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1 **Insects as zoogeomorphic agents: An extended review**

2
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5
6 **ABSTRACT:** Insects are the largest and most diverse group of living organisms on Earth, playing a
7 critical but underestimated role as agents of geomorphic change. Burrowing insects create micro-scale
8 landforms such as subterranean tunnels and surface mounds and, by this way, exert an influence on
9 hydrology, soil erosion and sediment transfer at a wider landscape scale. However, social insects
10 represented by ants and termites were the main taxa studied as geomorphic agents and ecosystem
11 engineers. This paper proposes an extended and critical literature review of insects as zoogeomorphic
12 agents, with reference to various taxonomic orders and families of insects having a burrowing behaviour.
13 It provides a large overview of their primary and secondary impacts on Earth surface systems, both
14 supported by naturalistic evidence and available quantitative data. Some evolutionary insights are
15 discussed based on fossil evidence of geomorphic work by insects and, at finer temporal scale, on recent
16 advances in radiometric and luminescence dating of insect mounds. Finally, this paper explores the
17 fruitful links between geomorphology and entomology, and suggests several research perspectives in
18 order to develop an integrated understanding of the importance of insects in Earth surface processes and
19 landforms.

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

21 22 **Introduction**

23 Insects are the most diverse and abundant class of animals on Earth, with ~1 million described species
24 – out of a total estimate of ~5.5 million species – that dominate animal biomass in many terrestrial
25 ecosystems (Stork, 2018). Their role as geomorphic agents has been recognized for more than a century
26 (Branner and Reid, 1900) but, since then, scientific studies and syntheses have mainly been focused on
27 select groups, especially ants and termites (e.g., Humphreys, 1981; Goudie, 1988; De Bruyn and
28 Conacher, 1990; Butler, 1995; Whitford and Eldridge, 2013). Overall, little attention was paid to the
29 geomorphic impacts of insect groups other than social ants and termites. Yet almost every insect order
30 has members that dig or burrow into soils or sediments at some stage in their life cycle (Eiseman et al.,
31 2010), with direct or indirect geomorphic effects to be considered from a very local scale to a wider
32 landscape scale. Compared to the geomorphic changes induced by vertebrates (for example, the well-
33 known and visible effects of dam-building beavers: Butler and Malanson, 2005), those by insects are
34 effectively more subtle except for the outstanding surface mounds created by social insects. Less visible,
35 but no less important, are the bioturbational effects of burrowing insects affecting both terrestrial (e.g.,
36 soils and weathering mantles) and aquatic environments (e.g., lake and river sediments). A
37 comprehensive overview of the geomorphic influences of entomofauna thus appears essential for a
38 global understanding of Earth surface processes and landforms.

39 Links between insects and landforms lie in the scope of zoogeomorphology, defined by Butler (1995)
40 as the study of geomorphic effects of animals. Based on extensive study of the behaviour of worms and

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

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

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

77

78 **Insect ethology and geomorphic processes**

79 Insect ethology, i.e. the study of insect behaviour, is a major aspect to consider in the understanding
80 of elementary geomorphic processes. Despite a certain lack of attention by geomorphologists on this
81 aspect, insect-induced processes have been variously discussed in several publications, mainly from a
82 pedoturbational perspective (e.g., Humphreys and Mitchell, 1983; Goudie, 1988; Mitchell, 1988; De
83 Bruyn and Conacher, 1990; Butler, 1995; Paton et al., 1995; Wilkinson et al., 2009; Butler et al., 2013;
84 Whitford and Eldridge, 2013). Readers interested in the pedoturbational actions of ants and termites are

85 asked to refer to the above-mentioned references for further details. In this section are examined the
86 elementary geomorphic processes of burrowing and digging induced by a wide variety of insect orders
87 and families (Table I) with respect to their morphological and ethological characters.

88 Burrowing behaviour for nesting and pupating

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

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

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

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

139 Contrary to the above-mentioned groups, a major part of insect orders has a transient burrowing
140 behaviour, mainly as larvae and nymphs, and become terrestrial or flying insects as adults. The
141 Lepidoptera (butterflies and moths, though only moth larvae are soil-dwellers) burrow into the soil to
142 pupate. Sphinx moths (Sphingidae) are one of those species that overwinter in the soil as pupae. Digging
143 behaviour for pupating is reported for a wide range of insect orders, including Coleoptera (dung beetles,
144 scarabs, chafers, weevils), Diptera (flies), Mecoptera (scorpionflies) and Megaloptera (alderflies,
145 dobsonflies, fishflies). In the Trichoptera order (caddisflies), larvae burrow and pupate into the bottom
146 sediment of streams, and have direct and indirect geomorphic effects by modifying the hydraulic
147 properties of bed material and the permeability of hyporheic zones (Johnson et al., 2009; Mason et al.,
148 2019). Some hemimetabolous insects (i.e., without pupal stage) may also have underground larval stages
149 whose duration is often much longer than the terrestrial adult stage. For example, in the Hemiptera order,
150 cicadas live underground as larvae for most of their lives at depths down to about 2.5 m, where they dig
151 their larval chambers. In the Odonata order, most species of petalurid dragonflies have a fossorial larval
152 stage; larvae typically excavate burrows in soft peaty soils in mires or along stream margins (Baird,
153 2014). In a similar way, Ephemeroptera (mayflies) do burrows into the substrate of lakes or streams
154 throughout most of their lives as aquatic larvae, a burrowing behaviour described along the river Marne
155 by the French naturalist Réaumur as soon as the 18th century (Réaumur, 1742; Figure 2).

156 Burrowing behaviour in relation to food provision and predation

157 After nesting and pupating, burrowing is involved in a variety of other functions relating to the
158 feeding behaviours of insects, including the search for below-ground food, food caching, geophagy,
159 predation as well as sheltering from predators. Belonging to the same order as termites (Blattodea)
160 despite strong differences in size and sociability, the Australia's giant burrowing cockroach
161 (*Macropanesthia rhinoceros*) spends most of its time in foraging for food. As highlighted by its
162 vernacular name, the species burrows an underground alcove at ~1-meter depth where the female
163 provides food for her larvae until they leave the nest and construct their own burrows (Rugg and Rose,
164 1991). Food provision for offspring in underground galleries and cells is, in fact, a common behaviour
165 reported in various insect groups such as termites, ants and bees, and is fully integrated in the nest
166 architectures and functions.

167 Hoarding or food caching in insect behaviour is also a common process involved in burrowing. One
168 fascinating behaviour of some granivorous ground beetle larvae (Coleoptera: Carabidae) is the creation
169 of burrows for caching seeds of grasses, particularly in the genus *Harpalus* (Kirk, 1972; Hartke et al.,
170 1998). Their burrows vary in size according to larval stage and species, with a diameter around 3-5 mm
171 and a depth up to 70 cm, and are generally topped with a small mound or tumulus (Figure 3A). In the
172 order Orthoptera, the ensiferan family Gryllidae has many subterranean members that live in
173 multifunctional burrows. Besides using the burrow as a calling site or as a temporary shelter from
174 predators (Gawałek et al., 2014), several species of burrowing crickets use it for food storage. This is

175 the case of the Tobacco Cricket, *Brachytrupes membranaceus*, which digs a burrow averaging 50 to 80
176 cm in depth, with an enlarged chamber in which the cricket stores food (Büttiker and Bünzli, 1958). The
177 burrow is dug by the mandibles, and the forelegs serve to push the excavated material out of the entrance,
178 where a mound can reach a height up to 30 cm (Figure 3B).

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

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

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

219

220 **Direct geomorphic effects of insects**

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

227 **Burrows as excavational landforms**

228 Insect burrows can be excavated into a wide diversity of substrates and can range in complexity from
229 a simple hole a few centimeters in depth, to a complex network of interconnecting tunnels and galleries
230 thousands of meters in total length. The most superficial and elementary microlandforms – comparable
231 in size and depth to micro-scale glacial landforms such as friction cracks and chatter marks – are the
232 surface scrapes and digs left by some foraging insects when collecting nest material, feeding or exploring
233 in order to dig a deeper, permanent burrow (Eiseman et al., 2010). Digging wasps, also called “mud
234 daubers” (Hymenoptera: Sphecidae), build aerial nests by collecting mud-balls in clayey humid soils,
235 leaving 6-8 mm scrapes printed by their mandibles at the soil surface (Chatenoud et al., 2012; Figure
236 6A). Other insects such as dune grasshoppers (Orthoptera: Acrididae) create shallow (2-3 cm deep), V-
237 shaped digs in sands in which they partially bury themselves, presumably for thermoregulation during
238 cold or windy nights (Papković and Jelinčić, 2019). These surficial features are often accompanied by
239 nearby surface trails and tracks made by insect displacements (Eiseman et al., 2010). Funnel-shaped or
240 conical pits are another shape of surficial entomolandforms with slightly higher dimensions (from 2.5
241 to 5 cm deep and 2.5 to 7.5 cm wide at the edge: Figures 3C and 6B), and are typical of predaceous
242 larval insects such as antlions and wormlions (Hollis et al., 2011; Dor et al., 2014). I-, J- and U-shaped,
243 non-branched holes can also be ranged in the category of simple burrows (Figure 5). U-shaped burrows
244 are generally produced by aquatic insect larvae from several orders, especially Diptera, Ephemeroptera,
245 Megaloptera and Trichoptera (Charbonneau and Hare, 1998; Figure 2). I- and J-shaped burrows – either
246 vertical, horizontal or inclined – may have been constructed by the same insect orders and by many
247 others, given their simple and common shape in the whole range of underground microlandforms. Their
248 detailed morphometric characteristics, however, are often group- or species-specific and can be used as
249 burrowing signatures for ichnoentomological research (Genise, 2016).

