Biogeomorphic Impacts of Invasive Species

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Abstract

Invasive species, often recognized as ecosystem engineers, can dramatically alter geomorphic processes and landforms. Our review shows that the biogeomorphic impacts of invasive species are common, but variable in magnitude or severity, ranging from simple acceleration or deceleration of preexisting geomorphic processes to landscape metamorphosis. Primary effects of invasive flora are bioconstruction and bioprotection, whereas primary effects of invasive fauna are bioturbation, bioerosion, and bioconstruction. Land-water interfaces seem particularly vulnerable to biogeomorphic impacts of invasive species. Although not different from biogeomorphic impacts in general, invasive species are far more likely to lead to major geomorphic changes or landscape metamorphosis, which can have long-lasting impacts. In addition, invasive species can alter selection pressures in both macroevolution and microevolution by changing geomorphic processes. However, the differing timescales of biological invasions, landscape evolution, and biological evolution complicate assessment of the evolutionary impacts of invasive organisms.

1. INTRODUCTION

1.1. Problem Statement

Ecosystem processes: the fluxes and transformations of energy and materials of an ecosystem

Ecosystem engineer: an organism that directly/indirectly modulates resource availability by causing short-term and/or long-term physical changes in biotic or abiotic materials

Geomorphological processes: the production, transport, and deposition of materials that modify Earth's surface

Biogeomorphology: study of the interactions between ecosystems and Earth surface processes and landforms

Invasions of exotic species can cause significant impacts on ecosystems. Comprehensive reviews have been conducted on the impact of invasive species on ecosystem processes (e.g., Ehrenfeld 2010, Pyšek et al. 2012, Simberloff et al. 2012, Ricciardi et al. 2013), but syntheses of effects on physical processes and structures are limited (Simberloff 2011). Since the introduction of the ecosystem engineer concept by Jones et al. (1994) and the connection of invasive species to ecosystem engineering by Crooks (2002), many studies have documented the alteration of physical structures by invasive species. Meanwhile, contemporary developments in Earth sciences saw an increasing realization of the pervasiveness of active geomorphic impacts of biota and explicit consideration of the reciprocal interactions between geomorphological and ecological phenomena (Viles 2011). However, the association between invasive species and geomorphic processes has been overlooked. These recent developments in both disciplines demand a review and synthesis of the biogeomorphic impacts of invasive species.

1.2. Purpose and Goal

Geomorphological and biological processes are often tightly linked. Many organisms have significant impacts on geomorphological processes and landforms, while landforms and surface processes are in turn critical aspects of habitat for organisms. It has long been recognized that landforms and organisms influence each other. However, the rise of biogeomorphology in recent years reflects the recognition that, beyond these one-way influences in either direction, there are often ongoing reciprocal interactions and tightly woven connections between, e.g., ecosystem and landform evolution.

Thus, just as major geomorphological change—erosion, sedimentation, landslides, etc.—can trigger ecological responses, biological and ecological changes might be able to trigger substantial geomorphic changes. Studies on general environmental impacts of invasive species often include consideration of their impacts on soils and sediments, landforms, and surface processes. Likewise, studies of biogeomorphology have addressed nonnative species. Thus, the time is ripe for an overview and synthesis of the biogeomorphic impacts of invasive species. In particular, we are interested in identifying the range of biogeomorphic effects of invasive species from minor side effects to complete landscape transformations. In doing so, we hope to identify trends and typologies that may assist in identifying high and low risks of adverse geomorphic impacts by invasive species.

1.3. Scope

Our review is focused on direct and indirect geomorphological effects of species recognized as invasive in the location where the effects are documented. We do not attempt to catalog all physical or chemical effects of invasive organisms even though some (e.g., changes in soil chemistry) could well have knock-on effects on geomorphic processes. We also acknowledge two other important interactions that are not within the scope of this review—influences of geomorphic processes on the invader's dispersal and establishment, and impacts of management or removal of invasive species on geomorphic processes.

2. CONTEXT AND CURRENT KNOWLEDGE

Biogeomorphology and ecosystem engineering are closely related. To better understand their tightly woven connections, we first provide a brief historical perspective on the development of the two fields and the important role of invasive species in understanding these connections.

2.1. History of Biogeomorphology

Biogeomorphology studies the feedback between geomorphic and ecological systems. Possibly the first to consider organisms as geomorphic agents was Charles Darwin. In 1881, Darwin published his book, *The Formation of Vegetable Mould, Through the Action of Worms, with Observations on Their Habits*, in which he outlined the process by which worms ingest soil at depth and deposit it on the surface as fecal castings (Darwin 1881). Many biogeomorphologists consider this book to be the starting point of biogeomorphology because it specifically examines the role of worms in the transformation of the regolith.

Coevolution: the dynamic, path-dependent, interrelated development of landforms and biota

Niche construction: modification of biotic and abiotic components in environments that result in changes in natural selection pressures

Other early examples of biogeomorphology research include studies by Nathaniel Shaler and Henry Cowles. Shaler (1892) discussed the effects of animals and plants on soils, including the influence of organisms on rocks underlying mineral soils, modification of soil through animal and plant interactions, and the contribution of organic remains. Cowles (1899) recognized the importance of biota on surface processes and landforms and vice versa (Sprugel 1980, Stallins 2006).

Though biogeomorphology and related terms were rarely used, the rediscovery of biomechanical (as opposed to chemical or biological) effects of organisms on soils and regoliths in both geomorphology and ecology was triggered by the work of D.L. Johnson and his students and colleagues around 1985–1990 (Johnson et al. 1987, Schaetzl et al. 1989, Johnson 1990). Johnson's work focused on direct effects of floral and faunal turbation, indirect effects on erosion and mass wasting, biogenic topography, and the creation of surficial biomantles. Butler (1995) discussed the geomorphic contributions of multiple vertebrate and invertebrate animal species, which marks an important historic moment in the field of biogeomorphology, as Butler criticized the field of geomorphology for overlooking the role of animals as geomorphic agents of erosion, transportation, and deposition. Other influential discussions of biogeomorphology in the past 30 years include those by Thornes (1985), Swanson et al. (1988), Viles (1988), Naylor et al. (2002), and Stallins (2006).

