



Aphaenogaster ants as bioturbators: Impacts on soil and slope processes

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ABSTRACT

Australian ants belonging to the genus *Aphaenogaster* excavate dense and frequently relocated nest systems in topsoil and deposit ephemeral, highly erodible (*type-I*) mounds at their funnel-shaped nest entrances. Rates of mounding are generally higher for this genus than for other Australian ant species, and are amongst the highest rates recorded for ant mounding anywhere in the world. Furthermore, tentative analysis of subsurface mixing suggests that overall rates of *Aphaenogaster* bioturbation are higher than indicated by mounding alone. This bioturbation has pronounced implications for soil and landscape processes, particularly in modifying soil fabric and texture and in impacting on soil hydrology and erosion. *Aphaenogaster* bioturbation may also be viewed as a form of ecosystem engineering, and affects the distribution of soil nutrients and the dispersal of seeds. This can lead to localized increases in soil fertility, although *Aphaenogaster* are notorious as a nuisance in agricultural landscapes.

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1. Introduction

1.1. Ants as bioturbators

The ant is the epitome of the well-organized invertebrate and their remarkable social behaviour has long fascinated myrmecologists. As this behaviour often results in large subterranean colonies and supercolonies with an immense potential to move soil material, ants

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are also of interest to contemporary pedologists and geomorphologists. Indeed, ants, along with earthworms, termites and small fossorial mammals, are one of the most prominent groups of the world's terrestrial 'bioturbators' (see Paton et al., 1995). Their extremely widespread distribution, having colonized all but the harshest and most remote of terrestrial environments, makes ants exceptionally important. Of course, many species of ant do not contribute to bioturbation, and the propensity to build mounds and mix soil varies enormously amongst those that do. Some species, though, have a particularly clear and intimate relationship with the soil in which they nest. This is exemplified here by members of the *Aphaenogaster* genus (Fig. 1), which are renowned 'soil specialists' (Lobry de Bruyn, 1999).

This review of the published literature provides a genus-level case study of bioturbation (i.e. the displacement of soil by animals and plants), a concept which has featured prominently in pedology, geomorphology and ecology in recent years (e.g. Paton et al., 1995; Gabet et al., 2003; Meysman et al., 2006; Wilkinson et al., in preparation). For this purpose, it is most convenient to consider *Aphaenogaster* bioturbation as consisting of two distinct components (cf. Wilkinson et al., in preparation); the deposition of soil material above ground at nest entrances (i.e. surface mounding), and all movement of soil material below ground (i.e. subsurface mixing), although these are inexorably interlinked. Bioturbation by ants not only redistributes soil particles but nutrients and organic matter as well, with important implications for both the physical and biological condition of their habitats. Accordingly, this review considers implications of *Aphaenogaster* bioturbation as a soil and slope process and as a form of ecosystem engineering, as well as its impacts in agricultural landscapes.

This genus has been influencing landscape and ecosystem processes in Australia since its probable evolution in the early Tertiary (c. 60 Ma), and certainly since the Oligocene or early Miocene (c. 20–30 Ma) (Humphreys, 2003). However, ichnofossil analysis by Hasiotis (2003) suggests that ants originate from prior to rifting of Pangaea (c. 250 Ma), and that they have acted as key ecosystem engineers ever since this time; a role of evolutionary significance (see Corenblit et al., 2008; Wilkinson et al., in preparation). In the wider context, the first burrowing animals evolved at the end of the Precambrian era (c. 550 Ma), and might have driven the 'Cambrian explosion' (see Meysman et al., 2006).

