Downward Thinking: Rethinking the "Up" in Soil Bioturbation

Alan F. Halfen[A], Stephen T. Hasiotis[B]

[A]Department of Geography, University of Kansas, 1475 Jayhawk Blvd., Rm. 213, Lawrence, Kansas, USA, Email afhalfen@ku.edu
[B]Department of Geology, University of Kansas, 1475 Jayhawk Blvd., Rm. 120, Lawrence, Kansas, USA, Email: hasiotis@ku.edu

Abstract
The nests of western harvester ants (*Pogonomyrmex occidentalis*) are extensive structures usually capped by a large conical mound. These ants have been documented to translocate significant amounts of soil and sediment to the surface; however, subsurface mixing patterns have not been investigated and documented. One thousand western harvester ants were added to a glass enclosure filled with discrete layers of homogeneous sediment to document this mixing. A 12-week experiment on nest development was conducted, during which (remarkable) translocation and mixing of sediment occurred. At the end of the experiment the distance and quantity of material translocated was measured. In sum, the ants excavated ~16% of the enclosure. Large amounts of this sediment were moved upward and significant amounts of material were moved down into the nest. Notably, ~51% of all excavated sediment was shown to be incorporated into the nest as backfill or tunnel lining. This material was neither translocated to the surface nor incorporated into the nest mound as traditionally thought. Our study demonstrates the significance of downward movement of sediments within soil. It also emphasises the underestimated role of soil-dwelling organisms, specifically the ant, in soil bioturbation and pedogenesis.

Keywords
Burrowing, pedogenesis, formicidae, soil biota, sediment mixing

Introduction
The acknowledgement that soil-dwelling organisms play a significant role in bioturbation, and thus pedogenesis, has been ascribed since the late nineteenth century (Darwin, 1881). Since Darwin's initial observations, a wide range of related studies have been conducted examining soil biota's role in pedogenesis. Many have recognized soil-dwelling social insects, particularly termites and ants, to be the most effect soil bioturbators found in soils today (e.g. Hasiotis, 2003). Some researchers have attempted to quantify the quantity of material excavated by ants (e.g. Baxter and Hole, 1967; Eldridge and Pickard, 1994; Humphreys and Field, 1998; Richards, 2009), while others have explored how excavated material influence the creation of soil mantels (biomantles) (e.g. Johnson, 1990). Other than Humphreys and Field (1998), these studies lack any observations of how ants move and mix sediment below the surface within and throughout subsurface. Understanding and quantifying the subsurface mixing of sediment by ants is important for understand the role soil-dwelling organisms play in soil pedogenesis. This paper quantifies and demonstrates the unobserved significance of the ant in the downward movement and subsurface mixing of sediments and soils.

Methods
Layers of sand, gravel, carbonate shells, and silty clay sediment were added to a 64 cm long x 120 cm high x 10.7 cm wide glass enclosure constructed as a three-sided wood frame with inset slots cut into the wood to hold two panes of glass, sealed with silicon caulk. Sediment was layered from the bottom of the enclosure as follows: 0-2 cm—carbonate shells, 2-12 cm—alluvial sand, 12-14 cm—red sand, 14-23 cm—alluvial sand, 23-24 cm—alluvial gravel, 24-32 cm—alluvial sand, 32-34 cm—green sand, 34-43 cm—alluvial sand, 43-44 cm—pink gravel, 44-54cm —alluvial sand, 54-56 cm—yellow sand, 56-64 cm—alluvial sand, 64-65 cm—blue gravel, 65-71 cm—alluvial sand, and 71-77 cm—silty clay top soil. Carbonate shells were coarse sand to granular in size; alluvial sand, medium to coarse; gravels, granular to pebble; and colored sand, medium to coarse. All layers were flattened and compacted before the next layer of material was added. Vegetation was transplanted with the silty clay top layer. Once filled, the entire enclosure was wetted. An ultra-violet (UV) light was placed atop the enclosure, and the grass was allowed to grow within the enclosure for 21 days. After 21 days, ~ 1000 western harvester ants were introduced to the enclosure. The ants were allowed to excavate uninterrupted for 12 weeks.

