



## Key processes and timescales of tropical earth formation

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### ABSTRACT

Understanding the formation of tropical yellow to red earth (TYRE) is essential for preserving soil multifunctionality in well-drained tropical landscapes. Weathering and bioturbation mutually interact in TYRE evolution, whereas allochthonous materials appear restricted to distinct (paleo)landscapes. A layered appearance of TYRE can result from quasi-constant deposition of invertebrate mound debris, outcompeting diffusional mixing. Age-depth profiles from optically stimulated luminescence (OSL) and charcoal radiocarbon ( $^{14}\text{C}_{\text{char}}$ ) data of TYRE sites in different tropical landscapes, both from the literature and the present study, all reveal quasi-constant soil upbuilding, in accordance with our model. The rates of soil upbuilding are mostly in the range of 100–200  $\text{mm}^2\text{ka}^{-1}$ , which conforms with published mounding rates of termites and ants. By comparison, geochemical transformation of rock to saprolite proceeds at rates at least one order of magnitude smaller. Termites mining saprolite, sometimes even below indurated subsoil, produce TYRE, thus linking the interconnected subsystems of differing process rates. The work of the bioengineers appears essential for transforming the deep-weathering products into well-structured TYRE. Future research may extend the provided database, the spatial scale, and the use of geochronology, coupled with paleoenvironmental proxies, in order to further enhance our understanding of tropical soil and landscape evolution, as one basis for advances in sustainable land use.

### 1. Introduction

Deep and strongly weathered soils cover large areas of the tropics,

hosting hotspots of biodiversity and deep soil carbon and water reservoirs (Balesdent et al., 2018; Gaston, 2000; Liang et al., 2022; Schaefer et al., 2022). The growing demand for food and fuel crops is partially

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satisfied by the conversion of tropical ecosystems into agricultural land, commonly supported by irrigation and fertilization (Laurance et al., 2014; Ray et al., 2012; Winkler et al., 2021). However, land use and land cover changes facilitate soil degradation and erosion, enhanced by high tropical rainfall erosivity (Borrelli et al., 2020; Labrière et al., 2015; Quinton et al., 2010).

Knowledge on soil forming processes and specifically soil (re-)production rates in the tropical zone is scarce but essential to evaluate the severity of soil degradation and loss (Alexander, 1988; Bronger et al., 2000; Montgomery, 2007), and to optimize or restore soil functions for sustainable land use. Furthermore, this knowledge increases our understanding of tropical critical zone dynamics (Braun et al., 2017; Mana et al., 2015; Moore et al., 2019; Schaefer et al., 2022) and landscape evolution (Heimsath et al., 2020; Nehren et al., 2016). It also permits to contextualize enclosed archeological findings (Johnson, 1990; Johnson, 2002; McBrearty, 1990; Mercader et al., 2002; Smith et al., 2020; Williams, 2019) and to use soils as paleoenvironmental archives (Bremont et al., 2017; Calegari et al., 2013; Desjardins et al., 2020; Gouveia et al., 2002; Pessenda et al., 1996; Pessenda et al., 2010).

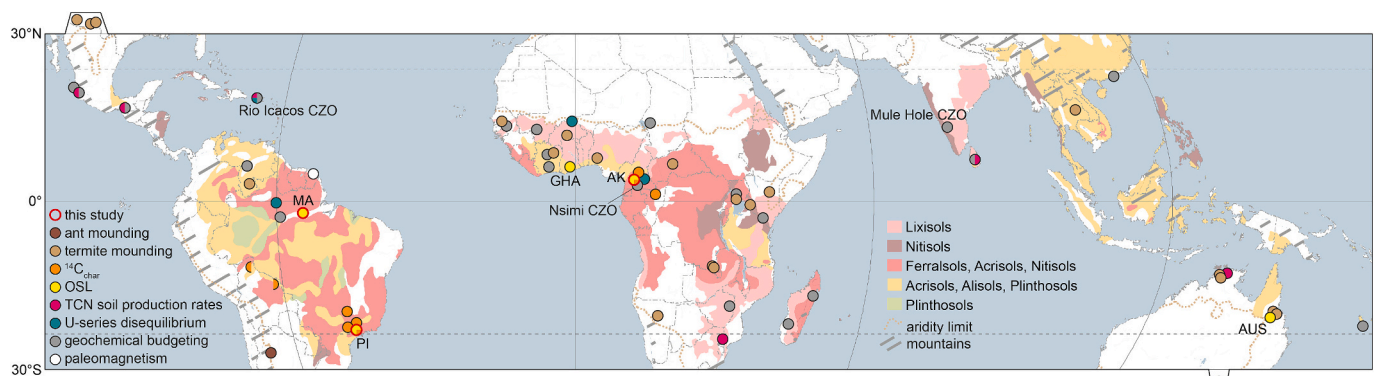
Well-structured and rather homogeneously oxidized soil of advanced weathering degree, herein referred to as tropical yellow to red earth (TYRE), is widely distributed in flat to undulating and hilly tropical landscapes above groundwater influence (Boulet et al., 1997; Lucas, 1989) (see Section 2, Fig. 1). In large parts of the tropics, TYRE are the few decimeters to several meters thick topmost parts of few meters to several decimeters deep tropical regolith profiles (TRP) (Anand et al., 2002; Thomas, 1974); the latter are often referred to as lateritic profiles (Balan et al., 2005; Monteiro et al., 2018; Schaeztl and Thompson, 2015) or (tropical) weathering profiles (Phillips et al., 2019). Stone lines and iron enriched zones often separate TYRE from saprolite, i.e., chemically weathered rock with visible lithological structure (Felix-Henningsen, 2016); between iron enriched zones and saprolite there may be iron depleted zones without rock structure (Anand et al., 2002). Iron-enriched zones are commonly referred to as laterite or, if allochthonous iron predominates (usually contributing to iron-crusts), as ferricrete (see review and references by Widdowson, 2008).

Various analytical techniques have been used to date selected components of TRP and to quantify specific soil-forming processes. Deep saprolite and well-developed laterite form over  $10^5$ – $10^7$  years through weathering and geochemical differentiation (Balan et al., 2005; Beauvais et al., 2016; Braun et al., 2012; Chabaux et al., 2013; Felix-Henningsen, 2016; Hewawasam et al., 2013; Mathian et al., 2020; Monteiro et al., 2014; Monteiro et al., 2018; Théveniaut and Freyssinet, 1999; Vasconcelos and Carmo, 2018). By contrast, TYRE appears to be frequently reworked at much shorter time scales ( $10^3$ – $10^4$  years), as

evidenced by radiocarbon ages of charcoal ( $^{14}\text{C}_{\text{char}}$ ) and optically stimulated luminescence (OSL) ages of quartz (Boulet et al., 1995; Heimsath et al., 2020; Johnson et al., 2014; Kristensen et al., 2015; Thiéblemont et al., 2014). Therefore, established (bio)geochemical models of tropical soil production and differentiation (Nahon, 1991; Tardy, 1993) need to be complemented by (bio)mechanical near-surface processes (Aleva, 1983; Johnson, 1993; Johnson et al., 2005b), leading to the incorporation of charcoal and minerals that had been exposed to sunlight.

The contributions of chemical weathering and pedogenic differentiation, bioturbation and geomorphic processes (e.g., colluvial, alluvial, eolian deposition) in the formation of TYRE and stone lines have stimulated decades of scientific dispute (Morrás et al., 2009; Nehren et al., 2016; Schaeztl and Thompson, 2015; Sharpe, 1938). Evidence of long-term weathering and bioturbation in the tropics (Aleva, 1983; Aleva, 1987; Nye, 1955; Schaefer, 2001) have inspired concepts of soil and landscape evolution that stress the presence of a (par)autochthonous biomantle above a stone line (not mandatory) and local weathering residue (Johnson, 1993; Johnson, 2002; Johnson et al., 2005b; Paton et al., 2000; Schaeztl and Thompson, 2015). In the temperate zone, however, climatically driven changes in morphodynamics leading to erosion, allochthonous additions, and layering of soil parent materials, are evident (Kleber and Terhorst, 2013; Lorz et al., 2011; Phillips and Lorz, 2008; Semmel, 1993; Semmel and Terhorst, 2010; Waroszewski et al., 2017). Apparently, both, autochthonous (in situ) processes and spatiotemporally distinct allochthonous contributions require consideration in concepts of soil and landscape evolution.

Despite decades of research, the extent to which climate changes have influenced tropical landscapes and soils remains controversially discussed. A widely agreed and intelligible model of TYRE formation, which integrates autochthonous processes and allochthonous material input, is lacking. This deficit is partly owed to the extent of tropical landscapes and the diversity of tropical soils but also to the variety of scientific disciplines and publishing languages (Richter and Babbar, 1991). A deeper knowledge of the mechanics of bioturbation and comprehensive information on process rates may help to widen the one-sided focus of either (bio)geochemical or geomorphological explanations of TYRE evolution. We reinforce the wide-held notion that mounding invertebrates lead to the accumulation of fine over coarse material (Johnson, 1990; Johnson et al., 2005b; Nye, 1955; Paton et al., 2000; Wilkinson et al., 2009; Williams, 2019). However, previous concepts largely ignore that mounds create layers within the surficial fine material (e.g., TYRE) that can be dated and used as paleoenvironmental archives (Boulet et al., 1995; Gouveia et al., 1999; Kristensen et al., 2015).



