Soil Animals and Pedogenesis: The Role of Earthworms in Anthropogenic Soils

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Abstract: The role of earthworms as one of the most important groups of ecosystem engineers in human-modified and natural environments has been increasingly recognized only during the last 30 years, yet earthworms and humans have been acting together in building landscapes for millennia. This relationship is well represented in the pre-Columbian raised fields, in flood-prone savannas around the rim of Amazonia, but also by the potentially significant role of earthworms in the formation and resilience of Amazonian Dark Earths. Through the bioturbating action of earthworms, soil is biologically, chemically, and physically altered; nutrients are translocated; organic matter is decomposed and transformed; and the surrounding biota interacts as a large orchestra where the soil musicians play together on the various instruments but where earthworms take a leading role, enhancing microbial activity and generally stimulating plant growth. In this article, we assess the remarkable role of earthworms at the center of soil pedogenetic processes within anthropogenic landscapes, dissecting their functions with a special focus on Amazonian Dark Earths.

Key Words: Amazonia, Amazonian Dark Earths, bioturbation, earthworms, nutrient cycling, soil formation

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The role of soil animals in soil formation was first recognized by Charles Darwin (1838) in 1837 and well exemplified in his last book *The Formation of Vegetable Mould Through the Action of Worms, With Observations on Their Habits* (Darwin, 1881; Feller et al., 2003). Unfortunately, this book became better known over the years as the "worm book," rather than as a "soils book" (Johnson and Schaetzl, 2015). This might be one of the reasons why the concept of bioturbation as a soil-forming process presented by Darwin was not widely adopted by other scientists for further development until decades later (see, e.g., Taylor, 1930), and it would be more than a century before soil scientists began incorporating bioturbation into their pedogenesis models (Johnson, 2002). This occurred despite efforts of many researchers proposing earthworms and insects not only as humus formers (Müller, 1889), but as soil formers and as pedoturbation agents (Anonymous, 1950; Langmaid, 1964; Nielsen and Hole, 1964; Taylor, 1930; Thorp, 1949; Wasawo and Visser, 1959).

It was not until the 1980s that research on the role of soil fauna in pedogenesis gained strength, with a bloom of articles describing and highlighting the role of earthworms in this process (Goudie, 1988; Hole, 1981; Lamparski and Kobel-Lamparski, 1988; Lavelle, 1988; Lee, 1983; Pop and Postolache, 1987; Tsukamoto, 1986). This trend continued into the 21st century, although it still has not become generalized: even nowadays, some soil genesis models are proposed that do not include soil fauna (Glaser and Birk, 2012).

Therefore, in the present article, we provide an overview of how soil fauna can affect soil genesis, with a focus on earthworms. We discuss how the interaction between soil fauna and human beings can create particularly dramatic anthrosols that can have major impacts on ecosystem properties and processes, as well as on sustainability of soil use, particularly for agriculture. We begin with an overview of the role of soil biota in raised-field agriculture, a historical example of soil-biota-human interaction, and then address the role of earthworms in pedogenesis and creation of anthrosols, particularly the Terra Preta de Índio, also known as Amazonian Dark Earths (ADE). Finally, we conclude with some speculation and ideas on the importance of these interactions in maintaining soil fertility in Amazonia.

Ecosystem Engineering and Raised-Field Agriculture in Peri-Amazonian Wetlands

In forested Amazonia, the transformation of soil properties by the addition of charcoal and nutrients is the dominant theme in the study of human-made soils (see following section). In flood-prone seasonal wetlands found around the rim of Amazonia, humans transformed soils in a very different way: they moved vast quantities of earth to create elevated structures on which they could farm (Fig. 1A). Pre-Columbian raised fields are widespread in peri-Amazonian wetlands from Bolivia, Ecuador, and Colombia to Venezuela and the Guianas (Denevan, 2001; Rostain, 2012). In a process of cultural niche construction (Laland and O'Brien, 2010), occupants of these environments created or enhanced topographic heterogeneity in wetlands, with a broad range of consequences for soil processes. As in forested Amazonia, macroinvertebrate soil engineers, including earthworms, appear to have interacted in important ways with humans to shape soils in these environments (Figs. 1B–D). Such animals are soil ecosystem engineers because they affect soil properties and the availability of resources for other organisms, including microorganisms and plants (Lavelle et al., 1997).

In fact, the adaptations expected to characterize soil engineers in wetland environments should make them an important—if currently little recognized—part of the natural capital from

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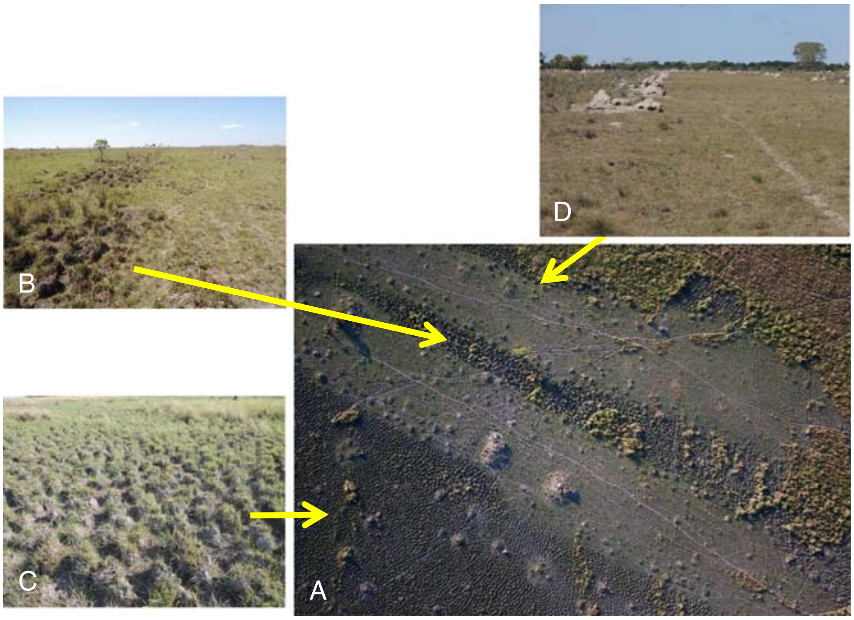

FIGURE 1. Interaction of raised fields and soil engineers in the Llanos del Beni, Department of the Beni, Bolivia. (A) The long, linear lighter-colored areas are *camellones*, vestiges of pre-Columbian raised fields (A). In the seasonal floodplain between the *camellones*, and surrounding them, are *sartenejales*, small mounds of natural origin resulting from the combined actions of earthworms and bunchgrasses (B, C). Large termitaria are concentrated along the borders between the *camellones* and the floodplain (D). A, Photo © D. Renard (2014); B–D, Photos © D. McKey (2014). A color version of this figure is available in the online version of this article. full color online

which raised-field farmers could benefit. Some earthworms, for example, have physiological adaptations enabling them to survive extended periods of flooding and anoxic environments (Maina et al., 1998). These wetland species presumably provide the same benefits for agriculture through their effects on soil porosity, soil mixing, and so on, as do earthworms in many other environments, although in some cases they have been blamed for creating problems in rice plantations primarily because of soil and plant root loosening (Bartz et al., 2009).

Soil engineering by these animals, particularly social insects (mainly termites) and earthworms, builds up mounds that rise above the high-water level, providing these organisms, and many others, with islands of well-aerated soil. These natural mound-field landscapes are often spectacular in their regularity and their spatial extent (Fig. 2). The mound-building activity by soil engineers could synergize with actions of human engineers in several ways. This is because mound building requires organisms that can conduct bioturbation at high rates. When they opportunistically colonize raised fields made by humans, soil engineers of wetlands continually move large volumes of soil (McKey et al., 2010; Renard et al., 2013), as they do when they make their own mounds. Thus, they contribute to favorable soil structure, breaking down the compact physicogenic structures that often dominate in clay-rich waterlogged soils. In addition, they move soil from anaerobic to aerobic compartments, thereby enhancing mineralization. When raised fields are left to fallow, soil engineers may maintain the mounds (McKey et al., 2010; Renard et al., 2013), reducing eventual costs of rehabilitating raised fields in the next cycle of cultivation. Finally, in parts of the landscape that are not cultivated, soil engineers provide a diversity of habitats for both semiaquatic and terrestrial plants (often in the form of shrubs or even small trees), increasing the availability of organic matter (OM) that can be applied to fields.

