Burrowing invasive species: an unquantified erosion risk at the aquatic-terrestrial interface

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Key Points:

- Burrowing invasive species represent a potentially significant but unquantified erosion risk at the aquatic-terrestrial interface

- Of global interest: over 100 countries, states or territories where at least one relevant example invasive species is established

- Our conceptual model demonstrates how burrows modify geotechnical, hydrological and hydraulic processes, influencing stability and erosion

Abstract

Invasive non-native species acting as 'ecosystem engineers' or 'geomorphic agents' can represent a major landscape disturbance. Quantification of their biogeomorphic impacts remains a key knowledge gap and aquatic-terrestrial transition zones may be particularly exposed to impacts. We demonstrate how burrowing invasive species represent a potentially significant but unquantified erosion risk at aquatic margins. We reveal a lack of quantitative research on geophysical impacts, despite increasing concerns over threats to waterways and flood defense infrastructure. We explore example animals of global interest, comprising crustaceans, fish, reptiles and mammals and reveal the global nature of the issue: over 100 countries, states or territories where at least one example species is established, and over 20 with 3-6 species present. We present a conceptual model for the impacts of burrows on stability and erosion at aquatic margins using established models of geotechnical, hydrological and hydraulic drivers. Burrows are hypothesized to (i) alter failure plane position, decrease failure plane length and increase failure plane angle (thereby decreasing bank shear strength); (ii) modify the spatial distribution of porewater pressure, thereby increasing subsurface flow (seepage), reducing cohesion and increasing the likelihood of slip failures at the bank face; (iii) increase turbulence and sediment entrainment at burrow entrances and (iv) alter flow resistance at the bank face. Most effects are expected to increase bank instability/erosion with the exception of (iv) which has the potential to offer protection from fluvial action. We call for

further research in these areas to quantify impacts for different environments and different invasive species.

Plain Language Summary

Animals and plants acting as 'biogeomorphic agents' can have profound impacts on earth surface processes. Numerous animals burrow into soils and sediments and this can yield a range of ecosystem benefits. The burrowing activities of some invasive or 'pest' species, however, may increase erosion risks and aquatic environments are particularly vulnerable to such impacts. Our study explores examples of burrowing invaders of global interest that have potential to pose an erosion risk to the banks and margins of rivers, lakes, ponds, marshes, estuaries and artificial drainage and flood defense infrastructure. We identify over 100 countries, states or territories with at least one example species present, and 20 with three or more burrowing invaders. There is no established framework for assessing the erosion risk from burrows, so we use existing theory from geophysics to explore the different ways in which these species may generate erosion at the margins of aquatic environments.

1 Introduction

The term 'ecosystem engineer' describes plants and animals that cause physical state changes in biotic or abiotic materials, either via their own physical structures or by transforming living or non-living materials (Jones *et al.*, 1994). The effects of ecosystem engineers on the environment is profound: they initiate, modify and maintain habitats and modulate resource flows in all ecosystems on earth (Jones *et al.*, 1994). A subset of ecosystem engineers, referred to as 'geomorphic agents' (Butler, 1995), 'geomorphic engineers' or 'biogeomorphic agents' (Fei *et al.*, 2014) alter earth surface processes and landforms at scales ranging from individual sediment grains to entire landscapes (Reinhardt *et al.*, 2010; Bertoldi *et al.*, 2011; Rice *et al.*, 2012). Biogeomorphic agents may construct new landforms (bioconstruction), break down and fractionate soils and sediments e.g burrowing or reduce protection from erosion e.g. herbivory, (bioerosion), disturb and rework soils and sediments (bioturbation) and offer protection from erosion of weathering (bioprotection), see Naylor *et al.* (2010), Fei *et al.* (2014) and Davidson *et al.* (2018). As a result, these organisms can increase habitat complexity, and potentially biodiversity (Crooks, 2002), and can be used to promote the recovery of degraded environments (Byers *et al.*, 2006; Polvi and Sarneel, 2017; Bailey *et al.*, 2018).

Invasive species acting as ecosystem engineers and biogeomorphic agents have been identified as a special case (Crooks, 2002; Harvey *et al.*, 2011; Fei *et al.*, 2014; Davidson *et al.*, 2018). While biological invasion is a natural process, species introductions (whether deliberate or accidental) have generated unprecedented increases in the rate of species invasions globally (Seebens *et al.*, 2016) as well as changes in the nature and pathways of invasions (Crooks, 2002). These trends are expected to persist (Seebens *et al.*, 2016). For many species, effective eradication strategies remain elusive (Stebbing *et al.*, 2012) and indeed may be inappropriate within the context of global change and novel ecosystems (Hobbs *et al.*, 2011). There is lively debate around the 'vilification' of nonnative and invasive species, the use of value-laden terminology (e.g. 'alien' and 'invasive'), the appropriateness of distinctions between non-native and native species in a rapidly changing planet and the suitability of existing management responses. These issues are illustrated by the

debate between Davis *et al.* (2011) and Simberloff *et al.* (2011) and in the recent synthesis by Boltovsky *et al.* (2018) and we refer the reader to these sources for further information. Here, we recognize a non-native species as that which is living outside its native distributional range as a result of intentional or accidental dispersal by human activities (sometimes referred to as 'exotic' or 'introduced'; UN Convention on Biological Diversity, 2019). 'Invasive species' generally refers to those non-native species that have the ability to spread and cause damage to the environment, the economy and human health (GBNNSS, 2019; Russell, 2012). We recognize that non-native species do not necessarily become invasive, that invasive species can have positive, neutral and negative effects on the invaded landscape and ecosystem, and that many have mixed impacts (Boltovskoy *et al.*, 2018). Native species may also be referred to as invasive or 'pest' species when environmental pressures result from the rapid dominance of a species (Valery 2013) or where their activities come into conflict with people, property or infrastructure (Bayoumi and Meghuid, 2011). We also recognize that invasive species do not possess ill intent and that their impacts have fundamentally been generated by the human activities that have facilitated their spread into non-native ranges. Notwithstanding the important epistemological issues, there is substantial and increasing evidence that many invasive species are capable of altering ecosystems and geophysical processes in ways that may generate environmental, economic and societal risks, at least within the context of current approaches to environmental conservation and management (Pimental *et al.*, 2001; Gallardo *et al.*, 2016). Irrespective of the suitability of management responses, improved understanding of the biogeomorphic impacts of invasive species is required to advance knowledge of biogeomorphology and invasion ecology and support environmental management (Fei *et al.*, 2014).

While the direct biogeomorphic impacts of invasive species are not unique in character, they can have profound geophysical effects that are disproportionate to their biomass and are more likely to lead to major geomorphic changes and stresses capable of inducing a landscape phase-state shift (Fei *et al.*, 2014; Butler *et al.*, 2018). Such impacts are possible since invasive species may be less constrained by factors that would limit their abundance in native habitats (Wolff, 2002), can be present in extremely high densities, and may exhibit behaviors and destructive traits that are not exhibited in the native range (e.g. Holdich, 1999). While some invasive species can generate increased habitat complexity and biodiversity, exotic animals in particular have been linked with disturbances that destroy physical structure and reduce heterogeneity in invaded landscapes (Crooks, 2002). Transitional areas between terrestrial and aquatic systems including fluvial systems, wetlands and marshes are highly connected within the landscape both laterally at the aquatic-terrestrial interface and longitudinally via the catchment-coast continuum, and have been identified as particularly exposed to the biogeomorphic impacts of invasive species (Moorhouse and Macdonald, 2015; Fei *et al.*, 2014). Despite these attributes, quantification of the biogeomorphic impacts of invasive species remains a key knowledge gap.

