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Insects as zoogeomorphic agents: An extended review

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ABSTRACT: Insects are the largest and most diverse group of living organisms on Earth, playing a critical but underestimated role as agents of geomorphic change. Burrowing insects create micro-scale landforms such as subterranean tunnels and surface mounds and, by this way, exert an influence on hydrology, soil erosion and sediment transfer at a wider landscape scale. However, social insects represented by ants and termites were the main taxa studied as geomorphic agents and ecosystem engineers. This paper proposes an extended and critical literature review of insects as zoogeomorphic agents, with reference to various taxonomic orders and families of insects having a burrowing behaviour. It provides a large overview of their primary and secondary impacts on Earth surface systems, both supported by naturalistic evidence and available quantitative data. Some evolutionary insights are discussed based on fossil evidence of geomorphic work by insects and, at finer temporal scale, on recent advances in radiometric and luminescence dating of insect mounds. Finally, this paper explores the fruitful links between geomorphology and entomology, and suggests several research perspectives in order to develop an integrated understanding of the importance of insects in Earth surface processes and landforms.

KEYWORDS: Zoogeomorphology; Entomofauna; Burrows; Mounds; Bioturbation; Soil erosion.

Introduction

Insects are the most diverse and abundant class of animals on Earth, with ~1 million described species – out of a total estimate of ~5.5 million species – that dominate animal biomass in many terrestrial ecosystems (Stork, 2018). Their role as geomorphic agents has been recognized for more than a century (Branner and Reid, 1900) but, since then, scientific studies and syntheses have mainly been focused on select groups, especially ants and termites (e.g., Humphreys, 1981; Goudie, 1988; De Bruyn and Conacher, 1990; Butler, 1995; Whitford and Eldridge, 2013). Overall, little attention was paid to the geomorphic impacts of insect groups other than social ants and termites. Yet almost every insect order has members that dig or burrow into soils or sediments at some stage in their life cycle (Eiseman et al., 2010), with direct or indirect geomorphic effects to be considered from a very local scale to a wider landscape scale. Compared to the geomorphic changes induced by vertebrates (for example, the well-known and visible effects of dam-building beavers: Butler and Malanson, 2005), those by insects are effectively more subtle except for the outstanding surface mounds created by social insects. Less visible, but no less important, are the bioturbational effects of burrowing insects affecting both terrestrial (e.g., soils and weathering mantles) and aquatic environments (e.g., lake and river sediments). A comprehensive overview of the geomorphic influences of entomofauna thus appears essential for a global understanding of Earth surface processes and landforms.

Links between insects and landforms lie in the scope of zoogeomorphology, defined by Butler (1995) as the study of geomorphic effects of animals. Based on extensive study of the behaviour of worms and their effects on the earth's surface, the final book by Darwin (1881) can be considered as the first study lying in the field of zoogeomorphology (Tsikalas and Whitesides, 2013). Although earthworms do not belong to the class of insects, this seminal work had a wide influence on the scientific community, especially for the subsequent study of ecological and geomorphic implications of entomofaunal activity. In this light, the work by Branner (1909) was one of the first zoogeomorphological studies dedicated to an insect group (ants), including accurate scientific examinations on ant mound morphometry and density as well as calculations of mounding rates which were suitably compared to Darwin's estimates on earthworm castings. Few studies or general considerations on the geomorphic impacts of insects were produced until the end of the 20th century, and were mainly focused on soil-dwelling ants and termites and their role as pedoturbational agents (De Bruyn and Conacher, 1990, and references therein).

Two important milestones in considering the potential of insects as geomorphic agents came in the decades 1980'-1990' with the publication of Viles's (1988) book *Biogeomorphology* and Butler's (1995) book *Zoogeomorphology – Animals as Geomorphic Agents*. However, in the first one, only one chapter was devoted to invertebrates through the geomorphic effects of termites and earthworms in the tropics (Goudie, 1988), a major part of the volume focusing on plant-landform interactions. In the second one, the emphasis of the book was clearly on the geomorphic influences of vertebrates, although a chapter specifically examined the geomorphic effects of invertebrates (in which insects – mainly termites and ants – were treated in company with earthworms, arachnids, crustaceans and molluscs). At the same time, the study of ecosystem engineering was being defined by Jones et al. (1994), with many subsequent studies that contributed to examine the role of insects as agents of landscape change, beyond their applied interest for the restoration of ecosystem functioning. However, the same scientific bias was observed, with studies focusing mainly on ants and termites as keystone ecosystem engineers (e.g., Lavelle et al., 1997; Dangerfield et al., 1998; Jouquet et al., 2006; Cammeraat and Risch, 2008; Meyer et al., 2013).

The aim of this paper is to provide an extended and critical literature review of insects as zoogeomorphic agents, and to contribute to exploring the links between geomorphology and entomology. Specific relationships between insect ethology and geomorphic processes are examined for a wide range of insect orders, including burrowing and digging for nesting, oviposition and pupation as well as for food provision and predation. The paper also examines the direct and indirect geomorphic effects of insects in a distinct way. Direct physical or geomorphic impacts of burrowing insects are first analyzed, leading to propose an original classification of entomolandforms – i.e. landforms directly created by insect activity. Indirect influences on landforms and geomorphic processes are then put forward through a review of the role of insects in the initiation of secondary landform construction and destruction as well as in enhancing soil erosion and sediment yield. Finally, a discussion opens on timescales for the impact of insect activity on geomorphic change, through the fossil records of entomogeomorphic activity and the recent insights provided by mound dating.

Insect ethology and geomorphic processes

Insect ethology, i.e. the study of insect behaviour, is a major aspect to consider in the understanding of elementary geomorphic processes. Despite a certain lack of attention by geomorphologists on this aspect, insect-induced processes have been variously discussed in several publications, mainly from a pedoturbational perspective (e.g., Humphreys and Mitchell, 1983; Goudie, 1988; Mitchell, 1988; De Bruyn and Conacher, 1990; Butler, 1995; Paton et al., 1995; Wilkinson et al., 2009; Butler et al., 2013; Whitford and Eldridge, 2013). Readers interested in the pedoturbational actions of ants and termites are asked to refer to the above-mentioned references for further details. In this section are examined the elementary geomorphic processes of burrowing and digging induced by a wide variety of insect orders and families (Table I) with respect to their morphological and ethological characters.

Burrowing behaviour for nesting and pupating

Numerous insects have a burrowing behaviour – although often transient – to survive and to accomplish various stages of their life cycle (from larva to imago). Nesting is one of the main geomorphic manifestations of burrowing insects. Social insects like ants, termites, bees and wasps build the most elaborate structures, able to maintain nearby constant temperature and humidity, and to resist to climatic hazards and heavy rains. The geomorphic processes induced by soil-dwelling ant and termite colonies are probably the most conspicuous evidences and best-known examples of the bioturbational impacts of insects as ground nesters, with various nest architectures of several meters high and deep, depending on the species. The termite nest of *Macrotermes michaelseni* is one of the most complex yet described (Turner, 2000; Figure 1A): the core of the mound forms the central living area with nursery galleries and fungus gardens, surrounded by a complex network of tunnels devoted to ventilation and thermoregulation (central chimney, surface conduits and radial channels). Ant nests excavated into the soil and saprolite layers are generally complex as well: their typical architecture consists of vertical tunnels connecting relatively horizontal chambers of oval to lobed outline, often surmounted by surface mounds derived from excavated soil material (Tschinkel, 2003; Figure 1B).

Belonging to the same taxonomic order as ants (Hymenoptera), bees, wasps, and sawflies also have many members that burrow into the ground for nesting (Cane, 2003; Sarzetti et al., 2013). Morphologically, digging wasps and bees have three basic tools that are involved in burrowing: mandibles, front legs and pygidial plates (Genise, 2016). Their remarkable adaptation to burrowing is responsible for a wide diversity of ground nest structures, ranging from simple burrows to complex tunnels or galleries with multiple cell houses – into which eggs are laid – and associated surface tumuli (Figure 1C). Contrary to ants and termites, digging wasps and bees are mainly unsocial or solitary species: this is the case of the so-called mining bees (family Andrenidae) which excavate vertical burrows connecting individual cells, that can finally form large nest aggregations up to several thousand units in favorable places, often in sandstones or sandy substrates.

Within the Orthoptera order, mole crickets (Gryllotalpidae) are a unique ensiferan clade distinguished from other true crickets by morphological and behavioural adaptations to burrowing and subterranean life-style, such as compact cylindrical bodies, reduced eyes and forelegs transformed into efficient digging tools very similar to those of true mammalian moles, a notable case of evolutionary convergence (Bidau, 2014). In the southern mole cricket *Neoscapteriscus borellii*, the male digs his burrow with a horn-shaped entrance acting as a resonator for calling (Nickerson et al., 1979; Figure 1D). After underground mating, the female builds a nesting chamber deeper in the soil for laying her eggs. Another ensiferan group of fossorial orthopterans is represented by the endemic Australian family Cooloolidae, notably its robust representant called Cooloola monster (*Cooloola propator*). Within the Caelifera suborder to which belong the grasshoppers, lesser-known families of endogean orthopterans are the worm-like sandgropers (Cylindrachetidae) and the pygmy mole crickets (Tridactylidae) endowed with a pair of strongly modified digging forelegs convergent with those of Gryllotalpidae. Many other orthopterans are not subterranean but actively participate in digging and burrowing processes through oviposition (Chopard, 1938). Indeed, numerous bush crickets and grasshoppers are soil-ovipositing species; the ovipositor appendages of females consist of a sabre-like, egg-laying apparatus in the cricket species, and of a pair of shovel-shaped valves in the acridid species that are both adapted to dig a deep chamber in the soil for egg burial.

Some minor, but interesting insect orders, are true fossorial animals adapted to successfully dig burrows in the soil for nesting. Close to the Orthoptera order, the Dermaptera (earwigs) are ground-dwelling insects having cylindric bodies and forelegs modified for digging. From an ethological viewpoint, female earwigs have the specificity to dig a deep nest burrow where they care for the eggs (Radl and Linsenmair, 1991). The Embioptera (webspinners) are members of a small order of insects and live in small colonies in subterranean nests of silk-lined burrows and galleries (Downing, 2008). The same behaviour of maternal care is observed in the webspinner females, which typically guard the eggs in the burrows and protect them with a silk covering, a particular behaviour shared with burrowing wolf spiders (McMillan et al., 2016).

Contrary to the above-mentioned groups, a major part of insect orders has a transient burrowing behaviour, mainly as larvae and nymphs, and become terrestrial or flying insects as adults. The Lepidoptera (butterflies and moths, though only moth larvae are soil-dwellers) burrow into the soil to pupate. Sphinx moths (Sphingidae) are one of those species that overwinter in the soil as pupae. Digging behaviour for pupating is reported for a wide range of insect orders, including Coleoptera (dung beetles, scarabs, chafers, weevils), Diptera (flies), Mecoptera (scorpionflies) and Megaloptera (alderflies, dobsonflies, fishflies). In the Trichoptera order (caddisflies), larvae burrow and pupate into the bottom sediment of streams, and have direct and indirect geomorphic effects by modifying the hydraulic properties of bed material and the permeability of hyporheic zones (Johnson et al., 2009; Mason et al., 2019). Some hemimetabolous insects (i.e., without pupal stage) may also have underground larval stages whose duration is often much longer than the terrestrial adult stage. For example, in the Hemiptera order, cicadas live underground as larvae for most of their lives at depths down to about 2.5 m, where they dig their larval chambers. In the Odonata order, most species of petalurid dragonflies have a fossorial larval stage; larvae typically excavate burrows in soft peaty soils in mires or along stream margins (Baird, 2014). In a similar way, Ephemeroptera (mayflies) do burrows into the substrate of lakes or streams throughout most of their lives as aquatic larvae, a burrowing behaviour described along the river Marne by the French naturalist Réaumur as soon as the 18th century (Réaumur, 1742; Figure 2).

Burrowing behaviour in relation to food provision and predation

After nesting and pupating, burrowing is involved in a variety of other functions relating to the feeding behaviours of insects, including the search for below-ground food, food caching, geophagy, predation as well as sheltering from predators. Belonging to the same order as termites (Blattodea) despite strong differences in size and sociability, the Australia’s giant burrowing cockroach (*Macropanesthia rhinoceros*) spends most of its time in foraging for food. As highlighted by its vernacular name, the species burrows an underground alcove at ~1-meter depth where the female provides food for her larvae until they leave the nest and construct their own burrows (Rugg and Rose, 1991). Food provision for offspring in underground galleries and cells is, in fact, a common behaviour reported in various insect groups such as termites, ants and bees, and is fully integrated in the nest architectures and functions.

Hoarding or food caching in insect behaviour is also a common process involved in burrowing. One fascinating behaviour of some granivorous ground beetle larvae (Coleoptera: Carabidae) is the creation of burrows for caching seeds of grasses, particularly in the genus *Harpalus* (Kirk, 1972; Hartke et al., 1998). Their burrows vary in size according to larval stage and species, with a diameter around 3-5 mm and a depth up to 70 cm, and are generally topped with a small mound or tumulus (Figure 3A). In the order Orthoptera, the ensiferan family Gryllidae has many subterranean members that live in multifunctional burrows. Besides using the burrow as a calling site or as a temporary shelter from predators (Gawałek et al., 2014), several species of burrowing crickets use it for food storage. This is the case of the Tobacco Cricket, *Brachytrupes membranaceus*, which digs a burrow averaging 50 to 80 cm in depth, with an enlarged chamber in which the cricket stores food (Büttiker and Bünzli, 1958). The burrow is dug by the mandibles, and the forelegs serve to push the excavated material out of the entrance, where a mound can reach a height up to 30 cm (Figure 3B).