The potential benefits that soil engineers may confer in wetland raised-field agriculture are for the moment speculative, because this type of farming virtually disappeared in the Neotropics

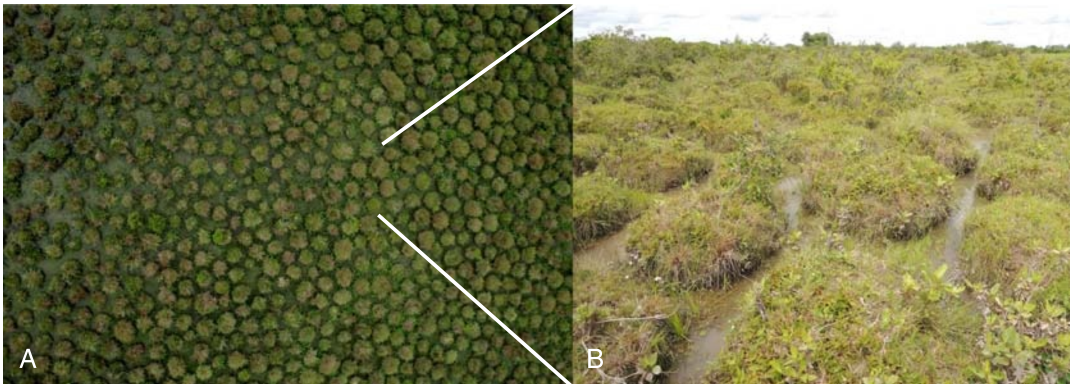

FIGURE 2. A *surales* landscape in the Orinoco Llanos in the Department of Casanares, Colombia, viewed from above (A) and from the ground level (B). The mounds are made by an as yet undetermined large earthworm species. Mounds are about 1.5 to 2 m in diameter. A, Photo © D. Renard (2012); B, Photo © D. McKey (2012). A color version of this figure is available in the online version of this article. full color online

with the European conquest and in some cases long before (McKey et al., 2014). The ideas sketched out here are beginning to be examined in field studies in African wetlands, where raised-field agriculture is still being conducted, in systems that show many apparent analogies with pre-Columbian systems in South America.

Soil engineers in wetlands may have an even more fundamental link with raised-field agriculture. Troll (1936), writing based on observations in the Beni Llanos of Bolivia, appears to have been the first author to wonder whether wetland raised-field farmers may have got their inspiration from observing the natural mound-fields made by termites (Figs. 1A, D). If so, this would be an intriguing case of human biomimicry at the ecosystem level.

The Potential Role of Earthworms in Pedogenesis

Earthworms affect pedogenesis in two main ways: first by modifying soil profiles through bioturbation and second by their effects on decomposition and nutrient cycling (Lee, 1983). Bioturbation through burrowing and casting moves material within and between soil horizons, mixing organic and inorganic fractions; furthermore, it destroys aggregates and creates new ones, altering porosity, aeration, and water infiltration (Fig. 3). Earthworm feeding on organic materials of various ages increases comminution, stimulating microbial activity and affecting decomposition rates and nutrient cycling (Fig. 3; Brown et al., 2000). Furthermore, soil abrasion and mixing in the crop and gizzard, together with digestive enzymes and microbial activity in gut passage (the "gut priming effect"), affect mineral weathering (Hodson et al., 2014; Liu et al., 2011) and the orientation of clay platelets (Barois et al., 1993) (Fig. 3).

The specific importance of earthworms to pedogenetic processes depends on the ecological category of the particular worm, which serves as a corollary of earthworm function in the soil. There are three main known categories (anecic, epigeic, and endogeic; Bouché, 1977), although intermediate categories among these can been used for species that do not strictly fit the system (e.g., endoanecic, epiendogeic). Anecic species feed on plant material usually mixed with soil (which they also ingest in large quantities) and make permanent burrows, generally in a more vertical direction. Epigeics live in and feed on surface litter, rarely ingesting soil particles, and produce basically organic castings. Endogeics are geophagous species that live in the soil and feed on soil OM of different quality (Lavelle, 1981): poly-, meso-, and oligo-humic species feed on C-rich, intermediate, and C-poor soil, respectively. Finally, Blanchart et al. (1997) also divided earthworms into compacting and decompacting species, depending on their ability to modify soil structure, and Lavelle (1997) divided them into litter transformers and ecosystem engineers.

Therefore, the effects of an active earthworm community on soil properties, processes, and genesis are dependent on the particular species present in the community (species composition), abundance of the species (numbers and biomass), and period of activity, factors determined by climate, soil and vegetation types, and human management (Lavelle, 1996). Some classic examples of earthworm effects on pedogenetic processes from the literature include the following:

- Darwin's pioneering studies on the formation of vegetable mould by earthworms, that revealed how they could contribute to the genesis of mull soils and the burial of archaeological remains, a topic that has not been much explored since Darwin's time (Johnson, 2002);
- studies by Müller (1889), a contemporary of Darwin, who first showed how earthworms contributed to the formation of mull soils in northern Europe;
- Buntley and Papendick's (1960) report on the presence and characteristics of Vermisols in South Dakota (United States), soils in which earthworm activity has drastically modified the Chernozem (Mollisol) soil horizons, cluttering them with casts up to a depth of 1 m;
- Nielsen and Hole's (1964) observations on midden formation, leaf-litter burial, and the formation of mull layers (coprogenous A1 horizons) in forest soils in Wisconsin (United States), due to

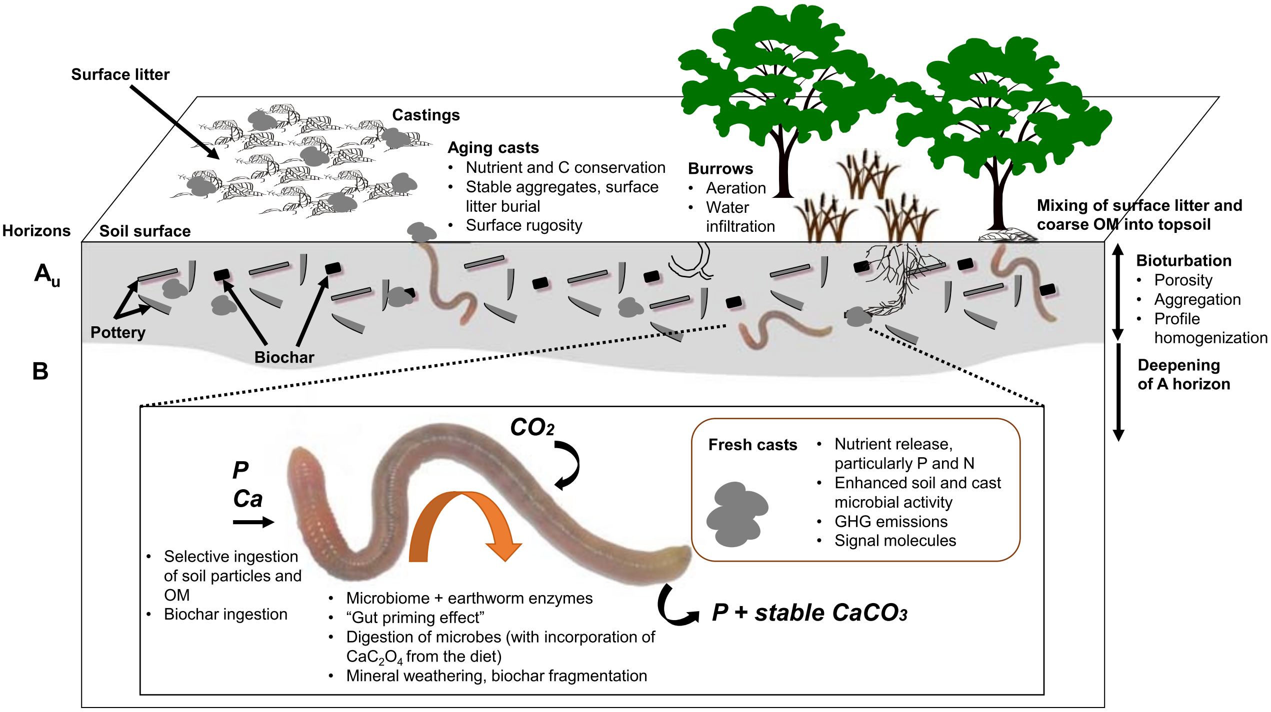

FIGURE 3. Diagrammatic scheme representing the role of earthworms in pedogenesis at different scales of time and space. A color version of this figure is available in the online version of this article.

the activities introduced of European earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*); and

- Langmaid's (1964) observations on the changes in the top 6 inches of the profiles of forested virgin podzols in Canada, 1 year after earthworm introduction; F, H, and Ae horizons disappeared and were replaced by Ap horizons as earthworms colonized these soils and began mixing and incorporating surface litter into the soil.

