impacts has been made from the large (e.g. grizzly bears (Butler, 1992), medium (e.g. earthworms (McKey, et al., 2010, Zangerlé, et al., 2016)) through to the small (e.g. weathering (Naylor, 2005, Naylor, et al., 2012, Viles, 1988). Recent research has indicated that sediment transport on river beds is likely to be significantly affected by biofilms (Gerbersdorf, et al., 2008, Vignaga, et al., 2013). Bioturbation through lotic animals may keep sediments in suspension (Butler, 2012, Statzner, 2012) and perturb bed sediments, aiding bed break up and entrainment (Pledger, et al., 2014). Foraging of riparian and aquatic plants by large animals such as elephants (Haynes, 2012), hippopotami, crocodiles, moose, warthogs (Naiman, et al., 1997) and cows have been reported to destabilize stream banks (Trimble, et al., 1995), but also might have an effect of in-channel processes (Haynes, 2012, Skeat, et al., 1996). The modification of rivers by beavers (*castor fiber* and *canadensis*) has recently received particular attention (Gurnell, 1998, Naiman, et al., 1988, Westbrook, et al., 2013), with their role as geomorphic agents including damming and digging (Giriati, et al., 2016, Hood, et al., 2015, Nyssen, et al., 2011), foraging trees on banks and floodplains (Naiman, et al., 1988) and introducing wood to rivers (Anderson, et al., 2014). Certainly in river-floodplain systems, the work done by both flora and fauna may be important.

In this commentary we argue that if fauna are important as geological agents, then understanding the complex response of geomorphic systems to fauna is necessary to understand the past, present and future of the fluvial environment. It is not surprising that studies of the Late Quaternary evolution of fluvial morphodynamics have largely focused upon changes in the sedimentary soil-sediment sequences that result from (i) climate change (Macklin, et al., 2012); (ii) vegetation change (Schirmer, 1995) and/or (iii) human impacts (Knox, 2006, Walter, et al., 2008). Reconstruction of vegetation and climate from pollen and other records facilitates these analyses. But if animals are shown to be an important influence on geomorphic processes today, then it is quite possible that they were also important historically. For example, conclusive interpretation of Holocene river changes may be limited because of an incomplete or partial account of the presence and/or absence of data on the role of ecosystem engineers in modifying the riparian and aquatic ecosystems, including hydro-geomorphic processes (Wolf, et al., 2007).

New molecular methods for assessing present-day and past biota

For vegetation, work on the palaeo-ecology of old river channels and floodplains has been possible through identification of botanical micro- and macro remains. The analysis of pollen provides information about past vegetation cover on a regional scale (for a review see Kalis, et al., 2003). However, fluvial processes are influenced by vegetation locally, and therefore pollen analysis may be limited with this regard. Botanical macro-remains (such as leaves, nuts, grains or wood) have been used to reconstruct past vegetation cover since the end of the last century (Becker, et al., 1977, Birks, et al., 2000), and are usually interpreted in combination with a pollen archive to cover regional

and local vegetation changes. However, due to decomposition processes in non-waterlogged surface conditions, botanical macro-remains are only rarely available. Analysis of Phytoliths (siliceous botanical remains) are another method used to understand past vegetation cover, but they are most consistently produced by grasses and sedges and therefore limited to these plant types (Alexandre, et al., 1999, Carnelli, et al., 2004, Fredlund, et al., 1997, Meister, et al., in press, Piperno, et al., 1996). Analysis of stable isotopes, mainly carbon isotope $\delta^{13}\text{C}$ from soil organic matter, can give evidence of the balance between C3 and C4 plants. While this is a powerful tool, the limitations lie amongst others in the natural variability, the limited global distribution of C4 plants and in a signature change over time (Meier-Augenstein, et al., 2009).

Geomorphologists in general, and fluvial geomorphologists in particular, have yet to embrace the new field of molecular proxies, encompassing numerous types of biomarkers, which are at present being explored in lake and offshore sediments for their ability to reconstruct palaeo-environments (for a review, see Dubois, et al. (2016)). A relatively well established biomarker for vegetation shifts are n-alkanes, a lipid class from leaf waxes originating in leaf litter, already used in loess deposits (Zech, et al., 2012), and more recently in fluvial deposits (Suchodoletz, et al., 2016). Other biomarkers, e.g. campesterol, sitosterol and 5 β -stigmastanol-like have successfully proven the presence of historical manuring techniques in soils (Simpson, et al., 1999), and thus could potentially give evidence of faeces and so the presence of animals.

More recently, DNA obtained from environmental samples such as surface water, sediment and permafrost (environmental DNA, eDNA; or PalEnDNA for palaeo-environmental DNA (Parducci, et al., 2015)) has become a widely used proxy of present-day and past biota (Pedersen, et al., 2015). For instance, many sedimentary deposits contain unique, genetic records of palaeo-environments (Willerslev, et al., 2003). Hence, the DNA found within historical deposits may be used to constrain the role of past ecosystem engineers. Analysis of ancient environmental DNA up to date includes palaeo-environmental DNA from disseminated genetic material found within sedimentary archives, including paleo-dietary ancient DNA (Rawlence, et al., 2014). The technique is based on the fact that species continuously expel DNA to their surroundings, deposited through skin flakes, urine, feces, hair, and saliva in the case of animals, root cap cells, dead leaves, and pollen in the case of plants (Pedersen, et al., 2015, Rawlence, et al., 2014, Thomsen, et al., 2015). However, the difficulty of analyzing PalEnDNA may give rise to erroneous results, especially in the sense of false positives (Ficetola, et al., 2015). Moreover, knowledge about contamination, transportation, incorporation, and preservation of DNA in sediments is a prerequisite (Birks, et al., 2016, Rawlence, et al., 2014).