Despite recognition of the impacts of biota on surface processes and landforms (and vice versa), geomorphologists only relatively recently started to engage the reciprocal adjustments between landforms and biota as well as the coevolution of ecosystems and landscapes. These kinds of tightly woven connections currently constitute the cutting edge of biogeomorphology research.

2.2. Ecosystem Engineers, Niche Construction, and Geomorphic Engineers

Similarly to the development of biogeomorphology, the concept of ecosystem engineers also has roots back to Darwin's earthworm work and links to other fundamental ecological concepts such as plant succession (Buchman et al. 2007, Cuddington et al. 2007). Jones et al. (1994) coined the terminology of ecosystem engineers and, later specifically, linked ecosystem engineering to geomorphological signatures (Jones 2012). Jones et al. (1994) classified ecosystem engineers as either autogenic or allogenic. Autogenic engineers alter the environment through their physical structures (e.g., corals, mussels, etc.), whereas allogenic engineers change the environment through mechanical or chemical means (e.g., beavers, ants, rabbits, etc.). (See the sidebar, Ecosystem Engineers, Niche Construction, and Geomorphic Engineers.)

A parallel concept is niche construction, which refers to the process whereby organisms, through their metabolism, activities, and choices, modify their own and/or others' niches (Odling-Smee et al. 1996, 2003). Niche construction theory recognizes the long-term impact of the environmental modification of an organism on the evolutionary processes via ecological inheritance (i.e., legacies of biotic and abiotic changes by niche-constructing organisms modify selection pressures on descendant organisms) (Odling-Smee et al. 2003, 2013). However, the linkage between niche construction and biogeomorphology is rarely explored (but see Corenblit et al. 2011), and

ECOSYSTEM ENGINEERS, NICHE CONSTRUCTION, AND GEOMORPHIC ENGINEERS

Ecosystem engineering focuses on the modification of habitats (i.e., the availability of resources to the ecosystem engineer and other species owing to the alteration of the physical structure). Geomorphologic engineering focuses on the modification of geomorphic processes and landforms. Niche construction focuses on the ecological legacy (i.e., the long-term impacts of environmental modification on the evolutionary processes).

Ecosystem engineers can cause both short-term and/or long-term impacts on the habitat of the ecosystem engineer and other species. Some ecosystem engineers can alter selective pressures on descendant organisms. Geomorphologic engineers, a subset of ecosystem engineers, are more likely to change selection pressures on descendant organisms because the changes in geomorphic processes and landforms often have impacts for several generations.

the consequence of exotic invasion in niche construction is rarely discussed (but see Keeley 2006, Dassonville et al. 2011, Warren et al. 2011).

According to Corenblit et al. (2011), there exists a direct parallel between the ecological concepts of ecosystem engineers and niche construction and the biogeomorphic concepts of biogeomorphic succession, functional ecogeomorphology, and biomorphodynamics (see also Stallins 2006, Viles 2011). Indeed, Corenblit et al. (2011) discussed geomorphologic engineers as a major subset of ecosystem engineer organisms and presented a typology of landform modifications by these species. The biogeomorphology perspective, however, includes interactions over longer timescales than are typical in ecology and also includes geomorphology initiated, in addition to biotically triggered, interrelationships. Geomorphologic engineers often have profound and drastic effects on surface processes and landforms that are disproportionate to their biomass, which in turn often have ecological effects and exert selection pressure on organisms.

2.3. Invasive Species and Biogeomorphology

In general, invasive species can impact one or a combination of ecological, ecosystem, and geomorphological processes (**Figure 1**). Changes in ecological processes can alter population and community structure; changes in ecosystem processes can lead to the shift of trophic levels and pool sizes; and changes in geomorphological processes can modify landforms. Moreover, all three processes are interrelated; therefore, changes in one of these processes can potentially have cascading effects on the other processes.

Direct physical or geomorphic impacts by invasive species are often studied through ecosystem engineer species. In an early study, Gordon (1998) reviewed the impacts of 33 invasive plants on ecosystem processes in Florida, USA. Gordon concluded that biological invasions can potentially alter geomorphic phenomena such as erosion, marsh surface elevation, and tidal channel morphology. Crooks (2002) reviewed the effects of biological invasions involving ecosystem engineers and provided 24 specific examples. Half of these involved direct geomorphic impacts, such as increasing erosion or sedimentation, or directly modifying topography or landform morphology; others were potentially geomorphologically relevant. Invasive species as a major group of ecosystem engineers, indeed, have attracted attention in the understanding of ecosystem impacts by ecosystem engineering, especially in the past 10 years (**Figure 2**).

Ecological processes: the interactions among organisms that regulate the dynamics of ecosystems and the structure of biological communities

Nevertheless, the association between invasive species and geomorphic processes has been overlooked. The review of feedbacks between biota and geomorphology provided by Corenblit