250 More complex are the burrows with a chimney-like extension (or turret), that is a recurrent feature
251 in entomolandforms. This turret extension of variable height above the burrow may have different
252 functions: in the larval tiger beetles (Coleoptera: Cicindelidae), the main functions are prey attraction
253 and thermoregulation (Knisley and Pearson, 1981). Some cicada nymph species (Hemiptera: Cicadidae)
254 use excavated sediment to construct turrets or chimneys up to 20 cm high in order to assist and maintain
255 emergence burrow humidity by reducing interior exposure to sunlight (Smith and Hasiotis, 2008; Figure
256 6C). Various digging wasps and bees also top their burrows with turrets (Eiseman et al., 2010), which
257 serve primarily to prevent burrow infilling by loose dust and debris, or to foil predators and parasites.
258 Given its complex nature, this type of burrow associated with turret construction can eventually be
259 considered as a hybrid landform of both excavational and constructional types.

260 Insect burrows forming a complex system of interconnecting tunnels and galleries have infinite
261 morphologies in terms of size, shape and depth. The majority of ant species nesting in soils excavate
262 extensive networks of tunnels and chambers below the earth’s surface (Buhl et al., 2006). The depth of
263 these tunneling networks vary widely from species to species: the Florida harvester ant (*Pogonomyrmex*

264 *badius*) build a subterranean nest of up to 3 meters deep each year, while Florida's largest ant species,
265 *Camponotus socius*, burrows only 60 centimeters into the soil. Japan's *Messor aciculatus* makes the
266 deepest nest in the world, with galleries up to 4 meters down into the earth. Semi-social and unsocial
267 insects can also dig complex systems of deep tunnels. The gregarious webspinners (Embioptera) produce
268 networks of silk-line galleries that can form an extensive tunnel system of aggregated nests (McMillan
269 et al., 2016). Crickets and mole crickets (Orthoptera: Gryllidae and Gryllotalpidae) individually
270 construct tunnel networks of relative complexity up to 60 centimeters long (Figures 1D and 6D). After
271 Held (2019), a single adult of southern mole cricket (*Neoscapteriscus borellii*) excavates 126,5 g (4.4
272 oz) of clay or 141 g (8.3 oz) of loamy sand while tunneling in 7 days; it also builds more longer and
273 more branched tunnels in loamy sand soils than in clay soils. In this species as in many others, the type
274 of substrate directly influences the shape of tunnels and the rate of burrowing.

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

297 Mounds as constructional landforms

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

309 Figure 7B). Somewhat analogous to the “mima” mounds of North America and “heuweltjies” of
310 Southwestern Africa, their origin has long remained enigmatic, until recent studies demonstrated their
311 close association with mound-building termites (Souza and Delabie, 2017; Martin et al., 2018). Unlike
312 most termitaria found in the tropics, these Brazilian mounds are not nest structures but amorphous
313 accumulations generated by the steady excavation of vast interconnecting tunnel networks from a single
314 termite species, *Syntermes dirus*. Estimated volume of excavated soil represents the removal and re-
315 deposition of ~10 km³ of earth – equivalent to ~4,000 great pyramids of Giza – over a period of ~4,000
316 years (Martin et al., 2018). These figures make it the greatest known example of ecosystem engineering
317 yet recorded worldwide by a single insect species.

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

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

336 Ant mounds (or anthills) are comparable to termite mounds in many aspects, but their morphological
337 features are less diverse, producing mainly cone-shaped and dome-shaped mounds (Figure 8B). In the
338 precursory work by Branner (1909), ant mounds as high as 5 meters, with bases 15-16 meters in
339 diameter, have been described from tropical South America, making these features among the biggest
340 anthills of the world. Ant mounds in cold-temperate ecosystems are substantially smaller, but can reach
341 up to 2 meters high in the red wood ants (*Formica rufa* group), with densities of 3-18 nests ha⁻¹ (Taylor
342 et al., 2019). Higher densities of mounds are reported for North American harvester ants
343 (*Pogonomyrmex* spp.: 20-150 nests ha⁻¹; MacMahon et al., 2000) and fire ants (*Solenopsis invicta*: 50-
344 220 nests ha⁻¹; Vogt et al., 2009). Exceptionally, the densities of anthills created by *Lasius flavus* can
345 reach up to 2,500 mounds ha⁻¹ in some parts of the Baltic region and the British islands (Elmes, 1991).
346 Such densities produce a hummock topography typical of several European landscapes of wet meadows,
347 peat lands and salt marshes where the ant mounds are an adaptation to seasonally flooded or waterlogged
348 soils (Whitford and Eldridge, 2013).

349 Many other insect orders have members that build earth mounds, generally with smaller dimensions
350 (1-30 cm in height) and simple morphologies (Figure 5). Thousands of solitary bee species are ground-
351 nesters and dig subterranean tunnels and galleries whose excavated material is pushed to the surface as
352 volcano-shaped mounds of 2-5 cm high, with an open crater <1 cm in diameter (Cane, 2003; Sarzetti et
353 al., 2013; Figure 8C). When tunneling horizontally with a burrow entrance on a wallslope, the excavated

354 soil is typically deposited in fan-shaped mounds. In the Coleoptera order, rove beetle adults and larvae
355 of the genus *Bledius* (Staphylinidae) make clusters of many small mounds very analogous to the castings
356 of earthworms (Eiseman et al., 2010; Figure 8D). Ground beetle larvae and cicada nymphs are also
357 mound-builders when excavating and pushing up a small mound of soil or tumulus that caps their larval
358 burrow. Endogean orthopterans, notably represented by mole crickets (Gryllotalpidae) and pygmy mole
359 crickets (Tridactylidae), also produce small mounds and miniature mole-like hills with a typical
360 elongated shape (esker-like landforms; Figure 8E). All these mounds correspond to loose material
361 simply deposited on the surface in the same way as earthworm casts, and are therefore ephemeral
362 landforms easily erodible by subsequent rainsplash and runoff processes. As such, they may be classified
363 as *type-I* mounds, as defined by Humphreys and Mitchell (1983) in their classification of ant mounds,
364 here extended to all insect mounds. At the opposite, a major part of the larger, more complex termite
365 mounds harboring nest structure, belongs to the *type-II* category of Humphreys and Mitchell (1983):
366 such mounds, often cemented by clay supply, are more resistant to erosion and therefore can persist in
367 the landscape for longer periods of time.

368 Quantitative estimates of mounding rates by entomofauna vary considerably between insect groups
369 and even within a same genus or species, depending on many environmental factors, but methods of
370 estimation probably contribute to observed variations. Despite some shortcomings in the quantification
371 of mounding, it is nevertheless possible to provide a global appreciation of the constructional potential
372 of some insect groups from a comparison of mounding rates with other world's major groups of
373 bioturbators (Table III). In the scientific literature, ants and termites are considered as active mounders
374 in a variety of environments, but their activity is globally considered to be much lower than that of
375 earthworms (Wilkinson et al., 2009; Taylor et al., 2019). Mounding rates reported for termites and ants
376 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
377 Blackith, 1962; Salem and Hole, 1968; Humphreys, 1981; De Bruyn and Conacher, 1990). Such high
378 mounding rates are similar to the constructional activity of crayfishes and fossorial mammals like the
379 European mole (*Talpa europaea*) or the pocket gopher (*Thomomys talpoides*) (Table III). Higher rates
380 of mounding up to 68 t ha⁻¹ y⁻¹ were exceptionally reported by Humphreys (1985) for the Australian ant
381 *Aphaenogaster longiceps*, that would exceed mounding rates of most burrowing animals. Table III also
382 provides some data on the rate of mounding by lesser studied insects such as cicadas and beetles, with
383 rates generally <0.5 t ha⁻¹ y⁻¹, although Kalisz and Stone (1984) reported mounding of up to 1.85 t ha⁻¹
384 y⁻¹ for the scarab beetle *Pelotrupes youngi*. For comparison, such moderate values are in the same order
385 of magnitude than those reported for the Indian desert gerbil (*Meriones hurrianae*) or the European
386 rabbit (*Oryctolagus cuniculus*) (Table III).