Geophagy, i.e. the eating or ingestion of soil, is another common phenomenon for pedofauna, especially earthworms, but it seems relatively uncommon in the feeding behaviours of insects. Soil-feeding termites are the most diverse and abundant termite group within tropical forests, and are unique among insects in feeding unselectively on mineral soil (Brauman et al., 2000). In particular, soil feeders of the genus *Cubitermes* are a successful termite group in the rainforests of Central Africa, with direct effects both on soil properties and on geomorphological heterogeneity (Donovan et al., 2001). Rare cases of geophagy are reported in insect larvae of Lepidoptera (moth species) and Diptera (e.g., *Bibio marci*), but they are mainly litter-feeding species only participating in the soil humification process (Dickinson and Pugh, 1974).

Digging and cratering as a consequence of predatory behaviour are no less original geomorphic processes reported in some insect species, either terrestrial or aquatic. Unique in the insect world for their highly sedentary predatory behaviour, pit-digging larval antlions (Neuroptera: Myrmeleontidae) have elaborated a special mechanism for trapping prey by digging funnel-shaped pits in sandy soils (Hollis et al., 2011; Figure 3C). The larva has a flat head and sharp mandibles with which it digs and throws the sand up and out of the hole. After that, it buries itself at the bottom of the pit and waits for an ant or another insect to stumble in. The shape of the funnel is designed with a critical angle of repose, by which the antlion can trigger a mini-landslide that causes the struggling prey to slide further down towards the bottom of the funnel. There is another group of insects, the wormlions (Diptera: Vermileonidae) whose larvae also build a similar trap in fine loose soils to ambush arthropod prey (Dor et al., 2014). A quite different, mobile predatory strategy in some aquatic insect larvae such as stoneflies (Plecoptera: Perlidae) is to search actively for prey, mainly invertebrates, by foraging the bottom material of streams, that contributes to bed erosion and bioturbation (Statzner et al., 1996; Zanetell and Peckarsky, 1996). In the retreat-making families of caddisflies (Trichoptera: Annulipalpia), the feeding strategy of burrowing aquatic larvae is a sedentary one, and consists in elaborating branched elongate tubes below the substrate surface of streams, including an enlarged chamber that houses a silk net used to filter suspended food particles and small organisms from the circulating water (Wiggins, 2007).

At the opposite or in a complementary way, many insects have developed a burrowing behaviour for sheltering and safety from predation. In terrestrial environments, the European field cricket, *Gryllus campestris*, lives in and around burrows and uses it as shelters to escape from predation by reptiles or birds (Rodríguez-Muñoz et al., 2011). In aquatic environments, the burrowing behaviour of the phantom midge *Chaoborus flavicans* is an interesting case (Gosselin and Hare, 2003): larvae of this dipteran species daily migrate between the water column of lakes, where they feed at night on zooplankton, and descent at day into the soft sediments where they find refuge from predatory fish, thus contributing to bioturbation. The retreat-making behaviour of aquatic larvae of caddisflies, as described above, is also employed as a strategy of sheltering and protection from predators. In fact, the sheltering function of burrows often overpasses that of a refuge from predation: in temperate regions, many insects use burrows as temporary shelters for thermal protection (overwintering) or even as permanent domiciles. The main ethological characters of insects having a geomorphic influence are summarized in Figure 4 and Table II. Each of the processes described has both direct and indirect geomorphic effects that are separately examined in the next sections.

Direct geomorphic effects of insects

Insects can exert a direct geomorphic impact through microlandform creation by acting as agents of erosion, transportation and deposition. Such entomolandforms – i.e. landforms directly created by entomofaunal activity – can be ranged into two categories: excavational landforms (i.e. burrows) and constructional landforms (i.e. mounds). Figure 5 illustrates the main shapes of microlandforms generated by entomofauna in the form of a multi-branch classification scheme. Literature estimates of corresponding burrowing and mounding rates are provided in the text and in Table III.

Burrows as excavational landforms

Insect burrows can be excavated into a wide diversity of substrates and can range in complexity from a simple hole a few centimeters in depth, to a complex network of interconnecting tunnels and galleries thousands of meters in total length. The most superficial and elementary microlandforms – comparable in size and depth to micro-scale glacial landforms such as friction cracks and chatter marks – are the surface scrapes and digs left by some foraging insects when collecting nest material, feeding or exploring in order to dig a deeper, permanent burrow (Eiseman et al., 2010). Digging wasps, also called “mud daubers” (Hymenoptera: Sphecidae), build aerial nests by collecting mud-balls in clayey humid soils, leaving 6-8 mm scrapes printed by their mandibles at the soil surface (Chatenoud et al., 2012; Figure 6A). Other insects such as dune grasshoppers (Orthoptera: Acrididae) create shallow (2-3 cm deep), V-shaped digs in sands in which they partially bury themselves, presumably for thermoregulation during cold or windy nights (Papković and Jelinčić, 2019). These surficial features are often accompanied by nearby surface trails and tracks made by insect displacements (Eiseman et al., 2010). Funnel-shaped or conical pits are another shape of surficial entomolandforms with slightly higher dimensions (from 2.5 to 5 cm deep and 2.5 to 7.5 cm wide at the edge: Figures 3C and 6B), and are typical of predaceous larval insects such as antlions and wormlions (Hollis et al., 2011; Dor et al., 2014). I-, J- and U-shaped, non-branched holes can also be ranged in the category of simple burrows (Figure 5). U-shaped burrows are generally produced by aquatic insect larvae from several orders, especially Diptera, Ephemeroptera, Megaloptera and Trichoptera (Charbonneau and Hare, 1998; Figure 2). I- and J-shaped burrows – either vertical, horizontal or inclined – may have been constructed by the same insect orders and by many others, given their simple and common shape in the whole range of underground microlandforms. Their detailed morphometric characteristics, however, are often group- or species-specific and can be used as burrowing signatures for ichnoentomological research (Genise, 2016).

More complex are the burrows with a chimney-like extension (or turret), that is a recurrent feature in entomolandforms. This turret extension of variable height above the burrow may have different functions: in the larval tiger beetles (Coleoptera: Cicindelidae), the main functions are prey attraction and thermoregulation (Knisley and Pearson, 1981). Some cicada nymph species (Hemiptera: Cicadidae) use excavated sediment to construct turrets or chimneys up to 20 cm high in order to assist and maintain emergence burrow humidity by reducing interior exposure to sunlight (Smith and Hasiotis, 2008; Figure 6C). Various digging wasps and bees also top their burrows with turrets (Eiseman et al., 2010), which serve primarily to prevent burrow infilling by loose dust and debris, or to foil predators and parasites. Given its complex nature, this type of burrow associated with turret construction can eventually be considered as a hybrid landform of both excavational and constructional types.

Insect burrows forming a complex system of interconnecting tunnels and galleries have infinite morphologies in terms of size, shape and depth. The majority of ant species nesting in soils excavate extensive networks of tunnels and chambers below the earth’s surface (Buhl et al., 2006). The depth of these tunneling networks vary widely from species to species: the Florida harvester ant (*Pogonomyrmex* *badius*) build a subterranean nest of up to 3 meters deep each year, while Florida's largest ant species, *Camponotus socius*, burrows only 60 centimeters into the soil. Japan's *Messor aciculatus* makes the deepest nest in the world, with galleries up to 4 meters down into the earth. Semi-social and unsocial insects can also dig complex systems of deep tunnels. The gregarious webspinners (Embioptera) produce networks of silk-line galleries that can form an extensive tunnel system of aggregated nests (McMillan et al., 2016). Crickets and mole crickets (Orthoptera: Gryllidae and Gryllotalpidae) individually construct tunnel networks of relative complexity up to 60 centimeters long (Figures 1D and 6D). After Held (2019), a single adult of southern mole cricket (*Neoscapteriscus borellii*) excavates 126,5 g (4.4 oz) of clay or 141 g (8.3 oz) of loamy sand while tunneling in 7 days; it also builds more longer and more branched tunnels in loamy sand soils than in clay soils. In this species as in many others, the type of substrate directly influences the shape of tunnels and the rate of burrowing.

Quantitative data on burrowing or mixing rates produced by insects remain very scarce because of the difficulty in procuring directly this information from simple and robust methods (Richards, 2009; Wilkinson et al., 2009). Indirect estimates of mixing by earthworms were classically obtained by deriving rates of soil ingestion (e.g., Evans, 1948; Satchell, 1967; Lavelle, 1978) but this method is unsuited to burrowing insects since most excavated material is carried or pushed away. Indirect quantification from cast production or mounding rates are regularly used to infer bioturbation rates by ants and termites, but this method only accounts for a small fraction of total bioturbation since a larger part of it occurs below-ground (Taylor et al., 2019). Field experiments using a soil column with colored layers were recently employed to quantify the amount of soil excavated and mantled by colonies of ant species in Florida (Tschinkel, 2015; Tschinkel et al., 2015; Tschinkel and Seal, 2016), with extrapolation of results to longer periods and larger areas using simulation procedures. A few earlier studies have used similar field experiments with a high degree of confidence. In an Australian study site dominated by mound-building ants (especially *Aphaenogaster longiceps*), Humphreys and Field (1998) carried out a unique 17-year, biofabric-based assessment of subsurface processes using a column of dyed soil experiment. Their results indicate mixing rates of 127 t ha^{-1} y^{-1}, that fits ~25 times the net rate of mounding. Such a strong difference between burrowing and mounding processes is consistent with estimated soil ingestion rates compared to earthworm castings in the study by Lavelle (1978) in Ivory Coast. The study by Humphreys and Field (1998) also showed that the rate of mixing declines non-linearly with depth following the proportion of open burrows and pedotubules, with notable differences between soil horizons. Such trends were confirmed for termites and were recently supported by soil mixing rates derived from cosmogenic ^{10}Be depth profiles and optically-stimulated luminescence (OSL) dating of individual quartz grains (Johnson et al., 2014; Kristensen et al., 2015).

Mounds as constructional landforms

Insect mounds are recurrent and common landforms in all morphoclimatic zones of the planet, except in polar and subpolar regions where they are quasi-absent. Termite mounds are undoubtedly the most conspicuous and impressive biogenic landforms in the tropics (Goudie, 1988). In some tropical regions, they are prominent and omnipresent features in the landscapes according to their size (up to 10 meters high) and density (up to 5,000 per hectare), respectively. These termitaria strongly modify the geomorphological landscape, generating a rough topography of regularly spaced mounds over large areas, as frequently observed in the African savanna landscapes where the distribution patterns of mounds are strongly influenced by hydrogeomorphology (Levick et al., 2010; Figure 7A). In the semiarid region of Northeast Brazil, approximately 200 million of 2-4 m high, conical earth mounds locally known as "murundus", are densely distributed over an area of ~230,000 km² of seasonally dry tropical forest – roughly the size of Great Britain – with a mean density of 35 mounds ha^{-1} (Funch, 2015;

Figure 7B). Somewhat analogous to the “mima” mounds of North America and “heuweltjies” of Southwestern Africa, their origin has long remained enigmatic, until recent studies demonstrated their close association with mound-building termites (Souza and Delabie, 2017; Martin et al., 2018). Unlike most termitaria found in the tropics, these Brazilian mounds are not nest structures but amorphous accumulations generated by the steady excavation of vast interconnecting tunnel networks from a single termite species, *Syntermes dirus*. Estimated volume of excavated soil represents the removal and re-deposition of ~10 km^3 of earth – equivalent to ~4,000 great pyramids of Giza – over a period of ~4,000 years (Martin et al., 2018). These figures make it the greatest known example of ecosystem engineering yet recorded worldwide by a single insect species.

Morphometrically, termite mounds are characterized by a wide variety of shapes and sizes, knowing that a single species may build more than one type of mound, and that multiple species may build similarly shaped mounds (Claggett et al., 2018). Following those authors and according to the vast literature on termite mounds, five primary shape classes of more or less complex mounds can be distinguished (Figure 5):

- Cone-shaped mounds, characterized by a height/width ratio typically >3, and a protruding peak extending a strong conical base;
- Dome-shaped mounds, with a lower height/width ratio (<3) and a more rounded mound top;
- Cathedral-shaped mounds, featuring complex forms with thin walls, buttresses and multiple peaks (Figure 8A); the tallest termite mounds of the world (up to 10 meters high) are of cathedral-type;
- Wedge-shaped mounds, also known as meridian or compass mounds, roughly aligned in a north-south direction (Korb, 2003); their unique shape is associated with endemic Australian species that use the earth’s geomagnetic field to accomplish this meridian orientation in ways to improve thermoregulation (Jacklyn and Munro, 2002);
- Mushroom-shaped mounds, notably built by the African species *Cubitermes fungifaber* (Donovan et al., 2001), with a sculpted morphology composed of distinctive mushroom-like stem and cap.

Ant mounds (or anthills) are comparable to termite mounds in many aspects, but their morphological features are less diverse, producing mainly cone-shaped and dome-shaped mounds (Figure 8B). In the precursory work by Branner (1909), ant mounds as high as 5 meters, with bases 15-16 meters in diameter, have been described from tropical South America, making these features among the biggest anthills of the world. Ant mounds in cold-temperate ecosystems are substantially smaller, but can reach up to 2 meters high in the red wood ants (*Formica rufa* group), with densities of 3-18 nests ha^{-1} (Taylor et al., 2019). Higher densities of mounds are reported for North American harvester ants (*Pogonomyrmex* spp.: 20-150 nests ha^{-1}; MacMahon et al., 2000) and fire ants (*Solenopsis invicta*: 50-220 nests ha^{-1}; Vogt et al., 2009). Exceptionally, the densities of anthills created by *Lasius flavus* can reach up to 2,500 mounds ha^{-1} in some parts of the Baltic region and the British islands (Elmes, 1991). Such densities produce a hummock topography typical of several European landscapes of wet meadows, peat lands and salt marshes where the ant mounds are an adaptation to seasonally flooded or waterlogged soils (Whitford and Eldridge, 2013).