Bioturbating activities, such as burrowing, frequently account for major effects in aquatic systems (Fei *et al.*, 2014). Many terrestrial and aquatic species excavate burrows for defensive, reproductive or refuge purposes (Haussman, 2017) and burrowing species can generate diverse ecosystem benefits and services, such as contributions to nutrient cycling, climate and water regulation and pollution remediation (Wilkinson et al., 2009; Blouin *et al.*, 2013). Burrowing

invasive and 'pest' species, however, have the potential to increase erosion risk at aquatic margins for the reasons outlined above. This risk remains unquantified, but increasing reports of damage to natural and artificial drainage channels suggests burrowing invaders and native pests represent a significant and growing threat to waterways and flood defense infrastructure (e.g. Hoover *et al.*, 2004; Panzacchi *et al.*, 2007; Ferriter *et al.*, 2008; Sementelli *et al.*, 2008; Nico *et al.*, 2009; Orlandini *et al.*, 2015; Davidson *et al.*, 2018) and historic waterside landmarks (e.g. Telegraph Reporters, 2016; BBC News, 2018). Improved understanding of the nature and extent of this risk is therefore urgently required to inform the effective and sustainable management of invaded systems.

This paper aims to demonstrate how burrowing invasive species alter geophysical processes and represent an erosion risk to aquatic margins in invaded landscapes. We highlight the lack of existing research into their impacts and identify example species of current concern at the global level. We then present a conceptual model which hypothesizes how burrows may influence erosion risk by modifying geotechnical, hydrological and hydraulic processes in river banks and indicate the relevance of these processes for other types of aquatic margin (e.g. lake margins, estuaries)

2 Burrowing invasive species: the knowledge gap

Numerous burrowing species have been introduced to aquatic ecosystems through a range of pathways including aquaculture, the aquarium and exotic pet trade, commercial shipping and the fur trade (Carter & Leonard, 2002; Kern, 2004; Nico *et al.*, 2009; Herborg *et al.*, 2003). Burrow excavation by invasive species occurs in a number of environments along the catchment to coast continuum, including the banks of natural and artificial channels, lake margins, salt marsh edge and creek habitats, and in and around flood defense structures including earthen dams, embankments/ levees and flood walls (see Figure 1). Some invasive animals have been observed to burrow in both native and invaded ecosystems (e.g. armoured catfish; Nico *et al.*, 2009), usually for reproductive and/or refuge purposes (see Table 1), while for others burrowing appears to be a behavior unique to invaded habitats and motivations are less clear (e.g. signal crayfish; Guan, 1994; Holdich, 1999). Burrowing habits have been linked to the invasiveness of some aquatic species, by contributing to increased environmental tolerance and protection from predation (Barbaresi *et al.*, 2004).

Geomorphological impacts of burrowing occur at different spatio-temporal scales, ranging from the excavation of the burrow itself (i.e. an instantaneous, low magnitude sediment input), to wider impacts on bank instability and erosion across impacted bank faces and sites (potentially higher magnitude inputs over longer timescales) (Guan, 1994; Holdich, 1999; Angeler *et al.*, 2001; Faller *et al.*, 2016). These impacts have the potential to generate catchment scale sediment management issues, depending on the magnitude of sediment inputs and system connectivity (Harvey *et al.*, 2011). Davidson *et al.* (2018) present a modified version of Parker *et al.*'s (1999) model for understanding and quantifying the impacts of invasive non-native species, focusing on the impact of bioeroders (including burrowing animals). The model proposes that the impacts of bioeroders, I_B can be expressed as a function of the geographical range of the species (R), the local abundance (A), and the per capita effects (E): $I_B = R \times A \times E$, mediated by the characteristics of the substrate exposed to bioerosion and influenced by the nature of the system and environmental change

(Davidson *et al.*, 2018) and by variations in the nature of relationships between R, A and E (Parker et al., 1999). In the case of burrowing species, burrow dimensions generally reflect body size, since it is not energetically efficient to construct burrows larger than the minimum requirement, resulting in a positive correlation between body size and burrow volume (Haussman, 2017; Figure 1). Magnitude-frequency relationships, however, are important: smaller species occur in greater numbers and may dig more excavations per individual per year, meaning that overall sediment removal rates may exhibit a negative correlation with body size (Haussman, 2017). The potency of smaller and less conspicuous animals such as aquatic invertebrates, therefore, has the potential to rival that of larger and more visible species such as mammals.

Our literature review is not exhaustive, but provides a selection of example invasive species with published burrowing impacts. Burrowing invaders include crustaceans (crayfish, crabs, isopod), fishes (armoured catfish), reptiles (iguana) and mammals (the semi-aquatic rodent 'coypu' or 'nutria'; *Myocastor coypus*; Table 1). Native mammals such as muskrats, beavers, porcupines, badgers and foxes are also sometimes considered 'pest' species when their burrowing habits cause damage to flood control structures (Federal Emergency Management Agency, 2003; Orlandini *et al.*, 2015). The conceptual model we present in section 4 is equally applicable to such cases and to terrestrial animals (in addition to aquatic and semi-aquatic species) that construct burrows at aquatic margins. Notably, we found that reports of burrowing impacts were largely confined to biological or ecological scientific journals or 'grey literature' (reports from government departments and academic/ research institutes). This reflects the fact that the burrowing impacts of invasive species tend to be reported as one of a number of detrimental ecosystem impacts, rather than the research focus in the majority of sources.We identified six publications that focus directly on quantifying the impact of invasive burrowers on slope stability or erosion at aquatic margins, but all of these linked burrowing with increased instability and/or erosion (Talley *et al.*, 2000; Rudnick *et al.*, 2005; Davidson and Riviera, 2010; 2012; Orlandini *et al.*, 2015; Aman and Grimes, 2016; Faller *et al.*, 2016).

Table 1 Impacted habitats and invasive range for example burrowing invasive animals of global interest, together with their burrowing behaviour and burrow characteristics. Bold numbers for invasive range show total number of countries/states/territories with established populations and superscript numbers show numbers of countries/states/territories where these have been amalgamated into regions for brevity (sources: GISD, 2019; DAISIE, 2019; NOBANIS, 2019). Data on burrowing behavior and burrow characteristics are derived from reports from both invasive and native ranges.

