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REVIEW AND SYNTHESIS

Bioerosion in a changing world: a conceptual framework

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Abstract

Bioerosion, the breakdown of hard substrata by organisms, is a fundamental and widespread ecological process that can alter habitat structure, biodiversity and biogeochemical cycling. Bioerosion occurs in all biomes of the world from the ocean floor to arid deserts, and involves a wide diversity of taxa and mechanisms with varying ecological effects. Many abiotic and biotic factors affect bioerosion by acting on the bioeroder, substratum, or both. Bioerosion also has socio-economic impacts when objects of economic or cultural value such as coastal defences or monuments are damaged. We present a unifying definition and advance a conceptual framework for (a) examining the effects of bioerosion on natural systems and human infrastructure and (b) identifying and predicting the impacts of anthropogenic factors (e.g. climate change, eutrophication) on bioerosion. Bioerosion is responding to anthropogenic changes in multiple, complex ways with significant and wide-ranging effects across systems. Emerging data further underscore the importance of bioerosion, and need for mitigating its impacts, especially at the dynamic land–sea boundary. Generalised predictions remain challenging, due to context-dependent effects and non-linear relationships that are poorly resolved. An integrative and interdisciplinary approach is needed to understand how future changes will alter bioerosion dynamics across biomes and taxa.

Keywords

anthropogenic impacts, bioerosion, biogeomorphology, biotic interactions, climate change, ecosystem engineering, habitat complexity, habitat structure, ocean acidification.

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INTRODUCTION

Bioerosion is a ubiquitous ecological process that transforms habitats and modifies resource availability in all of the major biomes of the world, from the tropics to the poles (Warme 1975; Cerrano *et al.* 2001). Bioeroding organisms break down and fractionate consolidated 'hard' persistent materials into smaller constituent components and thereby can have important biogeomorphic effects (Fig. 1, Box 1). For example, bioerosion by sea urchins, sponges and fishes reduce coral reefs to sand (Rützler 1975; Glynn *et al.* 1979), and lichens and microbes erode the surface of exposed bedrock, facilitating the creation of soil (Chen *et al.* 2000). Bioerosion occurs across a wide spectrum of abiotic and biotic materials, which differ in structure and degree of hardness, and is driven by diverse taxa that include microbes (e.g. bacteria, fungi, protists), lichens, vascular plants, invertebrates (e.g. sponges, molluscs, insects, crustaceans, echinoderms), fish, birds and mammals (Warme 1975; Bromley 1978; Butler 1995; Lisci *et al.* 2003). However, there are commonalities in the mechanisms of bioerosion across terrestrial, freshwater and marine ecosystems that suggest generalities in the forces that modulate bioerosion and its ecological outcomes. Here, we provide a unifying definition of bioerosion and a conceptual framework to evaluate its effects across ecosystems in a context of global change. Our aim is to advance a common framework across different systems that (1) allows conceptual understanding and predictions developed in one system to spur advances in other systems and (2) facilitates cross-comparisons and detection of novel linkages among systems.

A taxonomically diverse array of organisms erode and break down substrata through various physical and chemical mechanisms (Table 1). This bioerosion typically occurs as a consequence of organisms accessing nutrition from the trace elements or prey sequestered in (or on) substrata or by creating living space free from predators and harsh environmental conditions (Warme 1975; Cockell & Herrera 2008). Although organisms bioerode substrata for any number of different purposes, which fall into these broad categories, they cause a similar erosional effect on substrata, indicating bioeroders can be viewed as a functional group. This functional group therefore spans diverse taxa across traditionally defined ecological roles, such as primary producers, decomposers, herbivores, predators, parasites, mutualists and ecosystem engineers, and bioeroders sometimes play more than one such role (Table 1).

Studies from various disciplines have explored the dynamics and consequences of bioerosion. For example, ecologists, geologists and engineers have recognised the importance of this

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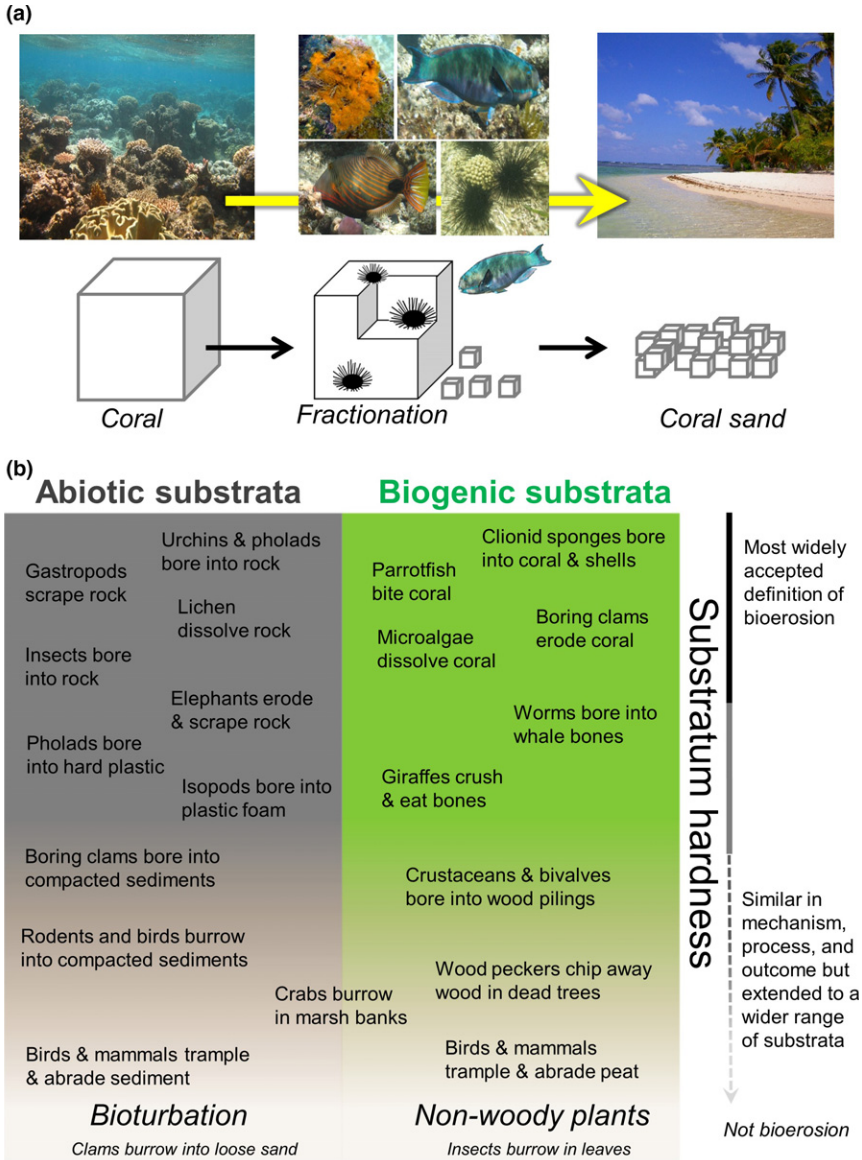

Fig. 1 Bioerosion is the process by which a hard substratum, such as coral, is eroded or fractionated by organisms, often converting hard substrata into loose sedimentary by-products (a). Bioerosion is manifested in diverse ways across a variety of substrata and taxa (b; see Table 1 for details). Colour differences distinguish abiotic (grey) from biogenic substrata (green). Colour gradation represents decreasing substratum hardness; examples in lighter coloured areas represent bioerosive activities that depart from the traditionally accepted definitions of bioerosion but share similarities in terms of impact and process. Most forms of bioturbation and biotic interactions occurring in non-woody plants are beyond the end of the spectrum and not considered bioerosion (see Box 1). Our objective is to demonstrate how bioerosion relates to multiple ecological processes and interactions within this conceptual diagram.

process from their disparate perspectives and often with their own specialised terminology (Box 1). Ecologists have described how bioerosion can affect the physical structure, complexity and abiotic properties of habitats, mediating community composition and ecosystem function (e.g. productivity, energy flow; *see next section*). Geologists have recognised the effects of bioerosion on the morphology of landscapes, interactions with other processes such as water flow, and changes in processes such as elemental cycling. To mitigate damage from bioeroders on infrastructure, engineers have developed technologies such as treated wood, corrosion-resistant concrete, antimicrobial chemical additives and various coverings or sheaths. The magnitude and interdisciplinary nature of challenges presented by bioerosion to society are evident in examples such as burrowing mammals and crustaceans that can destroy sea walls and levees that protect areas from flooding (Chilton 1919; Orlandini *et al*. 2015), shipworms that have toppled wooden wharfs and docks (Hill & Kofoid 1927), and mosses and lichens that corrode historical buildings and sites (Warscheid & Braams 2000).