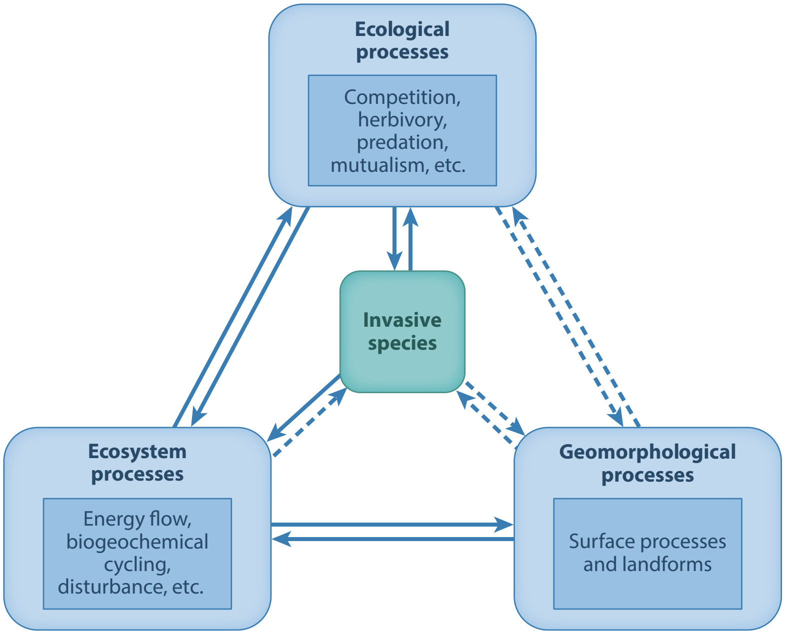

Figure 1

Impacts of invasive species on ecological, ecosystem, and geomorphological processes and their interactions. Dotted lines indicate interactions that are poorly understood at present. The diagram demonstrates the lack of understanding on (*a*) the impacts of invasives (and other organisms in general) on geomorphological processes and (*b*) the feedback of altered geomorphology on the selection pressure on community (macroevolution) and population (microevolution).

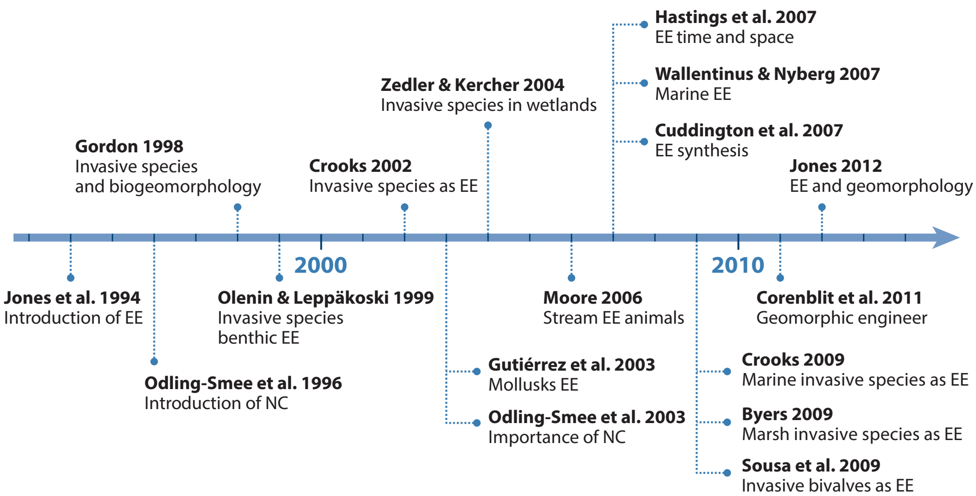

Figure 2

Selected important studies/reviews related to ecosystem engineering (EE), niche construction (NC), and geomorphic engineering concepts, with or without the inclusion of invasive species.

MAJOR BIOGEOMORPHIC PROCESSES AND THEIR RELATIONSHIPS

Bioweathering is a biotically mediated chemical weathering process. Bioerosion involves the removal of material by organisms or the indirect effect of protection reduction that facilitates erosion. Bioturbation is the biological reworking of soils and sediments. Bioconstruction is the production and accumulation of materials via organic means. Bioprotection is the prevention or retardation of mass removal or redistribution processes.

These processes are sometimes interrelated. Bioweathering and bioturbation can enhance erosion, whereas bioprotection can reduce erosion. Bioturbation and bioconstruction can occur simultaneously. Bioconstruction can enhance or reduce erosion.

et al. (2011) made only one passing reference to invasive species. However, among the eight suggested priorities for research on reciprocal interactions and adjustments between geomorphological and biological components on ecosystems, four of these priorities directly imply a key role for investigations of the geomorphological role of invasive species. Other recent reviews of geomorphology-ecology feedbacks and the geomorphic work of biota made little or no mention of invasive, introduced, or nonnative species (Atekwana & Slater 2009, Reinhardt et al. 2010, Osterkamp et al. 2012). Better understanding the biogeomorphic impacts of invasive species could help to advance our knowledge both in biogeomorphology and invasion ecology.

3. BIOGEOMORPHIC IMPACTS OF INVASIVE SPECIES

3.1. Type of Geomorphic Impacts

No invasive species is known to have completely unique geomorphic impacts. That is, the processes by which nonnative biota influence surface processes and landforms are the same as biogeomorphic impacts in general. These include bioweathering, bioerosion, bioturbation, bioprotection, and bioconstruction (a slight expansion of the typology by Naylor et al. 2002, who included weathering with bioerosion). (See the sidebar, Major Biogeomorphic Processes and Their Relationships.)

Bioweathering occurs directly due to "rock-eating" microbes and lichens, chelation by vegetation, and a number of microbially mediated chemical weathering processes. Indirect effects are also important, such as the formation of acidity due to water interaction with soil organic matter and CO_2 produced by respiration of soil organisms. Effects of invasive species on bioweathering are not well known, perhaps because so many of the key bioweathering species are microbes.

Bioerosion occurs due to trampling, vegetation destruction, digging, foraging, and tunneling by invasive animals. Severe erosion problems due to invaders are well documented in several cases, such as introduced European rabbits (*Oryctolagus cuniculus*) in Australia (see below). Bioerosion also can occur owing to the exclusion of soil stabilizers, increased uprooting, or increased landslides because of slope destabilizing effects by invasive plants.

Bioturbation may be related to erosion but in some cases is restricted to local mixing and redistribution of soil and regolith materials. Invasive species with burrowing, tunneling, or mound-building habitats may drastically increase bioturbation. The most effective floralturbation process is tree uprooting. Thus biological invasions that change vegetation cover and composition may increase or decrease floralturbation rates.