**Fig. 1.** Distribution of tropical earth and studies on its evolution. Map of tropical yellow to red earth (TYRE) as represented by related reference soil groups defined by the IUSS Working Group WRB (2022) and studies on aspects of TYRE evolution (between 30°N and 30°S, except studies that quantify termite bioturbation) referred to in this paper, including the supplementary data. This study: Akonolinga, Cameroon (AK); Piracicaba, SE-Brazil (PI); Monte Alegre, E Amazonia (MA). Previous studies that quantify bioturbation using OSL have been undertaken in Ghana (GHA) (Kristensen et al., 2015) and Australia (AUS) (Johnson et al., 2014). CZO: Critical Zone Observatory, TCN: Terrestrial cosmogenic nuclides. Figure based on a modified global soil map 1:25,000,000 (FAO et al., 2003). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Here, we (i) propose a model of TYRE formation that includes autochthonous and allochthonous particle transfers, highlighting the work of termites and ants giving TYRE the appearance of a deposit; (ii) present OSL and  $^{14}\text{C}_{\text{char}}$  age-depth profiles from six TYRE sites in upper slope positions in south Cameroon, eastern Amazonia, and southeastern Brazil, which are complemented by published data for assessing rates of TYRE upbuilding; (iii) review published mounding rates of tropical ants and termites, as well as (iv) tropical weathering rates; (v) discuss all data against the model of TYRE formation; and (vi) address some relevant implications for fundamental research and applied purposes.

## 2. Conceptual background

TYRE is a purely descriptive, pedologically and genetically neutral term, resembling “red and yellow earth” by Holt et al. (1980). TYRE as defined in Section 1 denotes common tropical soil material, independent of any existing classification system in use. To illustrate at global scale where TYRE can be found (Fig. 1), we tentatively attribute well-drained yellowish to reddish (including transitions) tropical soils with diagnostic argic (Acrisol, Lixisol, Alisol), nitic (Nitisol) and ferralic (Ferralsol) horizons to TYRE; thereby we consider internal differences in structure, geochemistry, textural gradient, and pedofeatures within these reference soil groups (IUSS Working Group WRB, 2022; Zech et al., 2022). Plinthosols may contain TYRE in the first half meter and are therefore shown as well, whereas Cambisols (even though some may fulfil the TYRE concept) are excluded due to their global omnipresence. TYRE replaces other terms like, e.g., soil (Anand et al., 2002; Vasconcelos, 1999), mixed soil (Heimsath et al., 2020), creep horizon (Nye, 1955), (upper) biomantle (Johnson, 1990; Johnson et al., 2005b), hillwash (Runge, 2001), or tropical loess (Iriondo and Kröhling, 2007), each associated with a particular concept of (tropical) soil and landscape evolution.

### 2.1. Allochthonous origin of TYRE?

Decades of debate on TYRE and stone line formation are owed to different, sometimes contradictory, perspectives of researchers from different disciplines, like pedologists, geochemists, ecologists, geomorphologists, and archeologists. Supposedly contradictory to a bioturbated (in the sense of mixing) weathering residue, some features make TYRE appear like a deposit: i) a vertical differentiation into horizons, which are sometimes well-visible (Almeida et al., 2015; Chiapini et al., 2018), but often weakly differentiated, with diffuse boundaries (Hartemink et al., 2020; Ker, 1998; Zech et al., 2022); ii) occasionally distinct charcoal layers (Kauffman and Uhl, 1990; Marques et al., 2011; Saldarriaga and West, 1986; Soubiés, 1980); iii) Holocene paleoenvironmental records of vertical successions of phytolith assemblages or stable carbon-isotope ratios (Bremond et al., 2017; Calegari et al., 2013; Desjardins et al., 2020; Gouveia et al., 1999; Pessenda et al., 1996; Pessenda et al., 2010; Piperno et al., 2021); and iv) stratified archeological features within TYRE (Araujo et al., 2017; McBrearty, 1990; Williams, 2019). In addition, v) often clear lower boundaries of TYRE and vi) the morphological appearance of many stone lines as coarse sediments may suggest an allochthonous origin of TYRE (Iriondo and Kröhling, 2007; Runge et al., 2013; Thiéblemont, 2013; Thomas and Thorp, 1995).

Repeated reworking of ancient TYRE may have occurred through long-term ( $10^5$ – $10^7$  years) pediplanation and etchplanation cycles influenced by regional tectonics (Muggler, 1998). However, late Quaternary  $^{14}\text{C}_{\text{char}}$  and luminescence ages from TYRE are frequently interpreted as evidence of recent colluvial (Runge, 2001; Runge et al., 2013; Sallun and Suguio, 2010; Thomas and Murray, 2001) or eolian accumulation (Iriondo and Kröhling, 2007; Lichte and Behling, 1999; Thiéblemont, 2013; Thiéblemont et al., 2014). Distinct phases of morphodynamic activity are usually attributed to dryer paleoenvironments with a reduced vegetation cover (Heine, 2019; Rohdenburg,

1969; Rohdenburg, 1970; Runge, 2001; Runge et al., 2013; Sallun and Suguio, 2010; Thomas and Thorp, 1995); yet the timing and spatial extent of dry periods with significant influence to TYRE remains to be established.

As colluviation is a downslope oriented process, it cannot create extensive plateau and upper slope TYRE. Fundamental paleotopographic changes as explanation for assumed (last glacial) colluvia in present-day hilltops (Semmel and Rohdenburg, 1979) appear not convincing on the comparably short, multimillennial time scales. Eolian mantles independent of the relief position require source material, usually deflated from (semi-)arid environments or dry beds of anastomosing rivers and glacier forefields (Smalley et al., 2009; Sprafke and Obrecht, 2016). Relevant mineral dust sources of such type are at present not observed in the humid tropics and not convincingly defined for presumed late Pleistocene to Holocene dry periods. Charcoal from TYRE is in most cases of Holocene age (Boulet et al., 1995; Bremond et al., 2017; Desjardins et al., 2020; Pessenda et al., 2010), but there are no obvious supraregional chronostratigraphic patterns to infer large-scale synchronous periods of deposition related to open, dry paleoenvironments. TYRE upbuilding by far-travelled eolian dust (Thiéblemont et al., 2014), which could occur independent of local (paleo)ecosystems, appears unlikely due to the large amount of material required and the fact that TYRE properties change in close relation to local bedrock geology (Boulet et al., 1995; Chiapini et al., 2023; Tardy, 1993). Neodymium-isotopes differing from bedrock as evidence for an eolian origin of TYRE (Thiéblemont et al., 2014) or at least a significant eolian contribution (Viers and Wasserburg, 2004) is debatable as this isotopic system is also affected by intensive weathering (Bai et al., 2023; Horbe et al., 2022; Ma et al., 2007; Ma et al., 2010). Overall, widespread colluviation or eolian deposition are unlikely key processes in TYRE formation. Locally, TYRE and stone line material may be found reworked, e.g., at or below steep slopes, related to (semi-)arid paleoenvironments, or due to past agricultural activity (Heckmann, 2014; Hiruma et al., 2012; Modenesi-Gauttieri, 2000; Modenesi-Gauttieri and de Toledo, 1996). Proximal to (paleo)deserts, or distal to deserts on very long time scales, dust may be relevant TYRE material, but otherwise it is merely a variable admixture to local weathering products (Brimhall et al., 1988; Chadwick et al., 1999; Li et al., 2016; Liu et al., 2019). Isotopic data do not refute that Sahara dust contributes nutrients to the Amazon rainforest, however, a relevant contribution to TYRE is not traceable (Abouchami et al., 2013).

### 2.2. Autochthonous formation of TYRE

TYRE formation and reworking by biota is largely independent of the geomorphic position and widely accepted as explanation for the in situ (autochthonous) differentiation of TYRE from stone lines, laterite or ferricrete, and saprolite (Johnson, 1993; Johnson et al., 2005b; Johnson et al., 1987; Miklós, 1992; Nye, 1955; Paton et al., 2000; Schaefer, 2001; Schaefer and Oliveira, 2022; Schaetzl and Thompson, 2015; Watson, 1961; Wielemaker, 1984; Wilkinson et al., 2009; Williams, 2019). A microgranular structure is characteristic for many TYRES and usually attributed to termite activity (Eschenbrenner, 1986; Jouquet et al., 2016; Jungerius et al., 1999; Martinez and Souza, 2020; Miklós, 1992; Reatto et al., 2009; Sarcinelli et al., 2009; Schaefer, 2001). Since the works of Darwin on earthworm casting (Darwin, 1881; Darwin, 1838), selective upward transfer of fine material is recognized as obvious sorting process. Isotropic (homogenous) fine biomantles are consequently differentiated from anisotropic (two-layered) biomantles with fine over coarse material, the latter commonly referred to as stone lines (Hole, 1961; Johnson et al., 1987; Schaetzl and Thompson, 2015).

Based on previous works, Johnson et al. (2005b) distinguish ‘mix-master’ organisms that stir soil without preferred orientation (diffuse bioturbation) from ‘moundmaker’ organisms performing conveyor-belt like bioturbation with upward biotransfer. Fungus-growing termites, several ant and earthworm species and some terrestrial vertebrates (e.g.,

armadillos) belong to the second category (Johnson et al., 2005b; Paton et al., 2000). Local soil and saprolite brought upwards (autochthonous) by moundmakers becomes new soil material upon mound erosion and local (parautochthonous) re-deposition (Bruand and Reatto, 2022; Bruand et al., 2022; Heimsath et al., 2020; Johnson, 2002; Miklós, 1992; Nye, 1955; Schaefer, 2001; Van Thuyne and Verrecchia, 2021).