387

388 **Indirect geomorphic effects of insects**

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

395 **Secondary landform construction and destruction**

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

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

422 At a finer scale, insects can also contribute to the shaping of distinct morphological features in stream
423 channels such as biogenic travertine deposits and tufa terraces (Humphreys et al., 1995; Marks et al.,
424 2006). In karst environments, aquatic insect larvae play an indirect geomorphic role in CaCO₃ deposition
425 at the microrelief level, as demonstrated by Drysdale (1998) from stream crusts and travertine deposits
426 in the Barkly karst region, Australia. Here the most conspicuous roles are played by fly larvae (Diptera:
427 Chironomidae and Simuliidae), moth larvae (Lepidoptera: Pyralidae) and caddisfly larvae (Trichoptera:
428 Hydropsychidae). By constructing cylindrical cases and capture nets on the travertine surfaces, they create
429 passive substrata for calcite precipitation while slowing the stream flow due to the roughness induced
430 by the many microreliefs. A similar process of travertine-building by a hydropsychid caddisfly,
431 *Smicridea travertinera*, has been described by Paprocky et al. (2003) from Venezuela. In fact, the
432 retreat-making behaviour of those insects appears to participate both in the bioconstruction and
433 bioerosion of the travertine formations.

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

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

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

482 Effects on soil erosion and sediment yield

483 Studying the effects of insect activity on soil erosion is a complex matter, because the hydrological
484 and erosional responses of watersheds are varied, depending on insect behaviours, nest morphologies,
485 and many other environmental factors. Burrowing insects can both reduce soil loss, by improving
486 porosity and infiltration capacity, and increase it, by diminishing soil stability as a result of organic

487 matter digestion and biomixing. Soil erosion can also be enhanced through upward biotransfer of fine-
488 grained material available for subsequent wash and creep action (Mitchell, 1988; Butler, 1995;
489 Dragovich and Morris, 2002; Jouquet et al., 2012; Schmidt et al., 2014; Li et al., 2019a). Moreover,
490 adjustments and interactions between geomorphic processes, insects and vegetation may be invoked in
491 some cases as an indirect mechanistic evidence for soil erosion. In particular, the relationship between
492 locust swarms and soil erosion is reciprocal. Locusts and grasshoppers consume vegetation and, when
493 they become numerous with a gregarious behaviour, can have large impact on land cover by stripping
494 vegetation and expose bare soils to rain splash, resulting in increased runoff and accelerated soil erosion
495 at the landscape scale (Dibble, 1940; Gillon, 1989; Latchininsky et al., 2011). Conversely, livestock
496 overgrazing and enhanced soil erosion are known to promote locust outbreaks in areas affected by land
497 degradation and desertification (Cease et al., 2012). At a more local scale, several ant species clear
498 vegetation around their nests, affecting soil hydrologic patterns around the mounds, with the overall
499 consequence to increase soil erosion and sediment transfers (MacMahon et al., 2000). Another indirect
500 effect of many insects is that they transport seeds and, by this way, determine the location of the new
501 plants and the vegetation patterns, that can indirectly influence infiltration paths and soil erosion.

502 Basically, all burrowing insects influence the hydrological properties of soils by producing water-
503 conducting macropores underground (voids, tubes, and galleries) and surficial nest entrances creating
504 preferential water infiltration paths. Experimental study of the effects of termites and ants on soil
505 infiltration rates has been investigated by many authors in a wide variety of environmental and
506 topographic settings (e.g., Elkins et al., 1986; Eldridge, 1993, 1994; Mando et al., 1996; Wang et al.,
507 1996; Cammeraat et al., 2002; Leonard et al., 2004; James et al., 2008; Cheik et al., 2018; Li et al.,
508 2019b). Most of these studies have demonstrated that soil infiltration rates and porosity were
509 significantly higher on termite- or ant-modified soils than on non-nest soils. One of the main controlling
510 factors of such differences is the existence of a dense network of tunnels and chambers resulting in lower
511 bulk density (i.e. increased porosity) and in larger flow percolation of water to deep soil layers (Whitford
512 and Eldridge, 2013). For example, Eldridge (1993) did a field experiment in a semi-arid woodland at
513 Yathong (eastern Australia) to study the influence of ant (*Aphaenogaster barbigula*) nest structures on
514 soil hydrological properties. Steady-state infiltration under ponding (i.e. saturated flow) on ant plots was
515 measured at a rate of $23 \pm 1.8 \text{ mm min}^{-1}$, which was four to five times greater than that on ant-free control
516 plots. He also showed a strong positive correlation between soil infiltration rate and the diameter of
517 *Aphaenogaster* nest entrances. A few studies have examined the role of lesser studied insects on soil
518 hydrologic processes and infiltration rates, especially dung beetles (Brown et al., 2010) and mole
519 crickets (Bailey et al., 2015; Li et al., 2018). All these studies highlighted the positive effect of
520 subterranean insect activity on soil porosity and water infiltration, resulting in 20% to 40% reduction in
521 surface runoff.

522 Paradoxically, and despite a general trend in runoff reduction, the same experimental studies have
523 shown that the burrowing activities of insects have the contrasting effect to exacerbate soil erosion and
524 sediment loss, because the earth mounds and the unstable soil aggregates made by burrowing insects at
525 the soil surface provide a large quantity of fine-grained material easily erodible by rainsplash and
526 slopewash. Such effects are classically reported for social insects (ants and termites) but also for unsocial
527 insects like dung beetles and mole crickets (Brown et al., 2010; Bailey et al., 2015; Li et al., 2018). The
528 relative importance of soil erosion and sediment yield notably varies with nest density and the type of
529 earth mounds (Aalders et al., 1989; Whitford and Eldridge, 2013). *Type-I* mounds are very susceptible
530 to erosion and are usually considered as a major source of sediment yield, because they consist of loose,
531 fine-grained material and often occur in high density (Humphreys and Mitchell, 1983; Paton et al.,
532 1995). At the opposite, *type-II* mounds are more compact and often cemented, and are therefore more

533 resistant to rain drop and wash erosion. For example, earth mounds constructed by the Australian
534 *Aphaenogaster* ants, which belong to the *type-I* category, are source of highly mobile sediment for
535 subsequent transport to be streambed (Richards, 2009). Similarly, in the tropical rainforest of Panama,
536 Schmidt et al. (2014) demonstrated high rates of erosion and sediment yield from *type-I* ant mounds in
537 a small experimental catchment, with a mean estimate of 725 kg ha⁻¹ calculated for an 8-month wet
538 period. Compared to the total sediment output reported for the same catchment (1–2 t ha⁻¹ y⁻¹), these
539 values potentially indicate a major contribution of ant mounding activity to sediment delivery.

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

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

567

568 **Past geomorphic effects of insects: some evolutionary insights**

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

574 **Fossil records of entomogeomorphic activity**

575 The oldest insect fossil records date back to the Devonian (Engel and Grimaldi, 2004; Garrouste et
576 al., 2012), even if the first insects probably appeared earlier, as soon as the Ordovician, concomitantly
577 with the appearance of bryophyte-like and land plants with which they largely coevolved (Misof et al.,
578 2014). A first diversification phase of insects is expected to have occurred between the Silurian and the
579 Late Devonian, and a second one during the Late Carboniferous, giving rise to the emergence of
580 numerous new major taxa in the subclass of Pterygota (winged insects). Most extant orders of insects
581 originated during the Permian, but many of the early groups became extinct with the Permo-Triassic
582 extinction event (Labandeira, 2005). Most modern insect families appeared in the Triassic and Jurassic
583 periods, and a number of successful groups of burrowing insects – especially the Hymenoptera (wasps,
584 bees and ants) and Coleoptera (beetles and scarabs) – developed in coevolution with angiosperms
585 (flowering plants) during the Cretaceous. Many modern insect genera emerged during the Cenozoic,
586 this last period recording the major part of insect traces and fossil landforms (paleo-burrows and paleo-
587 mounds) preserved in continental deposits and paleosols (Humphreys, 2003; Genise, 2016).

588 The identification of insect trace fossils (or ichnofossils), mostly represented by nests and pupation
589 chambers, has largely been based on comparisons with the morphological characteristics of modern
590 structures (Hasiotis, 2003; Tschinkel, 2003; Genise, 2016). One important issue of ichnological studies
591 for biogeomorphological research is to understand to what extent terrestrial bioturbation has evolved
592 since insects colonized the land areas of Earth in the Middle Paleozoic. Despite a lack of direct evidence
593 for pre-Mesozoic entomofaunal burrowing signatures, colonization of land by insects at the Silurian –
594 together with plants (Corenblit and Steiger, 2009) – probably represents a critical shift for geomorphic
595 changes on the Earth surface. Trace fossils and paleo-burrows found in Palaeozoic paleosols have been
596 used as evidence for the activity of burrowing invertebrates as soon as the Cambrian (Jensen, 2003),
597 indicating an emerging bioturbation by non-insect animals. The oldest and direct ichnologic evidence
598 of burrowing activity by insects was found in Early Mesozoic paleosols. Burrow traces made by cicada-
599 like nymphs have been recorded in Triassic paleosols from Antarctica and eastern Australia (Retallack,
600 1997), but insect traces remain scarce from those remote times. Complex ichnofossils and nest structures
601 constructed by termites, bees, wasps, ants and beetles are, however, common features in Cretaceous
602 paleosols (Genise, 2016). In particular, the intensity and distribution of bioturbation indicated by fossil
603 termite and ant nests in the Cretaceous geologic record suggest that these social insects played major
604 roles as geomorphic agents and ecosystem engineers at least since the Late Mesozoic (Hasiotis, 2003).
605 Given their abundance in paleosols, this also indicates a certain degree of coevolution between soils and
606 insects at that time (Philipps, 2009; Wilkinson et al., 2009).

