The role of ants in forming biomantles

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Abstract
Soil biomantles, not uncommonly sandy ones – called "sand plains" by some, are notable components of many midlatitude, subtropical, and tropical soilscapes. The role of ants in producing them has historically elicited genetic interest, and some controversy. Interest began in 1881 with the appearance of Darwin's book on soil formation by worm bioturbation, in which ants are mentioned. Subsequent attention to the theme involved leading scientists during the 19th-20th century transition period. Beyond touching on several post-Darwin highlights of ant bioturbation, this study reports on soil bioturbation volumes produced by *Lasius neoniger* and *Tetramorium caespitum* during one activity season in Illinois, USA. Extrapolating these data with time suggests that the two species play key bioturbative roles in producing comparatively thin (~30-60 cm) sandy and or silty biomantles in the upper Mississippi Valley region. Conversely, our recent work in Texas and Louisiana suggests that *Atta texana*, the leaf-cutter (parasol) ant -- a prodigious and legendary soil bioturbator and mound maker -- plays a key and probably dominant role in producing comparatively much thicker (~0.6-2+ m) sandy biomantles found in the southern Mississippi Valley and Texas-Louisiana Gulf Coastal plain.

Key Words
biotransfers, bioturbation, biosorting, turnover, Geoarchaeology, topsoil

Introduction
The year before he died, Darwin (1881) produced a soil process book that focused on animal bioturbations. In the book he showed how bioturbation by animals – mainly worms in his case (though he implicated other animals, including ants), promotes textural differentiation in soils, which leads to the formation of a surface layer of soil, first identified in 1975 as a soil biomantle (Soil Survey Staff 1975, p. 19; cf., Johnson 1989, 1990; Johnson *et al*., 1987, 2005). The biomantle is an approximate equivalent to what in Darwin's time was called 'mould,' or 'vegetable mould,' mainly topsoil. An important sub-theme of Darwin's book was how animal bioturbation leads to burial of surface-deposited objects (artifacts), in his case Roman coins dropped two millenia earlier on the English landscape, and how they gradually sink downward to subsoil levels. Darwin presciently noted "Archaeologists ought to be grateful to worms, as they protect and preserve for an infinitely long period every object, not liable to decay, which is dropped on the surface of the land, by burying it beneath their castings" (p. 308).

Because Darwin's book encouraged new questions, a flood of papers on animal bioturbations began appearing (e.g., Von Ihering, 1882; Gounelle, 1896; Drummond, 1885; 1988; Keilhack, 1899; Seton, 1904). Some authors emphasized the predominant role of ants in producing surface horizons (e.g., Von Ihering, 1882; Drummond,1888; Gounelle, 1996; Branner, 1900, 1910; Passarge, 1904), especially in the lower latitudes where, with bioturbation being year-round and involving more species, biomantles are comparatively thicker – in some cases significantly thicker, than those Darwin described in seasonal and comparatively ant-sparse England. Shaler (1888; 1891), likewise influenced by Darwin, was particularly impressed with the role of ants over other bioturbators in producing surface mantles in various fields of northeastern USA. Similarly, Passarge (1904) concluded that the collective bioturbations of African ants and termites play preeminently co-dominant roles in producing, and constantly replenishing, the latitudinally extensive Kalahari Sands, one of Earth's largest sand plains. Likewise, Branner (1900; 1910) extolled the preeminent mantle-producing roles of ants across Brazil, most notably the supremely bioturbating *Atta* (leaf cutter, parasol, town) ants that, along with termites, produce monster mounds that spread out over time to form thick biomantles (2-8 m) in the New World tropics. Such biomantles also occur in Central America and Cuba, and, while thinner (≤1-2+ m), also occur across much of the southern USA. The large-mound-builder *Atta texana*, however, occurs only west of the Mississippi River, in Louisiana and Texas, and south into Mexico. The thick sandy biomantles of Louisiana and Texas are notable among archaeologists for containing prehistoric artifacts, not infrequently scattered vertically (pocket gophers, *Geomys bursarius*, however, also are firmly bioturbationally implicated here). Two *Atta* mounds that we recently directly measured, with aboveground volumes calculated (not including either the huge belowground nest-chamber volumes, or the distal satellite heaps that erupt far beyond the mound perimeters), were: 24 m diameter x 50 cm high (452 m^2 area, 226 m^3 volume) on Davis Hill, Liberty County TX; and 18 m diameter x 48 cm high (254 m^2 area, 122 m^3 volume) in Natchitoches Parish LA (satellite heaps extend centripetally outward >95 m from the center of this mound!). Notably, mature *Atta* mounds in these southern USA states, and in the Neotropics generally, can have considerably greater areas and volumes than those we measured and calculated (pers. com. John Moser [USFS, LA], and Ulrich Mueller [U. TX, Austin], 2009; cf., Hölldobler and Wilson 2009, p. 457-463).