The properties of the mound debris determine the properties of the future topsoil, which in turn will be buried by the next generation of mound debris and so forth; at the same time, surficial charcoal, organic matter, phytoliths, quartz grains, artefacts, etc., may be incorporated into the morphologically rejuvenated topsoil. In Section 2.1, we have pointed to the presence of soil horizons, charcoal layers, meaningful  $\delta^{13}\text{C}$  and phytolith records of paleoenvironments, plausible chronostratigraphies, and artefact horizons along vertical sections of TYRE. Based on these findings it appears that conveyor-belt bioturbation does not only unmix fine from coarse material (stone line) but causes a layering within the fine material. In terminology of Johnson et al. (1987), proanisotropic processes of bioturbation may outcompete proisotropic ones in the presence of mounds, as common for TYRE. Linguistically, the term bioturbation implies mixing/confusion by biota and common images display circular arrows that apparently indicate the (homogenous) mixing of fine material (Dixon et al., 2012; Johnson, 1993; Johnson et al., 2005a; Stockmann et al., 2011); this notion inspires diffuse mixing models (Furbish et al., 2018a; Furbish et al., 2018b; Furbish et al., 2018c; Gray et al., 2020). However, in the presence of mounding invertebrates, the term bioturbation may be misleading, as biosorting may prevail over biomixing.

### 2.2.1. Key role of termites and ants in TYRE evolution

Probably the best-known mound-building termites are fungus-growing species, which aim for an adequate microenvironment for food production; however, Australian and American termites do not follow this strategy. Size, shape, material, and architecture of termite mounds reflect various functions and adaptations to the local environment; mounds and their materials in turn modify the local soil properties (Holt and Lepage, 2000; Salvucci et al., 2023; Van Thuyne and Verrecchia, 2021). Less noticeable earth constructions by termites, yet with considerable volume, are sheetings (Jouquet et al., 2022). Contrary to termites, ants have received less attention as tropical ecosystem engineers (Nascimento et al., 2024; Schaefer et al., 2021; Viles et al., 2021); some species, e.g., of the genus *Atta*, build vast underground nests and deposit large amounts of highly erodible debris on the soil surface; these are considered the most relevant bioturbators in the Neotropics (Nascimento et al., 2024). There also exist ant species that construct mounds as nests (Viles et al., 2021) and termite species that create debris mounds (Martin et al., 2018). The ecosystem engineering by termites and ants, influencing physical (e.g., structure, permeability) and chemical properties (e.g. carbon, nutrients, clay minerals) of local soils and the extent of ecosystem self-organization is reviewed elsewhere (Black and Okwakol, 1997; Folgarait, 1998; Jouquet et al., 2006; Lavelle et al., 2016; Van Thuyne and Verrecchia, 2021).

While ants typically favor soil or soft saprolite as host substrate for their cave systems and rarely dig deeper than a few meters, at maximum ca. 8 m (Forti et al., 2018; Moreira et al., 2004; Nascimento et al., 2024), some fungus-growing termite species are known to search for moisture or appropriate mound construction material up to tens of meters deep within TRP, even below stone layers and laterite horizons (Holt and Lepage, 2000; Lepage et al., 1974; Van Thuyne and Verrecchia, 2021). In the humid tropics, termites may seek for kaolinite in deeper levels of the TRP, trying to avoid TYRE dominated by gibbsite. Kaolinite enrichment in upper horizons of thick gibbsitic TYRE is commonly explained by biogeochemical processes, i.e., silica pumping by vegetation (Kleber et al., 2007; Lucas et al., 1993). Yet, termites also increase silica contents in the topsoil, likely by selecting their preferred building material at depth (Bruand and Reatto, 2022; Jouquet et al., 2020).

Deep dwelling biota and roots mutually enhance the permeability of

regolith, facilitating the weathering at depth, leading to a further deepening of the weathering front; therefore, bioturbation and weathering are tightly interlinked processes (Schaefer and Oliveira, 2022). In contrast, the common biomantle model suggests that in deep regolith profiles, weathering fronts advance rather independent of the biomantle, which apparently terminates below the stone line (Johnson, 1990; Johnson, 1993; Johnson et al., 2005b; Phillips et al., 2019).

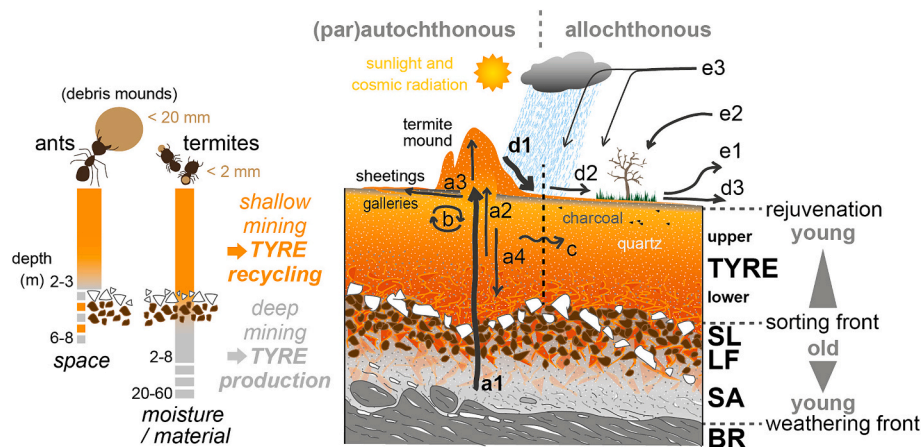
### 2.2.2. The influence of earthworms and roots

Earthworms are key bioturbators in the temperate zone, but in the tropics outnumbered by termites and ants (Barros et al., 2006). Earthworms can be grouped into three main ecological categories (Bouché, 1972; Bouché, 1977; Lavelle et al., 2007): anecic (litter-feeding, casting deep dwellers), endogeic (geophagous, eating through the upper decimeters of soil and casting), and epigeic (living in the organic layers on the soil surface, therefore not relevant for TYRE production). Available mounding rates in the tropics may even exceed those of termites and ants but are usually from endogeic species (Kollmannsperger, 1956; Nooren et al., 1995; Nye, 1955; Paton et al., 2000; Roose, 1981). These are vital for the improvement of biochemical and physical soil properties and influence the distribution of charcoal and luminescence dosimeters, but of minor relevance for deep TYRE production. Anecic earthworms perform conveyor-belt bioturbation and dominate in the temperate zone, where they can be found several meters deep. In the tropics, anecics only make up a small proportion (Lavelle, 1983) and mainly strive in the upper decimeters, recreating topsoil (Bottinelli et al., 2021; Jiménez and Decaëns, 2000; Jouquet et al., 2008; Kale and Karmegam, 2010). Yet, a key problem in recognizing the influence of earthworms on deep TYRE is the limited sampling depth in soil ecological studies. Reports from Brazil mainly obtained by the late G. Righi indicate numerous known and potentially unknown earthworms or their traces in several meters of depth (Barros et al., 2006; James and Brown, 2006) and once reliable data are available, earthworms may be included in advanced models of TYRE formation.

The wide-held perception of deep infertile tropical soils may lead to the false assumption that tree roots are rather shallow, but they can reach >5–10 m deep (Canadell et al., 1996). They may reach deeper in climate with stronger seasonal precipitation contrast, but the number of samples with sufficient depth is too limited for detailed statements (Pierret et al., 2016). Despite its relevance in the temperate zone, there are only few records of soil uprooting due to treefall from the tropics (Šamonil et al., 2010), indicating a very limited (or unknown) influence of treefall to TYRE formation. Reported pit depths reach from few decimeters, following a hurricane in Puerto Rico (Lenart et al., 2010), to <1.4 m (with an overall low treefall density) in Panama (Putz, 1983). Tropical rainforest soil uprooting in Papua New Guinea affected shallow soils (Šamonil et al., 2023). Overall, available local findings can hardly be transferred to the model of TYRE evolution. While near-surface biomechanical influence of tree roots is limited, they still contribute along with biota to increasing the permeability of regolith, thereby supporting chemical weathering at depth (Schaefer and Oliveira, 2022). Schaefer (2001) suggests a common evolution of termites and Angiosperm roots leading to deep TRP formation since the Late Cretaceous.

## 2.3. Assessing processes and rates of TYRE formation

Our conceptual model of physical processes essential for TYRE formation (Fig. 2) integrates autochthonous and allochthonous particle transfers. For plateau and upper slope TYRE in the (semi-)humid tropics the autochthonous and mutually connected processes of weathering and bioturbation are the key processes in TYRE formation (Heimsath et al., 2020; Johnson et al., 2005b; Kristensen et al., 2015). In foot slope and valley positions or close to (paleo)deserts, allochthonous contributions (colluvial, eolian) are possible or may even dominate, but these are not necessarily prerequisite for TYRE formation and require rigorous scientific evidence.



**Fig. 2.** Conceptual model of TYRE formation in the presence of termites and ants (details and references in the text). Key process is the upward transfer of deeply mined saprolite (a1) or shallowly mined TYRE (a2) material for (near)-surface constructions (a3), with some loss in biochannels (a4). While shallow mining means TYRE recycling, deep mining results in TYRE production. Termites may search moisture or specific building material even in the presence of laterite, whereas ants dig caves in TYRE and soft saprolite. Diffusive bioturbation (b) mainly takes place in the upper decimeters of TYRE but appears unable to completely destroy a certain stratigraphic integrity within the upper parts of TYRE. On millennial timescales, soil creep (c) blurs the boundary between (par)autochthonous and allochthonous. Mound erosion (d1) delivers particles back to the soil surface, with maximum likelihood for exposure to sunlight and cosmic radiation, relevant for various geochronometric techniques. Surficial reworking (d2) or erosion by water (d3) or wind (e1) occur primarily in mountainous and (semi-)arid regions. Regional eolian deposition (e2) can occur close to deserts but is different from far-travelled dust input by wet or dry deposition (e3). The youngest weathering products are found close to the weathering front, whereas young luminescence ages in TYRE are due to recent exposure of datable minerals to sunlight (morphological rejuvenation). Field observations show that upper TYRE is usually more porous than lower TYRE (details in Section 4.1). SL: stone line, LF: laterite/ferricrete, SA: saprolite, BR: bedrock.