Many other insect orders have members that build earth mounds, generally with smaller dimensions (1-30 cm in height) and simple morphologies (Figure 5). Thousands of solitary bee species are ground-nesters and dig subterranean tunnels and galleries whose excavated material is pushed to the surface as volcano-shaped mounds of 2-5 cm high, with an open crater <1 cm in diameter (Cane, 2003; Sarzetti et al., 2013; Figure 8C). When tunneling horizontally with a burrow entrance on a wallslope, the excavated soil is typically deposited in fan-shaped mounds. In the Coleoptera order, rove beetle adults and larvae of the genus *Bledius* (Staphylinidae) make clusters of many small mounds very analogous to the castings of earthworms (Eiseman et al., 2010; Figure 8D). Ground beetle larvae and cicada nymphs are also mound-builders when excavating and pushing up a small mound of soil or tumulus that caps their larval burrow. Endogean orthopterans, notably represented by mole crickets (Gryllotalpidae) and pygmy mole crickets (Tridactylidae), also produce small mounds and miniature mole-like hills with a typical elongated shape (esker-like landforms; Figure 8E). All these mounds correspond to loose material simply deposited on the surface in the same way as earthworm casts, and are therefore ephemeral landforms easily erodible by subsequent rainsplash and runoff processes. As such, they may be classified as *type-I* mounds, as defined by Humphreys and Mitchell (1983) in their classification of ant mounds, here extended to all insect mounds. At the opposite, a major part of the larger, more complex termite mounds harboring nest structure, belongs to the *type-II* category of Humphreys and Mitchell (1983): such mounds, often cemented by clay supply, are more resistant to erosion and therefore can persist in the landscape for longer periods of time.

Quantitative estimates of mounding rates by entomofauna vary considerably between insect groups and even within a same genus or species, depending on many environmental factors, but methods of estimation probably contribute to observed variations. Despite some shortcomings in the quantification of mounding, it is nevertheless possible to provide a global appreciation of the constructional potential of some insect groups from a comparison of mounding rates with other world's major groups of bioturbators (Table III). In the scientific literature, ants and termites are considered as active mounders in a variety of environments, but their activity is globally considered to be much lower than that of earthworms (Wilkinson et al., 2009; Taylor et al., 2019). Mounding rates reported for termites and ants are generally between 0.5 and 5 t ha^{-1} y^{-1}, with a few studies recording 5 to 10 t ha^{-1} y^{-1} (Waloff and Blackith, 1962; Salem and Hole, 1968; Humphreys, 1981; De Bruyn and Conacher, 1990). Such high mounding rates are similar to the constructional activity of crayfishes and fossorial mammals like the European mole (*Talpa europaea*) or the pocket gopher (*Thomomys talpoides*) (Table III). Higher rates of mounding up to 68 t ha^{-1} y^{-1} were exceptionally reported by Humphreys (1985) for the Australian ant *Aphaenogaster longiceps,* that would exceed mounding rates of most burrowing animals. Table III also provides some data on the rate of mounding by lesser studied insects such as cicadas and beetles, with rates generally <0.5 t ha^{-1} y^{-1}, although Kalisz and Stone (1984) reported mounding of up to 1.85 t ha^{-1} y^{-1} for the scarab beetle *Peltotrupes youngi*. For comparison, such moderate values are in the same order of magnitude than those reported for the Indian desert gerbil (*Meriones hurrianae*) or the European rabbit (*Oryctolagus cuniculus*) (Table III).

Indirect geomorphic effects of insects

In addition to their direct geomorphic effects, insects have indirect impacts on landforms and geomorphic processes at various spatial and temporal scales. In this section, the influences of insect activity on the initiation of secondary landform construction and destruction are first examined, with a special focus on fluvial systems and lateritic landscapes. Indirect effects of insects on the hydrological and erosional responses of watersheds are subsequently described, including the quantified impacts of their activity on soil erosion and sediment yield.

Secondary landform construction and destruction

Secondary geomorphic effects of insects on stream systems are diverse and may participate in fluvial landform construction as well as in stream bed erosion and transport. The role of termites in the initiation and growth of fluvial islands has been evidenced by McCarthy et al. (1998) and Gumbricht et al. (2004) in the Okavango delta, Botswana. They showed that the islands are initiated by the mound-building activities of the termite *Macrotermes michaelseni*, which construct large mounds above the maximum flood level. Changes induced by termite activity on the physico-chemical proprieties of the mound soil favor the subsequent colonization by pioneer shrubs and trees, which in turn results in increased transpiration. As a consequence, calcite and silica precipitate from shallow groundwater preferentially beneath the mounds, resulting in vertical and lateral growth, and finally island expansion. This is an interesting case where termites act as ecosystem engineers by a mechanistic evidence of passive niche construction: their activity indirectly causes a modification of the fluvial system through a series of feedback mechanisms between biota and geomorphic processes (Dangerfield et al., 1998; Corenblit et al., 2008).

In a similar way, McAuliffe et al. (2014) have demonstrated the role of termites in the initiation of *heuweltjie* earth mounds in South Africa, whose origin has long been controversial. Rather than being directly responsible for the mound formation, termites simply create nutrient-rich nuclei which support denser vegetation, thereby inducing aeolian accretion by sediment-trapping effect and correlative upward growth of mounds. The same kind of influence was reported for ant building nests, especially those of harvester ants of the genus *Pogonomyrmex* (MacMahon et al., 2000), which create islands of increased nutrient density favoring a larger vegetation growth than in surrounding areas. Otherwise, Eiseman et al. (2010) have observed some cases where ants have appropriated small, wind-driven dunes that were originally stabilized by plants, rather than having directly built these hills. In turn, the ants modify the structure of the mound by clearing the vegetation and by placing coarse gravels at their top in order to stabilize the denuded mounds. This is another interesting case of biogeomorphic succession dynamics, in the wider scope of examining the reciprocal interactions and adjustments between landforms, insects and vegetation.

At a finer scale, insects can also contribute to the shaping of distinct morphological features in stream channels such as biogenic travertine deposits and tufa terraces (Humphreys et al., 1995; Marks et al., 2006). In karst environments, aquatic insect larvae play an indirect geomorphic role in $CaCO_3$ deposition at the microrelief level, as demonstrated by Drysdale (1998) from stream crusts and travertine deposits in the Barkly karst region, Australia. Here the most conspicuous roles are played by fly larvae (Diptera: Chironomidae and Simuliidae), moth larvae (Lepidoptera: Pyralidae) and caddisfly larvae (Trichoptera: Hydropsychidae). By constructing cylindric cases and capture nets on the travertine surfaces, they create passive substrata for calcite precipitation while slowing the stream flow due to the roughness induced by the many microreliefs. A similar process of travertine-building by a hydropsychid caddisfly, *Smicridea travertinera*, has been described by Paprocky et al. (2003) from Venezuela. In fact, the retreat-making behaviour of those insects appears to participate both in the bioconstruction and bioerosion of the travertine formations.

In the field of fluvial biogeomorphology, some studies have been focused on the interactions between stream insects and the geomorphology of sand- and gravel-bed rivers, especially on their secondary effects associated with increased potential for fluvial erosion and transport (Statzner et al., 1996, 1999; Rice et al., 2012; Statzner, 2012). Globally, benthic and aquatic invertebrates are known to have strong impacts on gravel-bed sediments and processes (e.g., Meadows and Meadows, 1991; Butler, 1995). However, most studies have been limited to the bioturbational effects and sediment mixing caused by invertebrates such as sponges, gastropods and crustaceans, with poor attention to aquatic insect communities. Through field stream experiments and naturalistic observations, Statzner et al. (1996)

investigated the effect of mobile predaceous stonefly (*Dinocras cephalotes*) larvae on sand erosion. They showed that the digging stoneflies erode sand from stream riffles at a rate of 200-400 kg sand m^{-2} y^{-1}, thereby contributing significantly to the erosion of bottom material in streams. Similarly, river banks provide valuable habitats for many aquatic insect larvae, especially mayflies (Ephemeroptera), which in turn exert an influence on stream bank destabilization and erosion through burrowing microlandforms acting as weakness zones (Figure 2). Interestingly, some groups of silk-producing lotic insects (caddisflies, aquatic moths, and dipterans) have the contrasting effect to participate in the bioconsolidation of bed sediments with limited gravel erosion and transport (Statzner, 2012): their larvae create silk bridges of varying strength among sand and gravel particles, thus consolidating the bottom sediment of streams. In a 2-months experimental study on the effects of a silk-producing caddisfly (*Hydropsychseil talai*) on gravel transport in an Alpine river, Statzner et al. (1999) showed that the trichopteran community increases critical shear stress for gravel by a factor of 2, with the effect to stabilize the bed sediment of stream. Similar conclusions were found by Johnson et al. (2009) from a laboratory experiment regarding the impacts of net-spinning caddisfly larvae on the sediment stabilization of gravel-bedded rivers. The zoogeomorphic effects of case-building trichopteran larvae are less known and just start to be studied (Mason et al., 2019): larval case construction from sand and fine gravel results in altered sediment properties of bottom material and also contributes to bedload transport, but its effects on sediment mobility remain to be precisely quantified.

Outside stream channels, termite activity has also been suggested as a major contributing factor in the formation and evolution of duricrusted lateritic interfluves in the tropics (Tardy and Roquin, 1992; Thomas, 1994). Whether it contributes to ferricrete formation or to its degradation, however, has been a matter of debate (Goudie, 1988; Tardy, 1997; Runge and Lammers, 2001). Hard vermicular laterites, typified by inner tubes and cavities, have been classically ascribed to termite activity (Erhardt, 1951; Barros Machado, 1983). Furthermore, physico-chemical similarities between lateritic soils and termite material led to the assumption that termites could participate in the formation of ferricrete by an original process of ‘bio-aggregation’ of soil particles (Eschenbrenner, 1986). This last author has also suggested the probable role of termites in the alteration of parent rock and the deepening of the weathering front, thereby contributing to lateritic profile development. With the help of geochemical and mineralogical analyses, Tardy and Roquin (1992) have demonstrated both the upward and downward movements of soil material induced by termite activity within the whole lateritic profile, and especially the biomechanical transfer of clay-silt particles from the mottled zone to the surficial gritty horizon, a process also pointed out by Beauvais (2003). Consequently, this soft material overlying the duricrusted horizon becomes available for surface runoff erosion and lateral transport by colluviation from lateritic interfluves to alluvial valley floors (Figure 9). Another indirect consequence of vertical movements by termites is the ferricrete dismantling from underneath through zoogenic uptake of soil material in the deeper horizons (saprolite and mottled zone). The high amount of excavated soil underneath the ferruginous duricrust – with an uptake of soil calculated between 1.2 and 3.0 t ha^{-1} y^{-1} after a review by Runge and Lammers (2001) – is responsible for the formation of “cave systems” over which the duricrust tends to collapse, forming shallow pseudo-karstic depressions at the surface of lateritic mesas (Runge, 1996).

Effects on soil erosion and sediment yield

Studying the effects of insect activity on soil erosion is a complex matter, because the hydrological and erosional responses of watersheds are varied, depending on insect behaviours, nest morphologies, and many other environmental factors. Burrowing insects can both reduce soil loss, by improving porosity and infiltration capacity, and increase it, by diminishing soil stability as a result of organic matter digestion and biomixing. Soil erosion can also be enhanced through upward biotransfer of fine-grained material available for subsequent wash and creep action (Mitchell, 1988; Butler, 1995; Dragovich and Morris, 2002; Jouquet et al., 2012; Schmidt et al., 2014; Li et al., 2019a). Moreover, adjustments and interactions between geomorphic processes, insects and vegetation may be invoked in some cases as an indirect mechanistic evidence for soil erosion. In particular, the relationship between locust swarms and soil erosion is reciprocal. Locusts and grasshoppers consume vegetation and, when they become numerous with a gregarious behaviour, can have large impact on land cover by stripping vegetation and expose bare soils to rain splash, resulting in increased runoff and accelerated soil erosion at the landscape scale (Dibble, 1940; Gillon, 1989; Latchininsky et al., 2011). Conversely, livestock overgrazing and enhanced soil erosion are known to promote locust outbreaks in areas affected by land degradation and desertification (Cease et al., 2012). At a more local scale, several ant species clear vegetation around their nests, affecting soil hydrologic patterns around the mounds, with the overall consequence to increase soil erosion and sediment transfers (MacMahon et al., 2000). Another indirect effect of many insects is that they transport seeds and, by this way, determine the location of the new plants and the vegetation patterns, that can indirectly influence infiltration paths and soil erosion.

Basically, all burrowing insects influence the hydrological properties of soils by producing water-conducting macropores underground (voids, tubes, and galleries) and surficial nest entrances creating preferential water infiltration paths. Experimental study of the effects of termites and ants on soil infiltration rates has been investigated by many authors in a wide variety of environmental and topographic settings (e.g., Elkins et al., 1986; Eldridge, 1993, 1994; Mando et al., 1996; Wang et al., 1996; Cammeraat et al., 2002; Leonard et al., 2004; James et al., 2008; Cheik et al., 2018; Li et al., 2019b). Most of these studies have demonstrated that soil infiltration rates and porosity were significantly higher on termite- or ant-modified soils than on non-nest soils. One of the main controlling factors of such differences is the existence of a dense network of tunnels and chambers resulting in lower bulk density (i.e. increased porosity) and in larger flow percolation of water to deep soil layers (Whitford and Eldridge, 2013). For example, Eldridge (1993) did a field experiment in a semi-arid woodland at Yathong (eastern Australia) to study the influence of ant (*Aphaenogaster barbigula*) nest structures on soil hydrological properties. Steady-state infiltration under ponding (i.e. saturated flow) on ant plots was measured at a rate of 23±1.8 mm min^{-1}, which was four to five times greater than that on ant-free control plots. He also showed a strong positive correlation between soil infiltration rate and the diameter of *Aphaenogaster* nest entrances. A few studies have examined the role of lesser studied insects on soil hydrologic processes and infiltration rates, especially dung beetles (Brown et al., 2010) and mole crickets (Bailey et al., 2015; Li et al., 2018). All these studies highlighted the positive effect of subterranean insect activity on soil porosity and water infiltration, resulting in 20% to 40% reduction in surface runoff.