Soil biomantles of the loess belt of the upper Midwest of North America, as in Illinois, are considerably thinner (0.3-0.6 m) than those in the south, owed partly to erosional removals being greater than bioturbational renewals reflecting intensive agriculture during and since the 1800s. The role of ants and worms in producing such mantles was brought home to us – quite literally, in spring of 1971 soon after moving to a house at 308 Hessel Boulevard, Champaign IL (built in 1948, owned and managed then by University of Illinois Housing). During backyard gardening we discovered a buried, un-grouted 13.8 m^2 brick patio buried under ~ 7-10 cm of grassed sod, where the bricks, apparently, originally had been assembled on the lawn surface by a previous renter. After clearing the bricks of sod and soil, pleased with gaining a new patio – and perplexed why anyone would bury it (with absolutely no thought that it might have been buried naturally and biogenically), we left in early May for 3 months' out-of-state research. Returning in early August we discovered, to our astonishment, that our new patio was undergoing – again, burial, almost entirely by spoil heaps of ants and earthworms, formed above gaps between the ungrouted bricks, and which had spilled over onto them. Essentially the entire patio was being rapidly biogenically buried by ant-worm turnover, which mirrored Darwin's 19th century observations!

Apart from occasionally much larger, though spatially far fewer, harvester ant mounds in the Midwest, most ant contributions to upper Midwestern biomantles appear to be by *Lasius neoniger* (Emori) and *Tetramorium caespitum* (Linnaeus). This statement is based on their innumerable spoil heaps that form, then wash away after rains, and reform again. Such never-ending processes are observed in fields, gardens, forests, patio cracks, sidewalks, and driveways in many Midwest communities, including, of course, Champaign-Urbana. It was observed, for example, during April of 1978 soon after moving to our current residence that our gently sloping (< 1 %) brick walkway, linking the city sidewalk to our front porch, regularly sprouted ant heaps through cracks, particularly after rainstorms, especially during spring and summer months. The walkway was constructed in 1968, inadequately, such that by 1987 about 15 percent had cracked, particularly where cement grout had separated from the bricks. Ant spoil (heaps) regularly appeared above the cracks, and during periods between rainstorms, especially after them, such that spoil became notably conspicuous. The walkway was also observed to be generally lower than the surrounding lawn, and one badly cracked section had broken up, was uneven, and had noticeably sunk. This section, Area A, allowed (and of this writing still allows) more opportunities for ant burrowing and surface heaping, and clearly had (and has) experienced the greatest undermining and sinking.

Study area and methods

The study area is a 12.14 m^2 grouted, but somewhat cracked (~ 15 %) brick walkway at the authors' current residence, 713 South Lynn Street, Champaign, Illinois. The walkway proved useful for a study of ant turnover (i.e., soil biotransferred from depth to the surface), because most cracks were narrow enough (≤ 1 mm) to exclude earthworms and other mesofauna, but large enough to admit the two ant species indicated. The study began informally following a rain shower on 27 April, 1987, when ant spoil was observed to gradually grow over burrows along the cracks, reaching sizeable volumes. On 10 May, 12 days later, that accumulated spoil was collected by cordless vacuum, placed in a labeled dated container, oven dried, weighed, and recorded (displayed as the first column of fig. 1, which covers 2 weeks' time). For the rest of May, spoil was irregularly vacuumed as it accumulated, processed as above, with weights summed weekly (fig. 1).

Beginning 1 June, the procedure was refined, with spoil from each ant heap daily vacuumed, processed as before, but with identifying burrow numbers painted on bricks, matched to numbers on the collection canisters. A scaled map was made on which every brick and ant burrow was located. As new burrows appeared, ants were aspirated from them to match species with their burrow numbers, and their relative turnover volumes (ants identified by W. LaBerge, Illinois Natural History Survey, Urbana). Ant turnover ceased on 9 November with the onset of notably cold temperatures.

Results

A total of 2.08 kg of ant turnover spoil was produced jointly by *L. neoniger* and *T. caespitum* over an estimated 15% of the 12.14 m^2 walkway (the cracked portion) during the 196-day activity period (27 April-9 November) of 1987. During the last 163 days of this period (1 June-9 November), a total of 87 burrow openings were mapped, numbered, and matched with the respective volumes that the 2 species produced. Of the 87 burrows, 80 were by *L. neoniger*, which accounted for 88 percent of soil turnover by weight during this period, and 7 were by *T. caespitum*, accounting for 12 percent. The data were assembled in tables from which Figure 1 is derived. Assuming a topsoil bulk density of 1.3g/cm^3, the 2.08 kg of combined ant spoil equates to a soil layer 0.09 cm thick in one year, or 9 cm/100 years, 90 cm/1000 years, 4.5 m/5,000 years, and a 9 m thick biomantle in 10,000 years -- 88 percent of which would be produced by one small, insignificant-appearing ant: *Lasius neoniger*.