In the absence of allochthonous (eolian, colluvial) additions, TYRE develops exclusively in situ from weathered rock, supported by ecosystem engineers (Heimsath et al., 2020; Nye, 1955). We emphasize that the shallow mining of TYRE by moundmakers does not induce net growth of TYRE but rather represents a recycling process (Fig. 2). Termite and ant mounds contain variable contributions of saprolite (Jouquet et al., 2002; Nascimento et al., 2024; Van Thuyne and Verrecchia, 2021). Saprolite forms almost continuously at depth within the (semi-)humid tropics, whereas in arid environments, chemical weathering is limited to absent (Schaller and Ehlers, 2022). If the rates of upward biotransfer are known, the proportion of deeply mined saprolite to mined soil theoretically determines TYRE production rates. The latter equal rates of upward biotransfer when exclusively saprolite is mined, which is the case when TYRE is too shallow or of insufficient quality for earth constructions.

Rates of weathering and upward biotransfer are the essential parameters to quantify TYRE production (data compilation including all references in supplementary information 2A and 2B, respectively). Rates of rock to saprolite and soil conversion are determined from geochemical budgets within TRP and throughout river catchments (Braun et al., 2012; Hewawasam et al., 2013), by U-series disequilibrium calculations (Chabaux et al., 2013), and by terrestrial cosmogenic nuclides (Heimsath et al., 2020). Rates of upward biotransfer are obtained in various ways and commonly reported as mounding rates of particular species (Bétard, 2021; de Bruyn and Conacher, 1990). Age-depth profiles of TYRE based on  $^{14}\text{C}_{\text{char}}$  or OSL ages (supplementary information 2C) are long-term ecosystem integrals of soil upbuilding, though rarely applied (Boulet et al., 1995; Kristensen et al., 2015). Unlike charcoal, quartz is almost ubiquitously present in TYRE, therefore OSL dating has a high potential to determine rates of soil reworking (Johnson et al., 2014; Kristensen et al., 2015).

In recent years there have been fundamental advances in the application of geochronological techniques to quantify bioturbation (Bateman et al., 2007; Gray et al., 2020; Hanson et al., 2015; Heimsath et al., 2002; Madsen et al., 2011; Reimann et al., 2017; Rink et al., 2013; Román-Sánchez et al., 2019; Stockmann et al., 2013; von Suchodoletz et al., 2023; Wallinga et al., 2019), but very few results are available from TYRE (Johnson et al., 2014; Kristensen et al., 2015). As for the

large majority of studies that quantify bioturbation, OSL ages from semi-arid NE Australia (AUS) were interpreted as resulting from diffusional bioturbation (Johnson et al., 2014). In these cases, advection of particles is merely the soil production vector (Furbish et al., 2018a; Furbish et al., 2018b; Gray et al., 2020; Wallinga et al., 2019) and not related to dominating upward biotransfer. Yet, the widespread presence of termites at the AUS site (Coventry et al., 1988; Johnson et al., 2014) suggests primarily conveyor-belt bioturbation, as known for tidal flat lugworms (Madsen et al., 2011), anecic earthworms (Dreibrodt et al., 2022; Dreibrodt et al., 2023), and termites (Kristensen et al., 2015). The latter study from a profile close to a termite mound in semi-humid S Ghana (GHA) is particularly relevant, as it systematically compared data of single- and multi-grain OSL dating (Kristensen et al., 2015). Both tested approaches reveal a systematic increase in OSL ages with depth, consistent with the model of conveyor-belt bioturbation. This implies a constant deposition of soil material at the surface, where daylight exposure leads to the resetting of the luminescence signal, which builds up after burial (Kristensen et al., 2015).

### 3. Materials and Methods

#### 3.1. Optically stimulated luminescence (OSL) and charcoal radiocarbon ( $^{14}\text{C}_{\text{char}}$ ) ages

New chronometric data were obtained from six TYRE profiles from three different regions (1) on the S Cameroon plateau (profiles AK-Y, AK-R), (2) the Cerrado region in SE Brazil (PI-Y, PI-R), and (3) the Amazon (MA-Y, MA-R). Age information is based on quartz OSL dating and  $^{14}\text{C}_{\text{char}}$  data (coordinates, data and ages in supplementary information 2D).

OSL dating was carried out on small multi-grain aliquots (few  $10^1$  grains or few  $10^2$  grains) of quartz coarse grains (125–212  $\mu\text{m}$  or 180–250  $\mu\text{m}$ ) applying a single aliquot regenerative dose (SAR) protocol (Murray and Wintle, 2000; Murray and Wintle, 2003) with parameters adapted to the different study sites (for details, see supplementary information 1B).

Sample preparation was done under subdued red light using standard procedures including wet sieving, chemical pretreatments, density

separation, etching of the quartz extracts in hydrofluoric acid, followed by sieving. Measurements of aliquots mounted on metal discs, using silicon oil as adhesive, were performed on Risø TL/OSL readers.  $D_e$  calculation was performed with the software ‘Analyst’ (Duller, 2015) applying a single exponential fit for dose response curve construction. The central age model (CAM) (Galbraith et al., 1999), revised by Roberts et al. (Roberts et al., 2000), was used for burial dose estimation.

Dose rate measurements are based on low level gamma spectrometry. Element concentrations were converted to dose rates using the conversion factors of Guérin et al. (2011). The water content was assessed from the field samples, and the contribution of the cosmic dose rate was calculated according to Prescott and Hutton (1994).

Charcoal pieces for  $^{14}\text{C}_{\text{char}}$  dating were taken from charcoal layers or horizons with several charcoal pieces, excluding the presence of burned roots. Charcoal cleaning was done according to standard procedures in the Poznan Radiocarbon Laboratory and the Laboratory for the Analysis of Radiocarbon (LARA) at the University of Bern (details in supplementary information 1A). All  $^{14}\text{C}_{\text{char}}$  ages, including those compiled from the literature (Boulet et al., 1995; Bremond et al., 2017; Calegari et al., 2013; Desjardins et al., 2020; Gouveia and Pessenda, 2000; Hill et al., 2023), were (re)calibrated with Calib Rev. 8.1.0 (Stuiver and Reimer, 1993) using the Mixed NoHem SoHem calibration curve SHCal20 (Hogg et al., 2020) and plotted as median probability.

Our geochronological dataset (see supplementary information 2C) is complemented by OSL ages from GHA (Kristensen et al., 2015) and AUS (Johnson et al., 2014). We did not integrate luminescence ages from yellow to red tropical eolian, alluvial or colluvial deposits (e.g., Alappat et al., 2013; Perez Filho et al., 2022; Perez Filho et al., 2021; Sallun and Suguio, 2010; Sanderson et al., 2001; Singhvi et al., 1986; Storani and Perez Filho, 2015; Thomas and Murray, 2001; Zhang et al., 2019; Zhang et al., 2008; Zheng et al., 2021; Zöller, 2000). Yet, an unknown number of dated sites may contain bioturbated TYRE (Sanderson et al., 2001), especially those with quasi-continuous luminescence chronologies along vertical profiles. To reveal gaps of information as transparently as possible, we present the data in Figs. 3 and 4 in the original form and refrain from further statistical processing of ages (e.g., age-depth

models), as not to overinterpret the heterogeneous data.

### 3.2. Mounding rates

Published compilations of termite and ant mounding rates (Bétard, 2021; de Bruyn and Conacher, 1990; Paton et al., 2000; Viles et al., 2021) were combined into a unified database, cross-checked and complemented by more recent references (see supplementary information 2B). To harmonize the different data sets, all primary references were re-evaluated; all rates that are unclear or from artificial settings (e.g., laboratory-based, intermittent removal of mounds) were listed separately and excluded from Fig. 5. Rates of TYRE upbuilding derived from age-depth functions based on  $^{14}\text{C}_{\text{char}}$  and OSL dating are considered in our geochronological dataset (supplementary information 2C) and are therefore not included in the mounding rate database.

Publications date back to 1955, and methods to determine and report mounding rates as well as spatial scales and species differ considerably (Lobry de Bruyn and Conacher, 1990). For ants, there exist several reports on the extent of earth moved locally, given partly per time or per area (Nascimento et al., 2024), but to our knowledge there exists only one rate expressed as mass per time (Bucher and Zuccardi, 1967). Termite bioturbation rates are more common in literature; studies either report rates of material uptake, mound erosion, average soil upbuilding rates or use other terms that are provided in the database. Two studies from North Australia take into account soil erosion when reporting soil upbuilding (Lee and Wood, 1971; Williams, 1968), therefore we have selected the values independent of erosion, to be consistent with the other rates from the database. Most rates are reported from single species, but sometimes up to three species contribute to the rate provided as final estimate. Studies mainly report rates in  $\text{t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  or in  $\text{mm}\cdot\text{a}^{-1}$ , when referring to soil thickness, or use other measurement units. We use a soil density factor of  $1.2\text{ g}\cdot\text{m}^{-2}$  to calculate soil thickness equivalents from data reported in weight per area but keep the established term mounding rates (Van Thuyne and Verrecchia, 2021; Viles et al., 2021). To allow comparison to weathering rates (Fig. 5), we use  $\text{mm}\cdot\text{ka}^{-1}$  and the inverse  $\text{ka}\cdot\text{m}^{-1}$  scale.