1.2. *Aphaenogaster* species in Australia

Aphaenogaster (Mayr, 1853) belong to one of the largest and most diversified sub-families in the world, Myrmicinae. The genus itself is also large, diverse and widespread, containing some of the most



Fig. 1. An *Aphaenogaster* worker removing a clump of sand from its nest. Photograph by Steve Shattuck (Australian Ants Online – *Aphaenogaster*; reproduced with the permission of Steve Shattuck and CSIRO).

primitive and generalized ants (Saunders, 1967). It is found world-wide with the notable exception of southern and tropical Africa (i.e. the Ethiopian zoogeographic region), despite a recorded presence in Madagascar (Fisher, 1996) and in the north of the continent (e.g. Cagniant, 1996). There is also a supposed absence in South America (e.g. Shattuck, 1999), despite being very well documented in both North and Central America. It has been studied in a range of its territories, including the desert scrub of the south-western United States (Chew, 1995; Andersen, 1997), the temperate forests of northern Japan (Higashi et al., 1989), the grass- and shrubland of Spain (Cerdà et al., 2009), and the rainforests of New Guinea (Wilson, 1959; Smith, 1961). A very small proportion of the two to three hundred species of *Aphaenogaster* are present in Australia. Until very recently, just four species were recognized; *A. barbigula*, *A. longiceps*, *A. poultoni*, and *A. pythia*. In a much-needed revision, Shattuck (2008) increased the number to eight, adding *barbara*, *kimberleyensis*, *mediterrae* and *reichelae*. These eight species are morphologically similar, apparently closely related, and endemic; *A. pythia* is also found in New Guinea but it is the only species known to occur outside Australia (Shattuck, 2008). Whilst the focus of this review is on Australian research, as dictated by the state of the literature, it is supplemented with all available studies of direct relevance from elsewhere.

Three of the conventionally recognized four species of Australian *Aphaenogaster* have been studied in relation to some aspect of their bioturbation activities (Fig. 2); only *A. poultoni* has not been explicitly studied in this context, perhaps because of its particularly limited distribution, and therefore does not appear in this review. The four newly recognized species are also not discussed but it is possible that misidentifications have occurred in relation to these in the past (e.g. *A. barbara* might have been mistaken for *A. pythia*). Therefore, where this review uses only the genus name, *Aphaenogaster*, it will be a general observation from the available literature that does not necessarily apply to all Australian species, and certainly not to all *Aphaenogaster* species in the world (for example, *A. mariae* have arboreal nests). It should also be noted that the eight *Aphaenogaster* species coexist with well over a thousand other known ant species in Australia (as just one of the 100 or so identified Australian ant genera), most of which are similarly soil-nesting (Andersen, 1991). The effects of *Aphaenogaster* on soil are not necessarily unique, but of Australia's many invertebrate bioturbators they are certainly amongst the most notorious and conspicuous.

Their notoriety is bolstered by their extensive geographic distribution within Australia. *A. barbigula* and *A. longiceps* are common and widely distributed across eastern and southern areas and, due to reasonably discrete distributions of the eight species, the genus is present in all of the mainland's states and territories (Table 1) but is absent from Tasmania (Andersen, 1991; Shattuck, 1999, 2008). Furthermore, despite a common association with eucalypt forests (e.g. Wheeler, 1916) and semi-arid regions (e.g. Lobry de Bruyn, 1999), the genus occurs in a broad range of habitats (Table 1). At the species level, this applies to the widespread *A. longiceps* in particular, and to *A. pythia* in Queensland (Shattuck, 2008). Such a presence routinely requires survival through wildfires, which is aided by the immediate protection of their tunnel systems (Shakesby et al., 2007) and a relatively low sensitivity to fire interval (York, 1994). Fires can have both positive (e.g. Andersen and Yen, 1985) and negative (e.g. Andersen, 1988b) effects on the subsequent abundance of *Aphaenogaster* species.

Nevertheless, *Aphaenogaster* do have some habitat preferences. In particular, it is widely asserted that Australian species are most common on sandy soils (e.g. Hitchcock, 1958; Andersen, 1986, 1991; Eldridge, 1994; Eldridge and Pickard, 1994; Lobry de Bruyn and Conacher, 1994). *A. barbigula* exhibit a preference for aeolian soils in particular (Eldridge, 1993; Eldridge and Pickard, 1994), whilst *A. longiceps* have even been recorded in abundance on the loose, unstable coastal sands of Cooloola (Greenslade and Thompson, 1981) and on other sand dunes (e.g. Sloane and Sloane, 1964). However, at the other

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