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

621 active mounding by social ants may have been widespread at least since, and probably before, mid-
622 Tertiary times (Hasiotis, 2003).

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

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

651 Geomorphic implications of mound dating

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

661 The first clues to the lifetime of insect mounds were obtained by radiocarbon dating of material
662 within or at the base of termite mounds. Watson (1967) proposed a reliable age estimate of ± 700 years
663 BP for a termite hill built by *Macrotermes falciger* in Zimbabwe, based on ^{14}C dating of skeletal material
664 found inside the mound. This minimum age estimate was two to three times the age of the oldest

665 termitaria recorded in Africa at the time. Two decades later, Moore and Picker (1991) investigated a set
666 of eroded and intact earth mounds (*Heuweltjies*) of South Africa and provided new insights on the
667 longevity of these features, based on radiocarbon dating of basal calcrete of two mounds. Their results
668 showed that the mounds have been in existence for at least 4,000 years BP, i.e. an order of magnitude
669 greater than any previously recorded lifetime for termitarium inhabitation by a same species
670 (*Microhodotermes viator*). More recently, stable isotope and ^{14}C analyses of calcrete lenses in
671 abandoned termite mounds of the same region have provided new information about their age and the
672 paleoenvironmental conditions for their formation (Midgley et al., 2002; Potts et al., 2009). $\delta^{13}\text{C}$ and
673 $\delta^{18}\text{O}$ values together with ^{14}C dates indicate that *Heuweltjies* have not only formed during the Holocene,
674 as some of them have been present in the landscape for the last 36,000 years BP, i.e. at least since the
675 Last Glacial Maximum. However, the termite origin of these mounds has been questioned in those
676 studies and in many others, one of them recently attributing their formation to aeolian sediment accretion
677 rather than the direct building by termites (McAuliffe et al., 2014). Anyway, it appears that calcrete
678 frequently associated with termite mounds in tropical regions might be a useful proxy for dating insect
679 landform and reconstructing past environmental changes.

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

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

710 1979; Goudie, 1988; Whitford and Eldridge, 2013). However, quantitative constraints on such
711 accelerated erosion rates remain yet to be evidenced by OSL dating and/or other methods.

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

719

720 **Conclusions and perspectives**

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

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

- 738 (i) Additional research is needed to address both the primary and secondary geomorphic
739 impacts of insect groups other than the well-studied social ants and termites: quantitative
740 data on the mixing and mounding rates of major burrowing insects such as mole crickets
741 (Orthoptera: Gryllotalpidae) and solitary bees (Hymenoptera: Apoidea) are particularly
742 needed, as are the experimental studies of their indirect effects on soil erosion and sediment
743 transfer in a range of natural and human-modified environments.
- 744 (ii) The development of new tools and technologies such as high-resolution, multi-temporal laser
745 scanning and photogrammetry could help to quantify the volumes and rates of surface
746 mounding, in order to complement the simple, classic methods first employed by Darwin
747 (1881) and by many subsequent generations of scientists working on the bioturbation rates
748 of ants and termites.
- 749 (iii) The integration of insect behaviour and activity in soil loss equations and landscape models
750 would be a major advance in the understanding of the equivocal role of insects in soil erosion
751 at the catchment scale. Taking into account the richness and abundance of insects and their
752 positive and/or negative effects on soil erosion might contribute to a better incorporation of

- 753 biotic factors in landscape modelling, in a similar way as the “earthworm factor” recently
754 proposed by Orgiazzi and Panagos (2018). Such studies could indirectly participate in the
755 effort to achieve the Sustainable Development Goals (SDGs) related to soils, especially the
756 land degradation neutrality challenge (Keesstra et al., 2018; Visser et al., 2019), given the
757 importance of insects in the provision of soil ecosystem services.
- 758 (iv) An extended application of dating techniques to quantify the bioturbation of insects and to
759 estimate the age of mound landforms would be highly desirable: some studies have shown
760 the potential usefulness of radiocarbon (^{14}C and $\delta^{13}\text{C}$ on calcrete and insoluble organic
761 matter), cosmogenic (^{10}Be on quartz grains) and OSL dating techniques for quantifying the
762 rates of bioturbation by termites (e.g., Johnson et al., 2014; Erens et al., 2015; Kristensen et
763 al., 2015), thus encouraging further utilization of these proxies for other insect groups
764 shaping comparable features (e.g., ant mounds).
- 765 (v) The niche construction effects of insects may be further questioned in the wider scope of
766 geodiversity-biodiversity relationships: burrowing insects, in general, increase the
767 patchiness of the physical environment, or small-scale geodiversity (Bétard, 2013), which
768 creates localized patch habitat for other plants and animals, thereby increasing biodiversity
769 at the landscape scale (Zaitlin and Hayashi, 2012). This is the case of particular insect
770 landforms, such as termite mounds, acting as small-scale “biodiversity refuges” for other
771 soil macrofauna in tropical regions (Choosai et al., 2009).
- 772 (vi) In the recent debates on Anthropocene zoogeomorphology (Butler, 2018), new researches
773 are needed to study the ongoing decline in insect biomass and its potential impacts on Earth
774 surface systems (Sánchez-Bayo and Wyckhuys, 2019), with a possible decreasing influence
775 of insects on bioturbation and other geomorphic processes. In the range of human-induced
776 changes, invasive and alien species can also significantly alter geomorphic processes and
777 landforms (Fei et al., 2014), as shown by the drastic impacts of red imported fire ants
778 (*Solenopsis invicta*) on landscape change in many regions across the globe.

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

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795

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1233 **Figure captions**

1234 **Figure 1.** Sketch diagrams showing various nest structures for different insect species. (A) Nest
1235 architecture of the mound-building termite *Macrotermes michaelseni* (modified from Turner, 2000); (B)
1236 Nest architecture of the silky field ant *Formica subsericea* (modified from Drager et al., 2016); (C) Nest
1237 architecture of the desert bee *Cadeguala albopilosa* (modified from Sarzetti et al., 2013); (D) Nest
1238 architecture of the southern mole cricket *Neoscapteriscus borellii* (modified from Nickerson et al.,
1239 1979).

1240 **Figure 2.** Burrowing behaviour of aquatic insect larvae of Ephemeroidea (mayflies) and their geomorphic
1241 effects on a clay river bank, Marne, France (Réaumur, 1742). (A) Piece of the clay river bank showing
1242 burrows shaped by mayfly larvae; two close openings belong to the same burrow, whereas a single
1243 elongated hole corresponds to a burrow whose central tongue has been subsequently eroded; (B)
1244 Horizontal cross-section throughout the same piece of clay along a plane parallel to m-m-n-n, displaying
1245 a U-shaped burrow; (C) Specimen of a mayfly larva, one of those which live in the burrows of A and B
1246 at the same scale; (D) Magnified view of the same specimen of mayfly larva presented in C, showing
1247 the morphological details of the immature insect, particularly its robust legs and mandibles that help it
1248 to burrow.

1249 **Figure 3.** Cross-sections through three different hole systems related to feeding behaviours by foraging
1250 insects. (A) Sketch of a burrow of *Harpalus eraticus* showing tumulus and cached *Setaria* seeds 8-20
1251 cm deep; the larva is typically found at the bottom of its burrow (modified from Kirk, 1972); (B) Tunnel
1252 system of the Tobacco Cricket, *Brachytrupes membranaceus*, with its enlarged chamber for food storage
1253 (modified from Büttiker and Bünzli, 1958); (C) Cross-sectional view of a funnel-shaped, crater-like pit
1254 dug by an antlion larva (*Myrmeleon* sp.); note the thin ejecta blanket around the crater constructed by
1255 the insect from excavated sand (modified from Lehane and Ekdale, 2013).

1256 **Figure 4.** Flow diagram of the geomorphic impacts of insect behaviours.

1257 **Figure 5.** Direct geomorphic effects of insects: a proposed classification of entomolandforms.

1258 **Figure 6.** Some examples of excavational landforms shaped by insects. (A) 6- to 8 mm surface scarps
1259 and digs made by mud daubers (Hymenoptera: Sphecidae) when collecting mud balls at the soil surface
1260 to construct their aerial nests, Central Texas, USA (photo J. Evans - www.NatureTracking.com); (B)
1261 Cratered surface composed of individual funnel-shaped pits excavated by antlion larvae (Neuroptera:
1262 Myrmeleontidae) for trapping arthropod preys, Central Texas, USA (photo J. Evans -
1263 www.NatureTracking.com); (C) Mud turret, or chimney (~5 cm in diameter and 20 cm in height),
1264 standing above a deep hole (~1 m depth) excavated by a cicada nymph of *Fidicina chlorogena*,
1265 Amazonia (photo D. Culbert - CC BY-SA 2.0); (D) Male of *Gryllus campestris* (Orthoptera: Gryllidae)
1266 at the entrance of his tunnel (15 mm in diameter and 20-30 cm in length) in a dry meadow of NW France
1267 (photo F. Bétard).

1268 **Figure 7.** Two examples of termite mound fields in tropical ecosystems. (A) LiDAR-derived shaded
1269 relief revealing the prominence, regular spacing and high density of termite mounds on the rainforest–
1270 savannas boundary of central Cameroon, north of Yaoundé (DEM processing: N. Barbier); (B) Satellite
1271 view showing the spatial pattern of near-coalescing termite mounds in the semiarid landscape of
1272 Northeast Brazil, State of Bahia (image © 2018 CNES / Google Earth).