	Species	Habitat	Invasive range (no. countries/territories)	Burrowing life stage	Body length or *carapace width (cm)	Burrow function	Bank/margin type	Burrow architecture	Burrow position	Burrow entrance shape	Burrow depth (m) range, *mean or +max	Burrow density Areal (per m²) or *Linear (per m)	Refs
Crayfish	O. limosus	Pond/lake River Drainage channel	17 (Europe[18])	Adults	9–12	Reproduction	Silt/clay	Tunnel 2 entrances	Below water surface	Circular/D shaped	~0.1 (note value is for vertical burrow)		Momot (1988); Holdich and Black (2007); Kouba et al. (2016)
	O. virilis	Wetland Pond/lake River	32 (Canada[1], Europe[3], Africa[1], USA[27])	Adults	13	Refuge Reproduction	Earth, clay, silt	2 entrances, complex	Below or above water surface		1.0+		GISD, Hazlett et al. (1974); Momot (1988); Godfrey and Espino (2009)
	P. clarkii	Wetland Pond/lake River Rice paddy	46 (Africa[5], Caribbean[1], China, Central America[2], Europe[12], Georgia, Israel, Japan, Mexico, Phillippines, South America[3], Taiwan, USA[16])	Immature/juveniles	5.5–12	Protection from dehydration Refuge Reproduction	Silt/clay dominated	Simple/complex Tunnel/complex 'Chimney'/mud plug	Around water surface		0.28–0.58 4.2+	0.01–6.3	Correira and Ferreira (1995); Bararesi et al. (2004); Loureiro et al. (2015)
	Pacifastacus leniusculus	Pond/lake River	17 (Europe[18] and Japan)	Unknown	12–16	Unknown	Cohesive (silt/earth)	Simple and complex	Around water surface	Oval with flat base	0.1–0.5	2.8–5.6*	Bubb et al. (2002); Guan (1994); Harvey et al. (2011), Roberts (2012)
Crab	Eriocheir sinensis	Estuary	31 (Canada[2], Europe[19], Iran, Russia, USA[8])	Mainly juveniles	5–10*	Refuge protection from dessication	Silt, sand	Simple and complex	Between high and low tide lines	Elliptical	0.31*–0.44*	20* 30	Rudnick et al. (2000); Rudnick et al. (2005)
Isopod	Sphaeroma quoianum	Estuary	2 (USA[2])	Adults	up to 1.5	Filter feeding	Peat, silt, clay	Vermiform Single/complex ('galleries')		Circular	0.02*	778*	Talley et al. (2001); Davidson and Riviera (2012)
Fish	Pterygoplichthys (genus)	Pond/lake River Drainage channel	19 (Bangladesh, Caribbean[1], Central America[1], India, Indonesia, Japan, Malaysia, Philippines, Singapore, Thailand, Taiwan, Vietnam, USA[6])	Adult males	30–70	Reproduction	Silt/clay	Single Tunnels Colonies (~12) (2 openings/chambers - rare)	Around water surface	Triangular/arched/oval	0.20–1.30 0.78*	0.5–3.9	Nico et al. (2009); Van den Ende (2014)
Reptile	Iguana iguana	Pond/lake Drainage channel	10 (Caribbean[6], Europe[1], Fiji, Turks and Caicos, USA[1])	Adult females	up to 150	Reproduction Refuge	Earth	Single tunnels can extend to complex systems	Steep banks or terrestrial	Circular	0.3–2.4	0.2*	Sementelli et al. (2008); Rand and Dugan (1983)
Mammal	Myocastor coypus	Wetland Pond/lake Drainage channel	48 (Africa[1], Armenia, Azerbaijan, Canada[3], Europe[19], Georgia, Israel, Japan, Russia, Tajikistan, USA[16])	Adults	40–60 (70–105 including tail)	Refuge protection from thermal extremes Reproduction	45–90 degree bank slope, vegetated	Simple/complex Tunnel/chamber	Below water surface	Oval	1.0–5.0		Baroch et al. (2002); https://wdfw.wa.gov/living/nutria.html#facts; Sheffels et al. (2007); Sofia et al. (2017)

Although native burrowing animals are numerous (Haussman, 2017), there is no existing theoretical framework identifying the geotechnical, hydrological and hydraulic impacts of burrows that can be applied to burrowing species. Detailed understanding of the mechanics of burrowing is largely limited to hypothesized generalizations for idealized solids and experimentation with analog materials, failing to account for the complex and heterogeneous characteristics of natural sediments (Dorgan, 2015). Characterizing burrow-induced failure in natural substrates is therefore a critical knowledge gap requiring the development of new methods and approaches (Dorgan, 2015).

3 Example species of global interest

Crustaceans are the most successful aquatic invaders across the globe, accounting for 53% of invasive species in European freshwater ecosystems compared to 12% of native species (Hanfling *et al.*, 2011) and 28% of coastal invasions in North America (Ruiz *et al.*, 2011). They are the most widespread invasive aquatic organisms and are considered to be the most detrimental in terms of impacts on ecosystem services (Vila *et al.*, 2010). Several crustacean species of global interest are known to dig burrows into river banks, including a number of freshwater crayfish: spiny cheek crayfish (*Orconectes limosus*), virile crayfish (*Orconectes virilis*), red swamp crayfish

(*Procambarus clarkii*) and signal crayfish (*Pacifastacus leniusculus*). For some species the biological motivation for burrowing behaviour has been established (e.g. reproduction; *P. clarkii*; Loureiro *et al.*, 2015) while for others burrowing appears to be a characteristic unique to invaded ecosystems and motivations are less clear (e.g. *P. leniusculus*, Guan, 1994; Holdich, 1999; Table 1). Crayfish burrow architecture is often simple, comprising single openings with tunnels enlarging to a terminal chamber, although more complex architectures with multiple entrances have been observed (Correia & Ferreira, 1995). Evidence suggests that burrow construction is favored in fine, moist sediment; characteristics that also make vacant burrows more susceptible to collapse, potentially leading to further construction elsewhere (Barbaresi *et al.*, 2004; Figure 1a). Field observations at individual sites have linked invasive crayfish burrowing with increased bank erosion and sediment delivery (Guan, 1994; Holdich, 1999; Angeler *et al.*, 2001) and a recent extensive, multi-catchment study identified a statistical association between invasive crayfish burrows and bank erosion (fluvial action and mass failure processes) beyond the scale of individual burrows (Faller *et al.*, 2016). Faller *et al.* (2016) also reveal a tendency for burrows to be excavated on bare, eroding banks on the outside of meander bends. These are areas already exposed to erosional processes indicating potential for burrowing to accelerate erosion rates.