Sediment Mixing
A combination of digital images and traced gridded transparencies were used to estimate the quantity and distance of colored sediment moved from its respective horizons within the enclosure (see above for original

depths and thicknesses). A digital image of the front side of the enclosure was loaded in Adobe Illustrator ® and calibrated so that a 64 x 80 cm, 1 cm grid accurately fit the image. The image size was constrained, relative to the grid, so that actual distance was maintained. Translocated sediment was marked on the digital grid with different colors representative of the different sediment layers (e.g. yellow for yellow sand, blue for blue pebbles). In some cases not all translocated sediments were visible in the digital image (e.g. yellow versus green sand). Therefore, these sediments were traced on a 1 x 1 cm gridded transparency and then added to the digital grid. Once all translocated sediment was added to the digital grid, the grid was printed on 11 x 17 paper the occurrence and depth of movement was recorded. The same procedure was used for the rear side of the enclosure.

The distance of translocated sediment was measured by counting the occurrence of a specific sediment in cm from the original horizon. Because it was not possible to accurately count individual grains of colored sand, the 1 x 1 cm grid was counted whenever colored sand was present as one occurrence, regardless of how full this area was. This method is acceptable since we are only measuring the distance grains were transported, not the volume of sediment transported. For shell, blue gravel, and pink gravel, individual pieces were counted as single occurrences because they could be visually differentiated.

The occurrence and depth of red sand, green sand, yellow sand, carbonate shells, blue gravel, and pink gravel was documented for both sides of the enclosure. Because the enclosure was 10.7 cm thick, 85% of the fill could not be seen through the front or rear glass sides. To account for translocated material not visible, the front side and rear side measurements were averaged and applied to the remaining unseen sediment. This provided an accurate estimate of the distance and number of occurrences of specific translocated sediment. In using this estimation we assume that sediment-mixing patterns observed from the front and rear of the enclosure are the same in the middle of the enclosure.

Volumetric Calculations
The total volume of excavated sediment for each layer in the enclosure was also estimated allying the procedure describe above. Digital images and gridded transparencies were used to trace open and backfilled galleries and chambers visible through the front and rear of the enclosure on a digital 64 x 80 cm, 1 x 1 cm grid. Once all passageways were traced, they were printed at a 1:1 scale and measured using a nylon string. The total distance of all passageways, backfilled and opened, were tabulated for each sediment horizon (see previous sections for depths and thicknesses) for the front and the rear of the enclosure (Table 1). We then assumed a network of galleries and chambers in the middle sediment comparable to the averaged length of those tunnels visible in from the front and rear of the enclosure. In doing so, we created an equation to estimate the total volume of sediment excavated during nest construction (Eq. 1). Sediment mixing rates were also calculated based on the volumetric measurements and assumed average bulk density measurement of ~1.60 g cm^{-3}.

$$v = \left(\left(\frac{L_f + L_r}{2} \right)_h \times \left(\frac{10.7}{x} \right) \right) \pi \left(0.5x\right)^2$$

Equation 1: L_f represent the total distance of passageways, in cm, on the front size of the enclosure and L_r the rear of the enclosure. *h* serves as a delineator of individual horizons or any cumulative total of horizons. *x* represents the mean diameter, in cm, of all galleries and chambers in the nest.

Results
In general, the majority of all sediment was translocated upwards towards the surface, although the ants did not always place the sediment at the surface. Sediment was moved a maximum distance of 84 cm, from the lowest reaches of the enclosure to the surface of the nest mound. Vegetation was also moved down into the nest 82 cm from the surface. Some degree of mixing occurred in all colored sediment layers with carbonate shells being moved up 84 cm; red sand being moved 72 cm upwards and 10 cm down; river gravel being moved upwards 62 cm and 21 cm down; green sand being moved upwards 52 cm and 30 cm down; pink gravel being moved upwards 40 cm and 42 cm down; yellow sand being moved upwards 28 cm and 52 cm down; blue gravel being moved upwards 20 cm and 42 cm down (Figure 1). All colored sediments appear to have a bimodal distribution with sediment displaced to the surface and sediment normally distributed above and below the position of the original sediment layer (Figure 1).