Bioprotection effects reduce or inhibit erosion and weathering. Best known of these effects are the inverse relationship between vegetation cover (and associated litter and organic matter) and rates of water and wind erosion. Biotic crusts and films may also increase surface resistance of rock and soil surfaces.

Bioconstruction is the creation of landform by biota either directly from the organisms themselves (e.g., coral reefs, peat bogs) or by purposeful activities of biota (e.g., termite mounds, beaver ponds). In other cases, bioconstruction occurs due to sedimentary accretion caused or facilitated by invasive species or by formation of organically dominated surface layers (e.g., leaf litter).

The categories described above are descriptive and not meant as a strict classification of biogeomorphic effects. Some phenomena, such as termite mounds, could be considered bioturbation or bioconstruction, for instance. These groups of processes are sometimes closely linked (e.g., bioturbation and bioerosion, or bioprotection and bioconstruction; Naylor et al. 2002). In addition, the effects described above may sometimes also have independent biogeomorphic influences via changes in disturbance regimes (e.g., Mack & D'Antonio 1998). Where factors such as stream bank erosion and barrier island overwash are important geomorphic and ecological disturbance factors, bioprotection or bioconstruction that reduces these disturbances may be critical. Likewise, bioerosion or bioturbation, for example, may introduce new disturbance factors.

3.2. Prevalence of Geomorphic Impacts by Invasive Species

To get a general idea of the prevalence of geomorphic impacts by invasive engineering species, we examined the "100 of the world's worst invasive alien species" list from the Global Invasive Species Database (**http://www.issg.org/database/species/search.asp?st=100ss**). From the "general impacts" listing in the database for each species, we determined whether the impacts included direct geomorphic impacts. We also inferred whether the impacts included indirect geomorphic effects, for example by changing vegetation cover or by predation on biogeomorphic agent species. About 30% of the listed organisms have direct geomorphic effects; another 51% have potential indirect effects, whereas only 19% were judged to have no geomorphic impacts (**Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**).

Supplemental Material

3.3. Geomorphic Impacts by Invasive Flora

Primary geomorphic impacts by invasive flora are bioprotection and bioconstruction (**Table 1**). Many invasive plants were introduced as agents for bioprotection in terrestrial, riparian, and coastal ecosystems to reduce erosion. The classic terrestrial example is kudzu (*Pueraria montana*), a vine native to Asia widely introduced in the southeastern United States in the early twentieth century to control soil erosion. Kudzu is a legume that forms a dense protective cover and traps sediments from adjacent areas and infills eroded gullies (Winberry & Jones 1973). A well-documented riparian example is the invasion of *Tamarix* in the southwest United States. Its extensive root system alters the bioprotection processes, resulting in the reduction of bank erosion, increased sedimentation, and decreased channel width (Graf 1978, Di Tomaso 1998).

Like kudzu, American beachgrass (*Ammophila breviligulata*) was introduced along the barrier islands of North Carolina's Outer Banks to stabilize sand and trap aeolian transport. The invasion of beachgrass has resulted in much larger and taller dunes than had previously been present and the reduction in the prevalence of storm overwash. The barrier island morphology changed at a broad scale, transitioning from wider and lower elevation with low, scattered dunes and overwash features to narrower, higher dunes with fewer overwash features (Godfrey & Godfrey 1973). In the intertidal and near shore areas, invasive flora such as *Zostera japonica* can stabilize sediments with their roots, providing bioprotection from infrequent wave disturbance (Posey 1988). And the

Table 1 Summary of biogeomorphic impacts by invasive flora and fauna in major ecosystem types; see Supplemental Table 2 for examples

	Bioturbation		Bioprotection		Bioconstruction		Bioerosion	
Ecosystems	**Flora**	**Fauna**	**Flora**	**Fauna**	**Flora**	**Fauna**	**Flora**	**Fauna**
Terrestrial	+	++	++	0	+	++	+	++
Freshwater								
Riparian and wetland	0	++	++	0	++	++	0	++
Stream and lake	0	+	+	+	+	++	0	++
Marine								
Dunes	0	0	++	0	++	0	+	0
Salt marsh and estuary	0	++	+	+	++	++	0	++
Intertidal and near shore	0	+	++	0	+	++	0	++

Symbols: 0, limited or no evidence of impact; +, evidences of impact, ++, strong evidences of impact.

Supplemental Material

invasion of macroalgae such as red algae (*Acrothamnion preissii*) can form mats acting as traps for sediments (Piazzi & Cinelli 2003).

Bioconstruction of invasive flora is realized through increased litter accumulation rates, increased sedimentation rates, or reduced erosion rates compared with those of their native counterparts. Bioconstruction by invasive terrestrial plants often occurs in the form of excessive litter fall. Invasive plants such as cogongrass (*Imperata cylindrica*) can form excessive layers of litter, altering topography (Tamang et al. 2008).

Bioconstruction of invasive flora in freshwater and marine systems is often achieved by increased sedimentation rates. In streams and lakes, invasion of floating plants such as water hyacinth (*Eichhornia crassipes*) increases sedimentation rates owing to their complex root structure (Gopal 1987), whereas emerged plants such as papa grass (*Urochloa mutica*) and submerged plants such as water thyme (*Hydrilla verticillata*) can increase sediment accumulation rates by reducing flow velocity and adding organic matter accretion through litter fall (Langeland 1996, Bunn et al. 1998). The proliferation of papa grass in Australia had a dramatic effect on channel morphology, where channels choked by this aquatic macrophyte inevitably become sites of sediment deposition (Bunn et al. 1998).