Invasive crabs and isopods generate similar effects in estuarine and coastal margins. Perhaps the most widely-reported are Chinese mitten crabs (*Eriocheir sinensis*) which have spread across Europe and northern California via the transport of larvae and juveniles in the ballast water of commercial vessels (Herborg *et al.*, 2003). Their catadromous life cycle means that in addition to rapidly colonizing coastal and estuarine areas, *E. sinensis* can make significant migrations inland (Clark *et al.*, 1998; Herborg *et al.*, 2005). Burrows are generally excavated by juveniles following migration into brackish channels, for purposes of refuge during moulting and protection from dessication (Rudnick *et al.*, 2000; Bouma & Soes, 2010). The highest dispersal rates (> 400 km per year) have been observed along coastlines, but upstream or inland spread can also been rapid with rates of up to 49 km per year reported in the UK (Herborg *et al.*, 2005). *E. sinensis* burrow entrances are elliptical, reflecting the flat oval-shaped bodies of the crabs (Rudnick *et al.*, 2003) and architectures can range from single tunnel-chamber systems containing one crab, to more complex burrow systems with multiple entrances and tunnels containing multiple crabs, with the latter most likely reflecting reuse over longer time periods by multiple year classes (Rudnick *et al.*, 2003). As a result, burrow volume can vary by an order of magnitude, for example between 10^2 and 10^3 cm^3 (Rudnick *et al.* 2005) and burrow densities of up to 30 per m^2 have been reported (Rudnick *et al.*, 2000). *E. sinensis* burrows were linked with erosion as early as the 1930s in Germany (Panning, 1938) and erosion concerns have been raised more recently in the USA, UK and continental Europe (Herborg *et al.*, 2003; Rudnick *et al.*, 2005, Bouma & Soes, 2010).
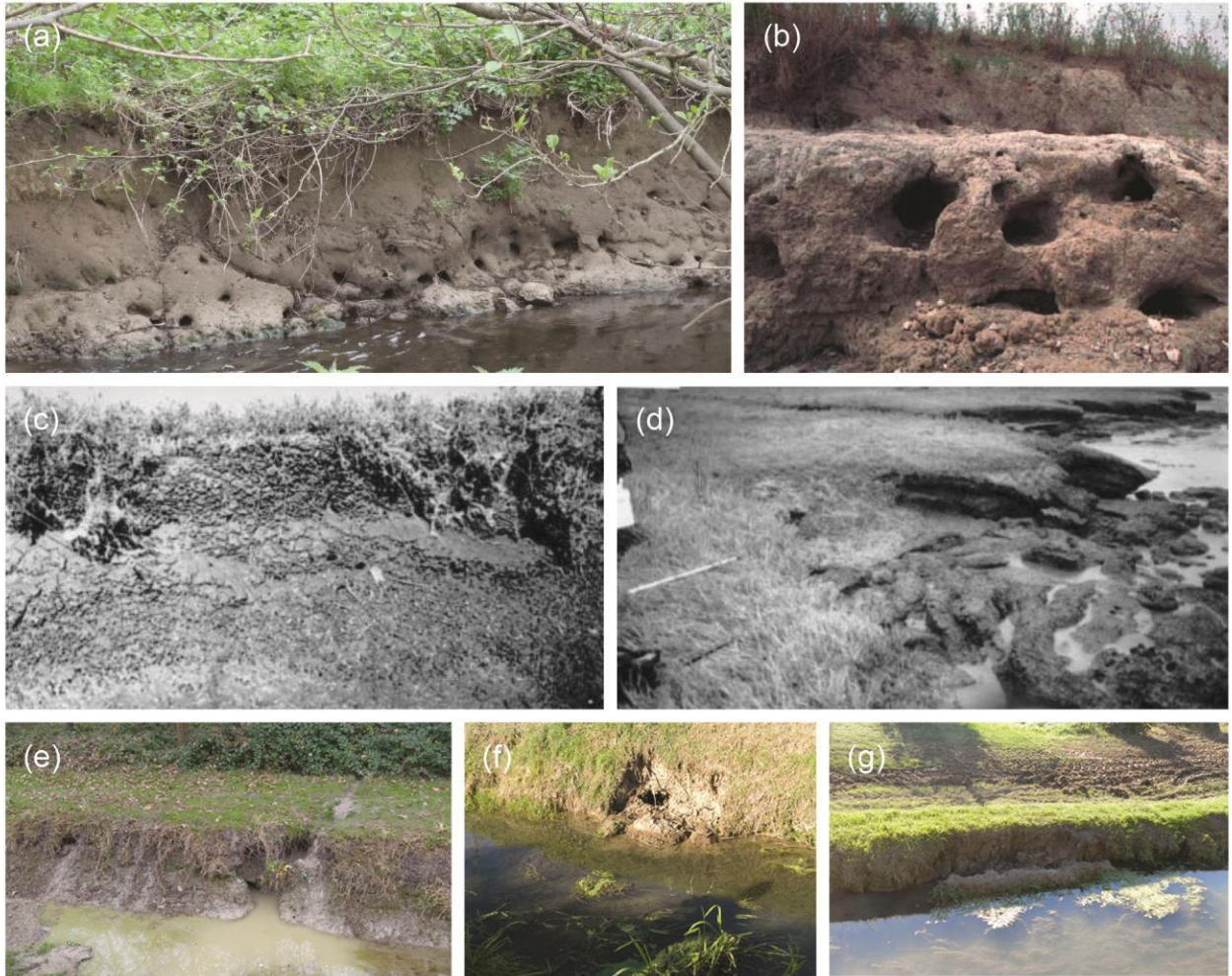
Figure 1 Examples of invasive species burrows in different types of aquatic margin: (a) *P. leniusculus* burrows on the River Enbourne, UK; (b) *Pterygoplichthys* sp. burrows on the San Antonio River, Texas, USA (reproduced from Hoover *et al.*, 2004); (c) Sediment loosened by extensive burrowing activity of *S. quoianum* and (d) collapse of marsh surface linked with *S. quoianum* burrowing, both from Paradise Creek, San Diego Bay, USA (both reproduced from Talley *et al.*, 2001, with permission from Springer Nature); and (e-g) *M. coypus* burrows and associated erosion on drainage channels in northern Italy (reproduced from Sofia *et al.*, 2016, with permission from John Wiley & Sons).

Another invasive crab species, the naturally aggressive and territorial European green crab (*Carcinus maenas*) is invasive in North America, Australia, South Africa, South America and Asia (GISD, 2019). Concerns over salt marsh erosion have been raised for some invaded areas as a result of burrowing into shore banks (Wallentinus & Nyberg, 2007; Aman & Wilson Grimes, 2016). Native burrowing crabs (*Sesarma reticulatum*) have also been linked with high magnitude peat displacement from New England salt marshes as a result of predator depletion and associated population density increases of ~400% (Coverdale *et al.*, 2013), illustrating the potential for similar effects from native species that become invasive. Interestingly, in this case *C. maenas* invasion assisted cordgrass recovery by reducing *S. reticulatum* functional density and herbivory through

burrow occupation and other effects (Coverdale *et al.*, 2013). Smaller animals can also have pronounced effects. For example, the Australasian isopod (*Sphaeroma quoianum*) has colonized at least 15 estuaries on the Pacific coast of North America (Davidson, 2008), creating dense networks of interconnected burrows in the peat and mud banks of tidal creeks and marsh edges (Talley *et al.*, 2001; Davidson, 2008; Figure 1c, d). While adult body size is small (11-13 mm), *S. quoianum* can occur in very high densities and a population of 100 000 adults burrowing for two months has the potential to remove approximately 176L of salt marsh bank (Davidson & Rivera, 2012). Infested sites have been associated with higher lateral salt marsh erosion rates (increases of up to 300%) and greater incidence of undercutting, calving and slumping (Davidson & Rivera, 2010).

Fewer invasive fish are known to excavate burrows, but suckermouth armoured catfishes (*Siluriformes: Loricariidae*) or loricariids, have the potential to contribute to instability and erosion at aquatic margins. Loricariids are a large and diverse group, native to South America, Panama and Costa Rica (Lienhart *et al.*, 2013). Many species are popular aquarium fishes and three genera (*Hypostomus, Pterygoplichthys* and *Ancistrus*), have been introduced outside their native ranges via the aquarium trade and established non-native populations across the globe (Nico *et al.*, 2009; Lienhart *et al.*, 2013). Both *Hypostomus* and *Pterygoplichthys* are known to excavate burrows (Nico *et al.*, 2009), primarily for nesting and spawning, but reports generally focus on *Pterygoplichthys* (including *Pterygoplichthys anisitsi; P. disjunctivus; P. pardalis;* and *P. multiradiatus*) since they also have large broods, are able to tolerate a wide range of environmental conditions (Lienhart *et al.*, 2013) and are the most widely introduced, occurring in drainage ditches and rivers across the USA, Central America, Asia and the Caribbean (Nico *et al.*, 2009). Adults are relatively large, measuring on average 30-50 cm and up to a maximum of 70 cm in length (Nico *et al.*, 2009). Simple, straight, single-tunnel burrows occur in both native and invaded habitats, commonly where population densities are high and habitat suitable, and are generally aggregated into 'colonies' of up to 12 burrows (Nico *et al.*, 2009; Figure 1b). Burrows can reach up to 1 m in length and may be randomly dispersed or clumped in higher density areas (van den Ende, 2014). As noted for *P. leniusculus* above, *Pterygoplichthys* appear to preferentially select locations already exposed to erosional processes as preferential burrowing sites: steep, exposed banks dominated by fine sediment (silt and clay) on the outer bends of meanders in natural channels (Nico *et al.*, 2009; van den Ende, 2014). Burrows have been found in a range of environments, however, including lake shores, canal banks, dikes and levees (Ferriter *et al.*, 2008) leading to concerns over erosion and undermining of structures (Hoover *et al.*, 2004; Nico *et al.*, 2009).

Impacts associated with burrowing reptiles have also been reported, although to a lesser degree. The green iguana (*Iguana iguana*) is a particular concern in south Florida where feral populations have established as a result of escape or deliberate release of animals imported as exotic pets (Kern, 2004). Burrows are excavated for nesting or refuge purposes (Krysko *et al.*, 2007) and have been observed in the banks of canals and levees and adjacent to seawalls. Burrows are sizeable, measuring up to 0.2 m in width and 2.4 m in depth, and hence have the potential to penetrate into flood defense infrastructure to a considerable extent (Sementelli *et al.*, 2008). As a result, *I. iguana* burrows have been linked with bank instability and erosion and the collapse of seawalls, and

similar impacts have been suggested for other species including the Mexican spiny-tailed iguana (*Ctenosaura pectinate*) and black spiny-tailed iguana (*C. similis*) (Kern, 2004; Ferriter *et al.*, 2008).