In fact, the effects of invading earthworms have been extensively studied more recently in many northern states of the United States as well as in Canada, particularly regarding the impacts of litter-feeding or burying species on areas devoid of earthworms. These invasions have caused, in addition to profound changes in soil structure and horizons, alterations in soil biota, soil nutrient cycling, fertility, and above-ground plant and animal biodiversity, activity, and productivity (Hale et al., 2005; Loss et al., 2012; Maerz et al., 2009; McLean et al., 2006; Nuzzo et al., 2009; Snyder et al., 2011; Szlavecz et al., 2011). In tropical Latin America, the invasion of pastures and forests by peregrine species such as *Pontoscolex corethrurus* has been associated with extensive soil bioturbation and changes in soil porosity, litter decomposition, and nutrient cycling (Barros et al., 2004; Chauvel et al., 1999; Liu and Zou, 2002) and competition with native worms (Fragoso and Rojas, 2009; Huang et al., 2006; Lapied and Lavelle, 2003). Under particular soil and climate conditions near Manaus, pedoturbation by invading *P. corethrurus* caused compaction, crusting, erosion, and pasture degradation (Chauvel et al., 1999). However, this phenomenon was not observed in Puerto Rico, even with denser earthworm populations (Gonzalez et al., 2006), and there are in fact very few examples of negative or harmful effects of earthworms on soils.

From the above, we can conclude that the pedoturbation effects of earthworms on soil processes and the populations of other organisms (including plants) are often profound and may lead to significant long-term changes in the soil. In agricultural areas, these changes are generally beneficial to soil fertility and plant production (Baker et al., 2006), but in native forests, they may be detrimental to the soil/litter layer and associated fauna and flora (Bohlen et al., 2004).

Although litter-burying (anecic) earthworms appear not to be as prevalent in tropical as in temperate climates (Lavelle, 1983), in oligotrophic tropical forests where communities are dominated by litter-feeding epigeic and anecic species, earthworms may have a major role in plant litter decomposition and incorporation (Fragoso and Lavelle, 1995). However, in areas dominated by geophagous endogeic (soil-living, soil-eating) species (e.g., many savannas), the role of earthworms in surface-litter decomposition and incorporation will be mostly indirect, through the deposition of casts on litter and the acceleration of microbial activity (Brown et al., 2000; Fragoso and Lavelle, 1995; Liu and Zou, 2002). Therefore, determination of the earthworm community present in a particular site is an important step toward understanding their potential role in pedogenesis.

In low-fertility, OM-poor tropical soils, such as some tropical pastures and savannas, earthworms may reach high biomass (Lavelle et al., 1994; Decaëns et al., 2004) and produce large amounts of castings (up to >1,000 Mg ha^{-1}), resulting in major effects on soil structure and nutrient cycling (Lavelle, 1978; Lavelle et al., 1997). In fact, the selection and transport of finer particles by these animals can affect soil surface horizon texture, altering contents of clay and coarse sand in the soil profile (Nooren et al., 1995). Unfortunately, vast areas of the tropics, particularly forests, continue to be unexplored and little studied in terms of earthworms, so the role of these organisms in pedogenesis remains poorly known compared with temperate regions. In the following section, we review and present novel information on earthworm communities and their potential role in tropical soils, focusing particularly on ADE.

Amazonian Dark Earths and Soil Engineers

Most Amazonian soils are nutrient-poor and highly weathered and affected by high turnover rates of OM; all these factors limit plant growth (Lehmann, 2009a). However, Amazonian Amerindians were able to sustain important food and trade crops, such as manioc, squash, gourd, maize, and fruit trees, in this highly challenging environment (Bozarth et al., 2009). Throughout Amazonia, there are small patches of high-fertility soils known as the ADE or Terra Preta de Índio, literally meaning "Indian dark earth" in Portuguese (Glaser, 2007). The dark color of Terra Preta (Fig. 4A) is due to the high concentration of pyrogenic charcoal and OM. The occurrence of these nutrient-enriched soils has been widely accepted as an indication of long-term human settlement (McMichael et al., 2014), mainly due to the frequent presence of high contents of pyrogenic carbon as well as large quantities of pre-Columbian ceramics. The addition of these materials, together with other organic materials to the soil, has led scientists to claim that ADE is of human origin (Neves et al., 2003), although it is well known that it is generally formed over the natural, original soil present on-site.

Amazonian Dark Earths may cover more than 150,000 km^2 or 3.2% of the total rainforest area (McMichael et al., 2014). These soils generally have higher pH, phosphorus (P), calcium (Ca), and magnesium (Mg) contents, cation exchange capacity, and base saturation than the surrounding soils (Table 1) and act as carbon sinks, potentially allowing long-term, sustainable, and highly productive agriculture (Glaser and Birk, 2012). Amazonian Dark Earths sites occur throughout Amazonia but are more concentrated in the center region of Brazil (McMichael et al., 2014; Clement et al., 2015).

It is known that plant and microbial richness associated with ADE is distinct when compared with that of adjacent sites (Arroyo-Kalin, 2010; Grossman et al., 2010; O'Neill et al., 2009). However, journal articles regarding soil animal biodiversity associated with ADE, in particular of macrofauna, are notably absent. Only one study was published to date on soil mesofauna in ADE (Soares et al., 2011). Soil macrofauna, including earthworms, have been sampled in many locations throughout Amazonia (Aquino et al., 2008, Barros et al., 2008, Brown and James, 2007; Lavelle and Lapied, 2003), but the only known assessments of macroinvertebrates in ADE were in the Manaus region and were either never published (M. Garcia, personal communication; unpublished data on earthworms) or included only as abstracts in proceedings of Brazilian conferences (Antony, 2005; Antony and van Roy, 2004; Sales et al., 2007; Silva et al., 2009). These studies showed that ADE has particular soil fauna communities that are different from those of the adjacent non-ADE soils, but that these communities also vary considerably among ADE sites, depending on the vegetation cover. Further information on the diversity, abundance, and biomass of soil fauna in ADE is urgently needed and should help clarify their potential role in soil properties and genesis.

Therefore, as part of the Terra Preta de Indio Network activities (for further details, please see Web site tpinet.org), soil macrofauna communities were recently (May 2015) sampled in four ADE (three of them forests and one of them a maize crop) and adjacent soils with the same vegetation types in Manaus and Iranduba counties, using the standard ISO–Tropical Soil Biology and Fertility (TSBF) method (Anderson and Ingram, 1993; ISO, 2006). Five 25 × 25-cm soil monoliths to 30-cm depth were taken per site, and the earthworms hand sorted from surface litter and

FIGURE 4. (A) A profile of an ADE (dystrophic Plinthosolic yellow Argisol with anthropogenic A horizon) in Rorainópolis Roraima, Brazil. The surface horizon (Au) shows the typical dark color of ADE, overlying a lighter-colored Bt horizon, as well as extensive mixing of the two horizons due to bioturbation. The inset in B shows details of pedotubules in Bt filled with friable macroaggregates from the A horizon; evidence of the mixing of both horizons of the ADE. Photos © Sérgio H. Shimizu (2015). A color version of this figure is available in the online version of this article. full color online

soil. In addition, earthworms were sampled qualitatively, by hand sorting separate samples from niches such as in and under rotting tree trunks, under stones, in the litter, and the soil. Soil macroaggregates from 10 × 10-cm soil blocks taken from the top 0 to 10 cm of the soil near the soil-monolith samples were also separated visually into different classes using the methodology proposed by Velásquez et al. (2007). The classes represented different origins of the aggregates, that is, biogenic aggregates produced by soil ecosystem engineers such as earthworms, termites, ants, and a few Coleoptera and Diplopoda, rhizosphere aggregates formed around and clinging to plant roots, and physical aggregates mainly produced by other factors (wet-dry cycles and mineral interactions). Other variables also separated included charcoal (biochar), organisms such as soil macrofauna present in the sample, nonmacroaggregated loose soil particles and unidentified aggregates of less than 5 mm, pottery shards, stones, and coarse organic material such as leaves, roots, seeds, and woody pieces. Because the number of fauna collected was very large, and the organisms have not yet been fully identified, only results for the earthworm communities and on soil macromorphology are presented here.