1273 **Figure 8.** Some examples of constructional landforms shaped by insects. (A) Cathedral-shaped mound
1274 (~5 m high) constructed by the termite *Nasutitermes triodiae*, Litchfield National Park, Northern

1275 Territory, Australia (photo J. Brew – CC BY-SA 2.0) ; (B) Dome-shaped mound (~80 cm high)
1276 constructed by a colony of red wood ants (*Formica rufa*) from a brown soil above shallow granitic grus,
1277 Bois des Jarries, Vendée, France (photo F. Bétard); (C) Volcano-shaped mound (~3 cm high, with a nest
1278 entrance of ~7 mm diameter) constructed by a solitary mining bee (*Dasypoda altercator*) from a sandy
1279 substrate (“Sables et Grès de Fontainebleau”), Bois de Rochefort, Yvelines, France (photo F. Bétard);
1280 (D) Cluster of small mounds, or castings (reminiscent to those made by earthworms), shaped by *Bledius*
1281 rove beetles adults and larvae, Los Olmos Creek, South Texas, USA (photo C. Eiseman); (E) Miniature
1282 mole-like ridges (~2 cm width) shaped by a mole cricket (Orthoptera: Gryllotalpidae) from a wet sandy
1283 stream bank, East Texas, USA. (photo J. Evans - www.NatureTracking.com).

1284 **Figure 9.** Ferricrete biogeochemical degradation, mechanical erosion and lateral transport of material
1285 induced by termite activity (modified from Tardy and Roquin, 1992).

1286 **Figure 10.** OSL dating of a termite mound: implications for quantifying the rates of bioturbation, mound
1287 erosion and surface deposition (modified from Pillans, 2002).

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1289 **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 (flies)	Bibionidae, Calliphoridae, Chironomidae, Coenomyiidae, Muscidae, Psychodidae, Sciaridae, Simuliidae, Stratiomyiidae, Syrphidae, Tabanidae, Therevidae, Tipulidae, Vermileonidae
EMBIOPTERA (webspinners)	Anisembiidae, Embiidae, Oligotomidae, Scelembiidae
EPHEMEROPTERA (mayflies)	Ephemeridae
HEMIPTERA (cicadas, 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

1290 **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 (cicadas, 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

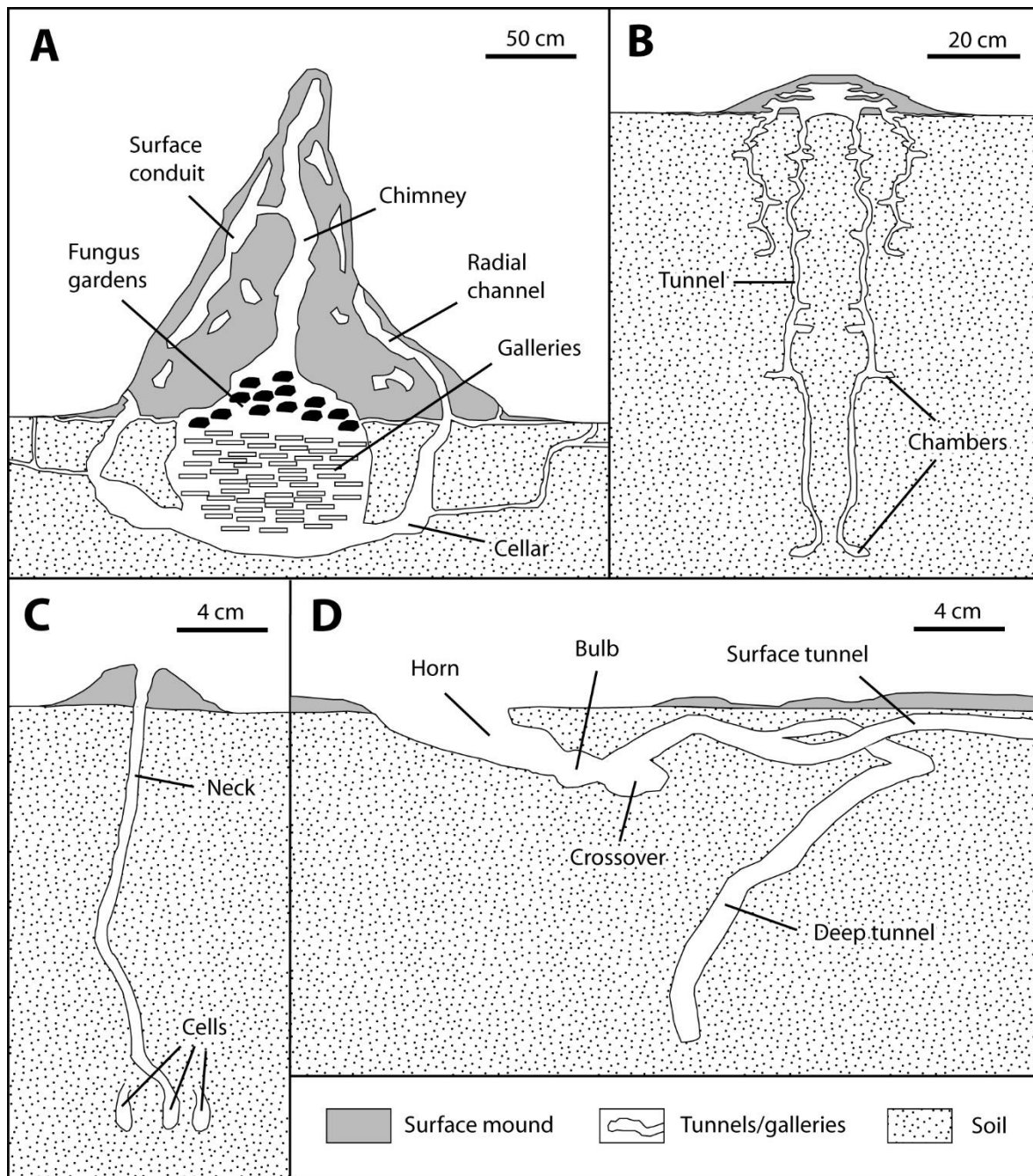
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1293 **Table III.** Mounding rates reported for some insect groups (termites, ants, cicadas, beetles), and
 1294 compared with other world's major groups of bioturbators (earthworms, crayfishes, fossorial mammals).

Group	Species	Location	Mounding rate (t ha ⁻¹ yr ⁻¹)	Reference
Termites	<i>Amitermes</i> sp.	N Australia	4.70	Lee and Wood (1971)
	<i>Cubitermes</i> sp.	S Congo	3.00	Aloni and Soyer (1987)
	<i>Macrotermes bellicosus</i>	W Africa	1.25	Nye (1955)
	<i>M. subhyalinus</i>	N Senegal	0.67–0.90	Lepage (1974)
	<i>Macrothermes</i> sp.	W Africa	0.3–1.05	Goudie (1988)
	<i>Odontotermes latericius</i>	N Kenya	1.06	Bagine (1984)
	<i>Trinervitermes trinewoides</i>	W Africa	0.35	Nel and Malan (1974)
	Ants	<i>Aphaenogaster longiceps</i>	SE Australia	68.38
<i>A. barbigula</i>		SE Australia	3.36	Eldridge and Pickard (1994)
<i>Lasius flavus</i>		Berkshire, UK	8.24	Waloff and Blackith (1962)
<i>Formica pratensis</i>		New York, USA	0.95	Levan and Stone (1983)
<i>F. exsectoides</i>		Wisconsin, USA	11.36	Salem & Hole (1968)
<i>Camponotus intrepidus</i>		SE Australia	0.19–0.28	Humphreys (1985)
<i>Solenopsis invicta</i>		N Louisiana, USA	1.60	Lockaby and Adams (1985)
Cicadas		<i>Psaltoda moerens, Thopa saccata</i>	SE Australia	0.03–0.19
	Beetles	<i>Copris tullius, Pinotus carolinus</i>	Kansas, USA	0.16
<i>Pelrotupes young</i>		Florida, USA	0.01–1.85	Kalisz and Stone (1984)
Earthworms		<i>Lumbricus</i> sp.	S England, UK	16.90–40.60
	<i>Allolobophora</i> sp.	Rothamsted, UK	2.20–51.10	Evans (1948)
	<i>Millsonia omodeoi</i>	Lamto, Ivory Coast	28.00–35.00	Lavelle (1978)
Crayfishes	<i>Cambarus</i> sp.	S Indiana, USA	6.30–8.40	Thorp (1949)
	<i>Eustacus hierensis</i>	SE Australia	7.30	Young (1983)
Mammals	<i>Talpa europaea</i>	Moscow, Russia	3.90–18.60	Abaturov (1972)
	<i>Meriones hurrianae</i>	Rajasthan, India	1.04	Sharma and Joshi (1975)
	<i>Oryctolagus cuniculus</i>	De Blik, Netherlands	0.81	Rutin (1992)
	<i>Thomomys talpoides</i>	Colorado, USA	3.90–5.80	Thorn (1978)

