Muddy waters: Mega-herbivores as agents of change in African shallow freshwaters

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RESEARCH NOTE

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Muddy waters: Mega-herbivores as agents of change in African shallow freshwaters

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Abstract

Large herbivores have been described as agents of change in terrestrial habitats. Their effect on aquatic ecosystems are, however, underexplored. We raise the question of whether elephants and hippopotamus have the potential to significantly alter limnological properties and, indirectly, primary and secondary productivity within small and shallow freshwaters in arid and semi-arid African landscapes. In this note we discuss hypothetical means by which elephants and hippopotamus alter shallow freshwater bodies. We further assimilate this with known ways by which these mega-herbivores alter aquatic environments giving an overview of their potential functional role in structuring aquatic habitats.

KEYWORDS
increased turbidity, semi-arid, shallow aquatic ecosystem, vertical mixing

Résumé

Les grands herbivores ont été décrits comme des agents de changement dans les habitats terrestres. Leurs effets sur les écosystèmes aquatiques sont toutefois peu étudiés. Nous nous demandons si les éléphants et les hippopotames ont le potentiel de modifier de manière significative les propriétés limnologiques et, indirectement, la productivité primaire et secondaire dans les eaux douces petites et peu profondes des paysages africains arides et semi-arides. Dans cette note, nous discutons des moyens hypothétiques par lesquels les éléphants et les hippopotames modifient les masses d'eau douce peu profondes. Nous assimilons ensuite ces résultats aux méthodes connues par lesquelles ces méga-herbivores modifient les environnements aquatiques, ce qui donne un aperçu de leur rôle fonctionnel potentiel dans la structuration des habitats aquatiques.

Disturbance plays a central role in the structuring of ecosystems (Sousa, 1984). Large herbivores can be agents of disturbance, altering terrestrial habitats through both foraging and non-foraging activities (Haynes, 2012; McCarthy et al., 1998; Mosepele et al., 2009; Ripple et al., 2015). Such altered habitats are particularly evident in many regions of Africa given the presence of the so-called mega-herbivores, such as hippopotamus (*Hippopotamus amphibious*), African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) (Ripple et al., 2015). Given the conspicuous and charismatic nature of these animals, and their recognised importance as ecosystem engineers, their roles in structuring terrestrial environments are well studied (Ripple et al., 2015 and the references therein). What is less known, however, are the effects of certain mega-herbivores on aquatic ecosystems. While catchment activities will certainly have indirect implications for aquatic ecosystems, through processes such as erosion, these animals also often have a direct association with water bodies. Semi-arid and arid regions on the continent are typically characterised by smaller, shallower and less permanent aquatic habitats that may be susceptible to structuring through mega-herbivore mediated activities. In many protected areas in the region, mega-herbivore numbers are burgeoning (e.g. Gough & Kerley, 2006), with implications for often scarce aquatic habitats.

We raise the question of whether elephants and hippopotamus have the potential to significantly alter limnological properties and, indirectly, aquatic communities within water bodies they frequent. In Africa, elephants and hippopotamus are among the largest of the herbivores (Ripple et al., 2015). While these species differ considerably in their behaviour, feeding and landscape exploitation, they are similar in that both have an affinity for water (Mosepele et al., 2009; Owen-Smith, 1992). Hippopotamus are considered semi-aquatic and diurnally, spend their time in aquatic environments such as rivers, lakes and impoundments, and thus utilise water not only for drinking purposes but also as habitat (Coughlin & Fish, 2009; Field, 1970; McCarthy et al., 1998). At night, hippopotamus leave their aquatic environments to forage in surrounding terrestrial habitats (Field, 1970). While elephants utilise water primarily for hydration purposes, these mega-herbivores also exploit water extensively for non-drinking activities such as mud-bathing and swimming (Mosepele et al., 2009; Owen-Smith, 1992; Vanschoenwinkel et al., 2011). As such, both hippopotamus and elephants regularly move between terrestrial and aquatic environments (Loarie et al., 2009; McCauley et al., 2015; Mosepele et al., 2009). In this research note we discuss hypothetical means by which elephants and hippopotamus could alter the limnology and ecology of water bodies. We further assimilate this theoretical information with known ways by which these mega-herbivores alter aquatic environments, by creating a conceptual model of their potential functional role in structuring small and shallow aquatic environments (Figure 1). Such conceptual models can be highly useful in conservation planning (Margoluis et al., 2009).

As a result of their size, elephants and hippopotamus have much potential for altering properties of the water column and the submerged benthos. Movement through aquatic environments by these mega-herbivores primarily involves contact with the bottom of waterbodies. Hippopotamus walk or bounce along the bottom of water bodies and rarely swim (Coughlin & Fish, 2009), while elephant also spend much of their time in contact with the substratum as their activities in water are largely restricted to shallower habitats (Owen-Smith, 1992; Wright & Luck, 1984). As such, they likely contribute to