Large earthworms ("minhocuçus") were absent from ADE sampled, whereas the pantropical earthworm species *P. corethrurus* was found at all ADE sites (based on qualitative samples), confirming previously unpublished observations of Embrapa researcher Marcos Garcia (personal communication, 2014). In fact, earthworms in the genus *Pontoscolex* predominated, representing 42% of all individuals collected (Fig. 5B), a value higher than in adjacent soils (30%). Abundance of *P. corethrurus* (from TSBF samples) ranged from 0 to 163 individuals m^{-2} in ADE and was significantly greater than in the adjacent soils at two of the three forest sites sampled (Fig. 5A), one of which was the Embrapa Caldeirão Research Station (Site 3), a well-known and well-studied ADE site. In sites used for agriculture (maize production at site 2), *P. corethrurus* abundance was low, and this species was found only in qualitative samples in the ADE. Site 4 had a sandier soil texture than the other sites, and *P. corethrurus* abundance was again low.

Pontoscolex corethrurus can produce 15 tons casts ha^{-1} y^{-1} (Pashanasi et al., 1992) and is an especially active surface caster when the soil is more compacted (Zund et al., 1997), as typically observed close to human dwellings such as huts and home gardens. This species has been associated with human-induced disturbance and land use changes (Brown et al., 2006; Lapied and Lavelle, 2003) and is able to feed and develop in environments where litter resources are decreased, but soils have been enriched in C and nutrients by deforestation and burning (Lavelle et al., 1987; Marichal et al., 2010; Ponge et al., 2006). Hence, this species may be a preferential ADE colonizer, and its relationships with soil properties and processes and the genesis of ADE deserve further attention (see the section on biochar below). Small,

TABLE 1. Some Selected Chemical and Physical Characteristics of the Topsoil of Two Alfisols, an ADE (Anthropic-A dystrophic Yellow Argisol) and Adjacent Soil (typic dystrophic yellow Argisol) Under Native Secondary Forest at Embrapa's Caldeirão Experiment Station, Iranduba, Amazonas, Brazil (from Macedo, 2014).

Parameter	ADE	Adjacent Soil	
	A horizon (0–40 cm)	A horizon (0–5 cm)	AB horizon (5–38 cm)
Physical		%	
Sand	57	63	51
Silt	10	2	1
Clay	33	35	48
Chemical			
pH (H_2O)	5.1	4.1	4.2
pH (KCl)	4.6	3.9	4.1
		g kg^{-1}	
C	24	27	14
		mg kg^{-1}	
P	56	1	1
K	25	29	11
		cmolc kg^{-1}	
Ca	6.4	0.04	0.03
Mg	0.58	0.11	0.04
Al	0.13	2.81	1.52
CEC	13.9	7.6	6.2
		%	
Base saturation	55	10	4

unidentified earthworms in the family Ocnerodrilidae were also found abundantly in ADE soils (Fig. 5B). These species may also be preferential ADE colonizers and contribute to a large number of small stable aggregates found in ADE (see below).

In fact,when soil aggregates from the four ADE and adjacent sites sampled were separated and weighed into various classes, the first two factors of the PCA explained 41%of variability in data, and the variables significantly separated ADE soils from the adjacent sites (Fig. 6B). Soils of these adjacent sites had the highest proportions of nonaggregated soil and physical aggregates produced by physical processes (e.g., drying and rewetting of the soil). On the other hand, in ADE, a higher presence of biological aggregates and earthworm biomass was associated with higher number of pottery shards (ceramics) in the soil (Fig. 6A). Such a relationship still lacks explanation but may reside in the fact that pottery, as any other surface, may influence soil physical properties by altering soil structure and affecting moisture content, ultimately creating a microhabitat used by soil biota. Further work on this exciting yet unstudied research topic is warranted, given these findings.

Earthworms and the Genesis of ADE

Although earthworms are one of the three top bioturbators and ecosystem engineers in soils, together with ants and termites (Jouquet et al., 2006; Lavelle et al., 1997), and their activities are known to affect pedogenesis, the currently accepted model for the genesis of ADE (Glaser and Birk, 2012) does not include

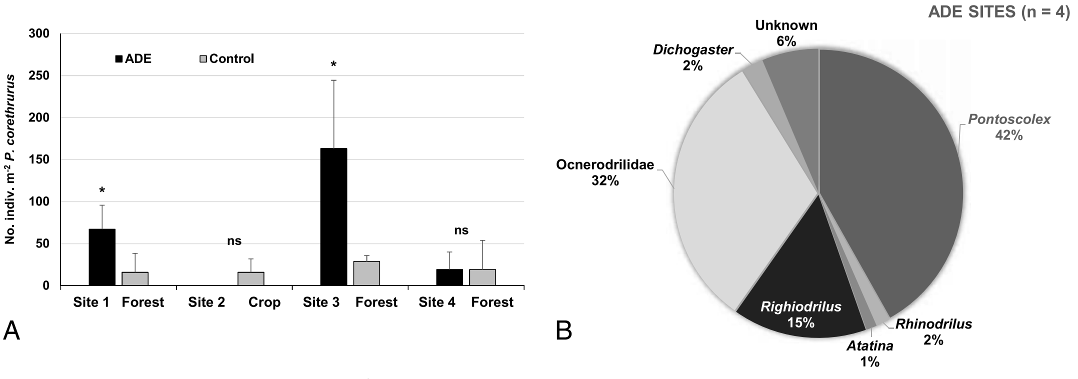

FIGURE 5. A, Abundance (mean no. individuals m^2 +/− S.D.) of *P. corethrurus* collected using TSBF-ISO methodology (hand sorting of 25 × 25-cm soil monoliths to 30-cm depth; Anderson and Ingram, 1993; ISO/WD, 2006) in ADE and adjacent (Control) soils at four sites with native forest or maize crops in Iranduba, Brazil, and (B) the proportion of *Pontoscolex* individuals in the overall ADE samples (quantitative-TSBF + qualitative samples). Asterisks above bars denote significant differences ($P < 0.05$) in abundance between a particular ADE and control site.