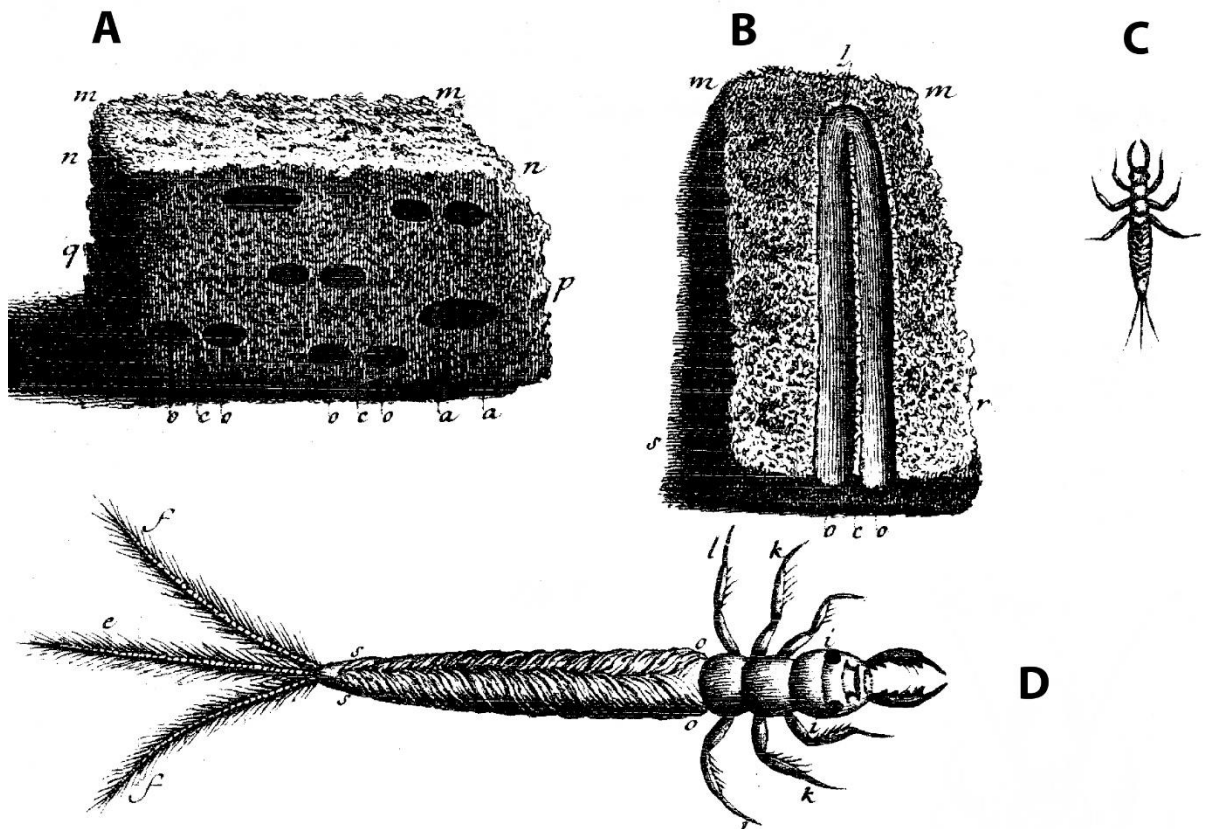
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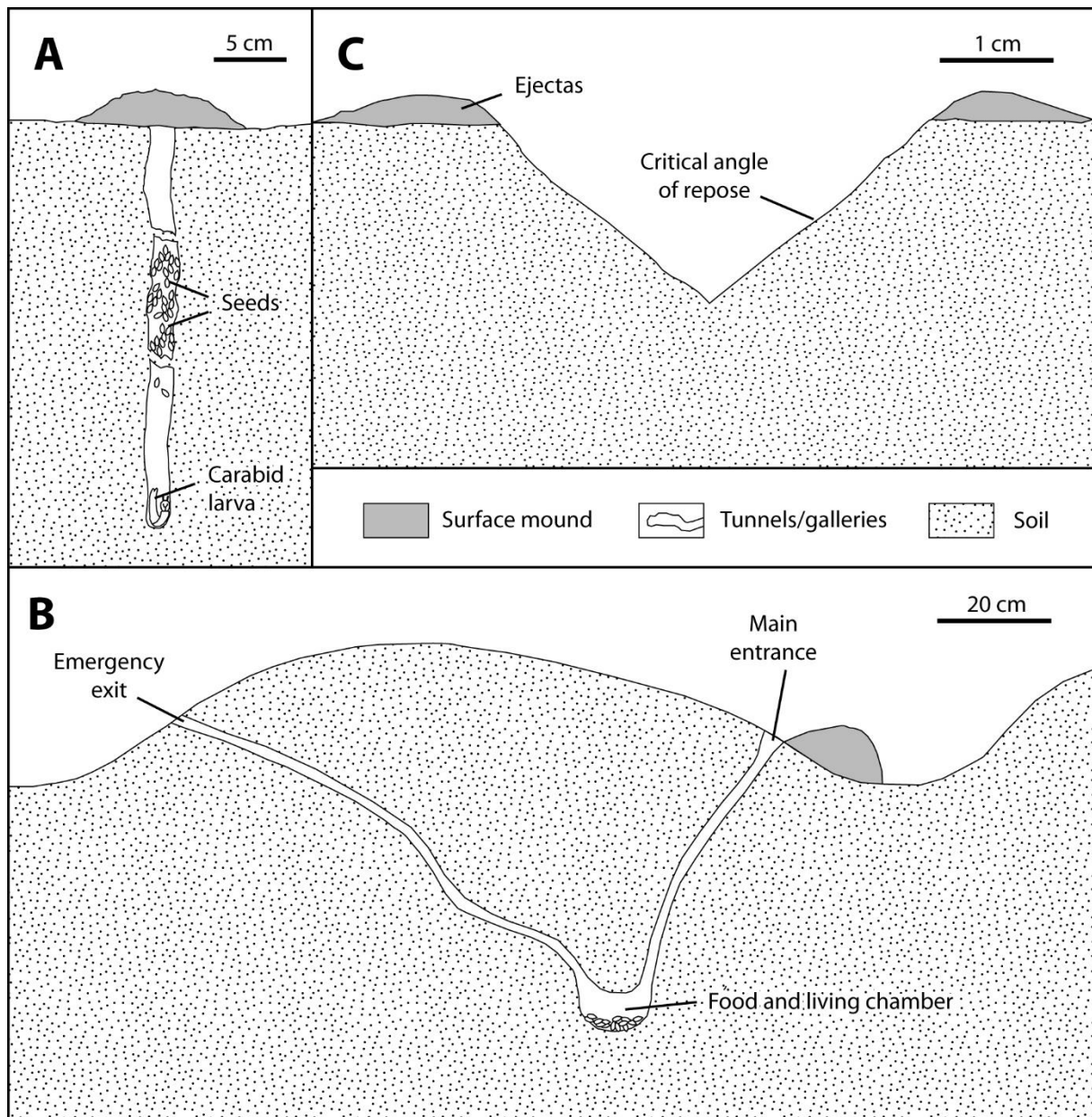
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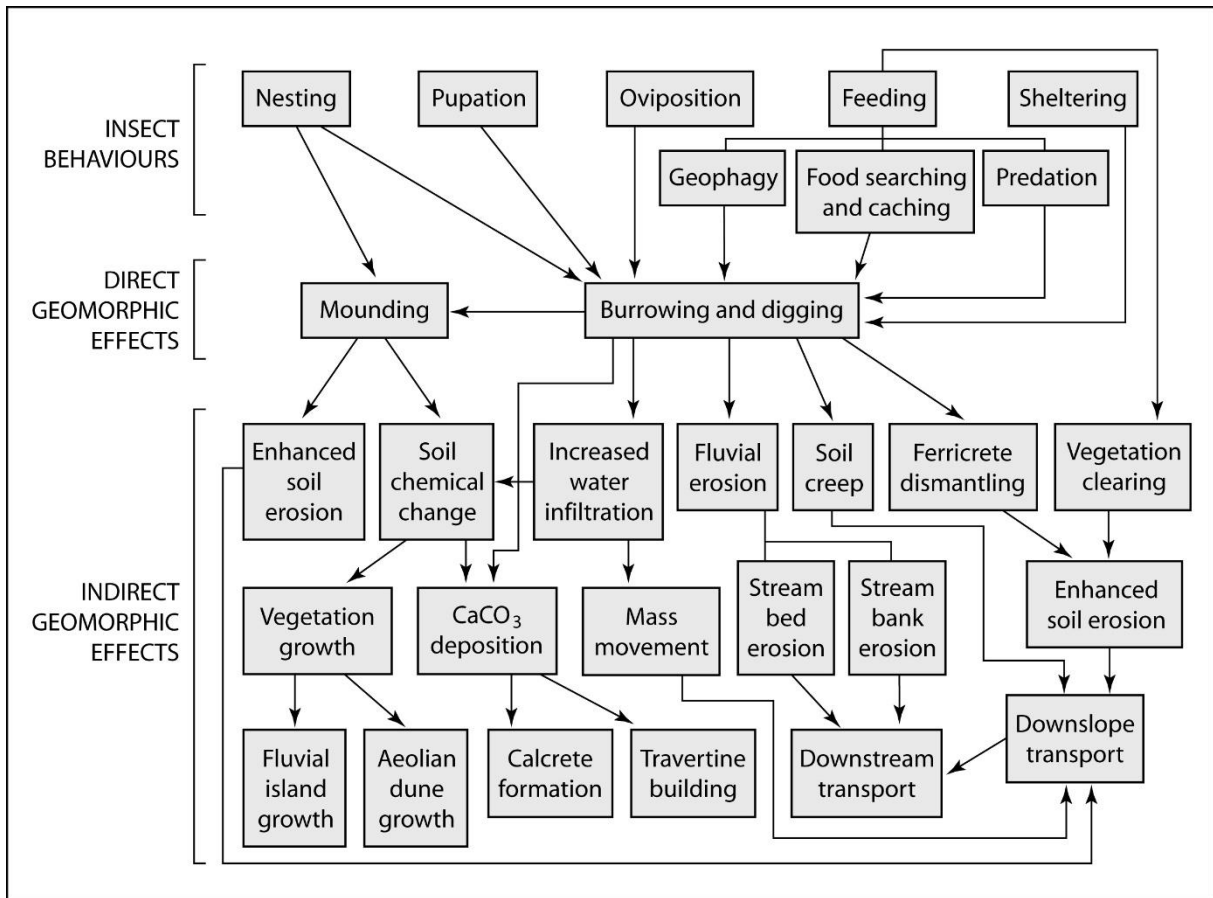
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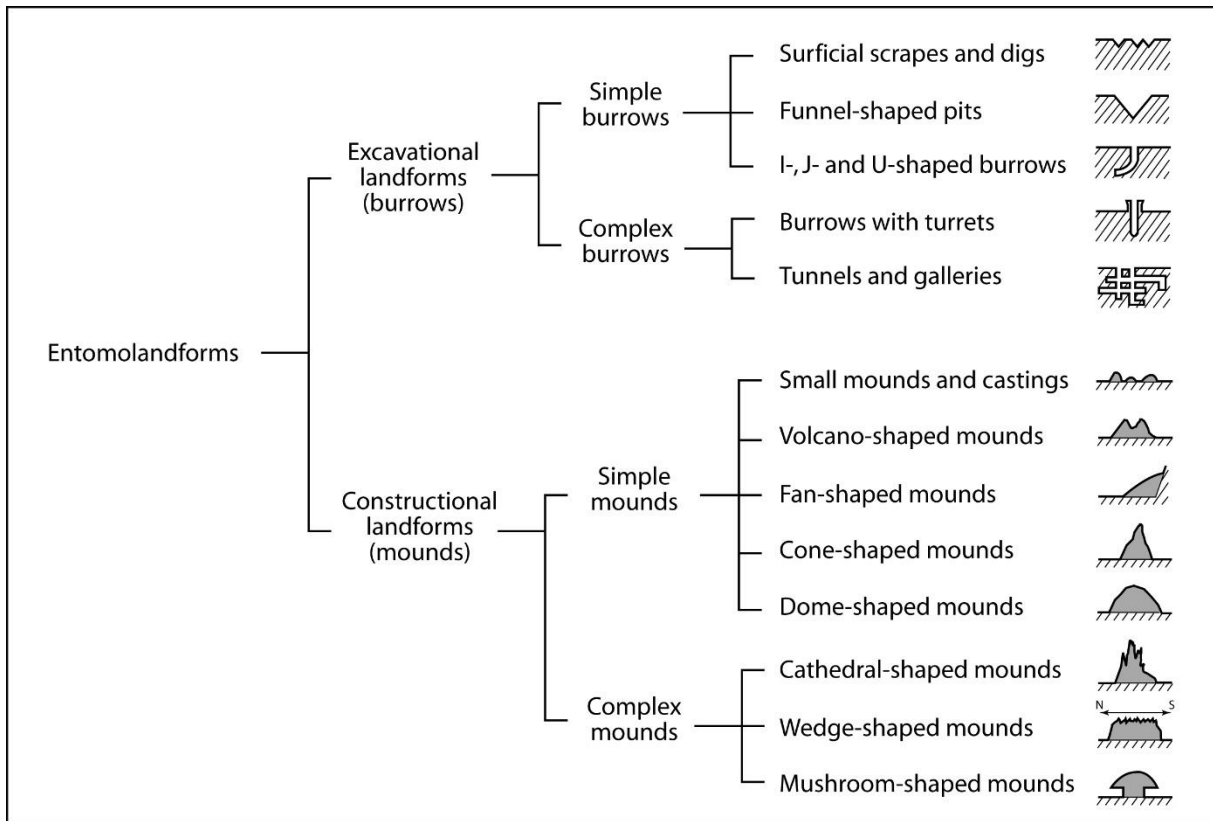
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1306 Figure 4