The literature on bioerosion is diffuse, and the full scope and effects of bioerosion are still emerging. Previous reviews have examined the concept of bioerosion and related processes from different perspectives, usually focusing on specific habitats including coral reefs (Hutchings 1986; Glynn & Manzello 2015; Schönberg *et al*. 2017), stone (Warscheid &

Box 1 What is Bioerosion? List of terms used to describe processes related to bioerosion.

What is Bioerosion?

Researchers use numerous non-exclusive terms to describe the various processes by which organisms alter, break down, and erode various substrata. These terms vary in scope, scale, substratum type, and by discipline of study. For example, the erosive activities of mycorrhizal fungi, lichens and microbes on minerals is called 'biotic weathering' by biogeochemists, the erosive effects of organisms on human-made substrata is termed 'biodeterioration' by engineers and microbiologists, and erosion of coral by microbes and invertebrates is called 'bioerosion' by marine biologists and palaeontologists. However, these terms all appear to describe similar processes and cause similar ecological outcomes. Indeed, the term 'bioerosion' (Neumann 1966) itself has been reinterpreted, expanded, and/or redefined by multiple authors over the last half century (Ekdale *et al.* 1984; Tapanila 2008; Schönberg *et al.* 2017) and is now used by several authors to represent the breakdown of any 'hard' substratum by biological activities (Wisshak & Tapanila 2008). Here, we use the term *bioerosion* to represent any biologically induced removal, destruction or deterioration that results in a transformation of persistent firm/hard substrata including rock, shell, bone, dead wood, peaty or compacted mud banks and cliff faces, and human-made substrata (metal, concrete, plastics, etc.). We consider 'hard' materials to be those that persist in ecological time and are resistant to environmental change relative to softer materials, such as loose sediment or exclusively herbaceous material. We recognise bioturbation (and related zoogeomorphological activities) cause key changes in ecosystems (Butler 1995; Meysman *et al.* 2006), but we exclude most forms of bioturbation from our synthesis because the reworking of sediment often does not constitute a transformative breakdown of a substratum but rather a reshuffling of unconsolidated material. Likewise, most forms of herbivory and predation are excluded, except where non-living structural material is eroded (e.g. bioerosion occurs when parrotfish consume algae living on coral reef). Damage occurring in wood is variable and may be analogous to bioerosion in some contexts (e.g. isopods boring into woody debris for habitat) and/or may be considered herbivory in other contexts (e.g. insects boring into and consuming woody tissue of a living tree). Here, is a list of the most important terms that have been used in association with bioerosional processes.

Allogenic ecosystem engineering – process where an organism alters the availability of resources to other biota through activities that change the physical or structural state of biotic or abiotic materials (Jones *et al.* 2010).

Biocorrosion – destruction or damage of a material from a chemical reaction caused by an organism. Most often refers to the work of microorganisms (Beech & Gaylarde 1999).

Biodegradation – process in which organisms decay or break down a waste material into a more useful form. Most often refers to the useful work of microorganisms (Allsopp *et al.* 2004).

Biodeterioration – breakdown, etching or marring of a material from the activities of an organism. Often refers to any undesired change caused by microorganisms (Allsopp *et al.* 2004).

Bioerosion (including biotic, biologic, biogenic or biological erosion) – 'destruction and removal of consolidated mineral or lithic substrate by the direct action of organisms' (Neumann 1966) – *seminal definition*. Others have expanded or redefined this process over the years. In this paper, we define bioerosion as the process by which organisms remove, breakdown, dissolve or fractionate consolidated 'hard' persistent materials often into smaller constituent components, which are removed or displaced.

Biogenic dissolution – dissolution of materials (typically minerals) by biologically derived chemicals (Tribollet 2008).

Biogeomorphology (and zoogeomorphology) – how biota alter, maintain or create geologic features or landforms (Butler 1995; Naylor *et al.* 2002).

Biotic or biological disturbance – incidental damage, displacement or mortality to biota caused by an organism, which can also include predation and herbivory (Sousa 1984).

Biotic or biological weathering – breakdown or weathering of rock and other substrata by biota (Viles 1995).

Bioturbation – Reworking of sediment or soils by biota through movement, feeding, respiration or other biological activities. Often refers to activities occurring in loose sediments (Meysman *et al.* 2006).

Boring – process of excavating a hole in a hard substratum by cutting across grains and cement, often creating a smooth wall (Ekdale *et al.* 1984). Many authors use burrowing and boring synonymously.

Burrowing – process of creating a hole in an uncemented substratum by shifting or moving grains aside (Ekdale *et al.* 1984)

Decomposition – breakdown of organic matter by abiotic or biotic means. Often refers to decay by microorganisms.

Erosion – process of wearing down or deteriorating material from the surface of the Earth. Often refers to the destructive activities of physical or chemical processes on rocks or sediment.

Braams 2000), alpine habitats (Hall & Lamont 2003), or rocky coasts (Naylor *et al.* 2012), or by focusing on specific taxa such as terrestrial macrofauna (Butler 1995), microalgae (Tribollet 2008), fungi (Hoffland *et al.* 2004), lichens and plants (Chen *et al.* 2000; Lisci *et al.* 2003) or trace fossils (Warme 1975; Ekdale *et al.* 1984). Despite apparent similarities in these processes and commonalities in the drivers of their dynamics, we lack a general understanding of bioerosion based on an integrative and comparative perspective.

Here, we examine the ecological and socio-economic effects of bioerosion and the dominant anthropogenic stressors that modify this process. We advance a conceptual framework that

Table 1 The process of bioerosion is manifested in diverse ways by a variety of taxa in different terrestrial, freshwater and marine habitats

Taxon	Habitat	Bioerosive effects & Ecological role*	Reference
External and internal abrasion (Physical)			
Scraping, etching and surface abrasion			
Gastropods, *Littorina* spp., *Nerita* spp., among others	Rocky intertidal and subtidal coastlines	Grazing on algae erodes rock, produces sediment, and helps develop tidepools; Herbivory	North (1954)
Gastropods, *Euchondrus* spp.	Deserts	Grazing on algae erodes rocks, affects nutrient cycling, and creates sediment; Herbivory	Jones & Shachak (1990)
Elephants, *Loxodonta* spp.	African savannahs, forests	Trampling, crushing and rubbing wears down rock and hardwood producing sediment; Ecosystem engineering	Haynes (2012)
Penguins, *Aptenodytes* sp., *Eudyptes sp.*	Sub-Antarctic islands	Trampling during migrations wears down rock and facilitates further surface erosion; Ecosystem engineering	Hall & Williams (1981)
Biting and Grinding			
Parrotfish, Scaridae	Coral reefs	Consumes algae living on coral reef causing reef erosion; Herbivory	Hutchings (1986); Smith (2008)
Giraffe, *Giraffa camelopardalis,* and other large ungulates	African Savannah, central Australia and North America	Osteophagia breaks down and recycles bone, horn and antler; Scavenging/detritivory	Hutson *et al*. (2013)
Sea urchin, *Eucidaris thouarsii*	Coral reefs	Preys on living coral causing reef erosion; Predation	Glynn *et al*. (1979)
Boring and burrowing			
Boring isopods *Sphaeroma* spp.	Temperate & tropical estuaries	Bore into rocks, wood, floats, and marsh for shelter; damages docks and foam floats; Ecosystem engineering	Chilton (1919); Cragg *et al*. (1999); Davidson (2012)
European bee eater (bird), *Merops apiaster*	Hard packed sediments & cliffs	Excavates nesting cavities and provides habitat for other organisms; Ecosystem engineering	Casas-Crivillé & Valera (2005)
Sea urchins*, Echinometra* spp, *Strongylocentrotus* spp.	Coral reefs, coastal rocks	Bore into rocks and/or coral for habitat and grazes epilithic algae; Ecosystem engineering, Herbivory	Warme (1975)
Masonry bee, *Centris muralis*	Shrub steppe in Argentina	Excavates nests in adobe buildings causing damage and facilitating collapse; Ecosystem engineering	Rolón & Cilla (2012)
Midge and caddisfly larvae, chironomids and trichopterans	Rivers in SE USA	Bores into sandstone and claystone bedrock in rivers for shelter; Ecosystem engineering	Savrda (2017)
Boring bivalves, teredinids, pholads, etc.†	Ubiquitous in all marine systems	Bore into rocks, coral and wood creating habitat for other organisms, destroy wooden structures, boats and marine facilities; Ecosystem engineering, Decomposition	Pinn *et al*. (2008); Cragg (1993); Cragg *et al*. (1999)
Fracturing (Physical)			
Plants (trees, shrubs, herbs)	Ubiquitous	Root growth in fissures fractures rocks, damages buildings and archaeological sites; Primary production, Ecosystem engineering	Lisci *et al*. (2003)
Endolithic lichens†	Ubiquitous	Growth of hyphae pit rocks and facilitate fracture during repeated freezing/thawing and wetting/drying; Ecosystem engineering, Primary production	Chen *et al*. (2000)
Corrosion (Chemical)†			
Boring sponges, *Cliona* spp.	Coral reefs, carbonate shorelines, shells	Erode coral and oyster reefs, rock and shell creating sediments, damages concrete structures; Ecosystem engineering, Decomposition, Parasitism	Neumann (1966); Snow (1988)
Microbes (bacteria, fungi, protists)	Ubiquitous	Dissolve substrata and alter nutrient cycling; Ecosystem engineering, Primary production, Decomposition	Schneider & le Campion-Alsumard (1999); Allsopp *et al*. (2004); Hoffland *et al*. (2004); Viles (2012)
Polychaetes, *Polydora* spp.	Worldwide in mollusc shells, coralline algae, coral	Weaken coral and coralline algae, damages shells of molluscs, including aquacultured species; Ecosystem engineering, Parasitism	Moreno *et al*. (2006)
Mycorrhizal fungi	Ubiquitous in terrestrial systems	Dissolve and fracture minerals in soil to supply plant symbionts nutrients; Ecosystem engineering, Mutualism	Wang & Qiu (2006); Thorley *et al*. (2015)