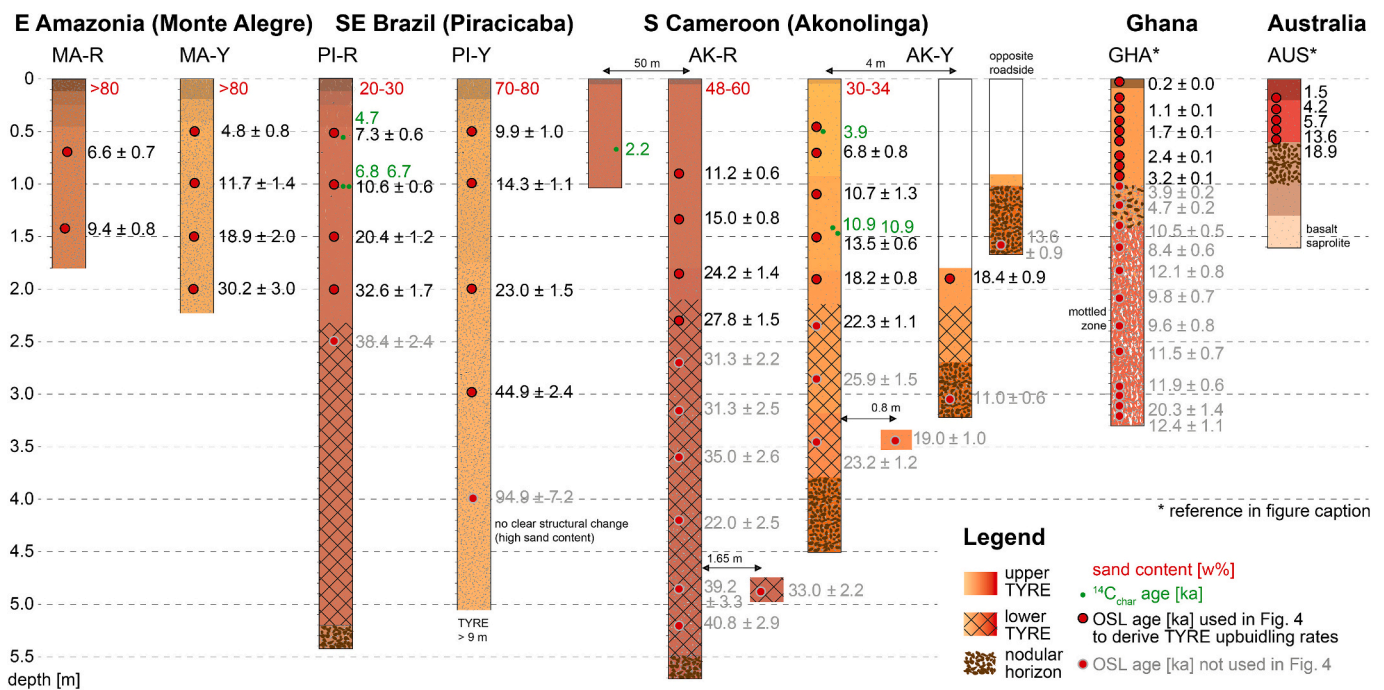


Fig. 3. Numerical ages and main morphological features of TYRE. Six sites studied by us in comparison to sites in Ghana (GHA) (Kristensen et al., 2015) and Australia (AUS) (Johnson et al., 2014; Pillans, 1997). Ages in black represent the last cycle of reworking and are used in Fig. 4 to derive rates of TYRE upbuilding; ages in gray reflect mixed OSL signals from lower TYRE, unsuitable for this approach. Data in supplementary information 2C and 2D.

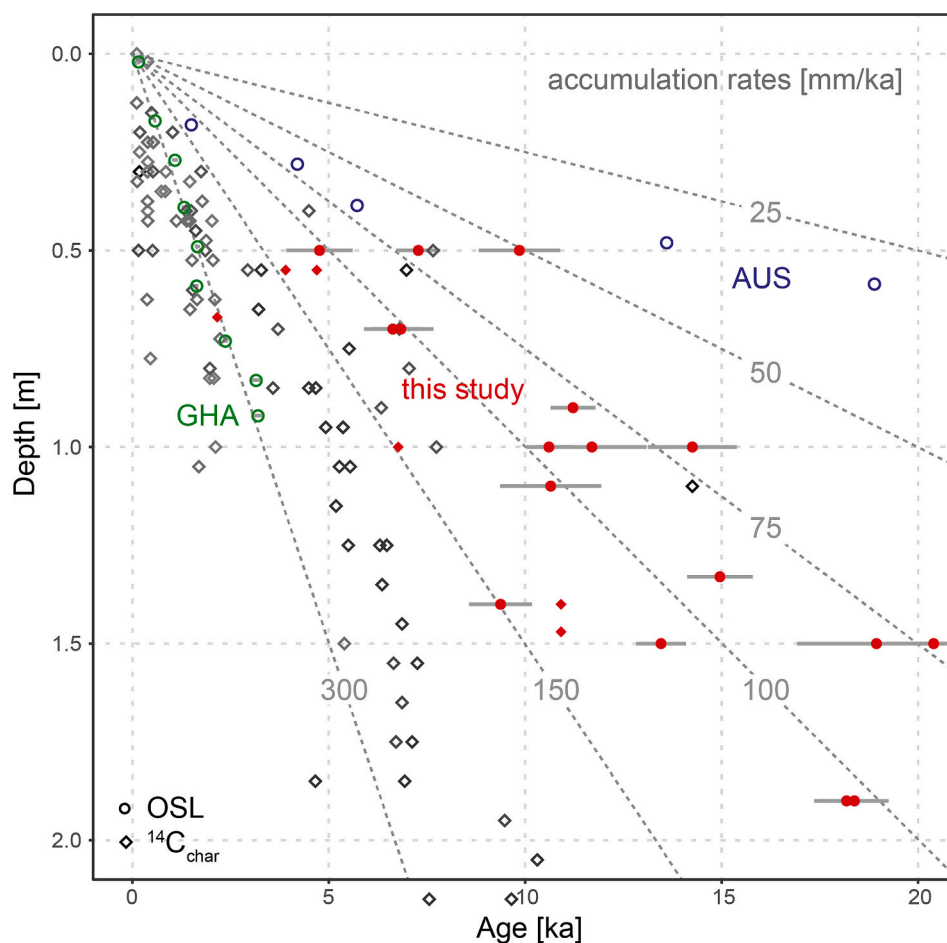


Fig. 4. Rates of TYRE upbuilding derived from age-depth profiles (upper 2 m). OSL ages from Ghana (GHA) (Kristensen et al., 2015) and Australia (AUS) (Johnson et al., 2014), and  $^{14}\text{C}_{\text{char}}$  ages from different studies in Africa and South America (all: greyscale open symbols) compared to data from this study (closed symbols). Details in text, all data are presented in supplementary information 2C.

The available studies publish one or several single rates or ranges. The termite global median is calculated from all single rates and the means of the ranges. As the inherent heterogeneity of the various types of information does not allow meaningful statistical data processing, the relevant data are graphically displayed in Fig. 5. All rates are presented with further information in the supplementary information 2B.

### 3.3. Weathering rates

A compilation of weathering rates by Stockmann et al. (2014) extends the database of Montgomery (2007); yet, both studies provide limited additional information. After initial removal of non-tropical data and adding more recent studies, individual checks were performed based on the primary references (see supplementary information 2A). Rates from high mountains and tectonically active regions, easily weatherable parent material (e.g., volcanic ash, limestone), and rates where original information was unclear or not available were listed separately in the data table and not included in Fig. 5.

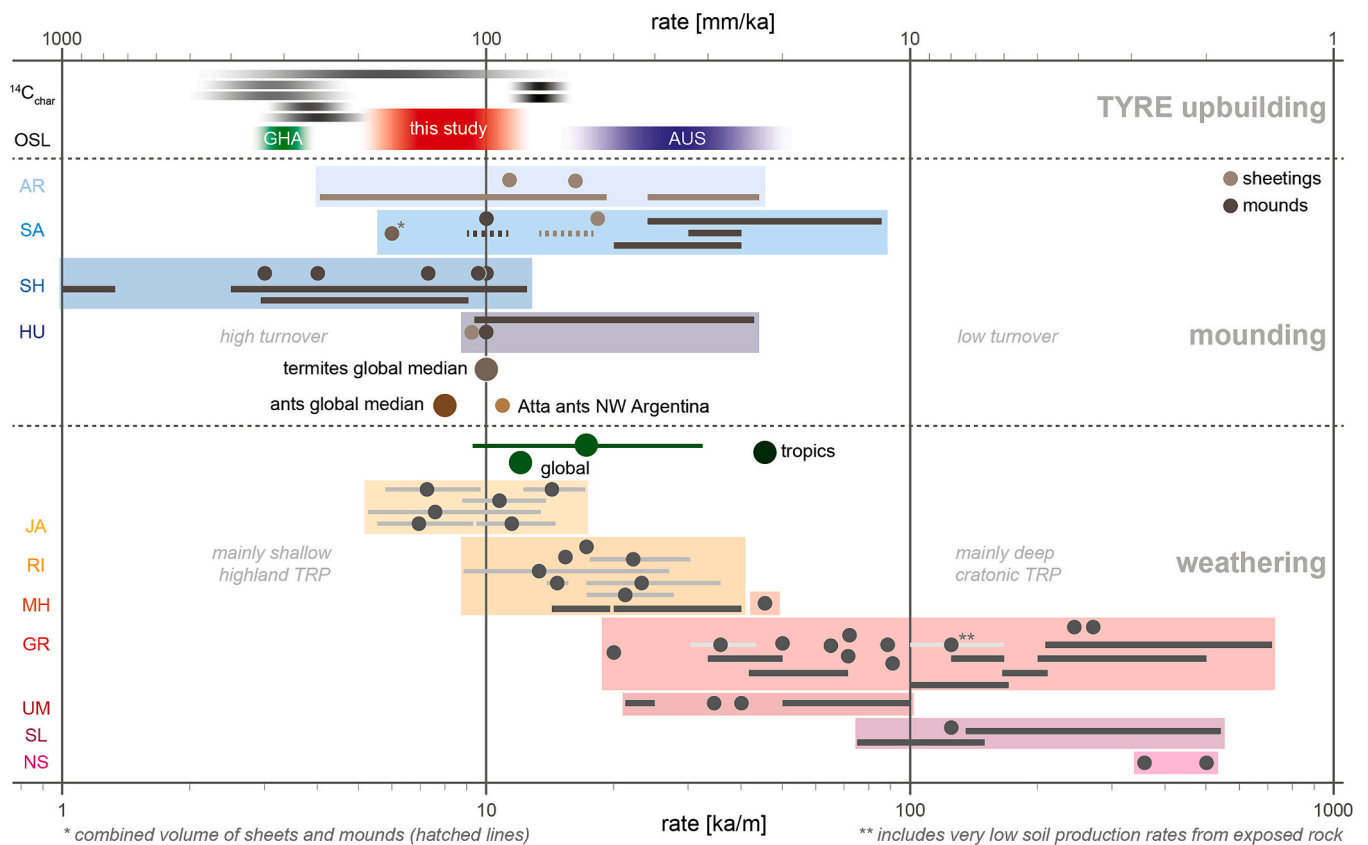
Publications date back to 1968 and spatial scales as well as methods to determine weathering rates and methods of reporting differ considerably. The majority of studies addresses silicate rich crystalline rocks from undulating to hilly catchments or localities. Studies that report (catchment) denudation rates but no weathering rates were excluded as steady-state soil thickness cannot be taken for granted (Phillips, 2010; Yu and Hunt, 2017). In Fig. 5, rates from specific study regions (critical zone observatories, mountainous highlands of Mexico) and from more easily weatherable ultramafic rocks of New Caledonia (e.g., Trescases,