In coastal ecosystems, common reed (*Phragmites australis*) was found to increase the trapping of minerals and organic sediment in salt marsh environments, which accelerated the rates of vertical accretion beyond the threshold of native plant assemblages (Lathrop et al. 2003, Rooth et al. 2003). Common reed also has the ability to fill in small creeks, reducing 8% of the length of first-order tidal creeks in a 20+ year period in New Jersey (Lathrop et al. 2003, Zedler & Kercher 2004). Another invasive exotic plant that has been shown to have a drastic impact on salt marsh environments, especially in China, is *Spartina* spp., which has converted more than 112,000 ha of mudflats to salt marshes in coastal China because of high sedimentation rates (An et al. 2007, Liao et al. 2007). The invasion of mangroves (*Rhizophora mangle*) in Hawaii reduced erosion and converted mudflats to monocultural mangrove forests (Allen 1998).

Although there is no reason to believe bioturbation rates by invasive species are significantly different compared with their native counterparts (e.g., native versus invasive trees), invasion of shrubs and trees into grasslands can significantly increase bioturbation rates. In particular, uprooting of invasive trees may induce significant bioturbation. Bioturbation rate by root growth and decay is four times higher in temperate forest than temperate grassland (Gabet et al. 2003). Storm-related uprooting of invasive trees can further impact bioturbation rates. For example, the invasion of Chinese tallow trees (*Sapium sebiferum*) in Texas, USA, can quickly convert native prairie to woodland (Bruce et al. 1995), subjecting soil to uprooting during major storm events.

In addition, invasions of exotic flora can indirectly increase erosion rates by eliminating soil stabilizers or increased uprooting and landslides. For example, the invasion of Australian pine (*Casuarina equisetifolia*) can increase erosion by excluding soil stabilizers through increased litter production (Gordon 1998). The invasion of broomsedge (*Andropogon virginicus*) can increase landslides due to its low transpiration rates during winter, resulting in oversaturated soils (Crooks 2002).

3.4. Geomorphic Impacts by Invasive Fauna

Primary effects of invasive fauna are bioturbation, bioerosion, and bioconstruction (**Table 1**). Bioturbation and bioerosion, which are often tightly linked, are the prevalent forms of geomorphic impacts by invasive fauna. According to Wilkinson et al. (2009), vertebrates, earthworms, ants, and termites displace great volumes of soil, with maximum global rates equivalent to maximum global rates of tectonic uplift. Some of the most familiar terrestrial examples include the common earthworm (*Lumbricus terrestris*) invasion in northern temperate forests, the European rabbit in Australia, and the invasion of red imported fire ants (*Solenopsis invicta*) across the globe. Bioturbation by earthworms can be evident in the subsoil up to 2.5 m below the surface (Darwin 1881), and the bioturbation rate can be as high as 40–63 tonne ha^{-1} $year^{-1}$ in temperate maritime systems (Wilkinson et al. 2009). The mounding and subsurface tunneling by fire ants have huge impacts on bioturbation rates. Porter et al. (1992) found mean mound densities at 51 sites in the southeastern United States to be 170 ha^{-1}, with a mean surface volume of 0.027 m^3, a bioturbation rate of about 460 mm ka^{-1} (greater than the typical rates of weathering and denudation in the southeastern United States).

Invasive animals in freshwater and marine systems often drastically change bioturbation rates and subsequent bioerosion rates through burrowing and nest construction activities. In streams, for example, invading Chinook salmon (*Onchorhynchus tshawytscha*) in New Zealand impacts geomorphology through bioconstruction by digging large redds in river beds during spawning (Field-Dodgson 1987). Invasion by exotic crustaceans, such as the European green crab (*Carcinus maenas*), Chinese mitten crab (*Eriocheir sinensis*), and various species of crayfish, have resulted in higher bioturbation and bioerosion rates (Gherardi 2006, Holdich & Pöckl 2007). In marine systems, for example, the construction of networks of tubes by the invasive amphipod crustacean *Corophium curvispinum* (van den Brink et al. 1993) and deep burrowing by the invasive worm *Marenzelleria viridis* (Żmudziński 1996) have increased bioturbation rates, resulting in a thicker surface sediment layer. The invasion by the isopod *Sphaeroma quoyanum* can convert marsh to mudflat by burrowing into mud banks of salt marshes and increasing erosion rates (Talley et al. 2001).

Both terrestrial and aquatic animals can also increase bioerosion rates by removing vegetation through grazing, browsing, or uprooting. The wide spread of feral pigs (*Sus scrofa*) has profound geomorphic impacts via grazing and associated alteration in surface vegetation around the world (Butler 2006, Barrios-Garcia & Ballari 2012). Trampling and uprooting by feral pigs have substantially increased bioturbation and bioerosion in many regions (2–3.6% in Australia and 6–11% in Hawaii) (Welander 2000, Barrios-Garcia & Ballari 2012). The common carp (*Cyprinus carpio*) can uproot aquatic macrophytes, resulting in increased bioerosion (Matsuzaki et al. 2009).

The invasion by coypu (*Myocastor coypus*) and muskrat (*Ondatra zibethicus*) in Europe have caused riverbank damage due to increased bioerosion from excessive vegetation removal and burrowing activities (Bertolino & Genovesi 2007).

Geomorphic engineers: organisms that modify sediment and landform dynamics, causing changes in Earth surface processes and landforms that often have long-term impact

Landscape metamorphoses: major, long-lasting changes in morphology and functioning of landscape or geomorphic systems

Invasive fauna can also change geomorphic processes drastically through bioconstruction. A classic example is the invasion by the North American beaver (*Castor canadensis*) in Tierra del Fuego in Chile. Beavers can dramatically alter geomorphology by felling trees and building dams, converting large areas of closed *Nothofagus* forest to meadows dominated by grasses and sedges, elevating water tables, and reducing stream velocities and inducing sedimentation (Lizarralde et al. 2004, Anderson et al. 2006, Butler 2006).