Note: Boldface text indicates the various mechanisms of bioerosion.
*The ecological role listed is specifically related to the bioerosive activity; many of these organisms also conduct other biotic interactions unrelated to their bioerosive activities (e.g. giraffes are herbivores but their osteophagy is scavenging/detritivory).
†Some species use both physical and chemical mechanisms to erode substrata including some species of boring bivalves (but not all), sponges, sipunculids, mycorrhizal fungi, lichens and others.

integrates across systems in several ways. First, the framework defines the scope of bioerosion as a ubiquitous process that includes diverse species (Fig. 1) unified by common mechanisms, which are driving change across terrestrial, freshwater and marine ecosystems. Second, our framework outlines a heuristic model that can be used to identify and predict the effects of anthropogenic stressors on bioerosion impact. Third, it identifies areas where future research is needed to better understand how bioerosion will respond to anthropogenic stressors in a rapidly changing world.

We include freshwater and terrestrial systems in our synthesis but focus in more detail on coastal ecosystems for our heuristic model, to illustrate potential effects of anthropogenic forces on the scale and direction of bioerosion impacts. Coastal ecosystems have a high diversity of bioeroders, including many functional groups that operate across a wide spectrum of substratum types, and thus serve to exemplify the generality of bioerosion. Furthermore, dominant anthropogenic stressors including temperature change, acidification and eutrophication affect many ecosystems but appear especially acute in coastal systems. Moreover, the dynamic land–sea boundary is a region high productivity and biological diversity, inhabited by nearly 40% of the global human population (Kummu *et al.* 2016), and provides 77% of the global value of ecosystem services (Martínez *et al.* 2007). Thus, there is some urgency to understand bioerosion in coastal regions, since its impacts may be affected by sea-level rise, rapid shoreline development and increased dependence on artificial structures in the trend of 'ocean sprawl' (Dugan *et al.* 2012; Firth *et al.* 2016). While we use well-studied coastal ecosystems to illustrate many points about bioerosion and its response to anthropogenic stressors, the core processes, perspectives and conclusions are broadly relevant to other ecosystem types as evident from the breadth of examples in Figures 1 and 2, and Table 1.

EFFECTS OF BIOEROSION

In this section, we compare the effects and mechanisms of bioerosion across systems using representative examples that underscore the importance of bioerosion as a driver of large-scale changes in the structure and function of ecosystems. Although many of the best recognised examples come from marine systems, the importance of bioerosion in freshwater and terrestrial systems is widespread but often poorly documented, being considered mostly as a side effect of biological activities (e.g. herbivory, burrowing), or within the context of other ecological concepts (e.g. disturbance, biogeochemical/nutrient cycling, ecosystem engineering). Nonetheless, we recognise that a wide diversity of bioturbators and consumers have strong bio- and zoogeomorphological influences on habitats composed of unconsolidated sediments or vegetation (such as bison, waterfowl, salmon, among others; Butler 1995; Meysman *et al.* 2006), and this literature provides a strong foundation for understanding the ecological context for bioerosion (Butler & Sawyer 2012). Here, we build upon this previous work and focus primarily on activities occurring in hard substrata, using substratum type (hardness or consolidation) to distinguish bioerosion from bioturbation (Box 1, Fig. 1).

Landscape and habitat modification

Bioeroders alter landscape features as a direct consequence of their activities and indirectly by accelerating physical erosional processes (Naylor *et al.* 2012). These activities can degrade existing habitats by simplifying them into homogeneous barrens and causing dramatic changes in habitat structure (Fig. 1). For example, intense bioerosion converts rocky coastlines and coral reefs to rubble and sand (Neumann 1966; Glynn *et al.* 1979; Schneider & Torunski 1983), erodes textured bedrock to a 'mirror-smooth finish' (Hall & Williams 1981; Haynes 2012), removes woody debris from water ways and estuaries (Cragg 1993), and collapses marsh banks and converts marsh to mudflats (Talley *et al.* 2001). In other cases, bioeroders create distinctive features and increase structural complexity of habitats used by other species. Boring by marine sponges and sea urchins, and the prodigious scraping of algae off rocks by aggregations of minute bioeroding gastropods, can convert rock benches and shelves into pools, channels, notches and many other heterogeneous landscape features (North 1954; Schneider & Torunski 1983; Taborosi & Kazmer 2013; See Figs S1–S4 in Supporting Information). In terrestrial environments, ubiquitous erosive microbes and lichens create pits, exfoliations and other surface irregularities in rock (Viles 1995, 2012; Chen *et al.* 2000). Even in caves, bats and bioerosive microbes create a complex topography of 'bell holes' and other textural features (Lundberg & McFarlane 2009; Phillips 2016). Small-scale and spatially limited bioerosive effects can result in larger scale changes if erosion is concentrated in critical locations (Naylor & Stephenson 2010), such as the joints between rocks or narrow bases of coral heads or in narrow bands in coastal rocks or marshes, causing undercutting and collapse (Figs S1–S4). This 'facilitative bioerosion' may accelerate physical erosion by wind or water movement, causing substantial alterations to the morphology of landforms and habitats (Naylor *et al.* 2012).

Modification of abiotic conditions

Like other allogenic ecosystem engineers, bioeroders can alter the abiotic conditions of habitats and landscapes. For example, excavations increase surface area (Hutchings 1986; Pinn *et al.* 2008), reduce desiccation or temperature stress (Viles 1995; Hendy *et al.* 2013) and shield biota from UV radiation (Cockell & Herrera 2008; Schönberg & Wisshak 2012). Burrows, depressions and similar bioeroded structures alter hydrodynamics (Vogel 1994; Eriksson & Eldridge 2014), water infiltration rate and absorption (Bertness 1985; Coombes & Naylor 2012), and the deposition of particles (Yager 1993) such as larvae, seeds and detritus. Burrows may even act as thermal or hydrological conduits, as observed with the burrows of rodents in the sub-Antarctic that help transport heat and water from the warmer subsurface to the frozen surface (Eriksson & Eldridge 2014). Bioeroded microhabitats may be particularly important refuge habitats in areas that experience high levels of physical stress or high predation (Schönberg & Wisshak 2012; Hendy *et al.* 2013). The erosion and fractionation of rocky benches and boulders into smaller rocks change