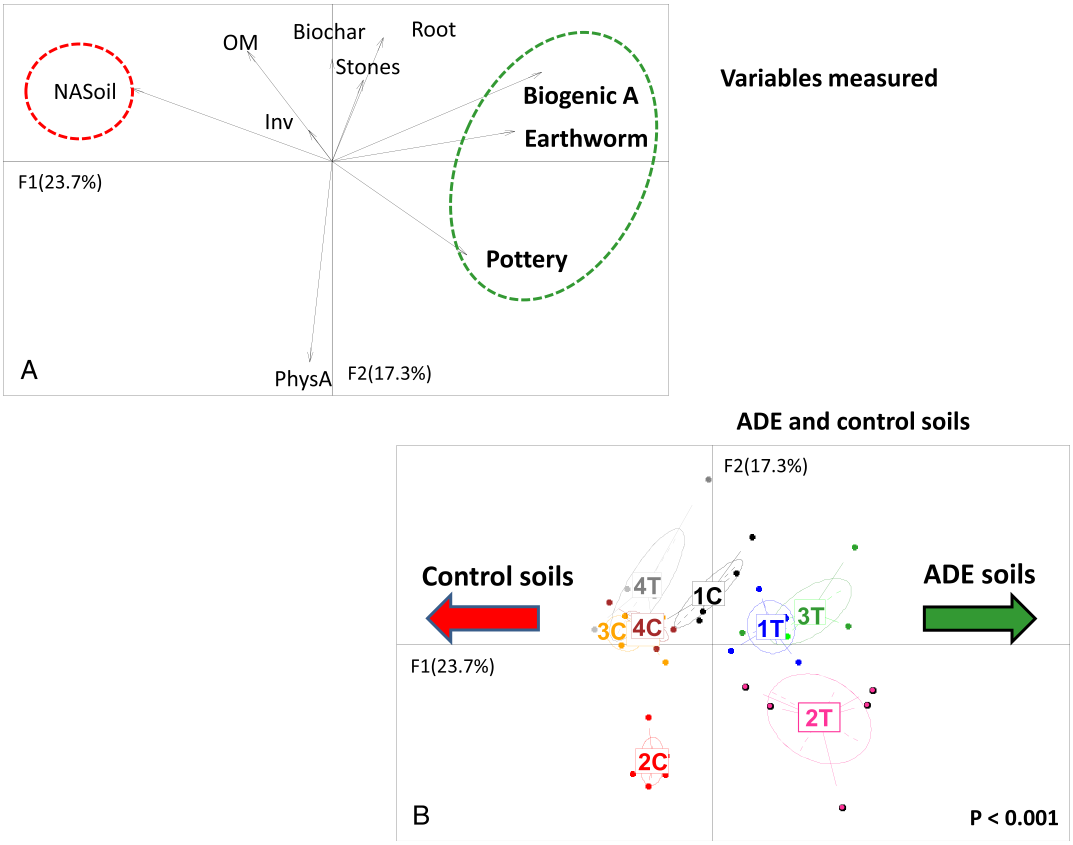

FIGURE 6. Principal components analysis of the soil macromorphology fractions taken to 0- to 10-cm depth in ADE (T) and adjacent soils (C) at four sites in Iranduba county, Brazil, using methodology of Velásquez et al. (2007). A, Bi-plot of variables and soil fractions measured; B, Bi-plot showing placement of the four sites with control (C) and ADE soils (T) along axes of first two principal components. Fractions measured (biomass) were biogenic aggregates produced by ecosystem engineers, rhizosphere aggregates (Root), physical aggregates (PhysA), nonmacroaggregated loose soil particles and unidentified aggregates less than 5 mm in size (NASoil), earthworms, other invertebrates (Inv), biochar, pottery shards, stones, and coarse organic material such as leaves, roots, seeds, and woody pieces (OM). A color version of this figure is available in the online version of this article.

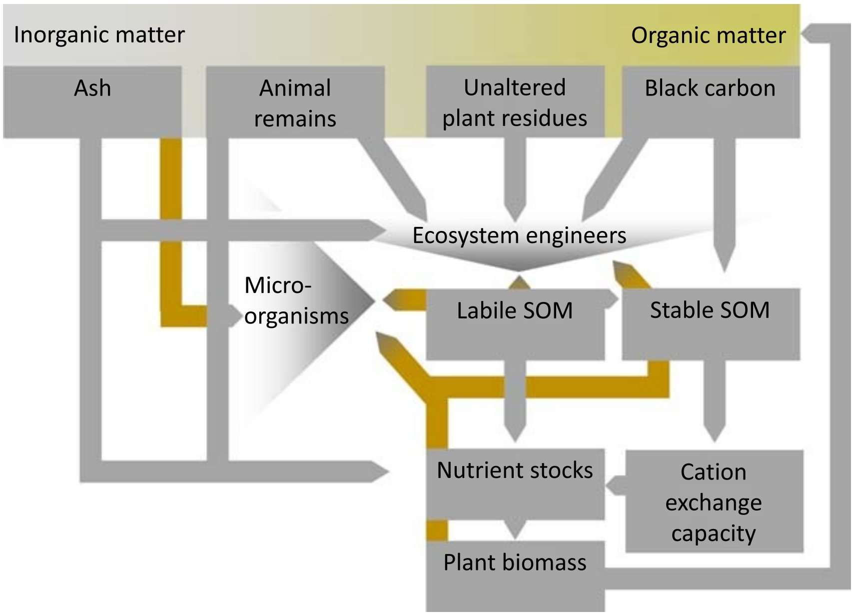

FIGURE 7. Amended version of Glaser and Birk's (2012) model of ADE genesis, incorporating the role of ecosystem engineers. A color version of this figure is available in the online version of this article.

the role of ecosystem engineers. These soil macroinvertebrates may be important “ingredients” in ADE genesis and maintenance, so this model has been amended in order to include the action of ecosystem engineers (Fig. 7). In this model, we argue that earthworms have three main functions within ADE that are important in its genesis and maintenance:

(1) the physical effects of bioturbation;
(2) ingestion and incorporation of charcoal into their casts, altering carbon stabilization and functionalization;
(3) alteration of nutrient and OM cycling and availability in soils, particularly litter and coarse OM fractions and stable forms of Ca and P.

Physical Effects of Bioturbation

Bioturbation is an important pedogenetic process in ADE and can be often observed in ADE profiles. The role of earthworm bioturbation is particularly visible when dark anthropic Au horizons overlie lighter-colored Bt horizons (Fig. 4A). Biopedotubules (Ø − 1.5 to 3 cm) filled with dark friable material from the Au horizon are easily visible in these Bt horizons (Fig. 4B). This shows an efficient mixing of material in ADE and the gradual thickening of anthropic horizons by soil fauna. Micromorphological analysis has shown that in ADE small pieces of charcoal predominate because of fragmentation caused by biological activity (Macedo, 2014). Anthropic horizons ranging from dark gray to yellowish brown have charcoal contents between 2% and 10%, whereas the yellowish subsurface horizons have a much lower proportion of fragments (<1%). With the incorporation of the charcoal and subsequent homogenization through bioturbation, the yellowish horizons become yellowish brown and dark gray (Fig. 8), transforming the subsurface horizons into anthropic and transitional horizons (Au and ABtu, respectively), thickening the overall anthropic horizon and darkening soil color.

Anthropic horizons show a microaggregated granular structure and subangular blocks of varying sizes sometimes formed by microaggregate coalescence. These microaggregates have been observed in ADE at Iranduba (near Manaus), where anthropic

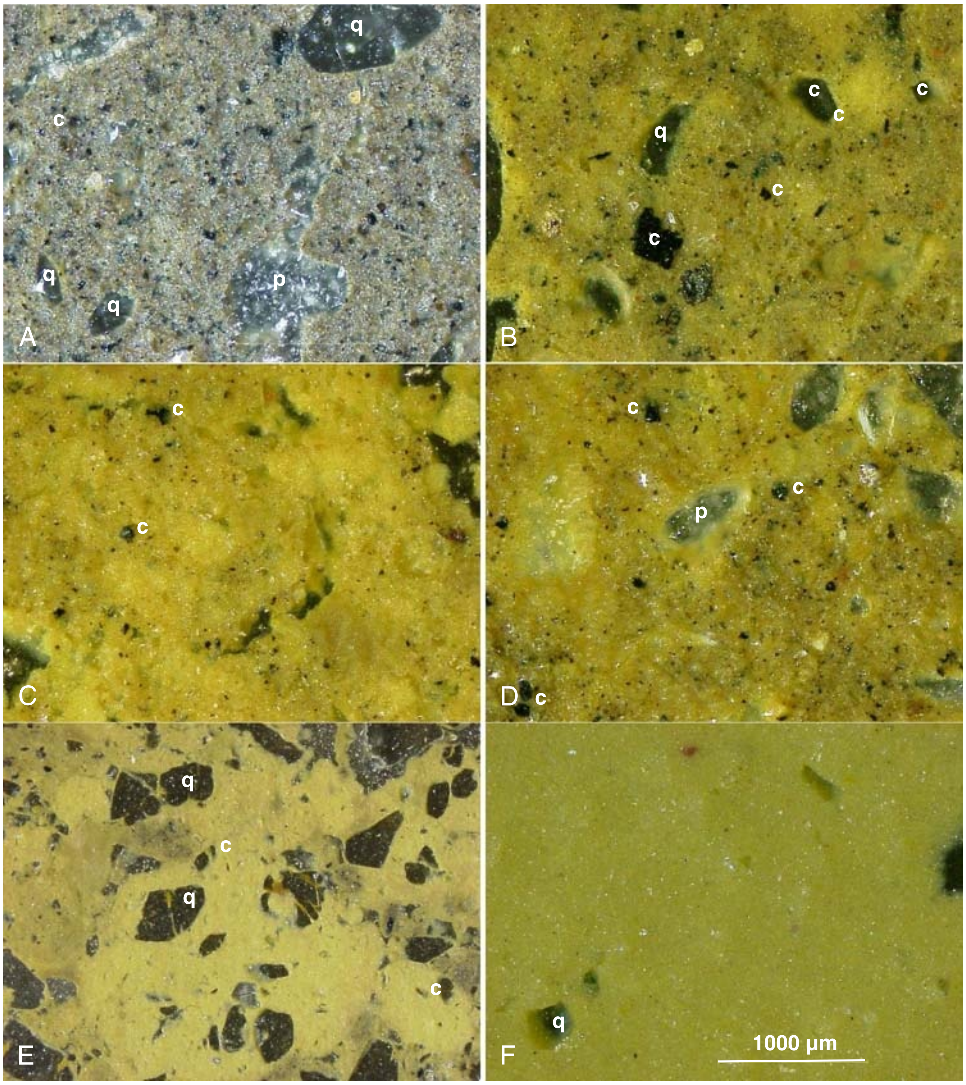

FIGURE 8. Photomicrographs (incident light) of anthropic horizons of the Anthropic Ultic Hapludalf at Embrapa’s Caldeirão Experiment Station in Iranduba, Brazil. A, Au$_1$ horizon: dark gray groundmass; B, Au$_2$: 50% brownish yellow, 40% yellow, 10% dark gray; C, Au$_3$: 70% brownish yellow, 30% yellow; D, Au$_4$: 45% brownish yellow, 35% dark gray, 20% yellow; E, Au$_5$: 50% yellow, 35% dark gray, 15% brownish yellow; F, Bt$_1$ yellow. q, quartz; p, pores; c, charcoal. Photos © R.S. Macedo. A color version of this figure is available in the online version of this article. full color online