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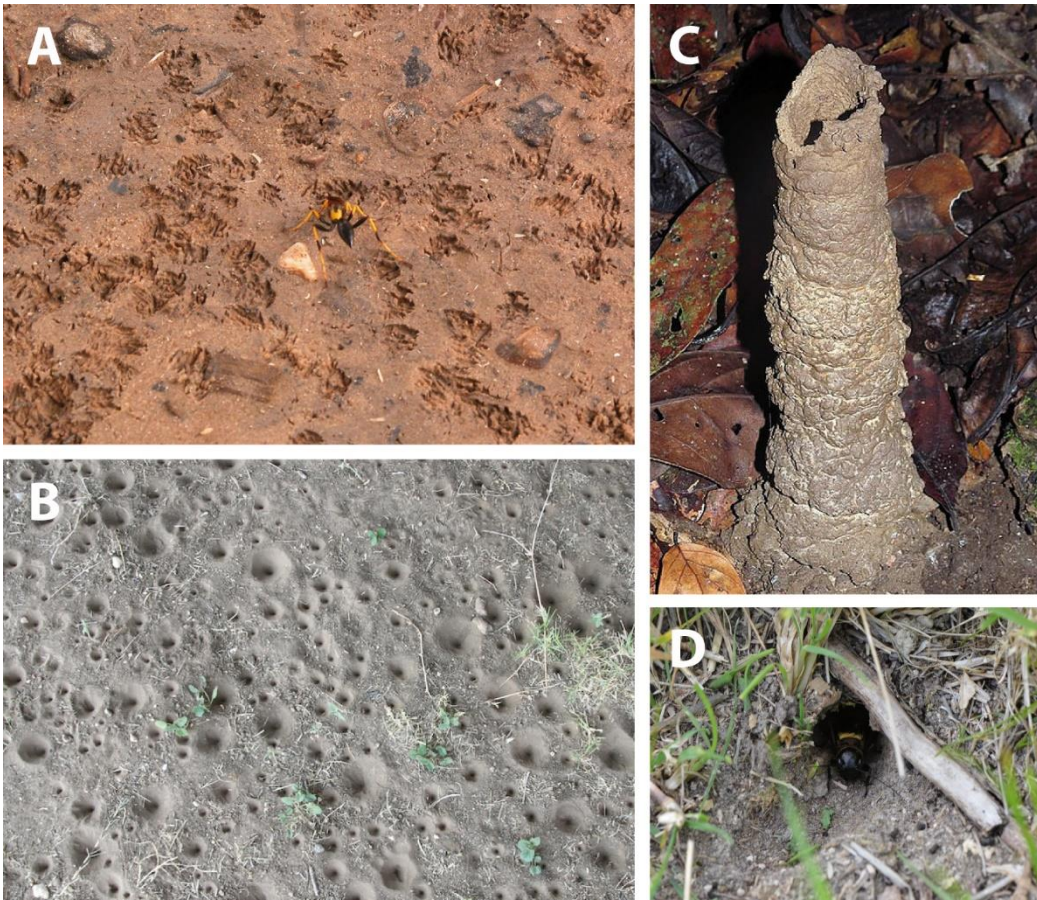