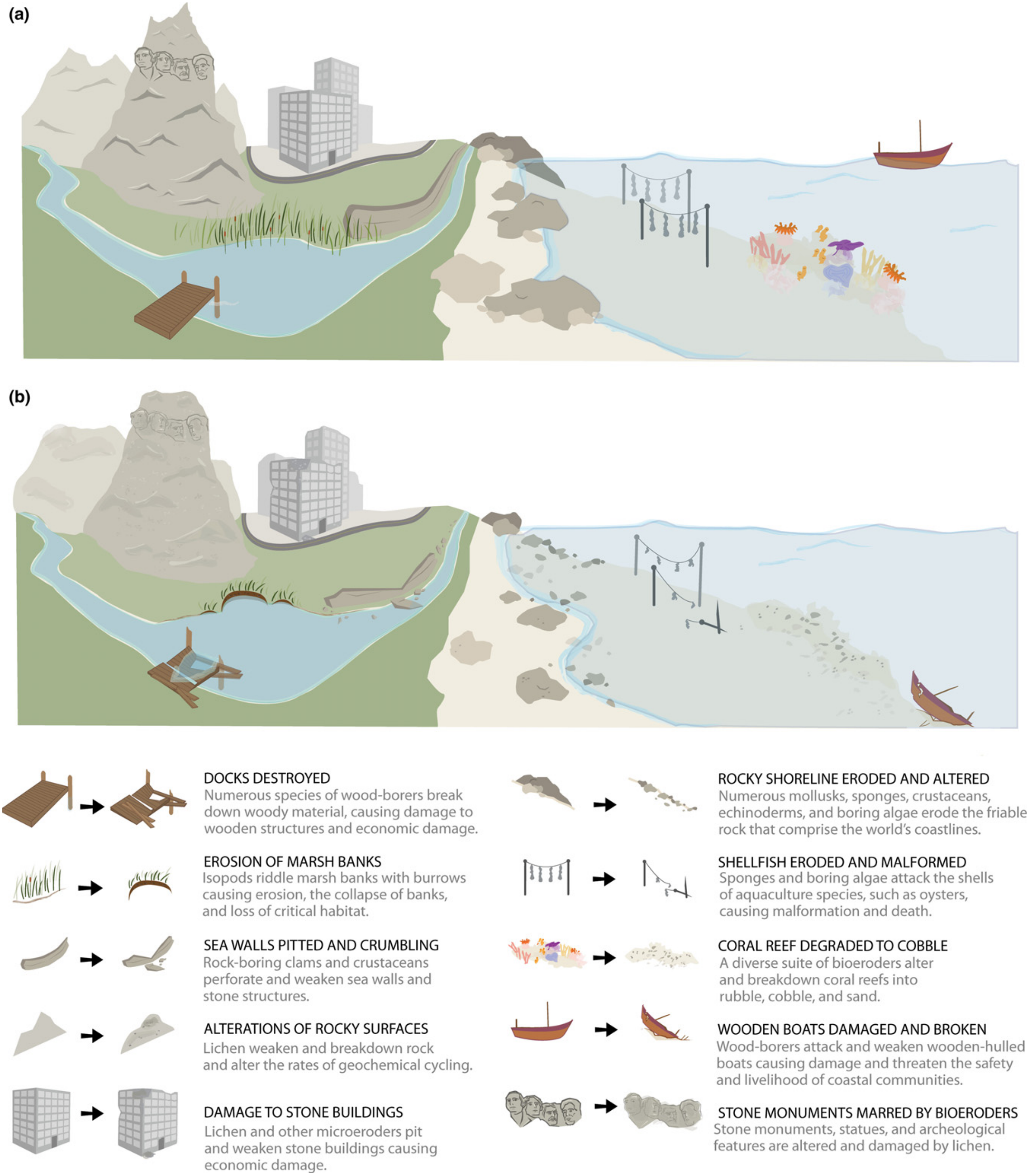

Fig. 2 (a) At normal levels, bioerosion is an important process for recycling elements for use by other organisms and can provide a complex heterogeneous habitat. (b) However, excessive bioerosion may alter the structure and function of ecosystems and cause more damage to structures and objects of economic, cultural or historical significance. Illustrated by Emily Roeder.

(a) the thermal regime, because smaller rocks experience greater temperature extremes and mortality of epifauna (Gedan *et al*. 2011) and (b) the disturbance regime, because smaller rocks are more easily moved by hydrodynamic forces (Sousa 1979).

Alteration of nutrient cycling and production

Bioeroders break down and release essential elements (nitrogen, phosphorus, potassium and numerous trace elements) sequestered within rocks and other hard materials, making the elements available to other organisms (Jones & Shachak 1990; Cragg 1993; Hoffland *et al.* 2004) and accelerating rates of geochemical cycling. In particular, lichens, fungi, cyanobacteria and other microbes are widely recognised for their essential role in biogeochemical cycling by eroding rock and releasing sequestered nutrients in terrestrial, marine and freshwater environments (Schneider & le Campion-Alsumard 1999; Chen *et al.* 2000; Hoffland *et al.* 2004; Tribollet 2008). Similarly, mycorrhizal fungi dissolve (bioerode) minerals in soils and then supply the nutrients to trees and other plants, which enhances primary production and concomitant sequestration of atmospheric carbon (Taylor *et al.* 2009). The increased production drives a positive feedback that enhances additional mycorrhizal activity and bioerosion. These ubiquitous plant mutualists are found in 80% of all land plants (Wang & Qiu 2006), making mycorrhizal fungi one of most widely occurring bioeroding taxa. Furthermore, bioerosion by mycorrhizal fungi on carbonates can enhance alkalinity fluxes between land, river and sea at ecologically relevant timescales (decades to centuries, Thorley *et al.* 2015).

Bioeroders that consume geologic substrates also provide important trace elements and key nutrients in food webs when they are fed upon (Chen *et al.* 2000). For example, snails enhance nitrogen cycling in the desert ecosystem by eroding rock to consume endolithic lichens (Jones & Shachak 1990). In freshwater and marine environments, bioerosion by cyanobacteria, and the associated consumption of this cyanobacteria by bioeroding invertebrates, plays a key role in the carbonate cycle (Schneider & le Campion-Alsumard 1999). Bioeroding microbial chemoautotrophs are the main primary producers in aphotic cave ecosystems and can support a food web of 48 terrestrial and aquatic species (Sarbu *et al.* 1996). Similarly, marine wood-borers break down terrestrial materials and make the sequestered carbon and nitrogen available in ocean ecosystems (Cragg 1993), thus enhancing linkages between terrestrial and marine ecosystems.

Effects on biodiversity

The complex habitats excavated by bioerosion can provide habitat for diverse and abundant species assemblages. In the rocky intertidal, the communities inhabiting boreholes created by bivalves had 2.7 times more species than assemblages on bare rock (Pinn *et al.* 2008). Coral reefs experiencing more bioerosion harboured richer cryptofauna compared to less eroded reefs in Panama (Enochs & Manzello 2012). Similarly, erosive activities by birds creating nest burrows in cliff faces create a unique habitat that is exploited by dozens of animals including vertebrates (other birds, rodents, snakes) and insects (Casas-Crivillé & Valera 2005). Even at the smallest scales, burrows of minute wood-boring isopods (millimetres in length) harbour diverse communities of microbes, nematodes, polychaetes, amphipods and copepods (Sleeter & Coull 1973; El-Shanshoury *et al.* 1994). In some cases, obligate associates are found living in bioeroded habitats, suggesting close evolutionary relationships, as observed between bioeroding sea urchins and their crab and sea star co-habitants (Schoppe & Werding 1996). Often the erosional cast-offs can create sedimentary habitats used by soft-sediment organisms. Bioerosion of rock and coral by fish, sponges and clams facilitates the creation of sand beaches (Neumann 1966; Glynn *et al.* 1979). Similarly, grazing by land snails and growth of lichens bioerode rocks into soils inhabited by plant communities in deserts, mountainous grasslands and other terrestrial ecosystems (Jones & Shachak 1990; Chen *et al.* 2000). However, we posit that intensive bioerosion can also decrease biodiversity where such activities diminish structural complexity or eliminate a habitat entirely.

Socio-economic impacts

Bioerosion can affect the quality and quantity of ecosystem services provided by natural habitats and compromise the aesthetics, longevity and function of materials and infrastructure. For example, bioerosion of living shorelines (e.g. marshes, oyster reefs, coral reefs) that serve as natural shoreline protection may make coastal zones more susceptible to storm surges, tsunamis and sea level rise. Bioeroders can also impact food industries, such as aquaculture operations where borers attack the shells of molluscs causing malformations or death (Moreno *et al.* 2006). They can also have indirect effects by destroying the infrastructure used in aquaculture operations (Davidson 2012).

The economic and social impacts of bioerosive species are perhaps most immediately apparent when they break down materials and structures created by humans (Fig. 2). Included here, bioerosion can inflict a cultural toll by degrading monuments (Warscheid & Braams 2000), archaeological ruins (Rolón & Cilla 2012) and shipwrecks (Müller 2010). There is a long history of wood-borers causing extensive damage to wooden-hulled vessels, which necessitated the development of costly anti-boring and fouling treatments (Cragg *et al.* 1999). Modern materials and infrastructure have proven susceptible as well, as studies have documented bioerosion damage to plastic pipes used to cool power plants (Jenner *et al.* 2003), cement pilings (Snow 1988) and even metal beams and piping (Beech & Gaylarde 1999). Levee failures and subsequent flood damage have also been attributed to the bioerosive activities of animals (Orlandini *et al.* 2015). Some components of coastal defence and infrastructure such as stone breakwaters, seawalls, floating docks and wooden pilings are also composed of materials susceptible to attack by bioeroders (Bulleri & Chapman 2010). As coastal development and shoreline armouring rapidly increases to combat threats of storms and sea level rise (Dugan *et al.* 2012; Firth *et al.* 2016), development and use of harder materials and/or preventive treatments would reduce structural failures from bioerosion and concomitant economic losses.