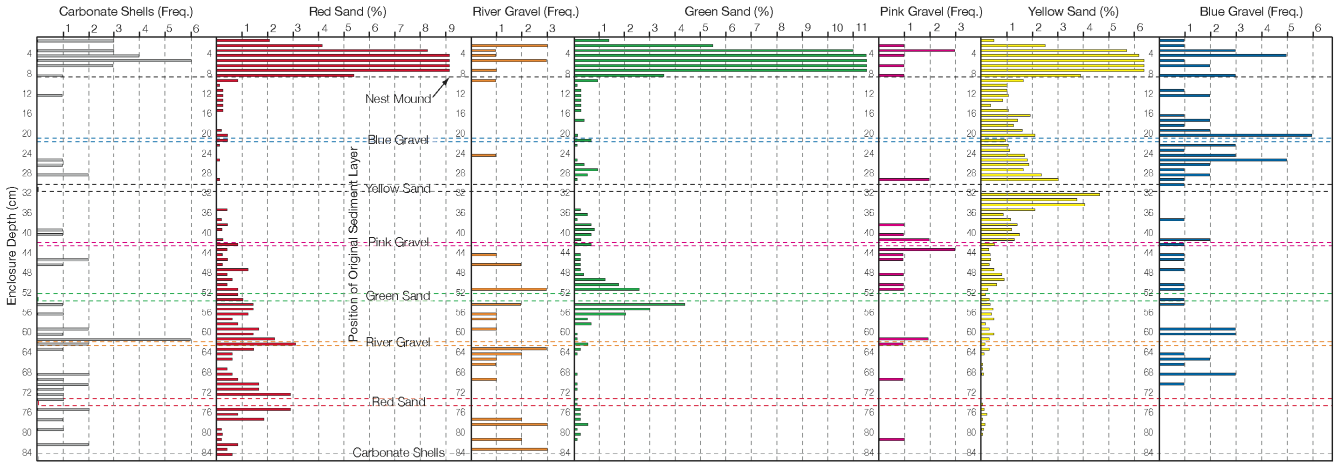

Figure 1. Distribution of colored sediment deposited at the end of the experiment. Depths are in cm and calibrated to the top of the nest mound. Original colored sediment horizons are marked with horizontal dashed boxes. Colored sand is represented as percent distributed of total. Colored gravel and carbonate shells are represented by frequency count of individual particles.

The calculated volume results show that 15.75% of the total 54,099.20 cm^3 sediment was excavated during the experiment (Table I). Considering individual sediment layers, most excavation took place in upper horizons (i.e., yellow sand and above) (Table I). The volume of the constructed nest mound was measured to be ~4,150 cm^3 and the total volume of excavated sediment was estimated to be 8,523.18 cm^3, indicating that ~51% of all sediment excavated in the nest was not placed at the surface and incorporated into the nest mound, but placed elsewhere in the nest below the surface. Simple sediment-mixing rates can be calculated with these data as well. A sediment-mixing rate of 28.55 kg yr^{-1} was calculated if examining the mound sediment alone. When incorporating the subsurface mixing, the rate of mixing increases to 58.64 kg yr^{-1}.

Discussion

Our experiment shows four significant results: 1) sediments were moved from all horizons to the surface, from horizons to other horizons, and from the surface back into the nest; 2) the distance of movement appears to be limited by the experiment, not the ants; 3) ~51% of all excavated material was either incorporated in the nest directly or after being deposited at the surface, not the mound; and 4) sediment-mixing rates can be calculated based on our results and indicate a much higher rates after accounting for surface and subsurface mixing of sediments.