Mollusks, as one of the common phyla of aquatic geomorphic engineers, often impact biogeomorphology through autogenic bioconstruction. Mollusks produce shells that can last for decades after the death of the animal, providing complex hard substrate on soft sediments (Gutiérrez et al. 2003, Sousa et al. 2009). For examples, the invasion by exotic bivalves such as *Musculista senhousia* (Crooks & Khim 1999), *Crassostrea gigas* (Ruesink et al. 2005), and *Dreissena polymorpha* (Vander Zanden et al. 1999) can significantly impact geomorphology through shell production and sediment trapping. One of the byproducts of these autogenic bioconstructions is bioprotection. For example, the creation of byssal mats by the invasive Asian date mussel (*Musculista senhousia*) can significantly increase the percent of fine sediments and combustible organic matter and sediment shear strength (Crooks 1998).

4. SYNTHESIS

4.1. Landscape Metamorphosis

Metamorphosis in geomorphology is used to describe major, long-lasting changes in morphology and functioning of landscapes or geomorphic systems, broadly analogous to state shift in ecology. The term has been most commonly applied in fluvial systems but is applicable to geomorphic systems in general.

Supplemental Material

Some of the invasive species impacts described above and listed in **Supplemental Table 2** constitute landscape metamorphoses. The transition from tidal flats to salt marshes wrought by invasive *Spartina*, for instance, involves changes in elevation, topography, substrate, mass flux regimes, hydrology, and both geomorphic and ecological functioning (Wang et al. 2006). Metamorphosis of channel systems associated with invasive *Tamarix* involves changes in channel dimensions, width/depth ratios, and flow regimes (Graf 1978). Nonnative beachgrass has led not only to growth and stabilization of sand dunes but to fundamental changes in barrier island morphology and washover dynamics on the Outer Banks, USA (Dolan & Godfrey 1973, Godfrey & Godfrey 1973, Godfrey 1977).

These cases of landscape metamorphosis associated with invasive species are instructive in several ways. First, there is not a one-to-one correspondence between impact severity and metamorphosis, at least not at a short timescale. The latter is associated with severe impacts, but severe impacts are not necessarily associated with landscape metamorphosis, as illustrated by examples of rabbits in Australia and feral hogs in the United States. Second, the available examples all involve geomorphic settings that are inherently dynamic—stream channels, intertidal zones, and barrier islands. Such environments are likely more susceptible to metamorphosis in general, and metamorphosis is certainly more likely to be observed and documented over contemporary and historical timescales in such environments than in less dynamic environments. In a general analysis of scale effects in biogeomorphology, Phillips (1995) presented several methods for comparing rates, time steps, and characteristic temporal scales of both geomorphic and vegetation processes to identify domains in which biotic and geomorphic effects are strongly codependent. This appears to be the case for the landscape metamorphosis examples above.

In two of the cases—barrier islands and intertidal zones—the nonnative species were deliberately planted to stabilize sand dunes and "reclaim" tidal mudflats. Thus in these cases the biogeomorphic engineer species were introduced precisely because of their geomorphic engineering potential. The expansion of *Tamarix* was not deliberate but was a direct outcome of human agency. The *Tamarix* tree is an opportunistic colonizer, which "occupied land made available by the plow, the bulldozer, and the shrinking of a channel depleted of flow by upstream water development" (Everitt 1998, p. 658). *Tamarix* did not actively displace native species; rather it outcompeted them for newly available habitats. This example suggests that landscape metamorphosis by invasive species (or colonizers in general) may depend on other anthropic disturbances or habitat modification (or on major natural disturbance events), at least during the introduction stage.

On geological timescales there is evidence of landscape metamorphosis associated with biogeomorphic effects, such as the role of vegetation (particularly woody plants) in transforming many braided and anabranching fluvial systems to meandering streams (Davies & Gibling 2013, Gurnell 2014) and the coevolution of grasses and herbivores in the development of soil and regolith covers (Retallack 2007).

However, biogeomorphic landscape metamorphosis on shorter timescales associated with ecological change may be restricted to highly dynamic environments where the timescales of ecological and geomorphological dynamics are commensurate and to situations in which disturbances (including deliberate introductions) occur. Nevertheless, cautions need to be made regarding the impacts of invasive species on landscape metamorphosis, especially in slow turnover ecosystems, such as forest ecosystems, in which geomorphic changes are difficult to assess because the impacts of invasive species may take decades to centuries to manifest themselves given the life spans of the taxa involved (Hughes et al. 2013).

4.2. Coevolution

Coevolution, in the sense of path-dependent landform/landscape and ecosystem development involving interactions of biota, geomorphic and ecological processes, and landforms (**Figure 1**), is evident from a number of the examples given above. An intriguing possibility is that insights gained from contemporary studies of geomorphic effects of newly arrived organisms can help shed light on the long-term coevolution of landforms and biota. Cotterill & De Wit (2011), for example, invoke "geoecodynamics" as a tool for developing a "unified narrative of landscape evolution." Their geoecodynamics is, in essence, application of biogeomorphology at the timescales of geological and biological evolution, with the recursive relationships between biological and geological evolutionary events at the core. In this section, we address the specific issue of coevolution in terms of invasive species exerting selective pressure via geomorphic influences.

Existing studies have noted the evolutionary consequences of biological invasions. The most direct evolutionary impact by invasive species is the hybridization between native and invading species. Invasive species also change selective pressure on native species through the alteration of ecological processes such as competitive exclusion, predation, mutualism, or facilitation, or the alteration of ecosystem processes such as biogeochemical cycling and disturbance regimes. In addition, invasive engineering species can modify selection pressures via the alteration of geomorphic processes. Erwin (2008) explicitly considered ecosystem engineering and niche construction as an important (and increasing, over geologic time) influence on selection and biodiversity.

Relatively few studies of coevolution have focused on invasive engineering species or on selection effects of biogeomorphic impacts of invasives, whether or not they involve engineering.