Bioerosion by microbial biofilms occurs in a diversity of hard substrata, including metal, plastics and stone in marine, terrestrial and freshwater environments, and causes billions of dollars of damage and maintenance costs yearly (Beech & Gaylarde 1999; Allsopp *et al.* 2004). Microbial bioerosion also presents a significant risk to human life when key components of infrastructure fail (e.g. bioerosion of gas pipes or power plant cooling pipes; Beech & Gaylarde 1999). Few materials are immune to microbial bioerosion although some materials, toxic coatings, chemical treatments, and routine maintenance and inspections can greatly mitigate their damage (Warscheid & Braams 2000; Allsopp *et al*. 2004). Conversely, microbial bioerosion may be harnessed as a powerful biotechnological tool, for example, in bioremediation of heavy metal-polluted soils or for biomining of precious metals (Mapelli *et al*. 2012).

BIOEROSION AND ANTHROPOGENIC CHANGE

Biotic and abiotic factors can affect various aspects of the bioerosion process by altering the distribution, abundance or *per capita* effects of bioeroders and their substrata. This can be further modified by anthropogenic factors, which may influence the bioerosion process and result in concomitant changes to habitat structure and community and ecosystem dynamics. Here, we establish a general predictive model to examine how dominant anthropogenic factors of environmental change alter the intensity of bioerosion (Fig. 3). These changes may vary in spatial scale, from global (e.g. climate change effects on bioerosion) to local (e.g. overharvesting of bioeroders).

To estimate and predict the impacts of bioerosion, we modify the model used to measure the impact of an introduced species proposed by Parker *et al*. (1999). Here, I_B is the bioerosive impact: $I_B = R \times A \times P$, where, R is the geographic range of the bioeroder, A is the abundance of the bioeroder and P is the *per capita* (or per abundance) bioerosive effect. Therefore, the total bioerosive impact of a species, such as a tropical boring sponge, may be locally important (high A or P

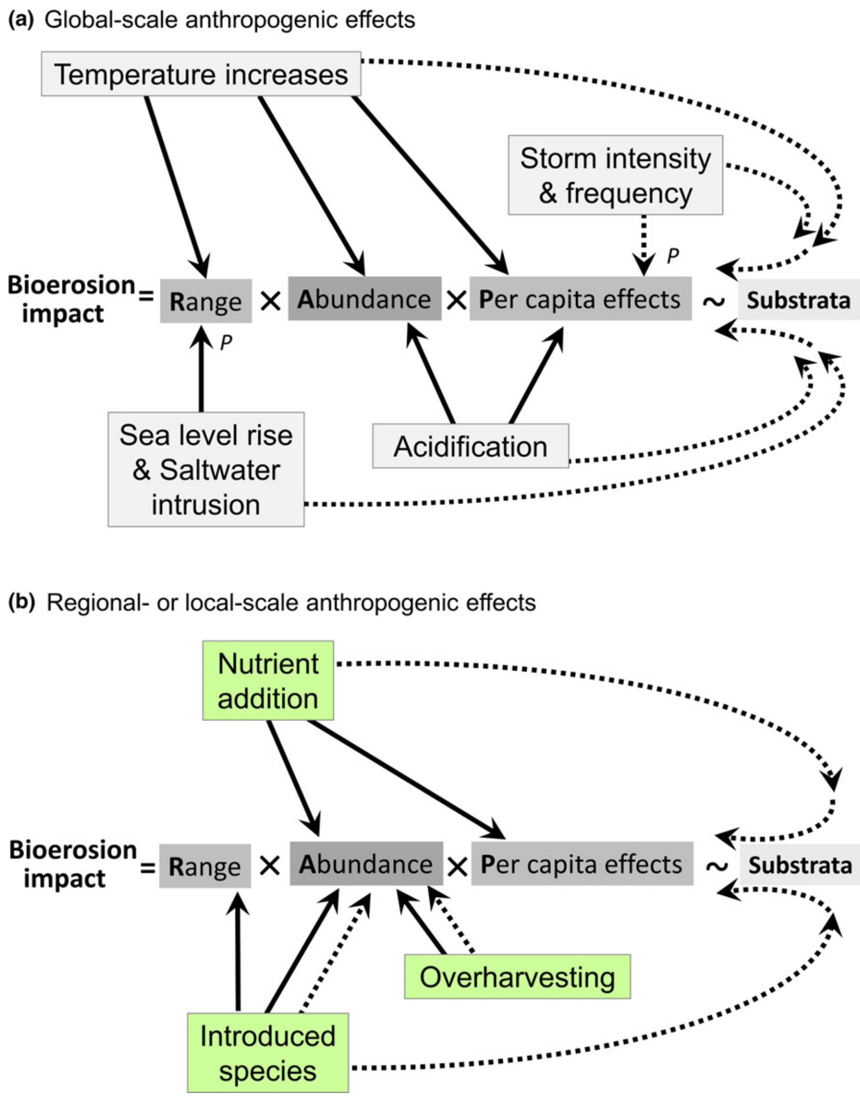

Fig. 3 Hypothesised effects of some global scale (a) and regional/local scale (b) anthropogenic changes on the process of bioerosion (= range × abundance × *per capita* effects of bioeroders, and mediated [~] by substratum characteristics), based on published studies (arrows) or generalised predictions based on responses of similar non-bioeroding taxa (arrows with a '*P*'). See main text for each respective anthropogenic effect for a more detailed discussion. Missing arrows indicate relationships that have apparently not been studied. Solid arrows indicate direct effects and dotted arrows indicate indirect effects, often by altering the integrity of or species interactions on substrata. We consider most physiological responses to anthropogenic stressors (such as changes to growth or activity) to be reflected in changes to *per capita* bioerosive effects, except extreme responses that result in broad-scale mortality, which should affect abundances.

value) but limited in geographic distribution to tropical coastal zones with carbonate substrata (low R). In contrast, ubiquitous bioeroders such as lichens, would have a broad distribution (high R) and/or high abundance (A), but a relatively low *per capita* impact (P). These impacts are mediated by the properties of the substratum, which can respond directly to environmental change.

For heuristic purposes, we examine how individual anthropogenic factors affect the process of bioerosion and substrata, but we acknowledge that nonlinear or threshold responses can arise from among multiple biotic and abiotic factors as discussed in Naylor *et al.* (2012). We illustrate some of these additional complexities in a broader flow diagram (Fig. 4), showing how anthropogenic alterations of the environment may interact with other biotic and abiotic environmental parameters to influence bioerosion impacts. For example, ocean acidification (anthropogenic change) decreases ocean pH (abiotic factor), which can increase dissolution and reduce cementation of coral framework (substratum) and, in turn, weakens the substratum to other agents of erosion (physical or chemical erosion and bioerosion; Manzello *et al.* 2008). However, acidification also affects different aspects of the bioerosion process (e.g. abundance and *per capita* effects; see Fig. S5 and the following section *Acidification* for details), and we use our conceptual model (Fig. 3) to better illustrate and predict these specific effects. We map other real-world examples using this model to illustrate how future outcomes could be predicted with specific bioerosive taxa and substrata (Figs S5–S7).

Our approach thus expands on the work of Naylor *et al.* (2012), who suggested that biological activity interacts with lithology and physical erosion to influence geomorphology. In the following sections, we focus on examining the implications and effects of bioerosion in an ecological context and under anthropogenic change. Our model (Fig. 3) links the key components necessary to predict the effects of bioerosion in a changing world. It is meant to serve as a baseline model that can be readily adapted using taxon-, substratum- and other context-dependent factors relevant to the respective study system. The model can be used to: (1) determine what components of the bioeroder impact ($R \times A \times P$) most influence bioerosion in different ecosystems, allowing for cross-system or cross-taxon comparisons, (2) predict how anthropogenic stressors may influence different components of bioerosion impact and quantify bioerosion for specific taxa and substrata under different anthropogenic influences and (3) summarise existing relationships to guide future research testing these predictions, investigate areas of uncertainty or test the dominant factors influencing bioerosion using a specific model system or taxon.