It has been known that ants could bring material to the surface from deep in their nest, but no studies to our knowledge have observed the deliberate downward movement of sediment by ants. This multidirectional movement of sediment significantly alters the perceived sediment-mixing rates of ants. To begin with, mixing rates of ants are difficult to quantify because ants do not ingest the soil like earthworms, a measurable behaviour. Baxter and Hole (1967) quantified the rate of soil turnover at 35 ha-cm over a period of 3500 years, Eldridge and Pickard (1994) estimated that ants contributed 0.28 mm to the thickness of a soil per year, and Humphreys and Field (1998) showed that over a period of 17 years, 127 t ha^{-1} y^{-1} of sediment was mixed by ants. Only the mixing rate provided by Humphreys and Field (1998) is based in part on subsurface mixing, although the actual method of analysis is unclear. When considering past estimates of mixing rates, our experiment clearly demonstrates that sediment-mixing rates are much higher when subsurface sediment mixing is quantified. Ants not only play a significant role is soil formation and soil turnover by adding sediment to the surface, but also by directly altering and adding soil to lower horizons. This behaviour has a direct influence on soil pedogenesis.

Table 1. Volumetric estimates of excavated sediment for each horizon.

Sed. Horizon	Thickness (cm)	Total Volume (cm^3)[a]	Side 1 Galleries (cm)[b]	Side 2 Galleries (cm)[c]	Mean Galleries (cm)	Total Galleries (cm)[d]	Total Galleries Volume (cm^3)[e]	Material Excavated (% of each)[f]	Material Excavated (% of total)[g]
White Shells	2.00	1369.600	12.50	5.10	8.80	104.622	66.558	4.86%	0.13%
Reg. Sand	8.00	5478.400	77.70	84.60	81.15	964.783	613.769	11.20%	1.18%
Red Sand	2.00	1369.600	6.40	10.10	8.25	98.083	62.398	4.56%	0.12%
Reg. Sand	10.00	6848.000	81.70	76.70	79.20	941.600	599.020	8.75%	1.15%
Reg. Gravel	1.00	684.800	10.90	4.80	7.85	93.328	59.373	8.67%	0.11%
Reg. Sand	8.00	5478.400	60.30	65.10	62.70	745.433	474.224	8.66%	0.91%
Green Sand	2.00	1369.600	8.30	17.80	13.05	155.150	98.702	7.21%	0.19%
Reg. Sand	9.00	6163.200	131.80	114.70	123.25	1465.306	932.187	15.13%	1.79%
Pink Gravel	1.00	684.800	2.30	3.30	2.80	33.289	21.177	3.09%	0.04%
Reg. Sand	10.00	6848.000	194.60	218.20	206.40	2453.867	1561.083	22.80%	3.00%
Yellow Sand	2.00	1369.600	99.50	62.70	81.10	964.189	613.391	44.79%	1.18%
Reg. Sand	8.00	5478.400	193.60	211.50	202.55	2408.095	1531.964	27.96%	2.94%
Blue Gravel	1.00	684.800	27.60	5.30	16.45	195.572	124.418	18.17%	0.24%
Reg. Sand	6.00	4108.800	113.80	118.20	116.00	1379.111	877.353	21.35%	1.69%
Silty Clay	6.00	4108.800	114.70	120.00	117.35	1395.161	887.563	21.60%	1.71%
Total	**76.00**	**52044.800**	**1135.70**	**1118.10**	**1126.90**	**13397.590**	**8523.179**	**16.38%**	**16.38%**

[a]Total volume calculated: horizon thickness x 10.7 x 64, [b]Total tunnel length network visible from side 1, [c]Total tunnel length network visible from side 2, [d]Total tunnel length network (see text for details) [e]Calculated usign equation 1 (see text for details), [f]Percent material excavated from each respective sediment horizon, [g]Percent material excavated from total enclosure volume

Conclusions

Quantities and distance of sediment moved by ants was estimated. In general, most movement was upward. Sediment was moved downward to the bottom of the nest as well. The volume of excavated sediment was calculated and shows that most excavated material was not placed at the surface and incorporated in the mound, but mixed and incorporated into the subsurface nest. This paper shows the significance of the ant in the deliberate downward movement and subsurface mixing of sediments and soils. This mixing plays an unobserved but present and important role in soil bioturbation and soil pedogenesis. More studies, specifically those that explore the mixing patterns of subsurface sediment, should be conducted on ants and other soil-dwelling organisms to further demonstrate their significance is soil pedogenesis.

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