Paradoxically, and despite a general trend in runoff reduction, the same experimental studies have shown that the burrowing activities of insects have the contrasting effect to exacerbate soil erosion and sediment loss, because the earth mounds and the unstable soil aggregates made by burrowing insects at the soil surface provide a large quantity of fine-grained material easily erodible by rainsplash and slopewash. Such effects are classically reported for social insects (ants and termites) but also for unsocial insects like dung beetles and mole crickets (Brown et al., 2010; Bailey et al., 2015; Li et al., 2018). The relative importance of soil erosion and sediment yield notably varies with nest density and the type of earth mounds (Aalders et al., 1989; Whitford and Eldridge, 2013). *Type-I* mounds are very susceptible to erosion and are usually considered as a major source of sediment yield, because they consist of loose, fine-grained material and often occur in high density (Humphreys and Mitchell, 1983; Paton et al., 1995). At the opposite, *type-II* mounds are more compact and often cemented, and are therefore more resistant to rain drop and wash erosion. For example, earth mounds constructed by the Australian *Aphaenogaster* ants, which belong to the *type-I* category, are source of highly mobile sediment for subsequent transport to be streambed (Richards, 2009). Similarly, in the tropical rainforest of Panama, Schmidt et al. (2014) demonstrated high rates of erosion and sediment yield from *type-I* ant mounds in a small experimental catchment, with a mean estimate of 725 kg ha^{-1} calculated for an 8-month wet period. Compared to the total sediment output reported for the same catchment (1–2 t ha^{-1} y^{-1}), these values potentially indicate a major contribution of ant mounding activity to sediment delivery.

Other experimental studies conducted in agricultural and forest-fire affected areas of southern Europe and eastern Australia have led to similar conclusions. In the study by Dragovich and Morris (2002), ant mounds are expected to contribute >90% to the total weight of slopewash and bio-transferred sediment in a post-fire landscape of the Sidney region. In a similar way, post-fire experiments conducted by Cerdà and Doerr (2010) in the Valencia province (Spain) confirm higher soil erodibility and larger sediment concentration for the ant mound plots than the control plots. In agricultural soils occupied by orange orchard plantations in a nearby region of Eastern Spain, Cerdà and Jurgensen (2011) have concluded to close observations supported by quantified data: soil erosion rates and sediment concentrations were nearly double in areas with ant activity (560-590 kg ha^{-1} h^{-1}), as compared to soil with no ants (310-360 kg ha^{-1} h^{-1}). In a citrus orchard of the same region, soil erosion rates were globally lower but evaluated to be 300% higher on plots with ant mounds (41 kg ha^{-1} h^{-1}), as compared to the plots without ants (12 kg ha^{-1} h^{-1}) (Cerdà et al., 2009).

In tropical regions, termite mounds and associated surface sheeting have the same effects to influence the secondary geomorphic processes of rain-splash detachment, surface wash, and soil creep. This biomantled material contributes significantly to soil erosion and sediment yield, with rates of 300–1,059 kg ha^{-1} y^{-1} reported in Sudano-Sahelian savannas (Goudie, 1988). Many erosional features on and around the mounds are obvious marks of intense denudation: small-scale landslides, rills, miniature wash pediments, and debris fans are common features associated with termite mounds. In Burkina Faso, the main erosion process of termitaria was identified as soil creep, with rates of 1,163 kg ha^{-1} y^{-1} from the mound to the corona around the mound (Lal, 1987). Bioturbation by burrowing insects, especially termites and ants, has been recognized as a key driver of soil creep and stone-line formation (Wilkinson et al., 2009; Richards et al., 2011; Pawlik and Samonic, 2018; Williams, 2019), whereas creeping has long been regarded by most previous authors as an entirely abiotic process – Darwin (1881) being a remarkable counterexample. One of the most commonly recognized and efficient factors of “biogenic creep” is tree uprooting, but soil-dwelling insects were also indicated to participate significantly in diffusive-like processes and mass wasting along slopes through burrowing and biomantling (Heimsath et al., 2002; Wilkinson et al., 2009).

Past geomorphic effects of insects: some evolutionary insights

Beyond the direct and indirect geomorphic impacts of entomofauna in apprehensible space, there is growing evidence of past geomorphic effects that can be examined along a temporal axis, in the light of recent advances in ichnoentomological research and radiometric dating of insect landforms. This paragraph is on timescales for the impact of insect activity on geomorphic change in the past geological history, from long-term evolutionary trends to more recent Holocene changes.

Fossil records of entomogeomorphic activity

The oldest insect fossil records date back to the Devonian (Engel and Grimaldi, 2004; Garrouste et al., 2012), even if the first insects probably appeared earlier, as soon as the Ordovician, concomitantly with the appearance of bryophyte-like and land plants with which they largely coevolved (Misof et al., 2014). A first diversification phase of insects is expected to have occurred between the Silurian and the Late Devonian, and a second one during the Late Carboniferous, giving rise to the emergence of numerous new major taxa in the subclass of Pterygota (winged insects). Most extant orders of insects originated during the Permian, but many of the early groups became extinct with the Permo-Triassic extinction event (Labandeira, 2005). Most modern insect families appeared in the Triassic and Jurassic periods, and a number of successful groups of burrowing insects – especially the Hymenoptera (wasps, bees and ants) and Coleoptera (beetles and scarabs) – developed in coevolution with angiosperms (flowering plants) during the Cretaceous. Many modern insect genera emerged during the Cenozoic, this last period recording the major part of insect traces and fossil landforms (paleo-burrows and paleo-mounds) preserved in continental deposits and paleosols (Humphreys, 2003; Genise, 2016).

The identification of insect trace fossils (or ichnofossils), mostly represented by nests and pupation chambers, has largely been based on comparisons with the morphological characteristics of modern structures (Hasiostis, 2003; Tschinkel, 2003; Genise, 2016). One important issue of ichnological studies for biogeomorphological research is to understand to what extent terrestrial bioturbation has evolved since insects colonized the land areas of Earth in the Middle Paleozoic. Despite a lack of direct evidence for pre-Mesozoic entomofaunal burrowing signatures, colonization of land by insects at the Silurian – together with plants (Corenblit and Steiger, 2009) – probably represents a critical shift for geomorphic changes on the Earth surface. Trace fossils and paleo-burrows found in Palaeozoic paleosols have been used as evidence for the activity of burrowing invertebrates as soon as the Cambrian (Jensen, 2003), indicating an emerging bioturbation by non-insect animals. The oldest and direct ichnologic evidence of burrowing activity by insects was found in Early Mesozoic paleosols. Burrow traces made by cicada-like nymphs have been recorded in Triassic paleosols from Antarctica and eastern Australia (Retallack, 1997), but insect traces remain scarce from those remote times. Complex ichnofossils and nest structures constructed by termites, bees, wasps, ants and beetles are, however, common features in Cretaceous paleosols (Genise, 2016). In particular, the intensity and distribution of bioturbation indicated by fossil termite and ant nests in the Cretaceous geologic record suggest that these social insects played major roles as geomorphic agents and ecosystem engineers at least since the Late Mesozoic (Hasiotis, 2003). Given their abundance in paleosols, this also indicates a certain degree of coevolution between soils and insects at that time (Philipps, 2009; Wilkinson et al., 2009).

Insects probably modify soils and landform dynamics to a greater extent during the Cenozoic, as indicated by the multiplication of trace fossils left by various groups of foraging insects from the beginning of the Paleogene. For example, bee cells of the ichnogenus *Celliforma* are one of the most common trace fossils in the Early Cenozoic paleosols of South and North America, Europe and Africa (Genise, 2016). Coleopteran and moth pupation chambers are also recurrent features preserved in Paleogene laterites and paleosols, as shown by Bellosi et al. (2016) in Lower Eocene laterites of Uruguay, with high insect ichnodiversity. Termite mounds were recognized in the fossil record since at least the Miocene (Bown and Laza, 1990), but polychambered termite nests with fungus combs are proved to have existed as early as the Oligocene (Roberts et al., 2016). A convergent evolution of symbiosis and associated complex nest structures with fungus gardens was observed in attine ants – especially in the genus *Atta*, *Acromyrmex* and *Trachymyrmex* – since at least the early Miocene (Tschinkel, 2003; Genise et al., 2013; LaPolla et al., 2013). Furthermore, common and widespread extant genera such as *Aphenogaster*, *Formica* and *Lasius*, known to be active mounders, date to the Oligocene period. Despite the absence of direct evidence for fossilized nest mounds, this implies that active mounding by social ants may have been widespread at least since, and probably before, mid-Tertiary times (Hasiotis, 2003).

In the light of ichnoentomological studies, it is thus possible to highlight long-term evolutionary trends of insect activity with their potential impacts on geomorphic change in the Earth's history. This perspective raises stimulating and important questions about coevolution between living organisms and landforms, and other biogeomorphic forms of ecosystem engineering and niche construction over time (Jones et al., 1994; Odling-Smee et al., 2003; Corenblit et al., 2008; Philipps, 2016). Biomantles and insect mounds clearly support the idea that long-term landform modulations reflect their reciprocal adjustments with the insect communities they support and help to shape since the Middle Palaeozoic, with an increasing degree of coevolution along the Phanerozoic. Following this idea, ant and termite mounds were used by Dawkins (1982) to illustrate the "extended phenotype" concept. Beyond the extended effects of organism's genes on the environment (including soils and landforms) and the positive feedback benefitting the engineer organism, this concept implies that biological variations and changes should be reflected in soil types and landform evolution (Philipps, 2016). It is obvious that insect mounds are biogenic landforms which have been defined genetically and that an evolutionary synchrony occurred between the mound-building insects and the landforms they create to nest. In a similar way, biomantles can be considered as "extended composite phenotypes" because of the cumulative, interacting, and overlapping effects of multiple organisms, including many burrowing insects (Philipps, 2009). This notion includes the effects of multiple generations of diverse organisms and may incorporate both positive and negative niche constructions over geological timescales.

As stated by Darwin (1881) in his final work, it appears that small-scale bioturbation caused by burrowing insects and other organisms partly governs the landform and landscape evolution at a large spatial scale – e.g. through increased sediment transfer by rivers from the land to the ocean (Meysman et al., 2006) – and on a geological time scale. As indicated by the fossil record, more and more burrowing insects have developed on long-term evolutionary timescales anatomical properties to improve their ability to dig, to move and to live in soils and subterranean galleries, thus occupying novel ecological niches (Odling-Smee et al., 2003). By means of natural selection, this evolutionary pathway also implies that biological speciation can be associated with the appearance of new landforms (e.g., the appearance of insect mounds during the Cenozoic), and that biological extinction can be accompanied as well by possible landform extinction (Philipps, 2020).

Geomorphic implications of mound dating

Shorter-term evolutionary insights and geomorphic responses at Holocene time scales can be discussed in the light of recent advances in mound dating. The age and persistence of insect mounds in the landscape has long remained unknown and enigmatic until the first radiometric dating of mound material. Theoretically, one can consider that the age of constructional, above-ground landforms increases proportionally to their size and to the hardness of the mound material (Humphreys and Mitchell, 1983; Paton et al., 1995). Therefore, *type-I* mounds of small size and loose material are formed and destroyed very quickly and generally represent ephemeral landforms. By contrast, *type-II* mounds of larger size and built of compact, cemented material – for example, cathedral-shaped termitaria – may survive for much longer, possibly over timescales of 10^3–10^4 yr.

The first clues to the lifetime of insect mounds were obtained by radiocarbon dating of material within or at the base of termite mounds. Watson (1967) proposed a reliable age estimate of ±700 years BP for a termite hill built by *Macrotermes falciger* in Zimbabwe, based on ^{14}C dating of skeletal material found inside the mound. This minimum age estimate was two to three times the age of the oldest termitaria recorded in Africa at the time. Two decades later, Moore and Picker (1991) investigated a set of eroded and intact earth mounds (*Heuweltjies*) of South Africa and provided new insights on the longevity of these features, based on radiocarbon dating of basal calcrete of two mounds. Their results showed that the mounds have been in existence for at least 4,000 years BP, i.e. an order of magnitude greater than any previously recorded lifetime for termitarium inhabitation by a same species (*Microhodotermes viator*). More recently, stable isotope and ^{14}C analyses of calcrete lenses in abandoned termite mounds of the same region have provided new information about their age and the paleoenvironmental conditions for their formation (Midgley et al., 2002; Potts et al., 2009). $\delta^{13}C$ and $\delta^{18}O$ values together with ^{14}C dates indicate that *Heuweltjies* have not only formed during the Holocene, as some of them have been present in the landscape for the last 36,000 years BP, i.e. at least since the Last Glacial Maximum. However, the termite origin of these mounds has been questioned in those studies and in many others, one of them recently attributing their formation to aeolian sediment accretion rather than the direct building by termites (McAuliffe et al., 2014). Anyway, it appears that calcrete frequently associated with termite mounds in tropical regions might be a useful proxy for dating insect landform and reconstructing past environmental changes.