The preservation and thus availability of eDNA greatly varies among different environments ranging from a few weeks e.g. in temperate water (Dejean, et al., 2011) to hundred thousands of years in permafrost (Willerslev, et al., 2003). In fact, there are multiple possible fates of eDNA in the environment, with both biotic and abiotic factors potentially interacting to degrade or preserve eDNA (Barnes, et al., 2014). Focusing on plants, Parducci and colleagues have recently suggested that eDNA may be best achieved using pollen grains rather than other vegetal tissues as the overlap between metabarcoding-derived plant composition and observation-based plant composition was higher when considering pollen than macrofossil remains (Parducci, et al., 2015). Generally, higher temperatures as well as oxic conditions may enhance microbiomes, resulting in eDNA degradation through extracellular nucleases (Nielsen, et al., 2007). Both exposure to oxygen and light, may also lead directly to eDNA damage. A number of studies document the important role that sediment and soil particles play in eDNA preservation, by both binding and protecting DNA molecules from other forces and by binding and inactivating extracellular nucleases (Barnes, et al., 2014). For example, DNA binds more strongly to clay particles than to sand or silt (Neumann, et al., 2013), and rates of

adsorption of DNA to clay differ among types of clays (Cai, et al., 2006). Despite these possible shortcomings, eDNA has been successfully applied to a variety of environments (for a review, see Thomsen, et al. (2015)), including marine e.g. (O'Donnell, et al., 2017, Thomsen, et al., 2016) and freshwater (Deiner, et al., 2016, Parducci, et al., 2015), soils (Hebsgaard, et al., 2009), silt (Fortin, et al., 2004), sand (Lakay, et al., 2007), peatbogs (Dedysh, et al., 2006), ice (Willerslev, et al., 2007), cave deposits (Haile, et al., 2007), permafrost (Bellemain, et al., 2013, Parducci, et al., 2012) and coprolites (Wood, et al., 2012).

Although the majority of eDNA studies in aquatic systems have been carried out in marine or lake environments, an increasing number of studies demonstrates that eDNA may be used to identify the presence of species in fluvial environments, such as rivers (Deiner, et al., 2016, Ma, et al., 2016) and river-floodplain lakes (Tessler, et al., 2017). For example, sequencing of CoxI (i.e., a mitochondrial marker commonly used in the context of metabarcoding applications, also referred to as COI) from eDNA samples obtained from surface water of a small temperate river led to the identification of 296 families of eukaryotes, ranging from relatively small to large vertebrates, including fish and beaver (Deiner, et al., 2016). Compared to surface water, eDNA appears to be much more concentrated in river sediments, presumably because the DNA is protected and thus can accumulate (Turner et al. 2015). In a geomorphological context, these studies show that eDNA enables observation of species that are otherwise difficult to identify and in some cases even reflect species abundances (Doi, et al., 2017).

Besides the application of metabarcoding markers, metagenomic approaches are emerging, enabling past flora and fauna reconstructions at high taxonomic resolution. Importantly, these studies have revealed that eDNA data and other proxies such as pollen and macrofossils complement each other showing wider diversity of species than if the methods are used separately (Gugerli, et al., 2013, Pedersen, et al., 2015). Depending on the research question, ancient DNA may also be isolated and analysed from subfossil plant and animal macro-remains. Such an approach could provide information on, for example, subfossil tree trunks found in fluvial deposits, enabling species identification (Gómez-Zeledón, et al., 2017)) and determining their (phylo)geographical origin (see Gurnell, et al. (2012)). Approaches relying on hybridization capture using RNA-based probes have revealed promising to identify fine-grain levels of genetic diversity in ancient plant samples from the early Holocene, even at the level of intra-specific variation (Schmid, et al., 2017).

Although highly promising for reconstructing present and past communities, the application of biomarkers and eDNA is not without pitfalls (Dubois, et al., 2016), especially regarding i) transport processes, linked to questions regarding their source, and also their quantitative representativeness (Dubois, et al., 2016), as well as ii) degradation processes (Barnes, et al., 2014, Buggie, et al., 2010). Several guidelines have been published so far to ensure proper (paleo-)environmental DNA analyses (Goldberg, et al., 2016, Thomsen, et al., 2015) and we recommend a careful setup of experiments in order to rule out recognized biases.

Conclusions

Geomorphology is within a new era, one that recognizes the role of biotic factors in governing geomorphic processes across a wide range of spatial and temporal scales. Environmental DNA has the potential to decipher species presence and composition from present and ancient samples, and so begin to reconstruct the web of interacting biotic agents associated with ecosystem engineering in rivers and floodplains, crucial for understanding the palaeo-sedimentary records of river-

floodplain sediments. Using non-DNA approaches may aid with vegetation, but we also need proxies for faunal activity that can be identified in river-floodplain deposits. Molecular proxies may allow the indirect identification of historical fauna activity, but, environmental DNA may offer much more potential. PalEnDNA has been shown in lake, bog and corrolites to be a reliable method for understanding palaeo-environmental conditions, and this may provide very valuable for reconstructing historical faunal activity.

To achieve this potential a careful choice of the depositional environment and experimental setup is necessary. Sediments should be waterlogged and have a large clay fraction. There is now compelling evidence that metabarcoding approaches allow deciphering past and present community composition (e.g. past vegetation). When aiming at identifying presence/absence of a single species (or genetic variation within), capture-based methods may reveal promising. Overall, PalEnDNA methods could substantially improve our understanding of biotic drivers of geomorphic processes in a short and longer (Quaternary) time perspective.

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Figure 1