An exception is Didham et al. (2007), who described selection consequences of invasive species in both marine (Mediterranean Sea) and terrestrial (California grassland) environments. Another is Gribben et al. (2012), who found the invasive seaweed *Caulerpa taxifolia* creates habitats with reduced water flow, siltier bed sediments, and lower dissolved oxygen. This selects for different phenotypes of the associated native bivalve *Anadara trapezia*.

Selection pressure also occurs in association with vegetation change on sand dunes, such as that associated with the introduction of beachgrass described above. As beachgrass promotes sand deposition and dune growth, plant burial becomes a significant stress. This favors more burial-tolerant species (including the invader) and more burial-tolerant genotypes and phenotypes within species (e.g., Maun 2008, Zarnetske et al. 2012).

The geological record shows several examples of coevolution involving biogeomorphic effects of evolutionary "invaders" (i.e., new species). For example, a major diversification of metazoan species occurred around the Ediacaran-Cambrian transition about 542 Ma. Erwin & Tweedt (2012) attribute this to ecological engineering feedbacks, which accelerated dramatically in the Cambrian. The most important feedback, according to their study, was chemical modification of the environment through biogeomorphic effects of engineer species such as sponges, via bioturbation and filtering of suspended solids. Likewise, evolutionary newcomers (the earliest land plants) had profound inputs on fluvial systems: decreased sediment yields and soil erodibility, reduced surface runoff and aeolian winnowing of fine sediments, and increased bank stability and hydraulic roughness (Davies & Gibling 2010). Stream systems were transformed in some cases from braided to single-thread meandering forms. This transition must have in turn created new habitats and niches and, thus, influenced selection.

Invading or colonizing species provide something of a modern, shorter-timescale analog of the evolutionary appearance of new varieties. Erwin & Tweedt (2012), for example, based their arguments in part on modern analogs (biogeomorphic effects of oysters). And the assumption that the appearance of new stream morphologies created new habitats and niches has a strong foundation in studies of modern fluvial biogeomorphology. Thus, though the study of the role of biogeomorphic feedbacks in natural selection is in its infancy, both modern examples and the paleoecological record suggest that coevolution associated with biogeomorphic effects of invasive species can provide key insights to evolutionary ecology and geomorphology more generally.

4.3. Generalizations About Biogeomorphic Impacts by Invasive Species

In general, direct geomorphic impacts of invasive species do not usually differ overall from biogeomorphic impacts. However, invasive or colonizing species are far more likely to lead to major geomorphic changes or landscape metamorphosis. Major biogeomorphic impacts, including bioturbation, bioerosion, bioconstruction, and bioprotection, are commonly observed in various systems invaded by exotic species. Invasive species probably have significant impacts on weathering. However, these are difficult to assess for two reasons: (*a*) biotic effects on weathering are largely microbial, and little is known about invasive microbes or weathering impacts of changes in microbial communities associated with invaders; and (*b*) plants are significant agents of weathering, but the relative weathering efficacy of invasive versus native vegetation has not been assessed.

Indirect geomorphic effects of invasive species often derive from their impacts on preexisting species via the alteration of ecological processes, such as herbivory, predation, competition, allelopathy, or mutualism. In some cases these are readily apparent, as when extensive herbivory or vegetation disturbance by invaders increases erosion. However, where the geomorphic influences of the stressed native species are poorly understood, these impacts are difficult to detect. Indirect geomorphic effects of invasive species can also derive from their impacts on the alteration of ecosystem processes, such as disturbance regime shifts. For instance, increased fire frequency and severity due to exotic plant invasion could lead to increased erosion rates. Therefore, biogeomorphologically significant invasive species include both engineering species with direct geomorphic effects and nonengineering species with indirect geomorphic effects. However, the consequence of geomorphic change to the invader can be beneficial (e.g., beaver), incidental or irrelevant (e.g., earthworms), or negative (e.g., ants) to their success (Jones et al. 1997, Christe et al. 2003).

Transitional areas between terrestrial and aquatic systems, such as fluvial systems, wetlands, salt marshes, and coastal beaches and dunes, seem particularly vulnerable to biogeomorphic impacts of invasive species (**Table 1** and **Supplemental Table 2**). Potential reasons include intermediate energy levels of these systems, dynamic geomorphic setting, and strong biogeomorphic coupling. This is similar to earlier findings of ecosystem engineering. Corenblit & Steiger (2009) found that geomorphic processes are controlled or modified by vegetation in terrestrial-water interfaces such as fluvial corridors, peatlands, and intertidal marshes. After reviewing ecosystem engineering species in stream systems, Moore (2006) concluded that ecosystem engineering is more important in streams with low to intermediate hydrologic energy and relatively unimportant in streams with overwhelming hydrologic energy. This is potentially because in ecosystems with intermediate energy, altered biogeomorphic processes by invasive geomorphic engineers occur at a perceptible rate, which allows landform alteration to be observed in ecological timescale.

Supplemental Material

Observation bias is inevitable. Geomorphic impacts are more likely to be noted and documented when they are visible (e.g., aboveground terrestrial versus belowground or benthic) invaders with high impacts per capita, when the invaders are viewed as problematic from a human perspective, and/or the invaded system is more susceptible to geomorphic change. For example, although earthworms move tremendous volumes of subsoil, geomorphic impacts are not obvious because terrestrial ecosystems have relatively slow geomorphic turnover, and earthworms live belowground for most of the time and have low per capita impacts. By contrast, the geomorphic impacts by beaver invasion are widely noticed, because beavers can be problematic for natural resource management, have high impacts per capita, and live in riparian systems susceptible to geomorphic change.

This review also revealed that biogeomorphic processes often transcend the categories of bioweathering, bioturbation, bioerosion, bioprotection, and bioconstruction. Burrowing and tunneling, or tree uprooting, for example, may involve construction, bioturbation, and erosion. Bioconstruction consists of at least four distinctly different phenomena: (*a*) direct construction from organisms (e.g., coral reefs, shell bars and shoals, peat), (*b*) initiation or increase of sediment deposition (e.g., marsh vegetation), (*c*) construction from organic matter of other species (e.g., beaver dams), and (*d*) construction from sediment or regolith materials (e.g., mounds, tunnels, burrows).