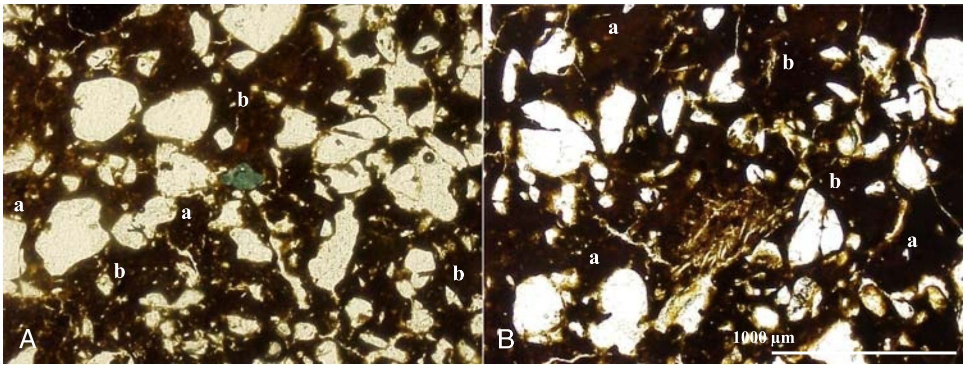

FIGURE 9. Photomicrographs of anthropic horizons of the Anthropic Ultic Hapludalf at Embrapa's Caldeirão Experiment Station in Iranduba, Brazil, showing different biological microaggregates (A, B). q, quartz; p, pores; a, microaggregates with well-selected quartz grains; b, microaggregates without or with a few quartz grains poorly selected. Photos © R.S. Macedo. A color version of this figure is available in the online version of this article. full color online

horizons showed structure similar to that of chernozemic A horizons, with a mixture of organic-mineral aggregates of different sizes (Lima et al., 2010). Most of this granular microstructure is due to faunal bioturbation. The similarity in size, shape, and structure to excrements produced by termites and/or earthworm casts that include very small and well-selected quartz grains, different from those in the overall soil matrix, confirms the biological origin of these structures (Fig. 9A). Microaggregates with or without a few poorly selected quartz grains also indicate biological origin (Fig. 9B), but geochemical processes are also involved in the formation of this type of structure. These microstructures have also been identified in B horizons of Latosols formed from different parent materials in Brazil (Cooper et al., 2005; Schaefer, 2001).

The soil fauna also exerts an indirect effect on some pedogenetic features of ADE (Macedo, 2014). Iron nodules of ADE, for example, can be found under a more advanced dissolved status than in the nonanthropogenic adjacent soil. During periods of increased precipitation, redox conditions are modified from time to time, contributing to solubilization and redistribution of iron (Fe) in the nodules through biotic oxidation of OM incorporated at greater depths. In addition to enhancing dissolution of Fe nodules (Fig. 10A), this process also contributes to increased transport and dispersion of clay (argilluviation) (Fig. 10B). In some anthropic horizons, clay and Fe linings are fragmented and embedded in the matrix (papules). The activity of soil fauna may effectively participate in the degradation of these features, which prevents the existence of slowly accumulated clay films (waxiness) during the morphological characterization of soils in the field.

Bioturbation also significantly influences the porosity of anthropic horizons. The number of biological channels is greater in ADE when compared with that in the adjacent soil (Macedo, 2014). Another difference is the occurrence of simple packing voids only in ADE, formed by the greater number of microaggregates. This causes the pedon to have more open porosity in the surface (anthropic) horizons and more closed porosity in the subsurface (Bt) horizons. Biological channels (biopedotubules) filled with organomineral material are common in ADE. These materials are mainly excrements and aggregates formed in situ by biological reworking. They may be spaced out (continued loose), aggregated (discontinued loose), or completely in-fill the pores (dense complete). They occur as old, coalesced materials with edges showing signs of aging (Fig. 11A), or as recently deposited materials, exhibiting a low degree of coalescence, clear shapes, and smooth edges (Fig. 11B). Furthermore, some biological channels of ADE show in-filling with SiO_2 and Al_2O_3 and are enriched in P_2O_5 and organic C. These forms of P-C-Al are most likely earthworm castings and microarthropod feces (Schaefer et al., 2004). The transformation of biogenic apatite results in secondary residual accumulations of P-Al, P-Fe, and organic P. This confirms the effectiveness of bioturbation in the process of mineral transformation in ADE. It also indicates the contribution of both past and present faunal bioturbation to the structuring and thickening of ADE.

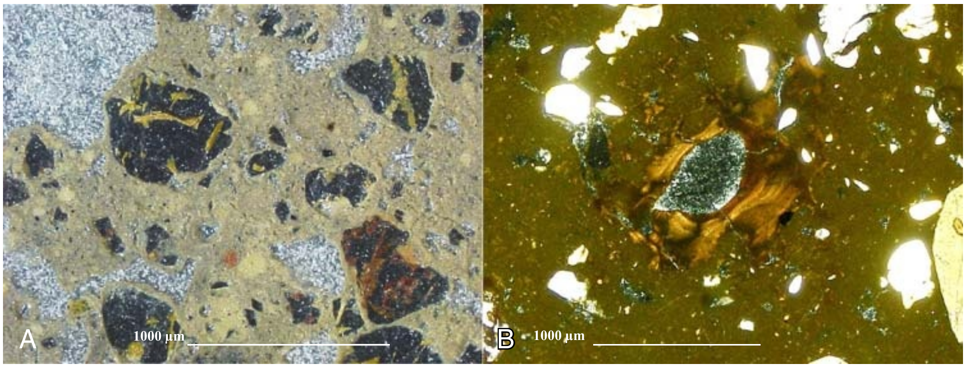

FIGURE 10. Photomicrographs (A: incident light; B: cross-polarized light) of anthropic horizons of the Anthropic Plinthic Kandiudox at Embrapa's Caldeirão Experiment Station in Iranduba, Brazil. A, Dissolution of Fe nodules; B, microlamination (clay coating) with strong and continuous orientation and clear extinction (argilluviation). Photos © R.S. Macedo. A color version of this figure is available in the online version of this article. full color online

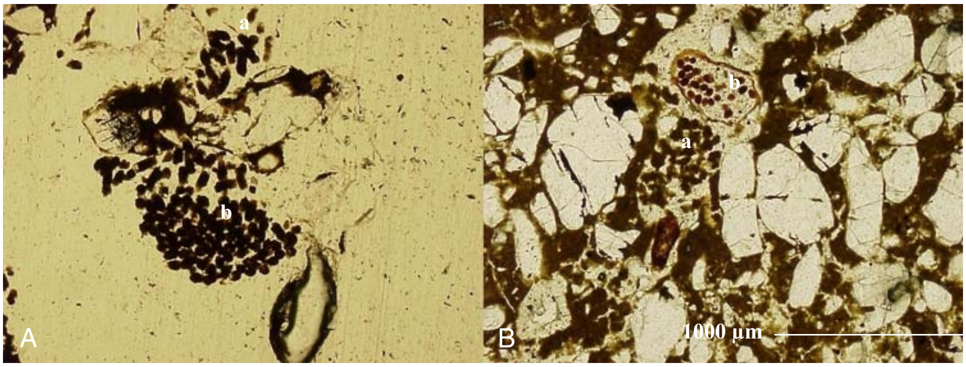

FIGURE 11. Photomicrographs of excrements and aggregates in anthropic horizons of the Anthropic Ultic Hapludalf at Embrapa's Caldeirão Experiment Station in Iranduba, Brazil. A, Old, coalesced, and with edges with signs of change; B, recently deposited materials, exhibiting a low degree of coalescence, clear shapes, and smooth edges. Photos © R.S. Macedo. A color version of this figure is available in the online version of this article. full color online