In central Africa, an age sequence of “true” termite mounds constructed by *Macrotermes falciger* has been determined by ^{14}C dating of the acid-insoluble organic matter along the central vertical axis of the mounds (Erens et al., 2015). This method has provided reliable age estimates around 2,335–2,119 years BP in the lower part of the oldest mounds, and allowed reconstruction of historical mound growth rates that are in good agreement with Holocene climatic changes, suggesting a relationship between past environmental conditions and mound occupancy. Comparable ages between 690- and 3,820-years BP were obtained for large termite mounds in Northeastern Brazil, using single-grain OSL dating of samples collected from the centers of 11 mounds (Martin et al., 2018). Those ages make them the world’s oldest known termite mounds constructed by several generations of a same species (*Syntermes dirus*). Such findings have strong geomorphic implications for the lifetime and temporal persistence of entomogenic landforms. Large termite mounds of the tropics appear as steady-state landforms produced by many generations of one or several species, as eroded mounds are continually repaired by termites until the colonies expire (Whitford and Eldridge, 2013). They can be further interpreted as the expression of an effect of “biogeomorphic resistance” in the landscape, or the way in which the mound landforms and their biological process-response system may survive as a result of dynamic equilibrium between mounding and erosion, at timescales ranging from 10^3 to 10^4 years.

Other important geomorphic implications about the quantification of bioturbation and the evolution of termite mounds can be inferred from the powerful application of OSL dating. A first attempt to understand and to quantify the rates of mixing by termites was made by Pillans et al. (2002) in north Queensland, Australia. They showed that mean luminescence ages of quartz grains increase with depth (up to 44.7 ka BP at 80 cm depth), suggesting that erosion of the termite hills led to the subsequent soil burial by progressive surface accumulation of mound-derived material (Figure 10). Later further study of the quantification of termite bioturbation has been achieved by Kristensen et al. (2015) in a savanna ecosystem of Ghana, using multi- and single-grain quartz OSL techniques. They calculated a surface deposition rate of ~0.28 mm y^{-1} that began about 4,000 years BP. Insights gained from OSL dating suggest that the simple, two-processes-based bioturbation model involving mound construction and erosion should be completed by two other geomorphic components, i.e. burial of subterranean galleries and surface deposition acting as an aggradation process on wash pediments. Rates of mound erosion are known to be accelerated after the abandonment by the colonies, mainly through the actions and interferences of other animals (e.g., trampling by elephants, foraging by other invertebrates; Pullan, 1979; Goudie, 1988; Whitford and Eldridge, 2013). However, quantitative constraints on such accelerated erosion rates remain yet to be evidenced by OSL dating and/or other methods.

Finally, all the above-mentioned studies based on optical dating have strong implications for the taphonomy of archaeological artifacts, because of the post-depositional and syn-depositional disturbance created by termite activity and other burrowing insects (Williams, 2019). Conversely, vertical and lateral displacements of mineral particles and artifacts occasioned by entomofaunal activity can seriously interfere with attempts to obtain a reliable chronostratigraphy based on radiocarbon and/or optical ages. These potential pitfalls in Holocene geoarchaeology and dating techniques should deserve more careful attention on the effects of biomixing and biomantling caused by insects.

Conclusions and perspectives

In contrast to the common assumption that the geomorphic effects of insects – apart from ants and termites – would be minor, this review paper shows evidence for the ability of many burrowing insects to change their physical environment by bioturbation, with direct and indirect geomorphic effects on landscape change. Indeed, the geomorphic influence of entmofauna has received little attention in the zoogeomorphological literature compared to other groups of burrowing animals. By shaping specific landforms and influencing geomorphic processes at various spatial scales and over geological time scales, insects as a whole should be considered as key drivers of geomorphic change. As reviewed in this paper, burrowing insects affect most of the Earth’s surface encompassing aquatic and terrestrial systems, from the micro-scale of landforms to the continental-scale of sediment transfers, and from long-term evolutionary trends to shorter-term Holocene changes.

As an integral component of zoogeomorphological research, the potential of insects as geomorphic agents should encourage the development of further links between geomorphology and entomology, with integrated researches on the role of insects on geomorphic systems and reciprocally. The success of these future researches will depend on interdisciplinary approaches crossing the expertise of geomorphologists and entomologists together with that of soil ecologists, landscape modelers and/or dating practitioners. Given the knowledge gaps in the study of insect-landform interactions and the need of further research on these issues, several perspectives can be identified:

(i) Additional research is needed to address both the primary and secondary geomorphic impacts of insect groups other than the well-studied social ants and termites: quantitative data on the mixing and mounding rates of major burrowing insects such as mole crickets (Orthoptera: Gryllotalpidae) and solitary bees (Hymenoptera: Apoidea) are particularly needed, as are the experimental studies of their indirect effects on soil erosion and sediment transfer in a range of natural and human-modified environments.

(ii) The development of new tools and technologies such as high-resolution, multi-temporal laser scanning and photogrammetry could help to quantify the volumes and rates of surface mounding, in order to complement the simple, classic methods first employed by Darwin (1881) and by many subsequent generations of scientists working on the bioturbation rates of ants and termites.

(iii) The integration of insect behaviour and activity in soil loss equations and landscape models would be a major advance in the understanding of the equivocal role of insects in soil erosion at the catchment scale. Taking into account the richness and abundance of insects and their positive and/or negative effects on soil erosion might contribute to a better incorporation of biotic factors in landscape modelling, in a similar way as the "earthworm factor" recently proposed by Orgiazzi and Panagos (2018). Such studies could indirectly participate in the effort to achieve the Sustainable Development Goals (SDGs) related to soils, especially the land degradation neutrality challenge (Keesstra et al., 2018; Visser et al., 2019), given the importance of insects in the provision of soil ecosystem services.

(iv) An extended application of dating techniques to quantify the bioturbation of insects and to estimate the age of mound landforms would be highly desirable: some studies have shown the potential usefulness of radiocarbon (^{14}C and δ^{13}C on calcrete and insoluble organic matter), cosmogenic (^{10}Be on quartz grains) and OSL dating techniques for quantifying the rates of bioturbation by termites (e.g., Johnson et al., 2014; Erens et al., 2015; Kristensen et al., 2015), thus encouraging further utilization of these proxies for other insect groups shaping comparable features (e.g., ant mounds).

(v) The niche construction effects of insects may be further questioned in the wider scope of geodiversity-biodiversity relationships: burrowing insects, in general, increase the patchiness of the physical environment, or small-scale geodiversity (Bétard, 2013), which creates localized patch habitat for other plants and animals, thereby increasing biodiversity at the landscape scale (Zaitlin and Hayashi, 2012). This is the case of particular insect landforms, such as termite mounds, acting as small-scale "biodiversity refugees" for other soil macrofauna in tropical regions (Choosai et al., 2009).

(vi) In the recent debates on Anthropocene zoogeomorphology (Butler, 2018), new researches are needed to study the ongoing decline in insect biomass and its potential impacts on Earth surface systems (Sánchez-Bayo and Wyckhuys, 2019), with a possible decreasing influence of insects on bioturbation and other geomorphic processes. In the range of human-induced changes, invasive and alien species can also significantly alter geomorphic processes and landforms (Fei et al., 2014), as shown by the drastic impacts of red imported fire ants (*Solenopsis invicta*) on landscape change in many regions across the globe.

Future improvements in those directions should open new chapters and original perspectives in the study of insects as zoogeomorphic agents, beyond the well-known and classical considerations on social ants and termites. It should also encourage new collaborations between geomorphologists and entomologists, in order to develop an integrated understanding of the importance of insects in Earth surface processes and landforms.

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Figure captions

Figure 1. Sketch diagrams showing various nest structures for different insect species. (A) Nest architecture of the mound-building termite *Macrotermes michaelseni* (modified from Turner, 2000); (B) Nest architecture of the silky field ant *Formica subsericea* (modified from Drager et al., 2016); (C) Nest architecture of the desert bee *Cadeguala albopilosa* (modified from Sarzetti et al., 2013); (D) Nest architecture of the southern mole cricket *Neoscapteriscus borellii* (modified from Nickerson et al., 1979).

Figure 2. Burrowing behaviour of aquatic insect larvae of Ephemeridae (mayflies) and their geomorphic effects on a clay river bank, Marne, France (Réaumur, 1742). (A) Piece of the clay river bank showing burrows shaped by mayfly larvae; two close openings belong to the same burrow, whereas a single elongated hole corresponds to a burrow whose central tongue has been subsequently eroded; (B) Horizontal cross-section throughout the same piece of clay along a plane parallel to m-m-n-n, displaying a U-shaped burrow; (C) Specimen of a mayfly larva, one of those which live in the burrows of A and B at the same scale; (D) Magnified view of the same specimen of mayfly larva presented in C, showing the morphological details of the immature insect, particularly its robust legs and mandibles that help it to burrow.

Figure 3. Cross-sections through three different hole systems related to feeding behaviours by foraging insects. (A) Sketch of a burrow of *Harpalus eraticus* showing tumulus and cached *Setaria* seeds 8-20 cm deep; the larva is typically found at the bottom of its burrow (modified from Kirk, 1972); (B) Tunnel system of the Tobacco Cricket, *Brachytrupes membranaceus*, with its enlarged chamber for food storage (modified from Büttiker and Bünzli, 1958); (C) Cross-sectional view of a funnel-shaped, crater-like pit dug by an antlion larva (*Myrmeleon* sp.); note the thin ejecta blanket around the crater constructed by the insect from excavated sand (modified from Lehane and Ekdale, 2013).

Figure 4. Flow diagram of the geomorphic impacts of insect behaviours.

Figure 5. Direct geomorphic effects of insects: a proposed classification of entomolandforms.

Figure 6. Some examples of excavational landforms shaped by insects. (A) 6- to 8 mm surface scarps and digs made by mud daubers (Hymenoptera: Sphecidae) when collecting mud bulls at the soil surface to construct their aerial nests, Central Texas, USA (photo J. Evans - www.NatureTracking.com); (B) Cratered surface composed of individual funnel-shaped pits excavated by antlion larvae (Neuroptera: Myrmeleontidae) for trapping arthropod preys, Central Texas, USA (photo J. Evans - www.NatureTracking.com); (C) Mud turret, or chimney (~5 cm in diameter and 20 cm in height), standing above a deep hole (~1 m depth) excavated by a cicada nymph of *Fidicina chlorogena*, Amazonia (photo D. Culbert - CC BY-SA 2.0); (D) Male of *Gryllus campestris* (Orthoptera: Gryllidae) at the entrance of his tunnel (15 mm in diameter and 20-30 cm in length) in a dry meadow of NW France (photo F. Bétard).

Figure 7. Two examples of termite mound fields in tropical ecosystems. (A) LiDAR-derived shaded relief revealing the prominence, regular spacing and high density of termite mounds on the rainforest–savannas boundary of central Cameroon, north of Yaoundé (DEM processing: N. Barbier); (B) Satellite view showing the spatial pattern of near-coalescing termite mounds in the semiarid landscape of Northeast Brazil, State of Bahia (image © 2018 CNES / Google Earth).

Figure 8. Some examples of constructional landforms shaped by insects. (A) Cathedral-shaped mound (~5 m high) constructed by the termite *Nasutitermes triodiae*, Litchfield National Park, Northern

Territory, Australia (photo J. Brew – CC BY-SA 2.0) ; (B) Dome-shaped mound (~80 cm high) constructed by a colony of red wood ants (*Formica rufa*) from a brown soil above shallow granitic grus, Bois des Jarries, Vendée, France (photo F. Bétard); (C) Volcano-shaped mound (~3 cm high, with a nest entrance of ~7 mm diameter) constructed by a solitary mining bee (*Dasypoda altercator*) from a sandy substrate ("Sables et Grès de Fontainebleau"), Bois de Rochefort, Yvelines, France (photo F. Bétard); (D) Cluster of small mounds, or castings (reminiscent to those made by earthworms), shaped by *Bledius* rove beetles adults and larvae, Los Olmos Creek, South Texas, USA (photo C. Eiseman); (E) Miniature mole-like ridges (~2 cm width) shaped by a mole cricket (Orthoptera: Gryllotalpidae) from a wet sandy stream bank, East Texas, USA. (photo J. Evans - www.NatureTracking.com).

Figure 9. Ferricrete biogeochemical degradation, mechanical erosion and lateral transport of material induced by termite activity (modified from Tardy and Roquin, 1992).

Figure 10. OSL dating of a termite mound: implications for quantifying the rates of bioturbation, mound erosion and surface deposition (modified from Pillans, 2002).

Table I. Main orders and families of burrowing insects.

Orders	**Families**
BLATTODEA (termites, cockroaches)	Termitidae, Blaberidae
COLEOPTERA (beetles, scarabs)	Anthicidae, Cantharidae, Carabidae, Cetoniidae, Cicindelidae, Chrysomelidae, Curculionida, Elateridae, Heteroceridae, Scarabeidae, Silphidae, Staphylinidae, Tenebrionidae, Vesperidae
DERMAPTERA (earwigs)	Anisolabididae, Forficulidae, Labiduridae
DIPTERA (flyes)	Bibionidae, Calliphoridae, Chironomidae, Coenomyiidae, Muscidae, Psychodidae, Sciaridae, Simuliidae, Stratiomyiidae, Syrphidae, Tabanidae, Therevidae, Tipulidae, Vermileonidae
EMBIOPTERA (webspinners)	Anisembiidae, Embiidae, Oligotomidae, Scelembiidae
EPHEMEROPTERA (mayflies)	Ephemeridae
HEMIPTERA (cidadas, bugs)	Cicadidae
HYMENOPTERA (ants, bees, wasps, sawflies)	Apidae, Colletidae, Crabronidae, Formicidae, Sphecidae, Vespidae
LEPIDOPTERA (moths, butterflies)	Noctuidae, Pyralidae, Sphingidae
MECOPTERA (scorpionflies)	Panorpidae
MEGALOPTERA (alderflies, dobsonflies, fishflies)	Corydalidae, Sialidae
NEUROPTERA (antlions, mantidflies, lacewings)	Myrmeleontidae
ODONATA (dragonflies, damselflies)	Gomphidae, Petaluridae
ORTHOPTERA (crickets, grasshoppers)	Cooloolidae, Cylindrachetidae, Gryllidae, Gryllotalpidae, Myrmecophilidae, Tridactylidae
PLECOPTERA (stoneflies)	Perlidae
TRICHOPTERA (caddisflies)	Glossosomatidae, Goeridae, Hydropsychidae, Limnephilidae, Leptoceridae, Rhyacophilidae, Sericostomatidae

Table II. Insect ethology and related geomorphic effects.