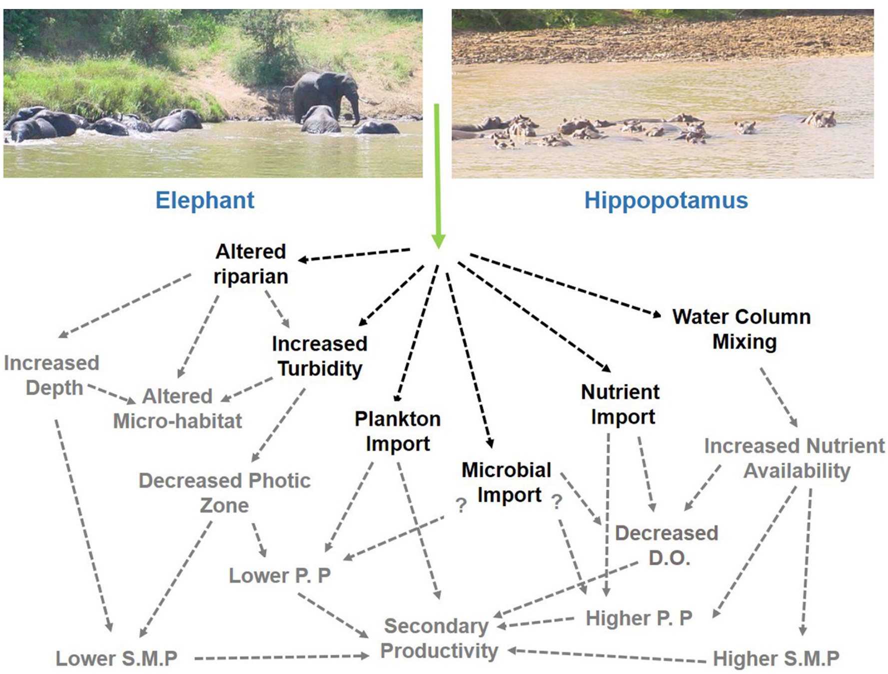

FIGURE 1 Conceptual diagram showing known and hypothetical (hyp) ways in which elephants and hippopotamus (mega-herbivores) directly (black arrows) and indirectly (grey arrows) alter aquatic systems through movement across and within these environments (green arrow). Mega-herbivores physically mix the water column (hyp), increase turbidity (hyp), decrease dissolved oxygen levels (Stears & McCauley, 2018) and alter the riparian (Mosepele et al., 2009; Ripple et al., 2015). In addition, they import allochthonous plant material (McCauley et al., 2015), viable plankton propagules (Vanschoenwinkel et al., 2011) and potentially harmful microbes (Ndlovu et al., 2018). These alterations have implications for micro-habitat structure, water transparency, nutrient availability and species augmentation, all of which are known to affect primary and secondary productivity in aquatic environments. D.O., dissolved oxygen; P.P., primary productivity; S.M.P., submerged macrophtye productivity.

resuspension of silt, nutrients and organic material and homogenisation of stratified waters. Since such effects will result in localised increases of turbidity and have implications for nutrient availability in the water column, mega-herbivore activity in shallow water bodies such as pans, river pools and reservoirs could have consequences for aquatic primary and secondary productivity. Although we present an untested hypothesis, the effects of homogenisation, nutrient resuspension and increased turbidity on plankton, macroinvertebrates and fishes have been well studied in freshwater environments (Arruda et al., 1983; Henley et al., 2000). The role of mega-herbivores as facilitators of such effects is, however, largely unexplored.

What has been observed is that the movement between terrestrial and aquatic habitats by mega-herbivores alters submerged and emergent aquatic and riparian vegetation (McCarthy et al., 1998; Mosepele et al., 2009). It has also been shown that mega-herbivores transport propagules, in the form of dormant cysts, between water bodies (Vanschoenwinkel et al., 2011) and contribute potentially harmful microbes associated with faecal matter, into aquatic ecosystems (Ndlovu et al., 2018). These animals can also physically shape aquatic habitats, forming and deepening channels and pools (McCarthy et al., 1998; Mosepele et al., 2009). Certain mega-herbivores are also known to facilitate cross-ecosystem subsidies through an introduction of dung, of terrestrial origin, into aquatic habitats (e.g. McCauley et al., 2015). Such animal-mediated allochthonous input has been shown to have implications for nutrient cycling, dissolved oxygen levels, food-web dynamics and productivity in certain aquatic environments (Marcarelli et al., 2011; McCauley et al., 2015; Stears et al., 2018; Stears & McCauley, 2018; Vanni, 2002). Given the known effects of elephants and hippopotamus on aquatic systems and their potential for altering the limnology of aquatic environments through physical activity- as raised in the present study, we propose that mega-herbivores may play a functional role in the structuring of shallow-water aquatic communities. We further hypothesise that these potential effects could be augmented in many regions given the practice of enclosing protected areas with fence (Loarie et al., 2009; Packer et al., 2013; Slotow, 2012). This practice ultimately limits movement of these large animals to within restricted boundaries (Gough & Kerley, 2006; Slotow, 2012) and can facilitate population numbers often higher than recommended for the maintenance of ecological integrity (Maciejewski & Kerley, 2014). While these issues have been well documented in the terrestrial context (Maciejewski & Kerley, 2014; Packer et al., 2013; Slotow, 2012), their potential effects on characteristic shallow aquatic ecosystems in arid and semi-arid regions, have yet to be adequately explored. We recommend future research address specific aspects outlined in the conceptual model, in an attempt to better quantify and understand how the known and unknown components interact. Such information is vital for better management of mega-herbivore disturbance dynamics at the landscape level.

AUTHOR CONTRIBUTIONS

Ryan J. Wasserman: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Tatenda Dalu**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

No conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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