1975) were grouped into separate categories. Most studies report weathering rates as depth per time period (mainly  $\text{mm}\cdot\text{ka}^{-1}$ ), whereas rates from Mexico (Riebe et al., 2004) and Sri Lanka (Hewawasam et al., 2013) are reported in weight per area per time period ( $\text{t}\cdot\text{km}^{-2}\cdot\text{a}^{-1}$ ), assuming a density conversion factor of  $2.7\text{ g}\cdot\text{cm}^{-3}$  (rock) and  $1.2\text{ g}\cdot\text{cm}^{-3}$  (soil), respectively. In soil erosion research, the unit  $\text{t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  is commonly used to quantify soil loss, however,  $\text{mm}\cdot\text{ka}^{-1}$  has a clear relation to soil depths. Agronomists concerned about the time required to form 1 m of soil may find the inverse unit  $\text{ka}\cdot\text{m}^{-1}$  useful, as used in the compilation by Nahon (1991); therefore this scale is added to Fig. 5. Due to the heterogeneous methods applied and the differing presentation of the results (units, numbers with and without errors or value ranges), meaningful statistical processing is hardly possible. Fig. 5 visualizes the original data for general comparison and to reveal the gaps of existing knowledge. All rates, including references and additional information, are provided in the supplementary information 2A.

## 4. Data and discussion

### 4.1. TYRE morphologies and age-depth profiles

Six TYRE age-depth profiles in three differing tropical landscapes investigated in our study are complemented by data from GHA (Kristensen et al., 2015) and AUS (Johnson et al., 2014; Pillans, 1997) as presented in Fig. 3. AK-R and AK-Y are located close to Akonolinga in semi-deciduous rainforest on the undulating S Cameroon plateau, made up of metamorphic rocks of the Panafrican orogeny (ca. 600 Ma). TYRE



**Fig. 5.** Rates of TYRE upbuilding as determined from age-depth profiles reflected against rates of mounding and weathering. Compilation based on literature and own data (for locations see Fig. 1). Age-depth profiles using OS� and  $^{14}\text{C}_{\text{char}}$  data are interpreted as ecosystem-integrals of soil upbuilding rates (colors and extents of vertical bars are based on Fig. 4). Termite mounding rates are differentiated by precipitation regime (AR: arid, SA: semi-arid, SH: semi-humid, HU: humid) and construction type (sheetings and mounds). Weathering rates are usually from TRP and/or catchments dominated by granite and comparable rocks (GR). Separated are weathering rates from easily weatherable ultramafic rocks (UM) from Sri Lanka (SL) (Hewawasam et al., 2013), from the Nsimi CZO (S Cameroon; NS), the Mule Hole CZO (S India; MH) (Braun et al., 2012), the Rio Icaos CZO (Puerto Rico; RI). The latter is considered as catchment with highest documented rates of weathering in the tropics. Data from the Jalisco region (W Mexico; JA) (Riebe et al., 2004) represent a semi-humid subtropical highland with equally high rates of regolith formation. Data and details are presented in supplementary information 2A and 2B.

at site AK-Y is a 3.5 m thick yellowish-brown clay (loam) and at site AK-R a 4.5 m thick red sandy loam; at the bottom of both profiles, there are nodular and quartzite stone lines forming the upper part of >1 m thick nodular laterite (pisoplinthite). TYRE at both sites has a mainly (micro) granular to subpolyhedral structure in the upper 2.0–2.5 m (upper TYRE), while the structure below is denser, with an increase of the coarse fraction (mainly quartz and Fe-Mn nodules; lower TYRE).

PI-R and PI-Y are close to Piracicaba in the transition zone of Cerrado (savanna) to Atlantic rainforest in the Peripheral Depression of Sao Paulo state, Brazil. Local Paleozoic to Mesozoic claystones and sandstones are in places intruded by Jurassic to Cretaceous diabase sills and dykes. TYRE at PI-R is a 5.2 m thick red clay loam, with a transition from a granular upper to a denser lower TYRE at ca. 2.5 m depth, whereas the 5 m deep profile at PI-Y is a homogeneous sandy loam, with no clear lower boundary of the upper TYRE.

The E Amazonian sites MA-R and MA-Y are located near the city of Monte Alegre in an edaphically controlled savanna of unknown age on Late Cretaceous sedimentary rocks (mainly sandstone). TYRES at MA-Y and MA-R consist of >1.5 m thick loamy sand of yellowish to reddish brown color (no lower TYRE exposed).

Despite the different geological contexts, OS� ages from the six study sites cover a similar age range from the Late Pleistocene to the Holocene (Fig. 3; data and further details in supplementary information 2D and 1B, respectively). All ages are in stratigraphic order, except for numeric age plateaus below 2.0–2.5 m in the S Cameroon profiles, which largely coincide with the change from upper to lower TYRE. The oldest age at

PI-R is from the top of the denser lower TYRE, with luminescence signals close to saturation. This was also the case for the lowermost sample of PI-Y, where no major structural change was observed. For the MA profiles, neither OS� ages nor soil structure point to a distinction into upper and lower TYRE.  $^{14}\text{C}_{\text{char}}$  ages from PI-R, AK-Y, and close to AK-R give somewhat younger ages with respect to their stratigraphic positions (supplementary information 2C, along with TYRE chronologies from literature). While the age-depth trends consistently confirm biosorting, we assume a 1.5 to 2 times overestimation of the OS� ages, likely due to the presence of “old” grains that were not exposed to sunlight during the last conveyor-belt cycle and/or mound erosion cycle, a phenomenon investigated in detail by Rink et al. (2013) and Kristensen et al. (2015) (Fig. 3).

The 0.7 m thick TYRE in semi-arid NE Australia (AUS) studied by Johnson et al. (2014) exhibits a constant, steep increase of OS� ages (up to 21 ka) with depth. At GHA, we interpret a marked increase in mottles and gravel below 1.0 m (Kristensen et al., 2015) as boundary between TYRE and mottled saprolite. In the gravel-free TYRE, ages constantly increase with depth from few hundred years up to 3–5 ka; below, there is no general trend and ages are artefacts of few “young” grains (OS� signal reset at the land surface) fall into biogalleries of the mottled zone (Figs. 3 and 4) (Kristensen et al., 2015).

Quasi-constant age increases with depth in individual profiles of upper TYRE indicate the absence of discrete phases of sedimentation. In all three study regions there is little synchronicity in the individual ages obtained from different profiles. Such a phenomenon is also visible in



some luminescence age compilations of tropical colluvial, alluvial, or eolian archives (Alappat et al., 2013; Perez Filho et al., 2022; Sallun and Suguio, 2010; Zheng et al., 2021). We have no field observations to doubt or confirm the respective geomorphological interpretations, but a quasi-constant reworking of near-surface material evidenced and dated by luminescence ages would require a nearly-continuously open landscape with little vegetation, different from today. Due to the upper relief positions of our records, colluviation would be less likely than eolian deposition. However, discrete pulses of sedimentation, especially if these are eolian, require major dry paleoenvironments, which appears unlikely in the given time frame, especially in the absence of intra-profile chronological synchronicity.

Increasing ages with depth in TYRE suggest a quasi-continuous structural rejuvenation, as typical for settings reworked by mounding invertebrates (see Section 2.2). We consider variations in mounding rates due to paleoecological changes possible but are unable to resolve these with the available data. There is a high potential for future high-resolution geochronological approaches, possibly involving luminescence screening approaches (May et al., 2018; Pfaffner et al., 2024; Sanderson and Murphy, 2010; Schulze et al., 2022; Schwahn et al., 2023).

Age plateaus and even inversions characterize the lower TYRE and underlying units and can be interpreted as artefacts resulting from an unknown share of “young” datable and too “old” grains (not-datable or saturated) (Kristensen et al., 2015; Rink et al., 2013). While OSL ages cannot resolve lower TYRE formation, OSL ages of the upper TYRE likely represent the last cycle of  $10^5$ – $10^6$  years of biomechanical reworking of long-term weathering products. Diffusional mixing is expected to be strongest close to the soil surface but frequently intact subsoil horizons and consistent vertical variations of paleoenvironmental proxies (see section 2) indicate that layering due to mounding invertebrates may outcompete diffuse mixing (Kristensen et al., 2015).