The semi-aquatic rodent *Myocastor coypus* (coypu or nutria), native to South America, has established feral populations across Europe, Asia, Africa and North America following introduction for fur farming (Carter & Leonard, 2002). *M. coypus* excavates burrows into river banks and levees for protection from predators and thermal extremes (Hong *et al.*, 2015). Burrows can extend for up to 5 m in depth and range from simple single-entrance systems to complex systems with multiple tunnels and entrances at different levels (Washington State Department of Fish and Wildlife, 2006). Burrowing activity by *M. coypus* has been linked to the undermining of banks and embankments on irrigation canals (Bertolino & Genovesi, 2007; Sofia *et al.*, 2016; Figure 1e-g) and burrow-induced collapse of weakened banks and levees has been linked to devastating flood events (Panzacchi *et al.*, 2007; Orlandini *et al.*, 2015). River bank management related to *M. coypus* has been estimated as in excess of € 1 million per year in Italy (Panzacchi *et al.*, 2007). Other mammal species, such as the North American beaver (*Castor canadensis*) which is invasive in Patagonia, are known to burrow but reported biogeomorphic impacts in invaded systems have, to date, focused on beaver meadow formation and how this differs from models developed for the native range (Westbrook *et al.*, 2017). The burrowing behavior of native rodents, including muskrats, beavers, groundhogs, porcupines, badgers and foxes, has also been identified as posing a significant threat to the integrity of earthen dams and levees (Federal Emergency Management Agency, 2003; Bayoumi and Meguid, 2011; Orlandini *et al.*, 2015).

Data on the non-native range of the example species/genera discussed above were sourced from the Global Invasive Species database (GISD, 2019), European Network on Invasive Alien Species (NOBANIS, 2019) and Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2019) for species listed as 'Alien' in status and 'established' in occurrence (unless accompanying notes indicated status was uncertain). This may omit invaded areas that are reported in the literature but have not yet been added to the databases, so the map is intended to provide an indication of the global relevance of the issue rather than a comprehensive assessment of individual species distributions. In total, there are 120 countries, states or territories where at least one species of interest has established a non-native population and 24 where there are between 3 and 5 species present. Six of the species discussed have established non-native populations in the Netherlands (4 crayfish spp., *E. sinensis*, *M. coypus*) and California (2 crayfish spp., *E sinensis*, *C. maenas*, *S. quoianum*, *Pterygoplichthys* spp.). The number of species per country, territory or state is summarized in Figure 2 and Table 1 presents further information at species level. The most globally widespread species/genera are *M. coypus* and *P. clarkii* followed by *E. sinensis* and the *Pterygoplichthys* spp. Table 1 also summarizes the main types of aquatic margin affected by burrowing invasive species as identified from the literature. All species are associated with either rivers, estuaries or artificial channels (and most commonly a combination of these), and most species also occur in pond and lake habitats and/or wetlands.
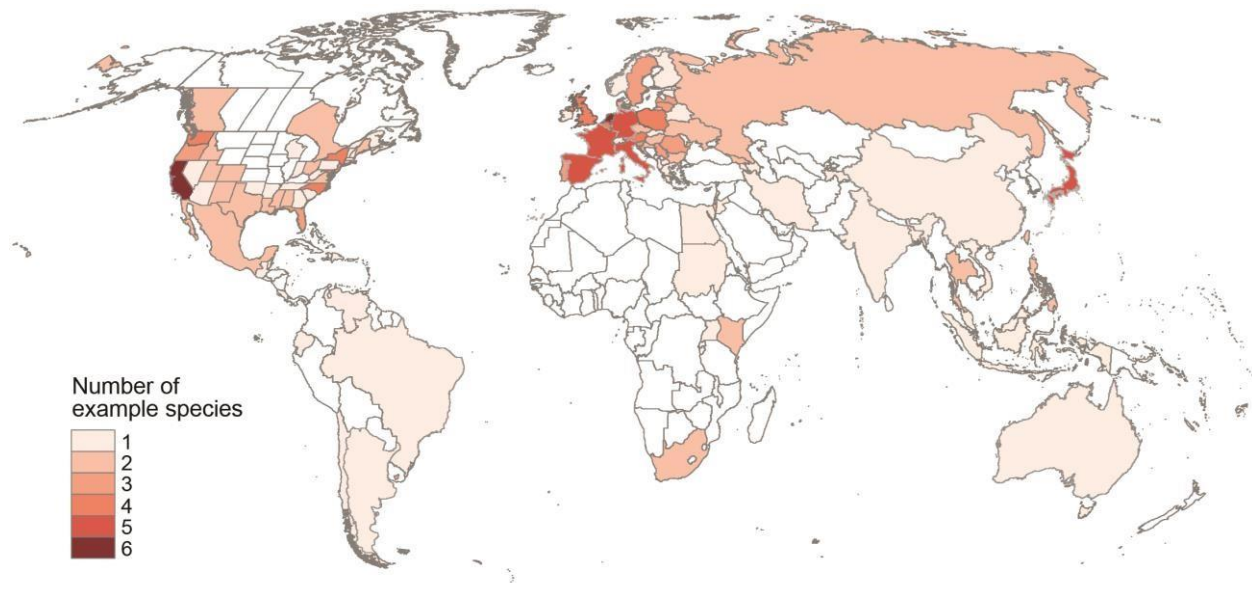
Figure 2 Map showing the number of example burrowing invasive animals discussed in the text for different countries (or states/ territories for the USA and Canada). Data sourced from GISD (2019), DAISE (2019) and NOBANIS (2019). Species included: *O. limosus*, *O. virilis*, *P. clarkii*, *P. leniusculus, E sinensis*, *C. maenas*, *S. quoianum*, *Pterygoplichthys* spp., *I. iguana*, *M. coypus.*

4 A conceptual model for burrow-induced bank erosion

The burrowing activities described above physically remove sediment from aquatic margins; primarily through the mechanism of excavation (pulling or scraping grains; Dorgan, 2015). Operating in isolation, this process will generate sediment flux from aquatic margins at a rate that is dependent on the size of burrows constructed by the species in question, its behavioral characteristics and the local population density. However, the construction of burrows by animals also has the potential to impact upon physical processes that operate on and within aquatic margins at scales much larger than an individual burrow. The following sections present a conceptual model hypothesizing how burrowing invaders will influence bank stability and erosion through geotechnical, hydrological and hydraulic effects. The primary focus is on river banks but we also indicate the relevance of each process to other types of aquatic margin. While similar mechanisms will be associated with native burrowing species, the potential for invasive species to establish high population (and burrow) densities and, hence, represent a system disturbance increases the potential extent and intensity of any impacts and, thus, the significance of any resultant conservation or management issues.

River banks retreat through a combination of fluvial (hydraulic) erosion and mass failure. Fluvial erosion refers to the dislodgement or entrainment of particles or aggregates of sediment due to the shearing action of flow at the water-sediment boundary. It occurs when forces acting to hold a particle or assemblage of particles in place (friction, interlocking and/or cohesion; Lawler *et al.*, 1997) are overcome by those acting to mobilize the particle or assemblage of particles (lift and drag, together with the downslope component of its submerged weight; Lawler *et al.*, 1997). Mass failure can be defined as the movement or collapse of bank material due to geotechnical instability.

Typically, this involves failure along a discrete plane deep within the bank and its occurrence depends on the balance between the forces acting to move a unit of bank material downslope (the tangential component of its weight) and those acting to resist that movement (see above; Lawler *et al.*, 1997). These two mechanisms are intrinsically linked, with the removal of material from the bank toe by fluvial erosion increasing the likelihood of mass failure due to an undercutting or steepening of the bank (Thorne, 1982). Eventual failure of the bank through mass failure delivers material to the bank toe which, in turn, protects the lower bank from further erosion until removal by subsequent fluvial erosion. This is referred to as basal endpoint control (Carson and Kirkby, 1972; Thorne, 1982) and is an important determinant of river bank retreat rates. Detailed understanding of how burrowing modifies these processes based on observational data is lacking but established models from soil science and fluid mechanics provide a theoretical basis upon which effects can be hypothesized. These are elaborated in the following sections.