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1312 Figure 6

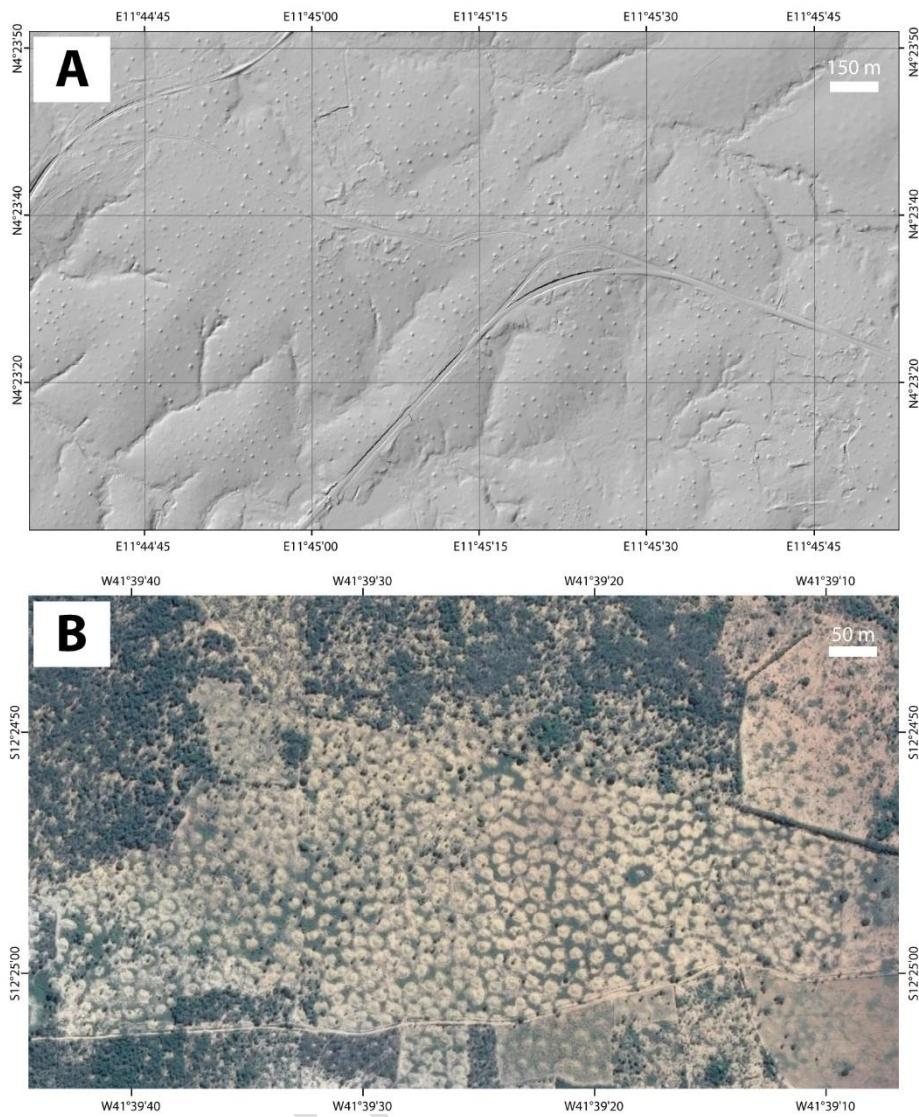


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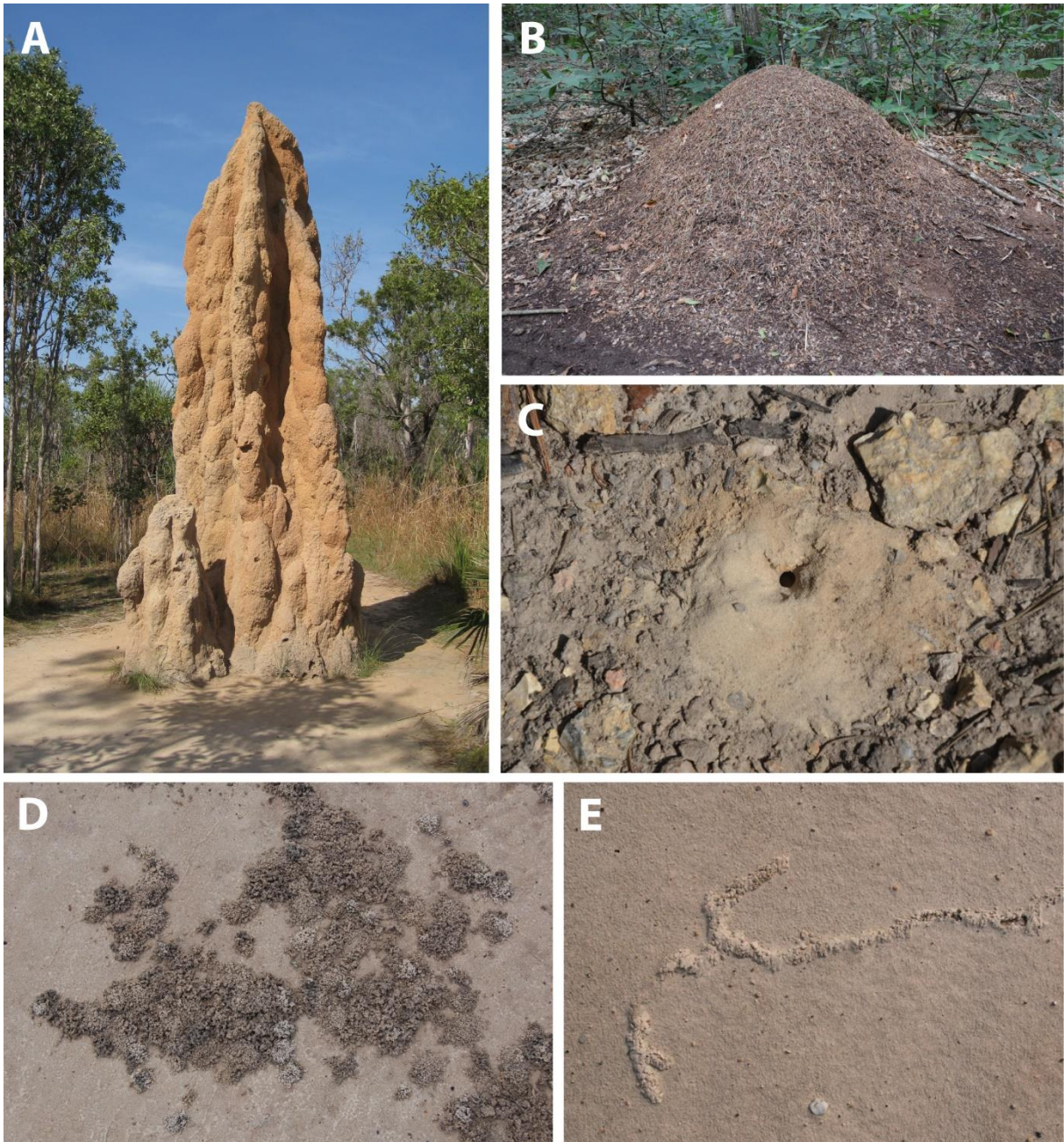
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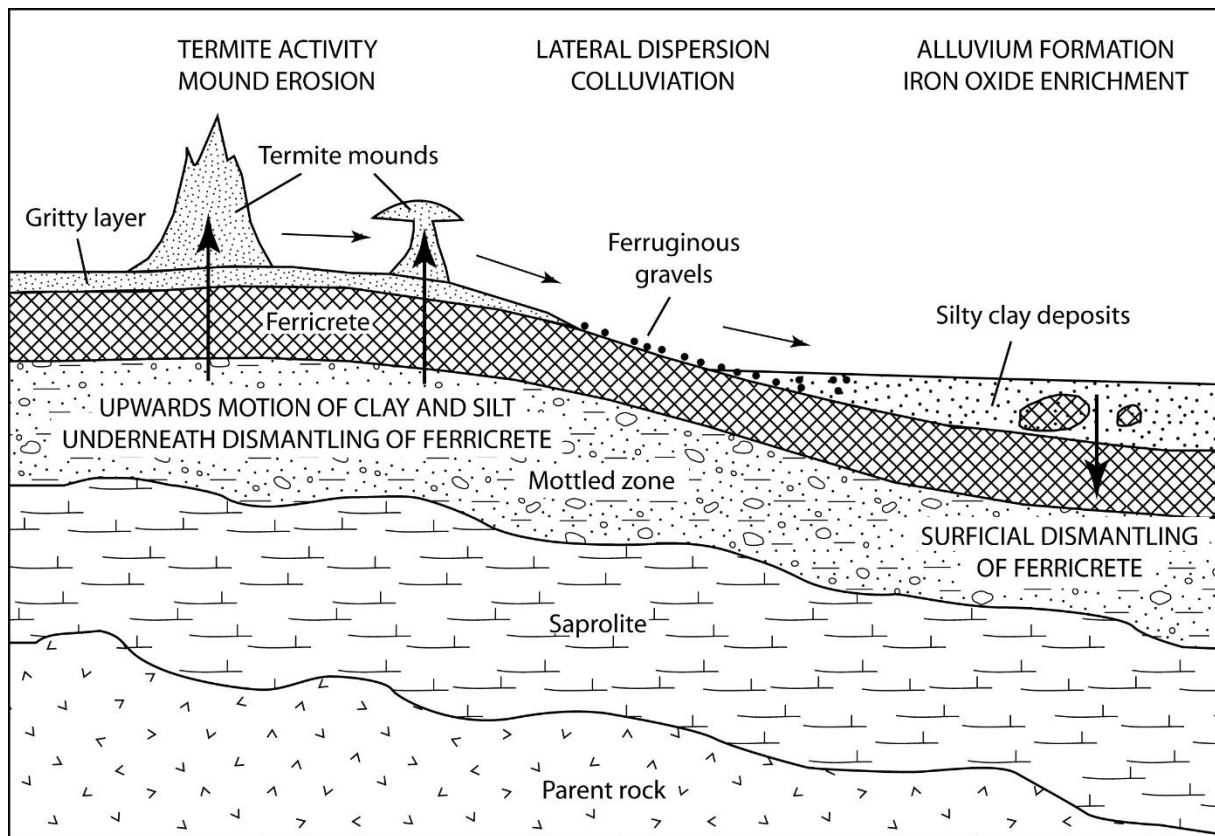
1318 Figure 8



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1321 Figure 9



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