Earthworms and Charcoal

Earthworms can ingest biochar particles both in situ (Topoliantz et al., 2005) and ex situ (Topoliantz and Ponge, 2003; 2005), that is, in the field and upon addition to the soil. There is some evidence that biochar may be toxic to earthworms, but not all studies have detected such an effect. Topoliantz and Ponge (2003, 2005) showed 100% survival of *P. corethrurus* in mesocosm experiments using natural charcoal and native soil. Gomez-Eyles et al. (2011) found that soil containing polycyclic aromatic hydrocarbons and other potentially toxic elements, amended with biochar, was not acutely toxic to *Eisenia fetida*, but the earthworms significantly lost weight in the soil with biochar. On the other hand, Liesch et al. (2010) observed 100% mortality in high concentrations of biochar made from poultry litter. Despite the considerable research on biochar interaction with earthworms (Weyers and Spokas, 2011), relatively few studies have focused on earthworm casts (Eckmeier et al., 2007), and none were performed over the long term. Further research on this is warranted, considering the potential effects of earthworm-microbe interactions on biochar properties and quality in casts, the earthworm gut, and worm-worked soils (Marhan and Scheu, 2005; Paz-Ferreiro et al., 2015; Topoliantz and Ponge, 2003).

To shed further light on some of these issues, we conducted a short-term microcosm experiment with 0% and 5% biochar (slow pyrolysis at 400°C for 8 h of hardwood in traditional kilns; Maia, 2010) by weight, in 100 g of an artificial soil substrate (sand 70%, kaolin 20%, and coconut fiber 10%; Garcia, 2004), fortified with glucose:fructose (1:1, 3 g kg^{-1}) as nutrients and vitamins for the earthworms. One *P. corethrurus* weighing ~1 g fresh weight was added to each container (n = 10 replicates of each treatment), and their survival and cast production assessed after 30 days. Furthermore, we also investigated the quality of cast OM using

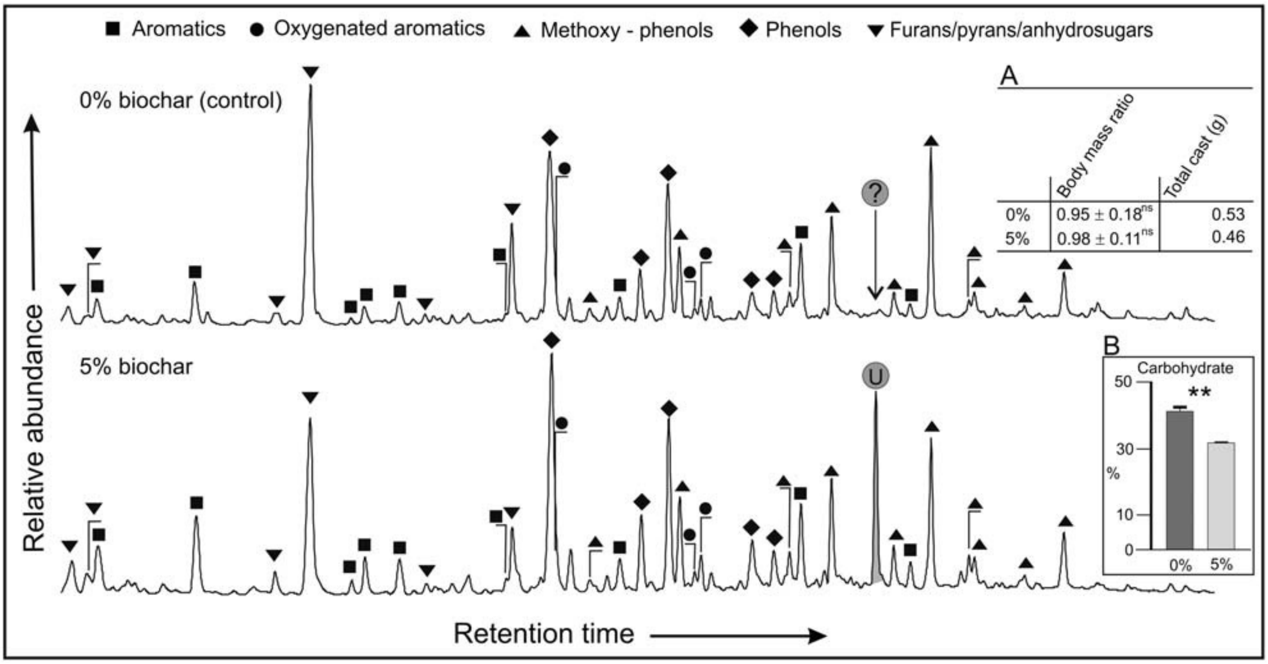

FIGURE 12. Partial total ion current (TIC) pyrograms showing the main classes of derived pyrolysis products in earthworm (*P. corethrurus*) casts from the control (0% biochar) and hardwood biochar addition (5% biochar) treatments. Insets, Worm body mass ratio ($mass_{initial}$:$mass_{final}$) and cast biomass after 30 days (A) and the relative distribution of carbohydrate-derived pyrolysis products in the casts (B). Letter U above peak in the 5% biochar treatment indicates an unknown compound. Significant levels in the *t* test applied: ns, $P > 0.05$; $^{**}P < 0.01$.

pyrolysis–gas chromatography–mass spectrometry. No earthworm mortality or weight loss was observed with biochar (Fig. 12A), and a total of 61 compounds were identified in the castings (Fig. 12), with the major chemical classes detected being aromatics (e.g., benzene and toluene), oxygenated aromatics (e.g., benzofuran and methyl-benzofurans), phenols (e.g., phenol and methyl-phenols), methoxy-phenols (e.g., guaiacol and vinyl-guaiacol), and furans/pyrans/anhydrosugars (e.g., furfural and levoglucosan).

The most abundant pyrolysis class was furans/pyrans/anhydrosugars (Fig. 12B), which are associated with carbohydrates (e.g., glucose and cellulose) in the casts (Kaal and Rumpel, 2009). Interestingly, the relative quantity of carbohydrates in the casts was lower with 5% biochar (Fig. 12B), and castings in this treatment showed an unknown pyrolysis compound (1.6 ± 0.7%) that was absent in the control treatment (Fig. 12). The presence of this unknown compound and the difference in the distribution of carbohydrate-derived pyrolysis products in the treatments (control and 5% biochar) indicate that cast quality is different when biochar is added and that this may be dependent on the type of biochar feedstock used, because it is well known that food type and quality affect cast quality as well (Buck et al., 1999; Jouquet et al., 2008). Also, a strong preference by earthworms for aged charcoal against fast-pyrolysis biochar indicates that age and decomposition stage may be crucial for efficient charcoal incorporation by earthworms (Elmer et al., 2015).

The interaction of earthworms and biochar may have significant effects on microbial communities (Paz-Ferreiro et al., 2015) and on plant growth (Noguera et al., 2010; Paz-Ferreiro et al., 2014; Topoliantz et al., 2002), although the few studies performed thus far have generally been short term (< 4 months). Little is known of the potential long-term interactions between these factors, as would occur in ADE. We hypothesize that bioturbation by earthworms such as *P. corethrurus* may have important effects not only on the properties of biochar (physical, chemical, and biological) but also on its potential function and effects in the soil, altering microbial communities, their activity, and ultimately soil fertility and plant production in ADE soils. This avenue of research is worth following and will help clarify the role of earthworms in the fertility of ADE.

Earthworms and Nutrient and OM Cycling in ADE

In the tropics, earthworm cast production can reach huge proportions and may account for a significant proportion of the total soil volume. At some sites, the whole topsoil profile may appear to have been ingested by earthworms, because many tropical endogeic species can consume from five up to as much as 30 times their weight per day (Lavelle, 1978, 1988). Therefore, the effects of earthworm burrowing and casting on nutrient and OM cycles can be different depending on the time scale considered and the earthworm community/ecological categories present (Brown et al., 2000).