Insect order	**Relevant ethology**	**Direct geomorphic effects**	**Indirect geomorphic effects**
BLATTODEA (termites, cockroaches)	Nesting Pupation Food caching Geophagy	Simple and complex mounds Tunnels and galleries	Soil erosion and creep Ferricrete dismantling Calcrete formation Fluvial island growth Aeolian dune growth
COLEOPTERA (beetles, scarabs)	Nesting Pupation Food caching Predation	Simple burrows Tunnels and galleries Small mounds	Soil erosion
DERMAPTERA (earwigs)	Nesting Hibernation	Simple burrows	
DIPTERA (flies)	Pupation Predation Geophagy	Simple burrows Funnel-shaped pits	Travertine building Bed sediment consolidation
EMBIOPTERA (webspinners)	Nesting	Simple burrows Tunnels and galleries	
EPHEMEROPTERA (mayflies)	Pupation	Simple burrows	River bank erosion
HEMIPTERA (cidadas, bugs)	Nesting Pupation	Burrows with turrets Small mounds	
HYMENOPTERA (ants, bees, wasps, sawflies)	Nesting Pupation	Surface scrapes and digs Burrows with turrets Tunnels and galleries Simple mounds	Soil erosion Creep process
LEPIDOPTERA (moths, butterflies)	Pupation Geophagy		Travertine building Bed sediment consolidation
MECOPTERA (scorpionflies)	Pupation	Simple burrows	
MEGALOPTERA (alderflies, dobsonflies, fishflies)	Pupation Predation	Simple burrows	
NEUROPTERA (antlions, mantidflies, lacewings)	Predation	Funnel-shaped pits Simple burrows	Soil erosion
ODONATA (dragonflies, damselflies)	Pupation Predation	Simple burrows	
ORTHOPTERA (crickets, grasshoppers)	Nesting Predation Oviposition	Surface scrapes and digs Simple burrows Tunnels and galleries Small mounds	Soil erosion
PLECOPTERA (stoneflies)	Predation	Simple burrows	Stream bed erosion
TRICHOPTERA (caddisflies)	Pupation Predation	Simple burrows	Travertine building Bed sediment consolidation

Table III. Mounding rates reported for some insect groups (termites, ants, cicadas, beetles), and compared with other world's major groups of bioturbators (earthworms, crayfishes, fossorial mammals).

Group	**Species**	**Location**	**Mounding rate (t ha^{-1} yr^{-1})**	**Reference**
Termites	*Amitermes* sp.	N Australia	4.70	Lee and Wood (1971)
	Cubitermes sp.	S Congo	3.00	Aloni and Soyer (1987)
	Macrotermes bellicosus	W Africa	1.25	Nye (1955)
	M. subhyalinus	N Senegal	0.67–0 .90	Lepage (1974)
	Macrothermes sp.	W Africa	0.3–1.05	Goudie (1988)
	Odontotermes latericius	N Kenya	1.06	Bagine (1984)
	Trinervitermes trinewoides	W Africa	0.35	Nel and Malan (1974)
Ants	*Aphaenogaster longiceps*	SE Australia	68.38	Humphreys (1985)
	A. barbigula	SE Australia	3.36	Eldridge and Pickard (1994)
	Lasius flavus	Berkshire, UK	8.24	Waloff and Blackith (1962)
	Formica pratensis	New York, USA	0.95	Levan and Stone (1983)
	F. exsectoides	Wisconsin, USA	11.36	Salem & Hole (1968)
	Camponotus intrepidus	SE Australia	0.19–0.28	Humphreys (1985)
	Solenopsis invicta	N Louisiana, USA	1.60	Lockaby and Adams (1985)
Cicadas	*Psaltoda moerens, Thopa saccata*	SE Autralia	0.03–0.19	Humphreys and Mitchell (1983)
Beetles	*Copris tullius, Pinotus carolinus*	Kansas, USA	0.16	Lindquist (1933)
	Peltrotupes young	Florida, USA	0.01–1.85	Kalisz and Stone (1984)
Earthworms	*Lumbricus* sp.	S England, UK	16.90–40.60	Darwin (1881)
	Allolobophora sp.	Rothamsted, UK	2.20–51.10	Evans (1948)
	Millsonia omodeoi	Lamto, Ivory Coast	28.00–35.00	Lavelle (1978)
Crayfishes	*Cambarus* sp.	S Indiana, USA	6.30–8.40	Thorp (1949)
	Eustacus hierensis	SE Australia	7.30	Young (1983)
Mammals	*Talpa europaea*	Moscow, Russia	3.90-18.60	Abaturov (1972)
	Meriones hurrianae	Rajasthan, India	1.04	Sharma and Joshi (1975)
	Oryctolagus cuniculus	De Blink, Netherlands	0.81	Rutin (1992)
	Thomomys talpoides	Colorado, USA	3.90–5.80	Thorn (1978)

Figure 1

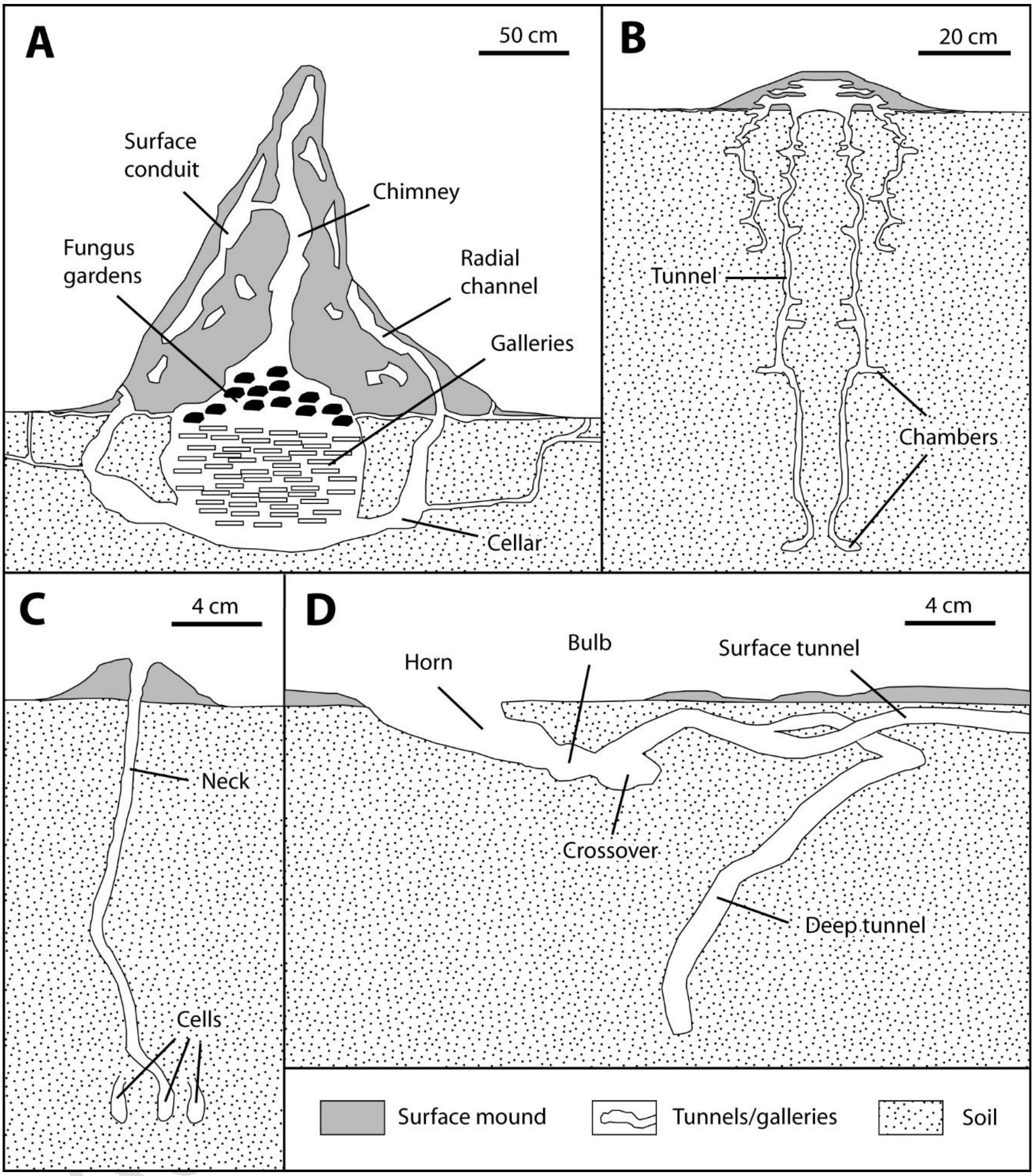

A
50 cm
Surface conduit
Chimney
Fungus gardens
Radial channel
Galleries
Cellar
B
20 cm
Tunnel
Chambers
C
4 cm
Neck
Cells
D
4 cm
Horn
Bulb
Surface tunnel
Crossover
Deep tunnel
Surface mound
Tunnels/galleries
Soil