4.1 Geotechnical and hydrological effects of burrowing
The shear strength of cohesive river banks under saturated conditions can be represented by the revised Mohr-Coulomb equation:

$$S_r = c' + (\sigma - \mu_w)\tan\varphi' \qquad\qquad \text{Equation 1}$$

where S_r is the effective shear strength *(kPa); c'* is the effective cohesion (kPa); σ is the normal stress (kPa); μ_w is the pore-water pressure (kPa) and φ' is the effective angle of internal friction in degrees (Fredlund & Rhardjo, 1993). The normal stress is computed by:

$$\sigma = W \cos\beta \qquad\qquad \text{Equation 2}$$

where W is the weight of the failure block per unit area of failure plane (kN m^{-2}) and β is the angle of the failure plane in degrees.

Banks will fail where the resistive strength, S_r, is exceeded by the driving gravitational force, S_d, as represented by:

$$S_d = W \sin\beta \qquad\qquad \text{Equation 3}$$

where S_d is the driving gravitational force (kPa), W is the weight of the failure block per unit area of failure plane (kN m^{-2}) and β is the angle of the failure plane in degrees. The ratio between these resisting and driving forces is known as the factor of safety, with failure occurring when its value falls below unity.

The presence of burrows will modify the value of key terms in the above equations. Their concentration and extension into the bank at and below the mean water level (see Table 1) can be considered akin to fluvial undercutting at the bank toe in that it will increase the potential failure plane angle and decrease the effective friction angle (c.f. Thorne & Tovey, 1991; Simon *et al.*, 2000; Figure 3), decreasing the factor of safety. Furthermore, the tendency of some species (e.g. *P. clarkii*, *M. coypus*) to dig tunnels that extend towards the bank top surface (see Figure 1e)

increases the likelihood that such burrows will act in a similar way to tension cracks. These are vertical voids that develop downwards from the ground surface some distance from the bank face due to horizontal tensile stresses generated behind steep banks and slopes (Terzaghi *et al.*, 1996). Their presence decreases bank stability by reducing the effective length of potential failure planes (and, thus, effective cohesion), with the eventual mechanism of collapse (e.g. slip versus toppling failure) being determined by the length of the tension crack relative to the height of the bank (Darby and Thorne, 1994). Natural undercutting and tension crack development tends to occur over lengths of river bank that are significantly greater than individual burrows, and between-burrow bank material will act to maintain stability. The significance of these effects are therefore likely to be determined by the lateral extent and intensity of burrowing, together with the burrow architecture, and revised stability equations will need to be developed to aid predictions of bank failure due to the geotechnical effects of burrowing. Similar processes will operate at other aquatic margins including estuaries, marsh edges and creeks and lake shores, with the nature of failure reflecting the sediment characteristics and geometry of the bank, shore or margin.

Physical changes to the internal structure of river banks caused by animal burrows may, alone, be sufficient to cause mass failure via the mechanisms described above. The probability of mass failure is, however, likely to increase where these effects are compounded by coincident hydrological changes within the river bank. The presence of animal burrows in river banks can significantly alter the hydrological behavior of the bank. Evidence from a limited number of studies suggests that crustacean burrows modify the spatial distribution of pore-water pressure within banks (Onda & Itakira, 1997; Xin *et al.*, 2009). This is significant as Equation 1 shows how increased pore-water pressures can reduce the strength of banks. The occurrence of positive pore-water pressures in banks during the receding limb of flood events where the water surface elevation in the channel falls rapidly has long been recognized as a cause of bank instability and erosion (Simon *et al.*, 2000) and the presence of burrows will enable such conditions to occur at greater depths within cohesive banks than might otherwise be expected. Even in unsaturated conditions, relatively small losses of negative pore-water pressures have been shown to be capable of generating bank failures (Casagli *et al.*, 1999; Simon & Curini, 1998). The following modified version of the Mohr-Coulomb equation demonstrates how an increase in pore-water pressure decreases the effective stress of the soil and, thus, the soil shear strength (Darby & Thorne, 1996; Fox & Wilson, 2010):

$$S_r = c' + (\sigma - \mu_a)\tan\varphi' + (\mu_a - \mu_w)\tan\varphi^b \qquad\qquad \text{Equation 4}$$

where S_r is the shear strength *(kPa); c'* is the effective cohesion (kPa); σ is the normal stress (kPa); μ_a is the soil pore-air pressure (kPa), μ_w is the pore-water pressure (kPa), φ' is the effective angle of internal friction in degrees, and φ^b is the angle indicating the rate of increase in shear strength relative to matric suction (Fredlund & Rahardjo, 1993; Simon *et al.*, 2000).

Onda & Itakira (1997) show that the presence of burrows modifies the location of the phreatic surface within the bank, increases the hydraulic gradient and concentrates subsurface (seepage) flow. Together, these effects have been shown to cause within-burrow erosion and the collapse of overhanging material (Onda & Itakira, 1997). These effects can be considered akin to horizontal

macropores (soil pipes) that develop in banks and hillslopes above water-restricting layers and act as preferential flow pathways (Hagerty, 1991a; Hagerty, 1991bFaulkner, 2006; Lindow *et al.*, 2009; Fox & Wilson, 2010). Concentration of subsurface flow along these pathways leads to bank undercutting, tension crack formation and eventual collapse due to mass failure (Hagerty, 1991a; Hagerty, 1991b; Fox & Wilson, 2010). We hypothesize that animal burrows will perform a similar hydrological function during the rapid drawdown of soil moisture following high magnitude flood events, with the extension of the burrow into the bank causing elevated pore-water pressures at the lower bank face and accentuating the likelihood of slip failures at the bank face once the water level falls below the elevation of the burrow entrance (Figure 3). Under baseflow conditions, however, increased drainage of the bank associated with burrow presence may reduce antecedent near-bank face pore water pressures, reducing susceptibility to erosion during lower magnitude flow events. A similar effect has been observed in artificially drained high, steep river banks (Shields *et al.*, 2009). Further research is needed to quantify the hydrological significance of burrows and their implications for bank stability. As with any potential geotechnical effects, the lateral extent and intensity of burrowing, together with the burrow architecture and typical position relative to the mean water level are likely to act as important determinants of the magnitude of any hydrological effect, in combination with the magnitude and frequency of water level fluctuations as determined by the hydrological regime. Similar processes will operate at other aquatic margins, but with key differences in the nature, magnitude and frequency of hydrological fluctuations associated with tidal and lentic hydrological systems.
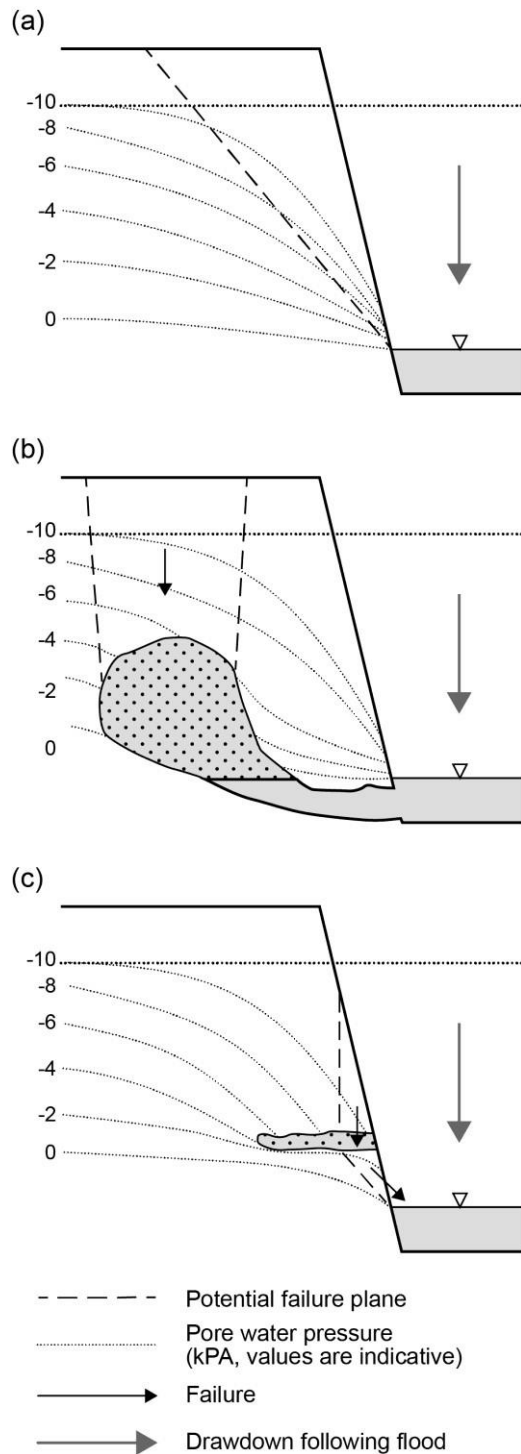
Figure 3 Conceptual basis for geotechnical and hydrological effects of burrowing. Hypothesized spatial distribution of pore water pressure and position, length and angle of potential failure planes immediately following a flood event under the following scenarios: (a) a cohesive river bank without burrows; (b) the same bank burrowed by *M. coypus*; and (c) the same bank burrowed by *P. leniusculus*. Note: the exact hydrological response of a bank following flood drawdown will be determined by its geometry, material properties and the nature of the event.