5. MANAGEMENT IMPLICATIONS

Because invasive geomorphologic engineers often have profound and drastic effects on surface processes and landforms that are disproportionate to their biomass, management priority should be given to biogeomorphologically significant invasive species for the following reasons. First, as suggested by Simberloff & Von Holle (1999), positive interactions among invasive engineers and other exotic species can lead to invasion meltdown. For example, the invasion of feral hogs in Hawaii has significantly changed the bioturbation rates during their rooting activities, which favors the invasion of several other exotic species (Aplet et al. 1991). Second, invasion-induced landscape metamorphosis can be irreversible and long lasting. The examples discussed earlier (e.g., *Spartina* and *Tamarix* invasion) illustrate that invasion can result in a total state shift in both landforms and ecosystem composition and structure. Third, geomorphic engineers can also alter selection pressure both at the population level (microevolution) and community level (macroevolution), resulting in evolutionary change and ecosystem alteration.

Among various ecosystems, geomorphically dynamic environments with strong biogeomorphic coupling are more vulnerable to major geomorphic impacts. Therefore, extra attention should be paid to these systems to minimize invasion-induced geomorphic process change or to avoid landscape metamorphosis. These geomorphically dynamic systems, especially land-water interface systems, are also often invasion epicenters due to high invasion propagule pressure and human-induced disturbances (Byers 2009). In addition, geomorphic disturbance (natural or human) is one of the key factors enabling establishment or spread of aliens. However, less geomorphically dynamic terrestrial systems should not be ignored, owing to the long-lasting impacts of certain organisms involved. For example, direct geomorphic impacts by shrubs and trees can last decades to centuries, without accounting for their postmortality legacy effects.

Complications could also arise in restoring ecosystems invaded by geomorphic engineering species. Invasive biogeomorphic agents may render habitat unsuitable for the restoration of natives. The geomorphic impacts of invasive engineers can persist after the engineer is dead or absent (legacy effect) through autogenic physical structure building or allogenic physical state change (Jones et al. 1994, Hastings et al. 2007). For example, control efforts that focus solely on the removal of *Spartina* via herbicide applications versus those that focus on both biomass and structure removal via mechanical methods can have a profound influence on the future course of restoration (Lambrinos 2007). Therefore, ecosystem restoration in systems that have experienced landscape metamorphosis can be extremely challenging.

6. KNOWLEDGE GAPS AND FUTURE DIRECTIONS

One big challenge in synthesizing the geomorphic effects of invasive species is the quantification of geomorphic impacts. Rates of biogeomorphic processes have been quantified using a variety of techniques, making comparisons and syntheses difficult. We recommend measuring or estimating impacts using mass per unit area per unit time whenever possible (perhaps in addition to other situation-specific criteria) to facilitate comparisons in energy-based units. In addition, a general framework, such as the one advocated by Parker et al. (1999), should be applied to account for important factors such as per capita rate and population density. A common framework with the same measuring unit will allow for a more objective comparison of geomorphic impacts among different systems.

Although microbes are prevalent in and important to many ecosystems, little is known relating the direct impacts of microbial invasion to geomorphic processes. Indirect geomorphic impacts by invasive microbes can sometimes be apparent, such as the region-wide mortality of American chestnut caused by the chestnut blight (*Cryphonectria parasitica*) invasion. As pointed out by Viles (2012), microbes play a key role in the connections between biota and landforms in all Earth surface processes. Therefore, invasion of new microbial species or groups or shifts of microbial communities associated with exotic plant invasions could have drastic effects on geomorphic impacts. Research is needed to better understand the geomorphic impacts of microbial invasions.

Invasive species can impact the evolutionary process. Direct evolutionary impacts such as hybridization and change of selective pressure via the alteration of ecological processes have been widely documented. By contrast, invasion-related coevolution of ecosystems and landforms is still not well studied. There exist limited case studies documenting the coevolution of landforms and ecosystems invaded by exotic species. Better understanding of the coevolution process using invasive engineering species could shed light on general principles of coevolution of biota, landforms, and soils by elucidating the biotically driven changes or metamorphoses of ecosystems and geomorphic landscapes associated with invasive organisms.

SUMMARY POINTS

1. Biogeomorphic impacts by invasive species are prevalent either through direct geomorphic effects by engineering species or through indirect geomorphic effects by nonengineering species.
2. Biogeomorphic processes often transcend the categories of bioturbation, bioerosion, bioprotection, and bioconstruction. Primary geomorphic impacts by invasive flora are bioprotection and bioconstruction, and primary effects of invasive fauna are bioturbation, bioerosion, and bioconstruction.
3. Transitional areas between terrestrial and aquatic systems, such as fluvial systems, wetlands, salt marshes, and coastal beaches and dunes, seem particularly vulnerable to biogeomorphic impacts by invasive species.
4. Invasion by some exotic species can result in landscape metamorphosis, especially in dynamic systems, which can have long-lasting effects on ecosystem, geomorphic, and evolutionary processes.
5. Invasive species can impact the coevolution of path-dependent landform/landscape and ecosystem development, altering selection pressures in both macroevolution and microevolution.
6. Management priority should be given to biogeomorphologically significant invasive species, especially in dynamic systems.

FUTURE ISSUES

1. Standard quantification of geomorphic impacts, such as energy-based units, is needed to synthesize the geomorphic effects of invasive species.
2. Understanding of geomorphic impacts by invasive species in soils, especially the direct impacts of microbial invasion on geomorphic processes, can advance our knowledge of key geomorphic processes such as bioweathering.
3. Better understanding of the coevolution process using invasive engineering species could shed light on general principles of coevolution of biota, landforms, and soils.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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