Figure 2

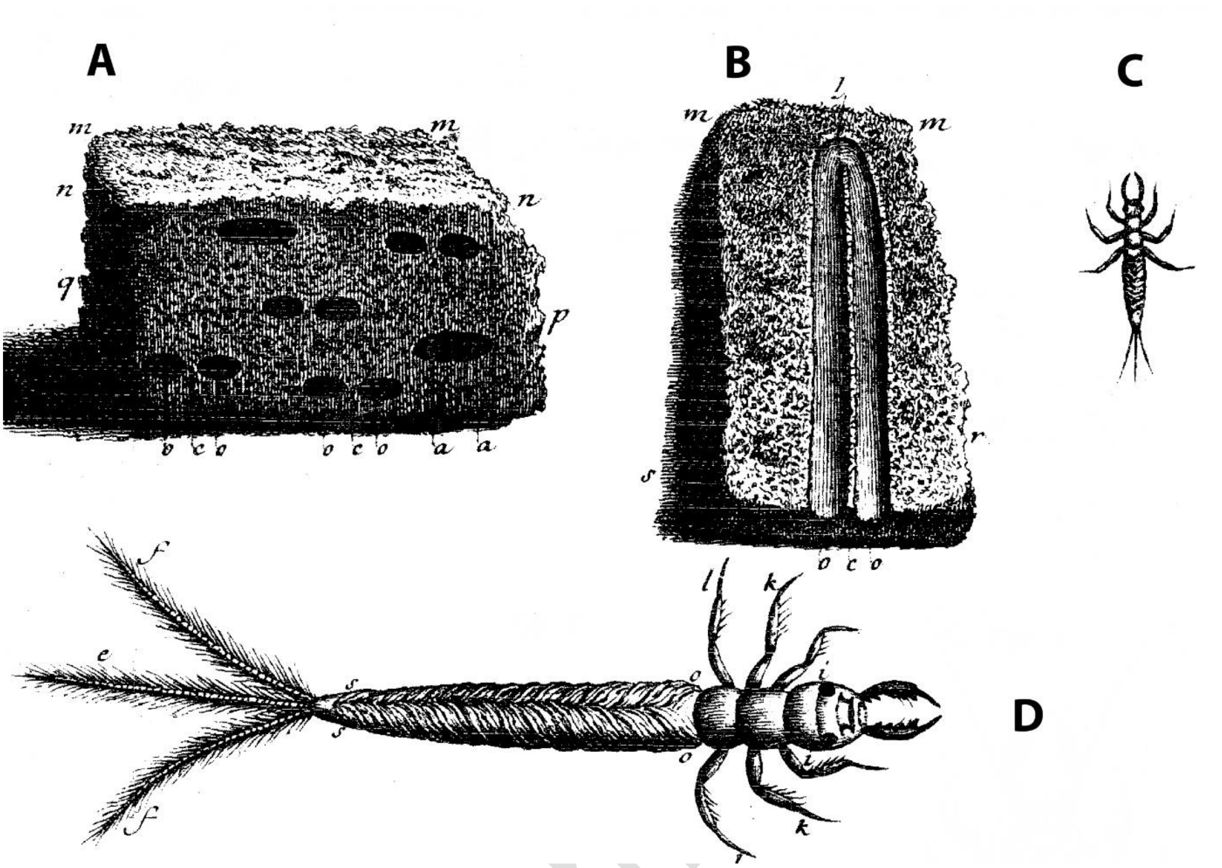
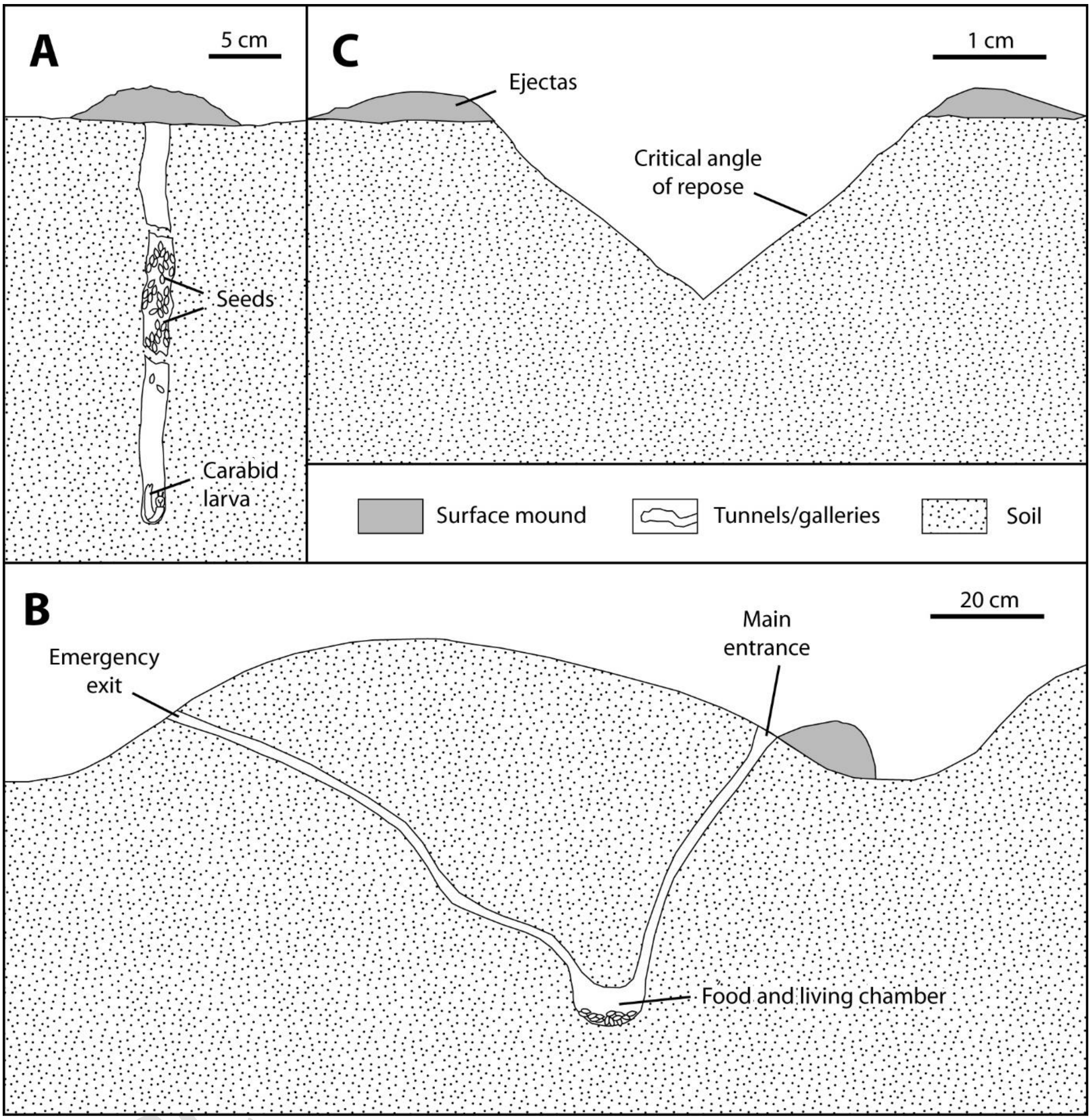
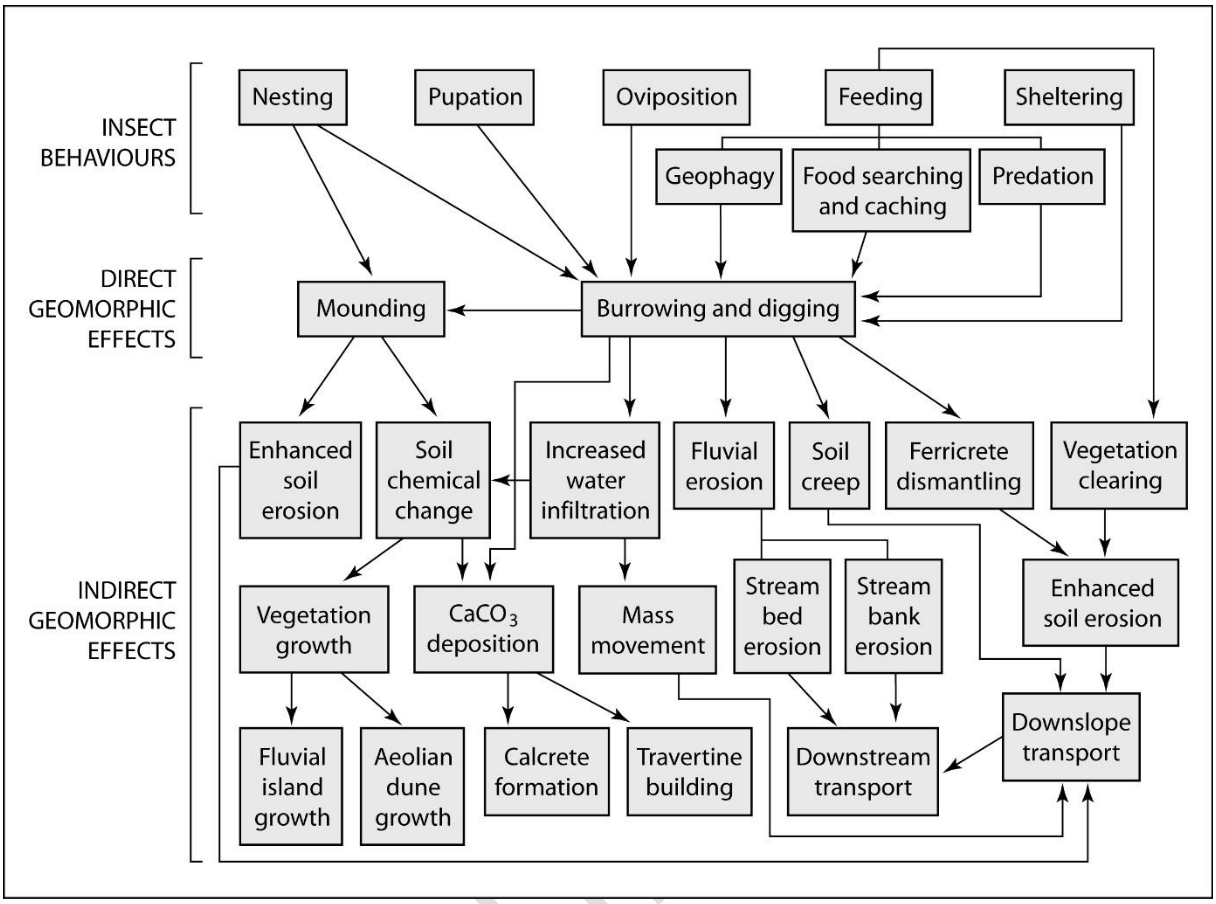


Figure 3


A
5 cm
Seeds
Carabid larva
C
1 cm
Ejectas
Critical angle of repose
Surface mound
Tunnels/galleries
Soil
B
20 cm
Emergency exit
Main entrance
Food and living chamber

1306 Figure 4



1307

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Figure 5

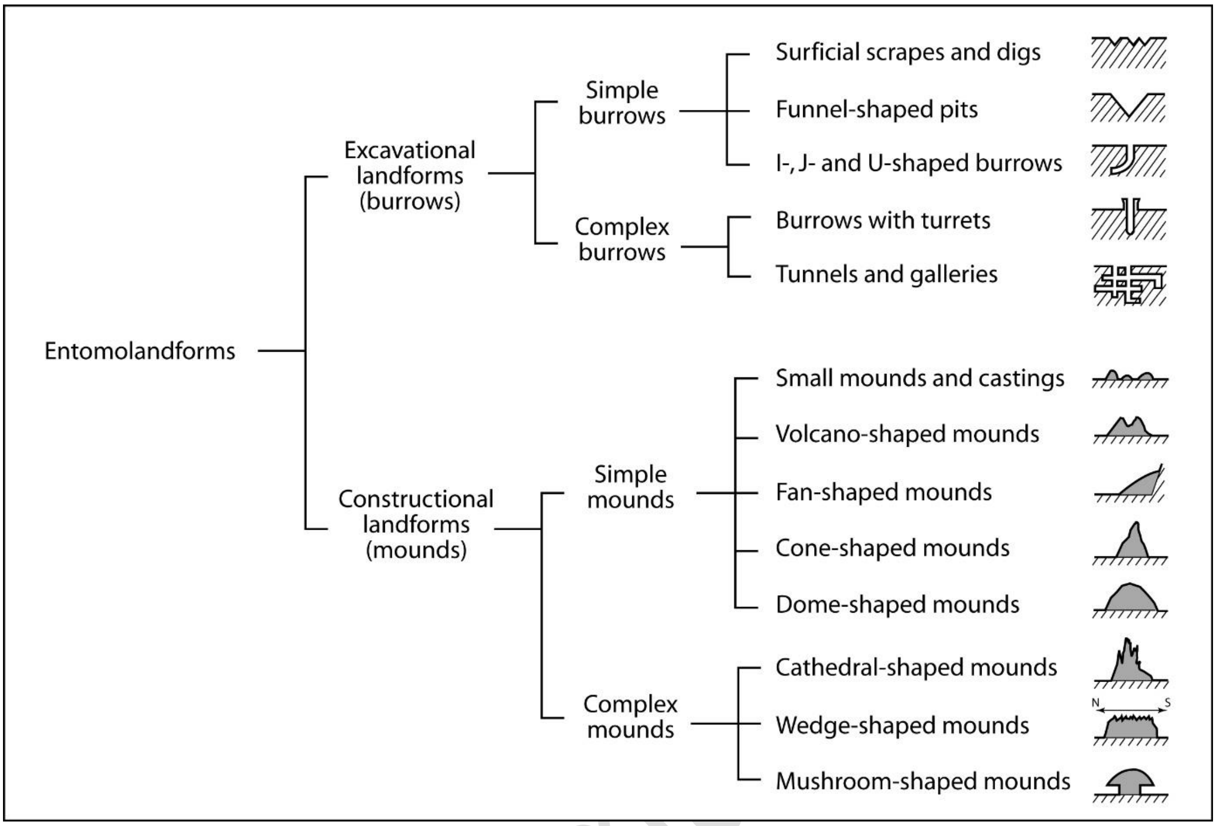

Entomolandforms
Excavational landforms (burrows)
Simple burrows
Surficial scrapes and digs
Funnel-shaped pits
I-, J- and U-shaped burrows
Complex burrows
Burrows with turrets
Tunnels and galleries
Constructional landforms (mounds)
Simple mounds
Small mounds and castings
Volcano-shaped mounds
Fan-shaped mounds
Cone-shaped mounds
Dome-shaped mounds
Complex mounds
Cathedral-shaped mounds
N
S
Wedge-shaped mounds
Mushroom-shaped mounds