EFFECTS OF CLIMATE CHANGE ON BIOEROSION

Changing sea and air temperatures

Mean surface temperatures are predicted to rise from 1.2 to 4.8 °C on land and from 0.8 to 3.1 °C in the ocean by 2100 (IPCC 2013). Ecological responses to temperature changes include shifts in mortality and demographic performance (Deutsch *et al.* 2008), species distributions (Parmesan & Yohe 2003) and species interaction strength (Sanford 1999). Such responses should affect bioeroders and the bioerosion process, impacting bioerosion intensity in several ways (Fig. 3a).

First, temperature increases may make the substratum more vulnerable to bioerosion. Biogenic substrata, such as coral reefs, can die due to gradually warming temperatures or periodic climate anomalies such as El Niño Southern Oscillation events (Glynn & Manzello 2015). Since reefs with living coral cover are attacked less frequently (Bromley 1978), dead coral reef material is particularly susceptible to bioeroders. Thermal stresses can also erode and weaken terrestrial rocks (Bonazza *et al.* 2009b) and may make surfaces more prone to bioerosion. Conversely, in colder climates, increasing temperatures should reduce the formation of ice that erodes and weakens rock, making substrata less prone to bioerosion.

Second, warming may expand the geographic ranges and abundances of warm-water bioeroders, consistent with recent range expansions of subtropical species into temperate zones (Vergés *et al.* 2014). Warmer temperatures are broadly predicted to increase abundances of warm-water species and decrease abundances of cold-water species (Poloczanska *et al.* 2016), and some studies link regional warming to increases in abundance of bioerosive urchins and gastropods (Schiel *et al.* 2004). Since warm-water communities tend to have more bioeroder species and/or higher bioerosion rates than temperate communities (Wisshak 2006; Wisshak *et al.* 2014), range expansions and higher abundances of warm-water bioeroders may intensify bioerosion in areas that experience warming.

Third, like other biological activities, bioerosion can be temperature-dependent, particularly in ectotherms (Cossins & Bowler 1987). However, fully predicting the direction and magnitude of the response of bioerosion to anticipated changes in temperature is challenging because bioerosion rates of some species increase in elevated temperatures (Brady & Carroll 1994; Smith 2008) and decrease in others due to physiological stress (Cossins & Bowler 1987), while other species appear unaffected (Duckworth & Peterson 2012; Stubler *et al.* 2015). Some species and bioerosion effects are influenced strongly by temperature variability, such as lichens whose thalli expand and contract inside rock in response to freeze–thaw cycles (Chen *et al.* 2000). Furthermore, the relationship between temperature and bioerosion is unlikely to be linear, but rather depends on the magnitude of the temperature increase and the physiological tolerances of the taxa, since high temperatures will eventually lead to stressful conditions that depress survivorship and bioerosive activities (Davidson *et al.* 2013). Such ambiguities reinforce the need for more controlled empirical studies to investigate the long-term effects of temperature on different bioeroder functional groups and comparisons across a broad latitudinal range before general predictions can be made.

Acidification

Acidification (increases in pCO_2, decreases in pH) can affect bioerosion through three primary mechanisms. First, acidification can increase dissolution of carbonate substrata (such as limestone, coral skeletons, and shell), which reduces the

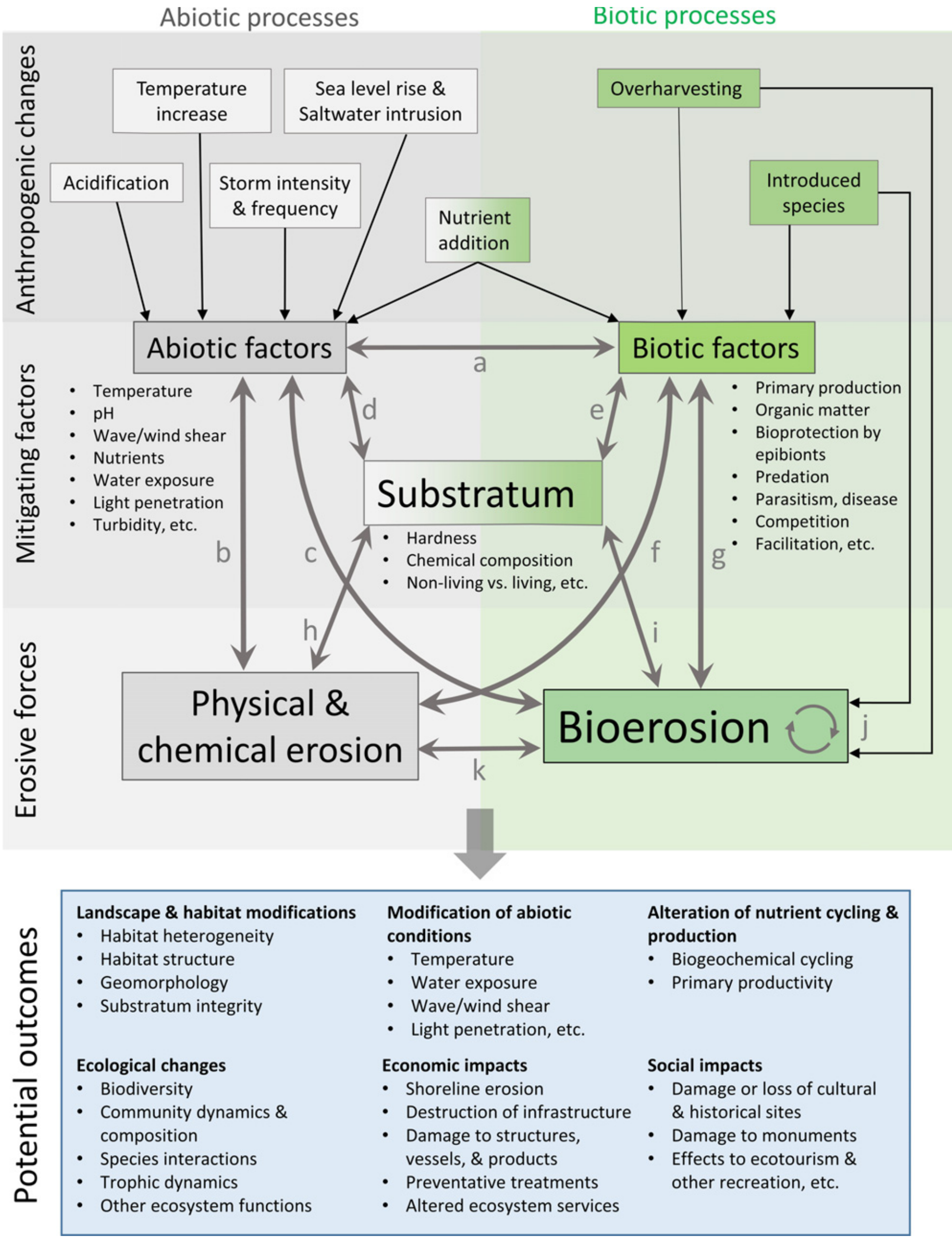

Fig. 4 Complex interrelationships between anthropogenic changes, mitigating factors (abiotic and biotic factors, substratum), and erosive forces (physical and chemical erosion and bioerosion) mediate the ecological and socio-economic outcomes of bioerosion. Colour differences reflect abiotic processes (grey, left side) and biotic processes (green, right side). Various anthropogenic changes (top boxes and small arrows) affect abiotic or biotic factors (middle grey and green boxes) or directly act on bioeroders (e.g. overharvesting, introduced species; see main text). Larger arrows represent relationships and feedbacks amongst biotic and abiotic factors, substratum, physical and chemical erosion, and bioerosion (see Appendix S1 for explanations and examples of each arrow [a–j]). Some key ecological and socio-economic outcomes resulting from bioerosion are presented at the bottom (blue box, see main text for details). The substratum can be living (coral, shell) or non-living (rock); this difference is reflected thematically using a green-grey colour gradient. We consider substratum separately from abiotic or biotic factors due to its critical role in mediating the rates, prevalence and effects of bioerosion. Similarly, nutrient additions could also be considered either an abiotic change (inorganic nutrients) or a biotic change (organic matter). We consider physical erosion to be erosion by physical or mechanical forces, like surface exfoliation caused by high temperatures, and chemical erosion to be erosion from chemical reactions such as the dissolution of carbonates when exposed to low pH conditions. For simplicity, we exclude interactions within each factor (e.g. interactions between biotic factors, like predation and competition) and exclude potential feedbacks and interactions between different anthropogenic stressors.

integrity of substrata making them more vulnerable to bioeroders (Fig. 3a). For example, Duckworth and Peterson (2012) found experimentally acidified seawater weakened scallop shells causing boring sponges to attack in greater intensity relative to normal seawater. In terrestrial environments, increasing concentrations of atmospheric carbon dioxide in rain (or sulfur and nitrogenous pollutants) accelerates dissolution rates and weakens carbonate substrata (through the karst effect or acid rain, Bonazza *et al.* 2009a), which we hypothesise may further enhance terrestrial bioerosion.