Implications for further pedological differentiation are beyond the aims and scope of this work, offering potential for future investigations. Yet, from our observations, it appears that deeper in TYRE there is more time and quiescence for the development and preservation of pedofeatures (e.g., clay coatings, iron-nodules; Eswaran et al., 1992) and structural changes, depending on the soil type in relation to local (paleo) environments and geology.

To give one example: dark humic subsoil horizons without lithic discontinuity in the (sub)tropics were initially explained by humus illuviation (Sys, 1960); however, such so-called sombric horizons (Almeida et al., 2015; IUSS Working Group WRB, 2022) rarely exhibit humus illuviation features, for example those recently studied in detail in SE Brazil (Chiapini et al., 2021; Chiapini et al., 2018). Mineralization of the upper part of a thick steppe soil under subsequent forest is one theory for the presence of a dark humic subsoil horizon (Caner et al., 2003), which implicitly excludes bioturbation. In the presence of mounds, the burial of a former (steppe) topsoil by local soil material mined at depth (Marques et al., 2011) appears to be a more likely explanation. This interpretation is supported by the omnipresence of bioturbation features in these soils (Chiapini et al., 2018). A comparable influence of autochthonous biogenic layering may be inferred for other types of TYRE subsoil horizons not formed by illuviation. In the presence of deep mining mounds, TYRE horizonation (or layering) is not necessarily in contradiction to bioturbation processes; just the term bioturbation itself appears misleading (see Section 2.2).

A combined effect of clay translocation and bioturbation in creating texture contrast soils was asserted for the temperate zone (Phillips, 2007), and is likely transferable to TYRE. Reduced porosity combined with an increasing length of rest time for soil formation appears to enhance the tendency towards redoximorphism in lower TYRE, as observed during fieldwork.

The oldest, not relocated weathering products of TRP can be expected directly below the stone-line, where laterite or ferricrete may occur, depending on local factors. Further down the TRP, until the

weathering front (Phillips et al., 2019), the ages of minerals formed by weathering decrease again (Fig. 2).

In this context, we suggest that deep bioturbation features in TYRE (Chiapini et al., 2023) can indicate deep reaching bioturbation but may also be due to thick burial of bioturbated units in the presence of deep mining mounds. Process vectors and mining depths of bioturbators strongly vary (Johnson et al., 2005b), which most likely influences the vertical differentiation of TYRE. The contributions of different bioturbators may have changed through time, with varying paleoenvironments, further discussed in Section 4.3.

#### 4.2. Rates of TYRE upbuilding, mounding and weathering

Where the conveyor-belt model applies, OSL and  $^{14}\text{C}_{\text{char}}$  age-depth profiles (Fig. 4) reflect rates of TYRE upbuilding (Boulet et al., 1995; Kristensen et al., 2015). These rates integrate the work of all mound-makers irrespective of particle origin, assuming soil loss by erosion is negligible in the presence of a closed vegetation cover. OSL based TYRE upbuilding at GHA with rates of ca.  $280 \text{ mm} \cdot \text{ka}^{-1}$  is related to the onset of deforestation ca. 4 ka ago, leading to the formation of a savanna with large termite mounds (Kristensen et al., 2015).  $^{14}\text{C}_{\text{char}}$  age-depth profiles in S Central ( $210$ – $230 \text{ mm} \cdot \text{ka}^{-1}$ ) and SE Brazil ( $210$ – $340 \text{ mm} \cdot \text{ka}^{-1}$ ) indicate comparable orders of magnitude (Boulet et al., 1995; Miklós, 2012). Charcoal ages from Central African TYRE (Bremond et al., 2017; Desjardins et al., 2020) point to the combined effect of bioturbation in the topsoil and biosorting throughout the profiles, with TYRE upbuilding rates of similar orders of magnitude as for Brazil and GHA. A much lower rate of TYRE upbuilding in the order of ca.  $50 \text{ mm} \cdot \text{ka}^{-1}$  is available from semi-arid AUS, when interpreting the OSL ages (Johnson et al., 2014) as representing conveyor-belt bioturbation. Our OSL age-depth relations from three humid tropical landscapes range in between those of AUS and GHA, suggesting bioturbation rates of ca.  $100 \text{ mm} \cdot \text{ka}^{-1}$ . Considering possible overestimations of the OSL ages indicated by available  $^{14}\text{C}_{\text{char}}$  ages, approximated rates of  $100$ – $200 \text{ mm} \cdot \text{ka}^{-1}$  appear as the most realistic scenario (Fig. 5).

The database of termite and ant mounding rates (Fig. 5, supplementary information 2B) is an update of previous compilations (de Bruyn and Conacher, 1990; Paton et al., 2000). The evaluation of the primary references from the last seven decades reveals diverse conceptual approaches, measuring techniques, and terminology. Rates of upward biotransfer span generally two orders of magnitude; mostly they are around  $20$ – $300 \text{ mm} \cdot \text{ka}^{-1}$  with a median rate of  $100 \text{ mm} \cdot \text{ka}^{-1}$ . Most data are available from semi-arid to semi-humid regions, where termites construct impressive termitaria. There is a trend to highest bioturbation rates in the semi-humid savanna. However, within rainforests, termites are equally abundant, but constructions are less prominent and studies are scarce (Eggleton et al., 1996; Hulugalle and Ndi, 1993; Maldague, 1964).

There exist a number of reports describing ants as widespread and powerful bioturbators in the tropics, especially leaf-cutter ants (genus: *Atta*) in Central and South America (Alvarado et al., 1981; Branner, 1896; Branner, 1910; Branner and Reid, 1900; Moutinho et al., 2003; Nascimento et al., 2024; Schaefer et al., 2021), but only a single estimate of soil turnover from N Argentina ( $73 \text{ mm} \cdot \text{ka}^{-1}$ ) by *Atta* ants (Bucher and Zuccardi, 1967). This figure appears small in relation to semi-quantitative reports of immense soil turnover by *Atta* ants in the Neotropics, exceeding the regional influence of termites (Nascimento et al., 2024). The global median of ant bioturbation is estimated to  $125 \text{ mm} \cdot \text{ka}^{-1}$  (Viles et al., 2021). Earthworms may be 1–2 orders of magnitude more productive than ants and termites (Bottinelli et al., 2021), but available reports from the tropics give a likely flawed impression that their work is largely restricted to the upper decimeters of soil (see Section 2.2.2) (Lavelle, 1978; Paton et al., 2000). The rates of TYRE upbuilding derived from  $^{14}\text{C}_{\text{char}}$  and OSL data in the present study ( $80$ – $150 \text{ mm} \cdot \text{ka}^{-1}$ ) are in the range of published species-related mounding rates ( $20$ – $200 \text{ mm} \cdot \text{ka}^{-1}$ ), yet other bioturbators also

contribute to TYRE evolution.

Published rates of tropical weathering, i.e., conversion of bedrock to soil or saprolite, span three orders of magnitude ( $2\text{--}100\text{ mm}\cdot\text{ka}^{-1}$ ; Fig. 5, supplementary information 2A). As for mounding rates, approaches to determine and report weathering or soil production rates and terminology differ between studies; rock type and TRP depth strongly influence the weathering rates. Deep tropical soil production from granitic rock takes place at a comparably low speed ( $2\text{--}20\text{ mm}\cdot\text{ka}^{-1}$ ), which may seem counter-intuitive, given the widespread notion of tropics as most intensive weathering environments. However, weathering is mainly related to available moisture and time; the latter is far more relevant in the tropics than a higher temperature in comparison to mid and high latitudes (Pope, 2013; Pope et al., 1995). Furthermore, published weathering rates are not corrected for profile depth, which is crucial here: once a certain depth of regolith is produced, weathering intensity strongly decreases with depth due to less atmospheric and biological influence (Humphreys and Wilkinson, 2007; Wilkinson and Humphreys, 2005). Compilations of global weathering rates (Montgomery, 2007; Saunders and Young, 1983; Schaller and Ehlers, 2022; Stockmann et al., 2014) include a large proportion of shallow soils, partly from humid mountain environments with high denudation rates. The example of soil production rates of subtropical mountains in W Mexico (based on the assumed equilibrium with total denudation rates) (Riebe et al., 2004) (Fig. 5) agrees with global weathering estimates of  $80\text{--}120\text{ mm}\cdot\text{ka}^{-1}$  (Stockmann et al., 2014; Troeh et al., 1999). This is in the order of magnitude of termite and ant bioturbation, but an order of magnitude faster than weathering front advances in deep cratonic regolith profiles. In general it seems plausible to follow Paton et al. (2000), who posit that near surface processes are generally one order of magnitude faster than epimorphic (weathering) processes.

#### 4.3. TYRE evolution and human-environment interaction

The still widespread notion of intensive tropical weathering and the availability of thick TYRE along with ecosystem engineers speeding up TYRE (re)production may result in less care against soil erosion. However, it is crucial to note that TYRE production only equals rates of upward biotransfer, if exclusively saprolite is mined. Even under these highly optimistic boundary conditions, one meter of TYRE requires some ten thousand years to form, which is orders of magnitude slower than common soil erosion rates in agricultural land (Montgomery, 2007). Furthermore, a minimum of fine earth regolith is required for efficient soil (re)production with the help of mounding invertebrates, as these are unable to process bedrock (Humphreys and Wilkinson, 2007).