Figure 6

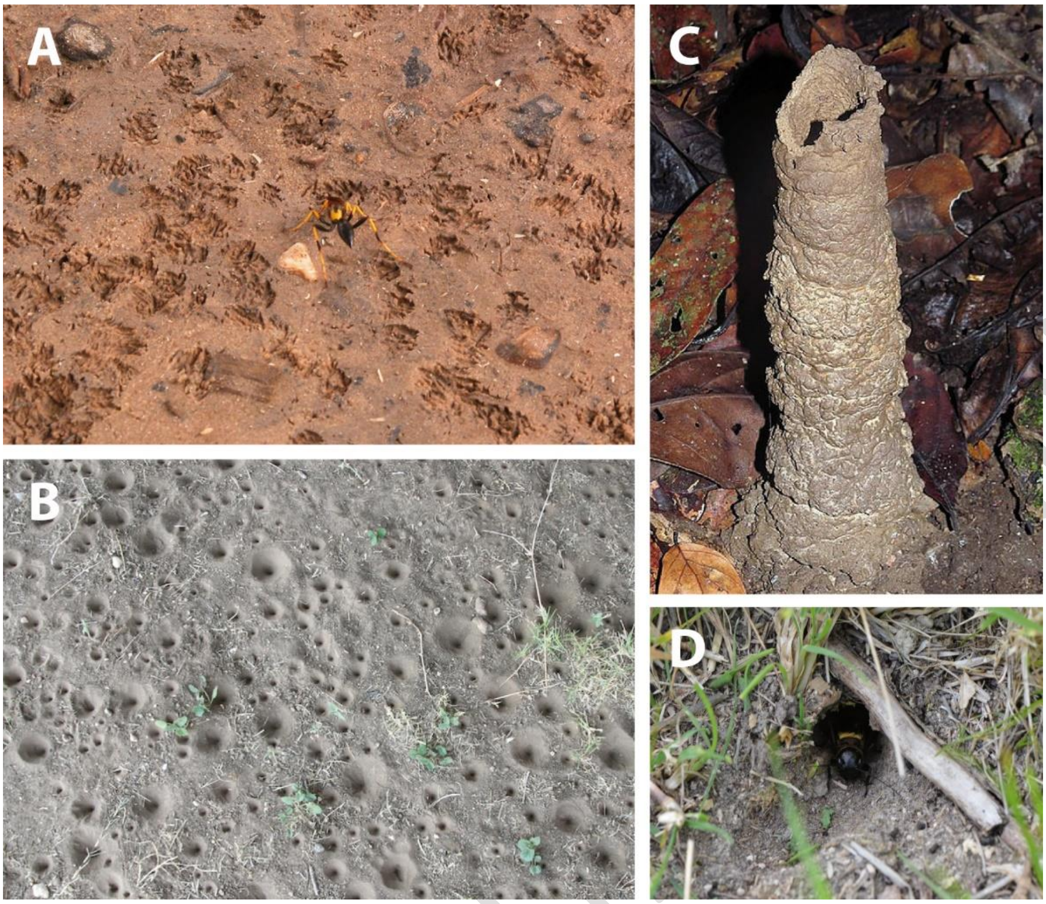


Figure 7

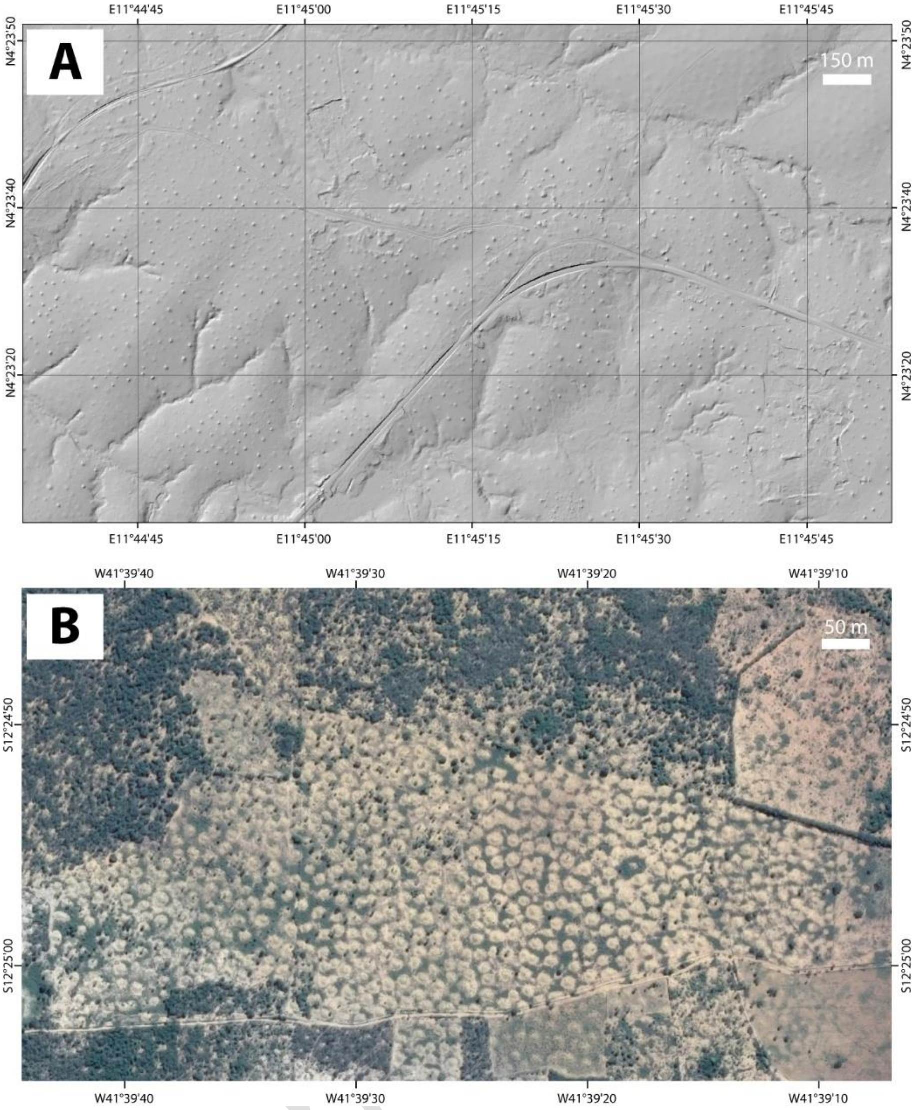

A
150 m
E11°44'45
E11°45'00
E11°45'15
E11°45'30
E11°45'45
N4°23'50
N4°23'40
N4°23'20
B
50 m
W41°39'40
W41°39'30
W41°39'20
W41°39'10
S12°24'50
S12°25'00

Figure 8

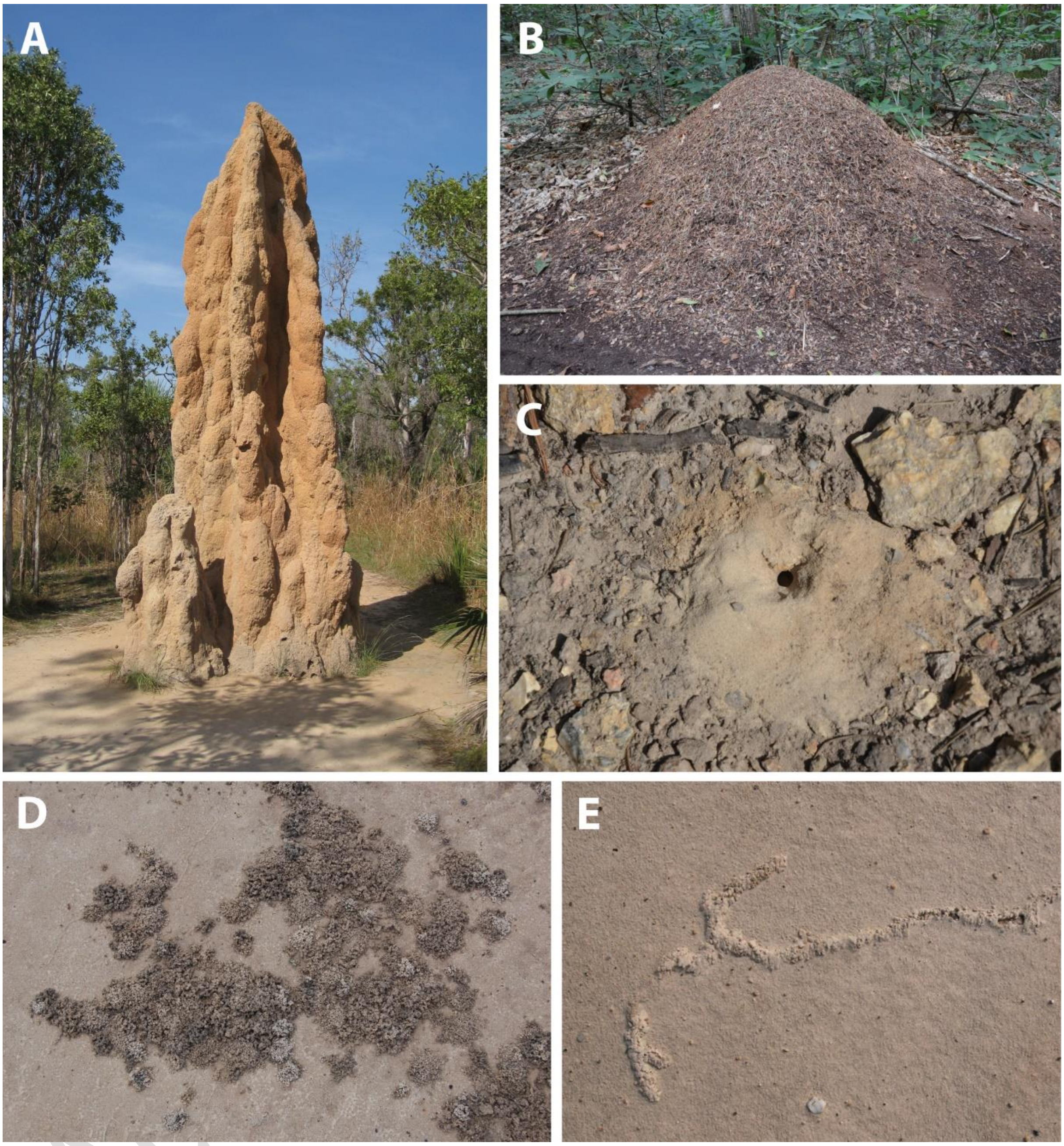
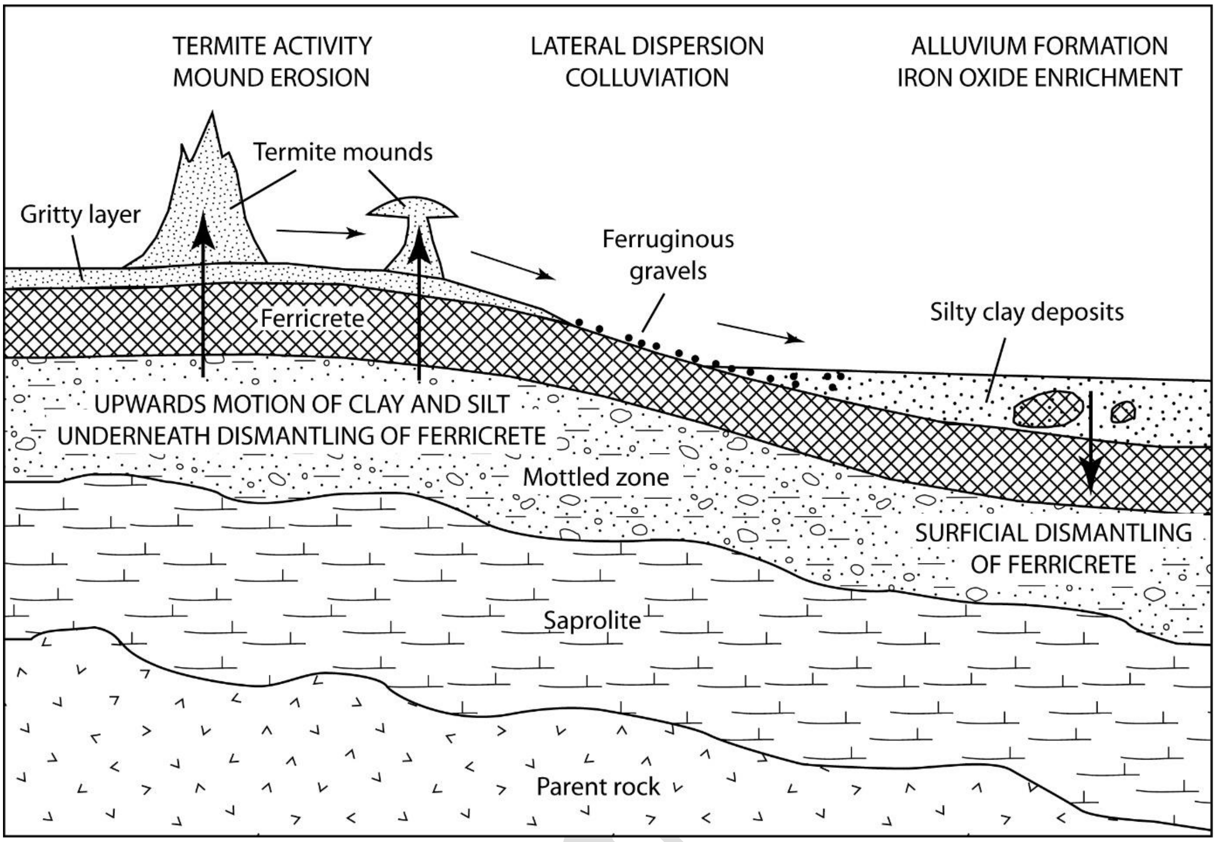
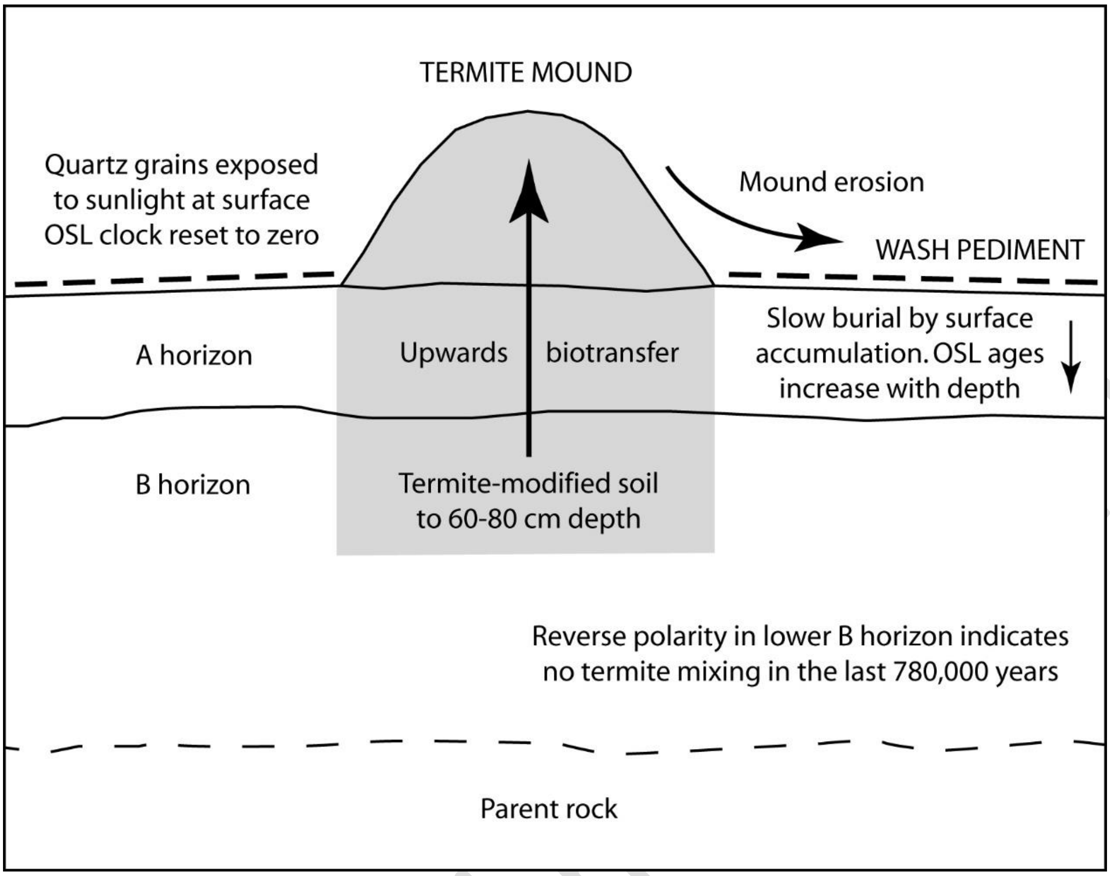


Figure 9


TERMITE ACTIVITY
MOUND EROSION
LATERAL DISPERSION
COLLUVIATION
ALLUVIUM FORMATION
IRON OXIDE ENRICHMENT
Termite mounds
Gritty layer
Ferruginous gravels
Silty clay deposits
Ferricrete
UPWARDS MOTION OF CLAY AND SILT
UNDERNEATH DISMANTLING OF FERRICRETE
Mottled zone
SURFICIAL DISMANTLING
OF FERRICRETE
Saprolite
Parent rock

1324 Figure 10



1325