Second, the chemical processes used by corrosive bioeroders (such as microbes and sponges) are often enhanced by lower pH conditions (Wisshak *et al*. 2012; Reyes-Nivia *et al*. 2013) or by increasing atmospheric CO_2 that fertilises bioerosive microbes (Brady & Carroll 1994), causing higher *per capita* bioerosive effects. For example, ocean acidification can increase rates of bioerosion (Silbiger *et al*. 2014; Enochs *et al*. 2016; Stubler & Peterson 2016), especially by sponges (Duckworth & Peterson 2012; Wisshak *et al*. 2012; Stubler *et al*. 2014) and microboring algae (Tribollet *et al*. 2009; Reyes-Nivia *et al*. 2013), two abundant bioerosive taxa. These effects are particularly strong in coral reef systems where acidification is predicted to increase sponge bioerosion by over 25% by 2100 (Wisshak *et al*. 2012). We predict similar increases in bioerosion in carbonate substrata in freshwater environments experiencing lower pH, although these effects apparently have not been examined. In terrestrial systems, lichens use acids in the erosion process (Chen *et al*. 2000) and further decreases in pH at the rock surface (derived from increases in atmospheric CO_2) may facilitate their bioerosion. Acidification may also interact with bioerosion through a positive feedback loop – if acidification increases the rate of bioerosion, bioerosion should in turn, increase the surface area vulnerable to acidification.

Third, acidification can directly affect bioeroders (Fig. 3a). Bioeroders that deposit calcareous exoskeletons (e.g. bivalves, echinoderms) may die or grow more slowly due to acidification (Fabry *et al*. 2008), thereby reducing their abundance and *per capita* effects. However, that response is not consistent among all calcareous species, as acidification did not affect long-term survivorship, reproduction or growth in boring urchins (Hazan *et al*. 2014). Additionally, non-calcareous bioeroding sponges also varied in their response, with some being unaffected (Stubler *et al*. 2014) and others suffering a minor decrease in survivorship with acidification (Duckworth & Peterson 2012). Thus, additional studies are needed to investigate the role of acidification in affecting long-term survivorship and growth of different bioeroders. Similarly, air pollution, especially by sulfur dioxide (which generates ‘acid rain’), can negatively affect the diversity and abundances of lichens, many of which are important bioeroders (Lisci *et al*. 2003). However, it is unclear if low pH conditions harm endolithic lichens that use acids in the bioerosion process. While acidification may negatively influence some calcareous bioeroders, overall, acidification appears to exacerbate bioerosion of carbonate substrata, particularly coral reefs, by weakening substratum integrity and facilitating the *per capita* effects of corrosive bioeroders (e.g. microbes, sponges; Fig. S5). Further studies are needed to examine how acidification affects bioerosion across a broader range of substrata and taxa.

Sea level rise and saltwater intrusion

As climate change drives sea level rise (up to 74 cm by 2100, IPCC 2013), coastal communities will become increasingly dependent on coastal infrastructure such as seawalls, breakwaters and levees to defend against rising sea level and storm surges, and stilts and pilings to elevate buildings and infrastructure above invading seas. Many of these coastal structures are composed of friable rocks, calcareous cements and stone, wood or other bioerodable materials (Scott *et al*. 1988; Cragg *et al*. 1999; Bulleri & Chapman 2010). Increasing suitable habitat for bioeroders through the addition of coastal infrastructure could provide yet another positive feedback between human alterations and bioerosion.

Natural structures are also threatened, such as coral reefs, where coral growth outpaced by sea level rise leads to coral death (Hoegh-Guldberg *et al*. 2007) and increases in subsequent bioerosion. Furthermore, as rising sea levels reclaim terrestrial areas, we predict that fronts of diverse marine bioeroders will expand their range (Fig. 3a), invading and eroding previously inaccessible terrestrial substrata. Such expansions could be particularly damaging to living shorelines such as saltmarshes that are already threatened by coastal squeeze and development (Firth *et al*. 2016).

Similarly, saltwater intrusion into terrestrial, riverine and coastal areas through sea level rise, freshwater diversion or drought could expand the ranges of bioeroding marine species, bringing them into contact with new substrata (James *et al*. 2003). For example, low rainfall and increased water withdrawal for irrigation around San Francisco, CA, USA during the early 20th century allowed a non-native shipworm (*Teredo navalis*) to move upriver and attack docks and pilings previously in low salinity refuge from shipworms (Hill & Kofoid 1927; Carlton 1979). In less than a decade, the non-native shipworm caused over a billion dollars of damage (adjusted to 2016 USD and Construction Cost Index) to private wharves, public infrastructure, and a US Navy shipyard (Neily 1927; Cohen & Carlton 1995). Similarly, wood-boring shipworms are predicted to expand inland along rivers in the Netherlands through increased saltwater intrusion associated with sea level rise (Paalvast & van der Velde 2011; but see Appelqvist *et al*. 2015). Since saltwater intrusion and the expansion of marine bioeroders will likely vary spatially and temporally based on changing freshwater output, the effect of bioerosion will also be dependent on regional precipitation and freshwater diversion.

Larger, more frequent storms and flooding events

The frequency and intensity of storms such as wind, rain and wave events are predicted to increase (IPCC 2013), which will likely exacerbate the effects of bioeroders (Fig. 3a). By excavating materials, bioeroders weaken substrata and make them more vulnerable to breakage or failure from chronic or extreme events (Highsmith 1980). Indeed, Scott & Risk (1988) found that a 10% loss in cross-sectional area in coral from boring clams reduced coral strength by > 36%. Similarly destructive results were found with fungi and termites in wood (Groot *et al*. 1998) and boring marine worms in bivalve shells (Bergman *et al*. 1982). Bioerosion may also facilitate propagation of cracks, fractionation, and ablation caused by microboring algae and snail rasping (Schneider & Torunski 1983) or facilitate crack formation by microbial biofilms inside steel-reinforced concrete (Sanchez-Silva & Rosowsky 2008), which could lead to increased rates of structure failure during extreme events.

Physical erosion associated with increased precipitation and river flows can scour sediment banks weakened by burrowing animals, causing erosional loss of marshes and river banks as well as economic damages to earthen dikes (Rudnick *et al.* 2005; Orlandini *et al.* 2015). Precipitation can also indirectly reduce bioerosion rates as increased rain can promote the growth of protective epibionts on terrestrial substrata (Gómez-Bolea *et al.* 2012), while low precipitation environments can reduce protective epibiota and can favour some terrestrial microbial bioeroders (Viles 1995). Furthermore, increased variability in precipitation may exacerbate bioerosion because repeated wetting–drying cycles can accelerate the erosive effects of lichens in stone (Chen *et al.* 2000).

There are synergisms between bioerosion and weather events that will likely play an increasingly important role with climate change. For example, coral reefs experiencing higher rates of bioerosion appear more damaged by storms (Clark & Morton 1999; Glynn & Manzello 2015). Similarly, burrowing by birds into consolidated sediments may facilitate toppling of trees by high winds (Cameron 1990). Bioerosive activities may also create channels or drainage lines that further concentrate physical erosion by moving water (Hall & Williams 1981) or weaken the surface to facilitate exfoliation by wind or water flow (Budel *et al.* 2004). Such synergisms between storm stresses and bioeroders will likely extend to terrestrial infrastructure and coastal defences and remain an important area for future research.

EFFECTS OF NUTRIENT ADDITION ON BIOEROSION

Excessive inputs of anthropogenic nutrients (nutrient pollution/eutrophication) have been linked to increased bioerosion of coral reefs (*summarised below*, Perry & Harborne 2016), stone by terrestrial microbes (Warscheid & Braams 2000) and wood by freshwater microbes (Gulis *et al.* 2004). Bioerosion typically increases with eutrophication because nutrient additions stimulate phytoplankton and macroalgae production, which are resources targeted by bioeroding filter feeders and grazers respectively (Glynn & Manzello 2015). Such increases in resources are thought to increase the abundance and *per capita* grazing activities of bioeroders and, therefore, their bioerosive effects (Fig. 3b, Rose & Risk 1985). Only in the most extreme circumstances does eutrophication likely reduce bioerosion through the creation of hypoxic waters that lead to mortality and decreased biological activity (Anderson & Reish 1967). Many human structures in the coastal environment coincide with sources of anthropogenic nutrient inputs (e.g. harbours and other urban water fronts), thus they may become more bioeroded with increasing eutrophication (Scott *et al.* 1988). However, increasing nutrient inputs may also stimulate the growth of non-bioeroding epibionts that act as a protective barrier from bioerosion (Naylor *et al.* 2002).