At the time scale of a few hours or days (Fig. 3), nutrient mineralization is high because of microbial priming in casts, although this may also result in nitrogen losses from the soil through greenhouse gas emissions, particularly of N_2O (Lubbers et al., 2013). But, as casts age, particularly in "compact" casts of endogeic species (Blanchart et al., 1997), microbial activity is reduced, and nutrients may be conserved, especially if casts dry out and harden. At the scale of months, C mineralization increases, but at longer time scales, it decreases (Brown et al., 2000). A modeling exercise undertaken using data from Peruvian Amazonia revealed a 28% reduction in C mineralization after 30 years of cultivation in soils with *P. corethrurus* (Lierman, 1997). Considering the presence and prevalence of this species in ADE, this topic deserves attention, especially given the long-term impacts of agriculture on C conservation in these soils.

In terms of ecological categories, as mentioned earlier, anecic earthworms are particularly important in leaf litter burial and decomposition, but their presence appears to be rare in ADE. Although surface casts are generally a small proportion of total earthworm casting for endogeic species (Lavelle, 1978), when these worms do produce surface casts, this behavior enables the worm to rapidly bury materials left on or that fall on the soil surface, accelerating their decomposition and mineralization rates (Fig. 3). For instance, in an Amazonian rainforest near Manaus, the giant earthworm species *Rhinodrilus priollii* produces large casts that cover more than 90% of the soil surface (Kuczak et al., 2006; Pereira, 2003). However, up until now, fewlarge earthworms have been seen in ADE, and no estimates of surface cast production are available for these anthrosols.

The earthworm community of ADE identified thus far by the authors does not include anecics and appears to be composed mainly of small epigeic and small- to medium-sized endogeic earthworm species, particularly mesohumic and polyhumic species that are more adapted to soils with human disturbance (Fragoso et al., 1999). The small epigeic earthworms live in ADE under forest vegetation and help break down the surface litter. They produce OM-rich casts that can be further consumed by other soil fauna and microbes. These species are particularly important in freeing up nutrients from surface litter and accelerating their release into the soil. Polyhumic endogeic earthworms (e.g., ocnerodrilids in Fig. 5B) feed on richer sources of OM in the early stages of decomposition closer to the soil surface or at the soil-litter interface, also helping to accelerate nutrient release from coarse organic materials, incorporating them into the surface horizons of ADE. Mesohumic endogeic species such as *P. corethrurus* tend to feed close to plant roots (Brown et al., 2000; Spain et al., 1990) and are particularly important in stimulating plant growth (Brown et al., 1999). This stimulation may be due not only to increased nutrient mineralization (particularly of N and P), but also to alteration of plant metabolism and gene expression induced by production of hormones by plants and signal molecules (mainly by microbes) in casts and worm-worked soils (Puga-Freitas and Blouin, 2015). This exciting topic will surely render many interesting results in the future and points to an as yet little-explored relationship among earthworms, microbes, and plants in ADE.

We believe that earthworms are not just followers of ADE, but rather that they also have a role in the generation of ADE and in their fertility. In fact, there is indirect evidence that earthworms may have an important role in the availability of two of the most important and abundant plant nutrients in ADE: P and Ca. Earthworm casts, including those of *P. corethrurus*, often show higher levels of organic P than surrounding soil, and selective ingestion of particles enriched in P, but also modification of P forms during and after gut passage, results in more labile or exchangeable P in casts (Chapuis-Lardy et al., 1998; Graff, 1970; López-Hernández et al., 1993). In fact, in an Amazonian agroforestry system, earthworm casts were estimated to constitute up to 41 kg ha^{-1} of total available P (Kuczak et al., 2006), and the inoculation of *P. corethrurus* in macrocosms increased maize plant P uptake by up to three times (Guerra, 1982) in a nutrient-poor Amazonian soil.

Earthworm biogenic mineralization of Ca may also be closely related to that of P. Morgan (1981) described Ca incorporation not only in the earthworm calciferous gland but also in the chlorogosome, revealing a bond between Ca and P. Many earthworm species, including *P. corethrurus*, have calciferous glands that affect pH and Ca availability in soil and earthworm casts (Bartz et al., 2010; Kale and Krishnamoorthy, 1980). The formation of amorphous calcium carbonate in the earthworm's calciferous gland is a notable case of biological mineralization (Gago-Duport et al., 2008; Lee et al., 2008). Nevertheless, precisely why earthworms produce amorphous calcium carbonate in the calciferous gland has never been satisfactorily explained, although the activity of carbonic anhydrase has been found (Clark, 1957). Some functions have been proposed, namely, pH buffering of the blood and the ingested soil, aiding not only digestion, egg formation, and excretion but also, and most importantly, respiratory functions (Chapron, 1971; Darwin, 1881; M'Dowall, 1926; Michaelsen, 1904). In fact, Darwin considered the calciferous gland to be an excretory organ that eliminates excess dietary Ca by fixing carbon dioxide (CO_2) to form $CaCO_3$. Recently Briones et al. (2008) showed by using ^{13}C-labeled CO_2 that environmental and metabolic CO_2 could, in fact, be fixed in this organ. The labeled isotope was found accumulating not only in the gland but also in the body wall.

Cromack et al. (1977) postulated that earthworms can sequester a great part of Ca by uptake of fungal calcium oxalate through their diet. In fact, oxalate-decomposing bacteria have been isolated from earthworms' digestive tracts and their casts (Jakoby and Bhat, 1958; Parle, 1963). Biogenic earthworm $CaCO_3$ is incredibly resilient and commonly found in archaeological sites (Canti, 1998). Considering the high biomass that earthworms represent in the soil, CO_2 fixation and $CaCO_3$ granule production may turn out to be a significant component of the biogeochemical cycling of C and Ca in soil (Lambkin et al., 2011) and therefore could help partially explain the high stability of Ca in ADE.

CONCLUSIONS AND RECOMMENDATIONS

The generation of new ADE ("Terra Preta Nova") is somewhat like a "holy grail quest" in sustainable agriculture research, with the potential to produce food for billions of people (Glaser, 2007). Although charcoal is one of the main constituents of ADE, ADE is more than just soil with charcoal added, and despite considerable scientific interest (Lehmann, 2007; 2009b), the promise of Terra Preta Nova has yet to be fully realized. A primary focus for future work should be to determine the extent to which soil engineers are required for the initial generation of ADE. This will require characterization of the biodiversity of ADE of different ages, in order to determine the characteristics of ADE that affect the variability in soil engineer biodiversity, and vice versa. In addition, there are areas within the Amazon rainforest where ADE is still being formed (e.g., upper Xingu; Schmidt et al., 2014), which are of particular interest for exploratory sampling, and much may be learned from native communities that live in these areas.

Other work should attempt to characterize the specific roles that the different constituents of ADE play by themselves and especially in combination with others. For example, what are the interactions of biota and charcoal and biota and ceramics (as evidenced in Fig. 6A)? Moreover, what is the role of the interaction of microbes with these components? Finally, how does bioturbation in ADE affect nutrient cycling and conservation? Amazonian Dark Earths appear to be a unique ecosystem in its own right, and these constituents are essential parts of it. Perhaps previous attempts to create Terra Preta Nova have fallen short because they have failed to adopt a more holistic approach that includes all the ingredients of ADE. Future work must therefore address not only the chemical and physical but also the biological, pedological, ecological, anthropogenic, and archaeological questions that are associated with ADE.

The preliminary results presented here indicate a high proportion of *Pontoscolex* species and Ocnerodrilidae in ADE. Future work must focus on determining whether this biodiversity is representative of ADE throughout Amazonia, both under agriculture and native forest. The high incidence of a unique diversity signature due to very distinct abundances of groups of earthworm families and genera in ADE potentially provides a robust biodiversity fingerprint. If this particular biodiversity signal is associated with ADE, then it will degrade as one moves away from ADE. It would be useful to understand better the selection pressures that individuals of different species are experiencing within and adjacent to ADE. In particular, tools such as comparative genetics/genomics may be useful in working toward a better understanding of biodiversity patterns found in ADE. A long-term scenario of coevolution should not be disregarded, where human cultural behavior, plants, earthworms, and the microbiota of ADE have evolved together in a mutualistic relationship, sustaining the high fertility of this anthropogenic ecosystem. Describing unique biodiversity and genetic attributes may hold promise in the future for identifying historical human disturbance and describing the extent of historic anthropogenic influence on parts of the Amazon rainforest.

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