4.2 Hydraulic effects of burrowing

We hypothesize that the hydraulic effects of animal burrowing (and, thus, their potential impact on fluvial erosion at the bank face) will vary with spatial scale. At the scale of individual burrows, cavities are known to modify near-bank flow structures in open channels, for example by generating high levels of vorticity as flow passes over their leading (upstream) and trailing (downstream) edges (Ozalp *et al.*, 2010; Jackson *et al.*, 2015; Figure 4). Enhanced turbulence around the entrances to animal burrows (in contrast to that typically encountered on smooth bank faces) may therefore amplify the direct entrainment of particles from the surface of the bank.
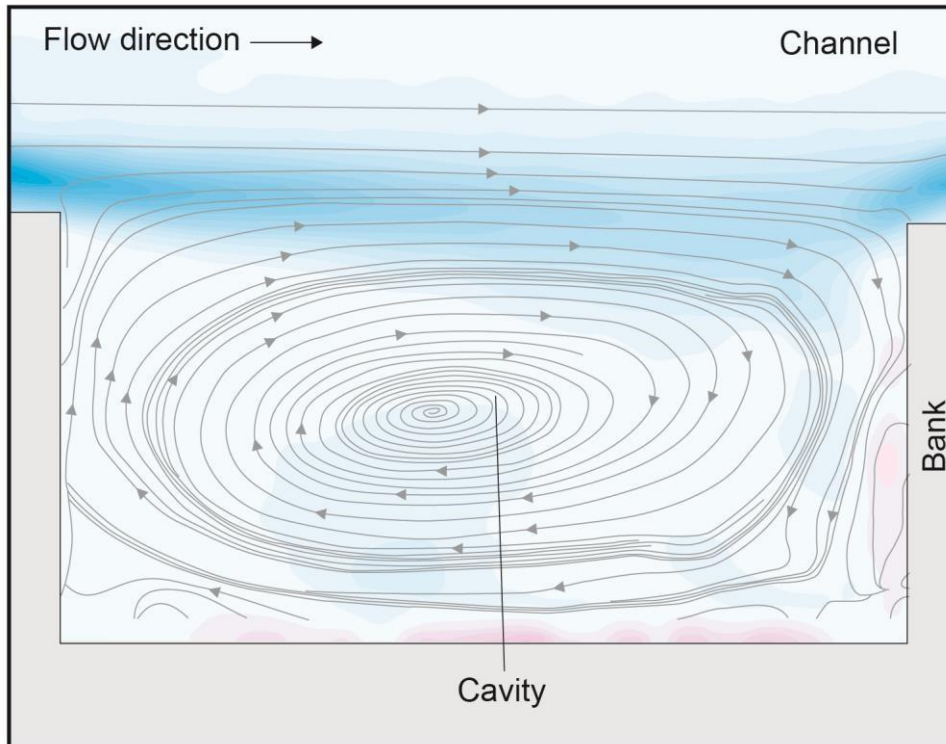

Figure 4 Conceptual basis for hydraulic effects of burrowing at the cavity scale, showing streamlines and contours for vorticity (Reynolds number = 1700; negative values in blue, positive values in red shading). Schematized diagram based on the experimental results of Ozalp *et al.* (2010), with permission from Elsevier (Figures 5 and 6).

At the wider bank section scale, however, the collective effect of multiple burrows may be to reduce overall rates of fluvial erosion as a result of increased roughness. Bank erosion rates are generally quantified using an 'excess shear stress' formula, whereby the erosion rate reflects the shear stress applied by the flow in relation to an erodibility coefficient and a critical shear stress value (Rinaldi & Darby, 2007). The total shear stress can be partitioned into 'skin friction', arising from the fluid stresses acting on the boundary and the 'drag stress' arising from the pressure differential created by flow past topographic irregularities (Kean *et al.*, 2009). Partitioning of skin friction and form drag is critical for accurate prediction of erosion rates, but understanding of relationships between bank roughness and erosion is relatively limited and largely derived from

laboratory experimentation due to the complexities associated with modelling the highly irregular surfaces of river banks.

For macrorough flow (where roughness elements approach the order of magnitude of channel dimensions) and under laboratory conditions, rectangular cavities can influence vertical mixing layers, wake zones, recirculation gyres, coherent structures and skin friction, with the overall effect of significantly increasing flow resistance (Meile *et al.*, 2011). Smaller-scale topographic features characteristic of natural river banks may have similar effects. Natural banks (without burrows) are characterized by small scale topographic undulations produced by erosional processes and/or vegetation which create near-bank disturbance layers, exerting form drag that can profoundly modify flow resistance (Kean & Smith, 2006a; 2006b; Figure 5). Such effects can be sufficient to drive periodic changes in erosion potential associated with changes in the relative magnitude of form and skin stresses through time (Leyland *et al.*, 2015). For instance, bank failures resulting from high magnitude flows can generate complex bank geometries, increasing form drag relative to skin friction and offering protection from further erosion, while smoothing of the bank face in intervening periods of lower-magnitude flows can increase erosion potential by reducing form drag in relation to skin friction (Leyland *et al.*, 2015). We hypothesize that the nature and magnitude of the hydraulic effect of burrows will be influenced by burrow size, shape and density. Individual or widely spaced burrows may generate localized increases in turbulence intensity and particle entrainment around burrow entrances, with burrow size and shape determining the nature of alterations to the flow field. In contrast, for banks with higher burrow densities the combined effect of multiple burrows may increase flow resistance and potentially reduce hydraulic erosion rates. Hydraulic effects of burrows are likely to be most pronounced for aquatic margins in river and tidal systems, but wind-induced turbulence in lentic systems may also be relevant.
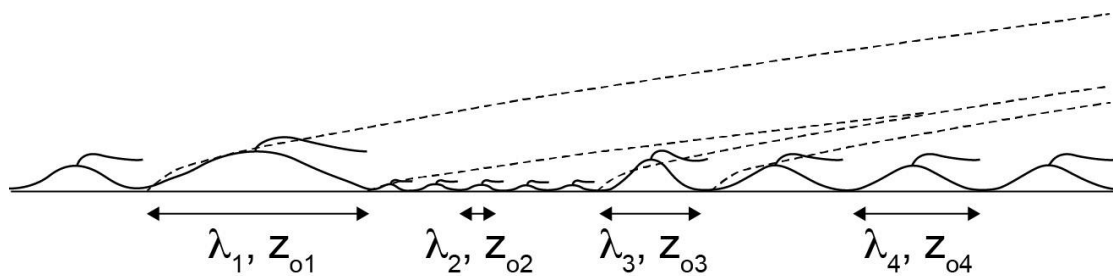
$$\lambda_1, Z_{o1} \qquad \lambda_2, Z_{o2} \qquad \lambda_3, Z_{o3} \qquad \lambda_4, Z_{o4}$$

Figure 5 Conceptual basis for hydraulic effects of burrowing at the bank section scale showing the effect of multiple bank protrusions on the near-bank disturbance layer, reproduced from Kean and Smith (2006b). Dashed lines represent the multiple disturbance layers generated by four types of roughness element, with faster growing layers (e.g. Z_{o3}) envelop slower growing layers of smaller elements (Z_{o2}). Solid lines represent the first part of the wake for each element.