The relationship between eutrophication and bioerosion is best studied in coral reefs where numerous observational studies link increased rates of bioerosion in coral reefs with the presence of nutrient pollution and areas with more terrigenous runoff (see references in Glynn & Manzello 2015). These observational studies are supported by experimental results that found that the addition of inorganic nutrients (N + P) increased bioerosion by microborers on shells by 920% (Carreiro-Silva *et al.* 2009) and by microborers and bioeroding grazers on coral blocks by 120 and 167%, respectively (Chazottes *et al.* 2017). However, some studies did not find a relationship between eutrophication and bioerosion (Pari *et al.* 2002; Kiene 1997) or found bioerosion rates varied by functional group (microborers, macroborers, grazers; Hutchings *et al.* 2005; Chazottes *et al.* 2017). These contrasting results underscore the importance of distinguishing; (1) the effects of nutrients on different bioeroder functional groups from (2) potentially confounding factors such as sedimentation and turbidity, which may prevent the establishment of erosive microborers and algae (Hutchings *et al.* 2005) or interfere with the respiration of macroborers. Additional manipulative studies will help disentangle the effects of eutrophication from co-varying stressors (e.g. sedimentation, turbidity, hypoxia). Studies should also explore if the response of bioerosion to nutrient additions is consistent in temperate and nutrient-rich environments.

EFFECTS OF OVERHARVESTING ON BIOEROSION

Overharvesting can alter bioerosion impact by reducing the abundances of bioeroders or the predators of bioeroders (Fig. 3b). Many fisheries target bioerosive organisms including temperate and tropical urchins, parrotfish and boring bivalves (Mumby *et al.* 2006; Guidetti 2011). The aquarium and curio trade also harvests bioeroding organisms such as fish (e.g. puffers, parrotfish), urchins and gastropods (Wabnitz *et al.* 2003). The selective removal of the largest organisms by fishers can greatly reduce bioerosion rates, because the largest bioeroders often have the highest *per capita* effects (Carreiro-Silva & McClanahan 2001).

Overexploitation of consumers can have indirect effects on the bioerosion process by releasing populations of bioeroding organisms from consumer control (McClanahan *et al.* 1999). Overfishing of predators resulted in increased urchin abundances, which in turn led to bioerosion rates 20 times greater on unprotected reefs than reefs protected from fishing (Carreiro-Silva & McClanahan 2001). These effects can extend to larger scales, as seen in New England marshes where recreational fishing of predatory fish led to increases in burrowing crabs (Altieri *et al.* 2012). The burrowing ultimately caused substantial shoreline erosion and widened creek channels by over an order of magnitude (Coverdale *et al.* 2013).

EFFECTS OF INTRODUCED SPECIES ON BIOEROSION

Species introductions can dramatically alter the bioerosion of habitats and infrastructure both directly and indirectly (Fei *et al.* 2014). For example, between 1910 and 1920, San Francisco Bay suffered from over \$1.3 billion of damage when non-native shipworms *T. navalis* destroyed supportive pilings causing the collapse of over 50 structures (Hill & Kofoid 1927; Cohen & Carlton 1995; USD, adjusted for the December 2016 Construction Cost Index). Bioeroding organisms are inherently prone to accidental introductions because they inhabit structures and materials that are transported around the world. For example, numerous invasions of wood-boring species (e.g. shipworms and other bivalves, boring crustacea) have occurred throughout human history due to their association and transfer with wooden ship hulls (Carlton &

Ruckelshaus 1997). Translocation of oysters for aquaculture is another mechanism that has led to global redistribution of bioeroders including clionid sponges, polychaetes and gastropods, which hitchhike in, on and among shells to new coastlines (Ruiz *et al.* 2000; Moreno *et al.* 2006). The export of live rock and coral for the aquarium trade is a largely unrecognised, but potentially significant, vector for the introduction of bioeroders. The live rock and coral trade in SE Asia alone exported an estimated 17.8 million pieces (2.4 million kg) of live coral in just one decade (Nijman 2009); each piece of which can contain an entire community of animal, plant, and microbial bioeroders. Other bioeroders have been intentionally introduced for harvesting (e.g. Chinese mitten crab, nutria, pigs or rabbits) or to serve as pack animals (e.g. feral horses, burros) without consideration of their burrowing or trampling effects (Cohen & Carlton 1995; Butler 2006). Introduced species can also have indirect effects on bioerosion. For example, introduced predatory rats decimated populations of ground-dwelling burrowing birds (Jones *et al.* 2008), introduced crabs preyed on native marsh-eroding crabs (Bertness & Coverdale 2013) and introduced algae reduced herbivory of a bioerosive urchin (Tomas *et al.* 2011).

Furthermore, the introduction or emergence of disease-causing parasites and pathogens can have positive and negative effects on bioerosion. For example, populations of bioeroding sea urchins in the Caribbean (Lessios *et al.* 1984) and the Atlantic coast of Canada in the 1980s (Scheibling & Stephenson 1984) suffered from large-scale die-offs due to diseases of unknown origin. Diseases can also indirectly expose biogenic substrata to bioerosion by damaging protective living tissues over calcareous skeletons or shell (Kim *et al.* 2005), facilitating attack by bioeroders.

CONCLUSIONS AND FUTURE DIRECTIONS

Bioerosion is a major structuring force in natural communities and can have wide-ranging ecological and socio-economic impacts. By synthesising a disparate body of bioerosion studies into a unifying framework, we reveal how bioerosion is a prevalent and important process that alters ecological communities and ecosystem function. We demonstrate that this process is widespread and driven by multiple mechanisms and diverse taxa, across terrestrial, freshwater, and marine biomes and human-made systems. Furthermore, we advance a general approach and model to predict how anthropogenic factors operating at local, regional and global scales may affect rates of bioerosion activity and the susceptibility of geological, biogenic and human-made substrata. In some cases, human activities appear to exacerbate the effects and consequences of bioeroders (e.g. acidification on sponge bioerosion in coral reefs, Fig. S5), but other activities reduce bioerosive effects (e.g. overharvesting of coral bioeroding urchins and fish). Indeed, some system-specific responses of bioerosion to anthropogenic changes can be inferred (e.g. the role of storms in exacerbating bioerosion damage in coastal systems), but it is still difficult to make broad generalisations and fully predict whether net bioerosion rates will increase or decrease at various spatial or temporal scales across the globe, given the current state of knowledge. However, we hope our model for bioerosion in a changing world (Fig. 3, Figs S5–S7) will facilitate more targeted theoretical and empirical studies to quantify bioerosion by specific taxa and functional groups interacting with anthropogenic stressors. When combined, multiple studies from a broad range of taxa will allow more generalised and multispecies predictions of the effects of anthropogenic changes on bioerosion operating at local or regional scales.

Considering the widespread consequences of bioerosion to natural systems and human infrastructure, and the interaction between bioerosion and human activities, further research across disciplines is needed urgently to broaden our understanding of bioerosion and predict myriad effects, especially under rapidly changing conditions throughout the world. Specifically, we call for more experimental studies to examine the separate and interactive effects of multiple anthropogenic factors on bioerosion (such as potential synergisms between eutrophication and acidification, DeCarlo *et al.* 2015) and to identify specific threshold effects on bioerosion, such as quantifying the likely nonlinear relationship between storm intensity and surge and the failure of reef, docks, sea walls or marshes weakened by bioerosion. Studies that integrate from species to ecosystems will allow for the identification of nonlinear responses, positive feedbacks and tipping points of bioeroding systems under human-induced changes. The need is particularly acute in coastal systems, where we predict bioerosion will change rapidly due to global and regional forces, affecting natural shorelines, coastal defences and infrastructure. As human populations expand along the coast and their dependence on coastal resources and infrastructure escalates (Dugan *et al.* 2012), the effects of bioerosion will be of increasing relevance ecologically, economically and socially. An integrated approach by interdisciplinary teams of biologists, geologists, economists and engineers will be key to determining the potential consequences and mitigating the future effects of bioerosion in a rapidly changing world.

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AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the conceptual framework for this synthesis. TMD conducted the literature review. TMD wrote the first draft, and all authors contributed substantially to subsequent drafts.

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SUPPORTING INFORMATION

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