In tropical savanna regions, soil erosion may not directly expose bedrock, but laterite, which hardens upon exposure and limits plant growth and agricultural activity. The traditional Zaï soil restoration technique for degraded lateritic soils in semi-arid Burkina Faso makes use of the ability of termites to penetrate laterite and mine the saprolite underneath for mound construction (Kaiser et al., 2017; Mando and Miedema, 1997). In the model of TYRE production (Fig. 2), we highlight this key ability of termites to produce new soil from saprolite even in the presence of soil crusts (Beauvais, 2009; Schaefer et al., 2016). TYRE production is limited by the presence of saprolite to be mined and in (semi-)arid regions saprolites are largely relicts of weathering under more humid paleoclimate. Deep red soils in semi-arid regions of India, for instance, are mainly developing from Eocene to Miocene weathering relicts (Bronger et al., 2000), when the subcontinent was closer to the equator. Nowadays, saprolite formation in India is limited to the most humid southern regions of the subcontinent (Bonnet et al., 2016).

Long-term landscape evolution is an important element to explain local TRP and TYRE formation. An increasing number of techniques is applied to date specific components of well-developed TRP and to reveal complex weathering histories, e.g., based on Si isotopes of kaolinite (Guinoiseau et al., 2021).  $^{40}\text{Ar}/^{39}\text{Ar}$  and K-Ar dating of (K-)Mn oxides (Beauvais et al., 2016; Bonnet et al., 2014; Colin et al., 2005; Deng et al.,

2016; Feng and Vasconcelos, 2001; Spier et al., 2006; Vasconcelos et al., 1992; Vasconcelos and Carmo, 2018), (U-Th)/He dating of goethites (De Campos et al., 2023; Heim et al., 2006; Monteiro et al., 2014; Monteiro et al., 2018; Riffel et al., 2016; Shuster et al., 2005; Vasconcelos et al., 2019), both primarily found in laterite and ferricrete, as well as electron paramagnetic resonance (EPR) dating of kaolinite (Balan et al., 2005; Mathian et al., 2020) reveal, with few exceptions, ages in the range of  $10^6\text{--}10^7$  years. These ages are in line with the results of paleomagnetic measurements in laterites, suggesting their largely relict nature in semi-arid tropical landscapes (Schmidt et al., 1983; Théveniaut and Freyssinet, 1999).

Concentrations of  $^{10}\text{Be}$  in TYRE of Brazil and Central Africa point to several hundred thousand years of TYRE exposure and mixture (Braucher et al., 1998a; Braucher et al., 1998b). The unexpectedly good luminescence dating behavior of quartz from the studied TYRE profiles indicates multiple events of quartz bleaching and burial, indicating that OSL dates the last of an unknown number of cycles of TYRE reworking. For this reason, we can assume that a large part of TYRE is repeatedly recycled by mounds and not produced from deep mining.

For semi-arid NE Brazil, however, a stripping of TYRE during the dry last glacial maximum and a subsequent rebuilding by termites is suggested (de Freitas et al., 2021), a scenario possibly repeated during several glacial-interglacial cycles (Schaefer et al., 2023). Thus, a continuous TYRE above stone line configuration may not be true for (paleo)climatically and geomorphologically extreme regions. We do not preclude the presence of fine and coarse alluvial or colluvial materials in well-defined tropical landscape compartments (Hiruma et al., 2012; Kirchner et al., 2015; Modenesi-Gauttieri, 2000; Modenesi-Gauttieri and de Toledo, 1996; Nehren et al., 2016). Transitions between TYRE and colluvia are possible along slopes (de Melo and Cuchierato, 2004), where surficial particle transport of soil material exceeds (par-)autochthonous TYRE upbuilding. A continuum between eolian deposits and residual soils exists along climatic gradients (Sprafke, 2023).

However, yellow to red fine above coarse material close to rivers does not necessarily imply the presence of alluvial/eolian fines above fluvial gravel, but may also correspond to TYRE above stone line as part of a TRP in an ancient eroding landscape (Löffler and Kubiniok, 1996). Some tropical sedimentary deposits (colluvial, eolian, fluvial/alluvial) may require reevaluation in the future, to reliably reconstruct the influence of (past) morphodynamics on landscape and ecosystem evolution (Lira-Martins et al., 2022). Interpretations of age-depth profiles in assumed sedimentary records require at first a rigorous assessment of a possible bioturbation influence.

According to the model of TYRE evolution (Fig. 2), in the absence of allochthonous additions, the maximum mining depth over a considerable period of time determines TYRE thickness. This may be almost 10 m for PI-Y or even more for profiles in e.g., Minas Gerais (Marques et al., 2021). The structural and chronological transition at 2.5 m depth in the up to 5 m thick TYRE profiles in Cameroon (Fig. 3) may be explained by a differentiated depth of certain bioturbators and longer biomechanical quiescence in the lower TYRE. Equally possible appears a change in the mining depth and activity of key bioturbators, likely related to paleo-environmental changes. The considerable global climatic fluctuations during the Quaternary (Wang et al., 2017) resulted in the expansion and shrinking of rainforests, mainly determined by atmospheric moisture availability (Garcin et al., 2018; Hessler et al., 2010; Maley et al., 2017) and ecosystem engineers and their imprint may have varied as well. More work is needed to refine time scales and processes of TYRE and stone line formation in relation to paleoclimatic changes based on advanced geochronological approaches and higher vertical sampling resolution (May et al., 2018; Pfaffner et al., 2024; Schulze et al., 2022; Schwahn et al., 2023), ideally coupled with paleoenvironmental proxies like phytolith and  $\delta^{13}\text{C}$  depth profiles (Bremond et al., 2017; Calegari et al., 2013; Desjardins et al., 2020; Pessenda et al., 2010; Piperno et al., 2021).

Knowledge of TYRE formation helps unravelling numerous tropical

soil archives of human evolution and vice versa at high spatial resolution (Cruz-y-Cruz et al., 2022; McMichael et al., 2012; Mercader et al., 2002; Smith et al., 2020; Watling et al., 2017; Williams, 2019). While contributing to the understanding of tropical landscape evolution and critical zone dynamics, we also suggest to further evaluate biomechanical carbon sequestration potentials (Martinez et al., 2021; Martinez and Souza, 2020). Last but not least, an awareness on limited soil (re)production on human time scales (Montgomery, 2007) is important for environmental education and to support targeted nature-based approaches to soil restoration (Kaiser et al., 2017) and optimization towards a sustainable land use.

This work at the interface of disciplines like geology, geomorphology, pedology, ecology, archeology, sustainable land use, education, etc., contributes to a common understanding of TYRE evolution, however, based on still limited observations and data. Here we suggest a not exhaustive list of topics to be investigated in more depth in the future: 1) internal differentiation of TYRE leading to distinct soil types, 2) spatiotemporal differentiation of allochthonous contributions to TYRE, 3) re-evaluation of yellow to red fine over coarse deposits (colluvial, eolian, fluvial/alluvial) in tropical landscapes, 4) standardizing reports on soil production and weathering rates; increasing the database for tropical regions, 5) standardizing the quantification of bioturbation, enhancing the database, evaluation of the influence of, e. g., earthworms and trees on TYRE evolution, 6) advancing concepts of soil and landscape evolution, e.g., depth of biomantle, sorting versus mixing processes, 7) increase sampling resolution and decrease aliquot size (single grain approach) in luminescence dating, 8) investigating TYRE and TRP evolution during changing paleoenvironments on multimillennial to million-year time scales.

## 5. Conclusions

The literature overview and presented data reinforce the importance of (bio)chemical weathering and biomechanical work (by, e.g., termites, ants) in the formation of tropical yellow to red earth (TYRE), i.e., the uppermost, well-structured, multifunctional element of tropical regolith profiles (TRP). Luminescence and radiocarbon age-depth profiles of TYRE from various tropical landscapes differing in geology and ecosystems indicate quasi-constant soil upbuilding with common rates of ca. 100–200 mm\*ka<sup>-1</sup>. Relief positions and a far distance to (paleo) deserts exclude significant allochthonous contributions or erosion at the study sites. These figures are in line with termite (ca. 20–200 mm\*ka<sup>-1</sup>) and ant (ca. 125 mm\*ka<sup>-1</sup>) mounding rates and are about one magnitude larger than chemical weathering of bedrock in the tropics (2–100 mm\*ka<sup>-1</sup>; 2–20 mm\*ka<sup>-1</sup> for deep TRP).

TYRE production by mounding invertebrates only takes place when material below TYRE (saprolite) is transferred upwards, whereas shallow mining within TYRE leads to its recycling. As ecosystem engineers are unable to process solid rock, TYRE production by mounds requires the presence of saprolite to be mined, which is only slowly produced by chemical weathering. In (semi-)arid regions, saprolite is a currently not renewable relict and therefore represents an even more limited resource. The knowledge of processes and timescales of TYRE formation is crucial for the understanding of tropical landscape evolution and Late Quaternary human-environment interaction. Above all, it is essential for nature-supported solutions of sustainable land use (e.g., soil protection, restoration, optimization; carbon sequestration) and basic environmental education. This study reveals the high potential of luminescence dating of tropical soils and hopefully encourages more efforts to quantify rates of bioturbation, weathering and possible allochthonous contributions.

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## Author contributions

Conceptualization: TS, PVT, HV, CT; Methodology: TS, AK, CT, FL, FCGR, AOS, JT, SS; Investigation: TS, AK, FL, FCGR, CT, JT, LZ, TAS, PT, SS; Visualization: TS, FCGR, FL, AK; Supervision: HV, PVT, PDN; Writing–original draft: TS; Writing–review & editing: AK, FL, FCGR, AOS, CT, JT, LR, TAS, LZ, SS, PT, PDN, UL, PVT, HV

## Declaration of competing interest

The authors declare that they have no competing interests.

## Data availability

All data are available in the main text or the supplementary information.

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