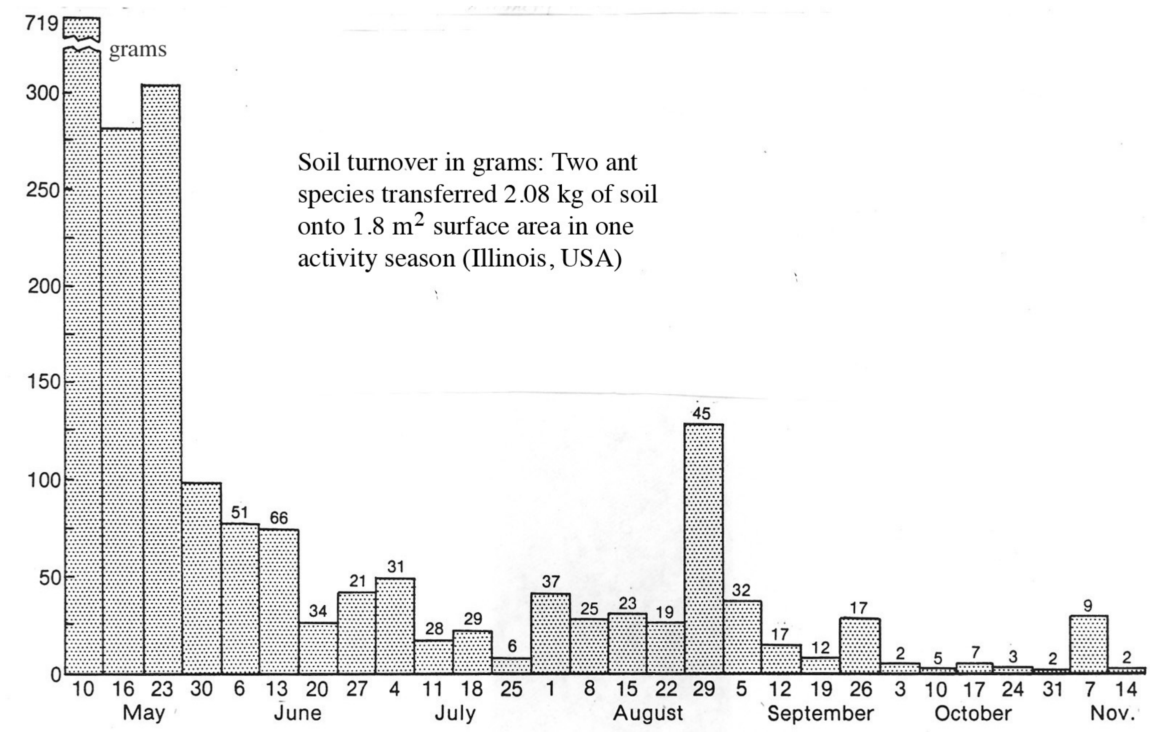

Figure 1. Total turnover of ant surface spoil, 2.08 kg, produced jointly by 2 ants, *L. neoniger* and *T. caespitum*, during a 196-day ant activity season in Illinois, 1987 (April-November). First column (10 May) represents 2 weeks' turnover (27 April-10 May). All other columns, except last, represent weekly summed turnovers. Last column (14 November) represents several days' turnover, to November 9. Numbers at column tops (June-November) represent numbers of ant burrows (both species) that produced turnover during that week.

Caveats

One assumes that the walkway was intact when constructed in 1968. Grout failure, cracking, and subsequent bioturbation began afterward, being underway upon our arrival in 1977, continuing until the study began in 1987. Cracking and breakup processes are still occurring, as of this writing, with about 85% of the walkway still intact (un-cracked). A point we stress is that if the entire walkway had been un-grouted, like the backyard patio at 308 Hessel Boulevard described earlier, then eminently more bioturbation involving the full retinue of invertebrate bioturbators – with consequent far greater walkway undermining, sinking, and expected soil-sediment turnover -- would have occurred. Our numbers, therefore, are preeminently more conservative than had that been the case! Furthermore, an unknown but sizeable quantity of ant spoil was lost to rainstorms before it could be collected, rendering our numbers even more conservative.

Conclusions

Our conclusions and projections for biomantle formation, based on the above data and caveats, are as follows. We estimate, very conservatively, that two common ant species *L. neoniger* and *T. caespitum* alone contribute significantly to Midwestern soil biomantles in amounts of at least 90 cm/1000 years, 4.5 m/5000 years, and 9 m/10,000 years. These estimates assume that such turnover volumes are neither offset by erosional removals, nor augmented by either other soil infaunal turnover, or by eolian infall. Turnover by the two ant species -- increasingly augmented since 1987, in Area A especially, by other mesofauna (earthworms, sphecoid wasps, killer wasps, etc.) -- still occurs on our walkway, every spring, summer, and fall, usually beginning in mid-April, and usually ending in late October-early November. The entire walkway, again especially Area A, is still slowly sinking!

Regarding the comparatively thicker sandy biomantles of Texas and Louisiana, unlike ants in the upper Midwest, *Atta* ant turnover in this more southerly region -- except during occasional winter cold snaps -- is largely year-round, and augmented by many other ant species in these lower latitudes. One must, in fact, take time to travel widely in the region in order to bear witness to and fully appreciate the size and density (in places), and extent of *Atta texana* mounds, and project back to pre-plow times. Only then can one begin to comprehend the key role these ants play, and have played, in the origin of soils and landscapes of this large area. Their volume contributions to the comparatively thicker biomantles in the region, though unquantified, are unquestionably very great -- and very greatly deserving of thesis attention.

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