4.3 Geochemical and biological effects on sediment stability and erodibility
Geochemical and biological factors also play an important role in determining the stability or erodibility of soils and sediments (particularly cohesive sediments), although these factors are less well understood (Grabowski *et al.*, 2011). The clay fraction in cohesive sediments is the most electrochemically active, characterized by high particle surface area and strong electrochemical charges and, as a result, strongly influences cohesive behavior. These properties mean that the

chemistry of the pore water, as well as the characteristics of the sediment, influence the erodibility of cohesive banks and margins. Spatial and temporal variations in factors such as temperature, pH and salinity will therefore influence the stability and erodibility of cohesive aquatic margins and hence the processes discussed in the previous sections (Arulanandan *et al.*, 1971). Microscopic and macroscopic organisms in soils and sediments also have diverse effects on sediment stability including biostabilisation through biofilms and root or fungal networks (Mermillod-Blondin and Rosenberg, 2006; Grabowski *et al.*, 2011; Wilkes *et al.*, 2019) and changes to organic matter content and particle size distributions through feeding and egestion (e.g. Wharton *et al.*, 2006). Again, spatial and temporal variations in these effects will influence the nature and magnitude of processes outlined in the previous sections.

Bioturbating animals increase the mixing of the various constituents of sediment including inorganic particles, organic matter, oxygen and nutrients (Grabowski *et al*., 2011). Burrowers may, therefore, also influence stability and erosion through changes to geochemical and biological properties of the sediment and pore water. This may include effects associated with burrow construction and maintenance, subsequent exchanges between the burrow and the outer flow, and the non-burrowing effects of burrow occupants, such as feeding and egestion. For example, burrow construction and maintenance has been shown to increase oxidation of sediments through mixing of oxidized and less oxidized sediment, potentially changing the reduction potential of the sediment (Pulmans *et al.*, 2014). Animal burrow networks are also flushed with water originating from the sediment-water interface ('bioirrigation'). This process can significantly influence solute exchange, for example by return of nutrients to the outer flow, and introduction of oxidants into burrows at depth (Miele *et al.*, 2001). The effects of bioturbation on biogeochemical processes, however, depends on the physical (hydrodynamic) properties of the system (Mermillod-Blondin and Rosenberg, 2006). Burrowing has also been linked with the exclusion of plants that might otherwise have a biostabilizing effect on the sediment (e.g. Hughes and Paramour, 2004) and can contribute significantly to the mobilization and transport of fine sediment and increased water turbidity (Harvey *et al.*, 2014; Rice *et al.*, 2016). This generates potential for indirect effects on sediment stability and erodibility through changes to light penetration, water chemistry and aquatic organism health (Harvey *et al.*, 2011). Additional effects of burrowing invaders on the biological factors contributing to sediment erodibility may include consumption of biofilms (Scott *et al.*, 2012), processing of organic matter and alterations to microbial communities (Boeker & Geist, 2015). Here, we recognize the potential importance of geochemical and biological effects on sediment stability and erodibility in combination with those discussed in sections 4.1 and 4.2, and emphasize that these will vary spatio-temporally, and according the burrowing species and their wider ecological interactions.

5 Conclusions and future directions
Burrowing animals can make numerous contributions to ecosystem functioning, but invasive species can represent a special case as a result of their potential to cause major geomorphic changes and environmental stresses. Concerns over threats to waterways, flood defense infrastructure and waterside landmarks from invasive burrowers are raised in numerous scientific contributions and media reports, but there is a lack of quantitative research on the geophysical impacts. Our review

explores a range of animals of global interest, including crustaceans, fish, reptiles and mammals. Example species are widely distributed at the global level, and we identify the potential for combined impacts from multiple species in over 20 different countries, states or territories worldwide. The group of species explored is not exhaustive and is intended to illustrate the nature and global relevance of the issue. Furthermore, the current trajectory of global species invasions means that other species of interest will likely emerge in the future. A range of environments are exposed to the impacts of burrowing invasive species, including pond and lake margins, the banks of rivers, creeks and estuaries, salt marsh edges, wetlands, canals and drainage ditches in addition to flood control structures including earthen dams, levees and flood walls.

Using established models of geotechnical, hydrological and hydraulic drivers of bank instability and erosion, we have demonstrated four ways in which burrows can be expected to influence bank stability and erosion. We hypothesize that burrow presence will: (i) alter failure plane position, decrease failure plane length and increase failure plane angle (thereby decreasing bank shear strength) in banks and slopes at aquatic margins; (ii) modify the spatial distribution of pore water pressure, thereby increasing subsurface flow (seepage), reducing cohesion and increasing the likelihood of slip failures at the bank face; (iii) increase turbulence and sediment entrainment at burrow entrances and (iv) alter flow resistance at the bank face. The first three effects are expected to increase bank instability/erosion in most cases, while in contrast higher densities of burrows may increase flow resistance at the bank face, and hence potentially reduce erosion by fluvial action. The density, architecture and positioning of burrows together with the characteristics of the sediment and the hydrodynamic environment will determine the relative importance and interactions of these different effects and, in turn, the net effect on erosion rates. Alongside the geotechnical, hydrological and hydraulic effects of burrows on sediment stability and erosion, burrowing animals may also influence geochemical and biological factors that can contribute to sediment erodibility, including through changes to pore water chemistry and bio-stabilization or -destabilization of sediment. As a result of the interacting factors described above, the effects of burrowing invasive species on instability and erosion may include increases, decreases or no significant effects depending on the species and the environment in question. Our conceptual model is applicable beyond invasive species, and may, for example, support investigation of the impacts of native 'pest' species.

Burrowing impacts of invasive species have the potential to generate distal as well as local sediment management issues, including downstream increases in sedimentation arising from increased fine sediment delivery to the river network. The extent and magnitude of distal impacts will depend upon the connectivity of the system as well as the magnitude of site-level sediment inputs. Further research is required to test these hypotheses and quantify the magnitude of impacts in different environments and for different invasive species. Quantification of bank stability and erosion is notoriously challenging as a result of practical limitations of field measurement, high spatial variability and the event-driven nature of the process. However, physical modelling and mesocosm experiments along with numerical modelling of flow hydraulics and slope stability in 3D can be used to explore the effects of burrow properties (density, morphology/architecture, positioning) on the geotechnical, hydrological and hydraulic processes in different environments. The information on burrow characteristics (e.g. density, morphology) provided in this review can

be used to inform the design of these experiments. Enclosure/ exclosure field experiments and longer-term monitoring will be required to demonstrate the 'real world' magnitude and significance of changes in erosion rates and associated sediment transfer. Addressing these knowledge gaps will require novel, interdisciplinary approaches to field and modelling studies.

Acknowledgments, Samples, and Data

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