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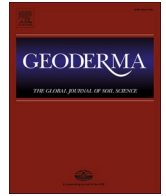
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Long-term quantification of the intensity of clay-sized particles transfers due to earthworm bioturbation and eluviation/illuviation in a cultivated Luvisol

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ABSTRACT

As a result of the limited knowledge on eluviation/illuviation and bioturbation rates, these two processes of soil particles translocation are qualitatively described either as synergic or competing processes. Here we take the opportunity of the recent development of an image analysis procedure to quantify illuvial clay and earthworm's porosity to quantify the intensity of illuviation and bioturbation cumulated over soil formation in a temperate cultivated Luvisol. The key objectives of the study are i) to quantify the total intensity of illuviation and bioturbation and their depth distributions and ii) to assess the possibility for bioturbation to limit or compensate the depletion of the clay-sized fraction in topsoil horizons due to eluviation. The total quantity of illuvial clay is 1,100 t.ha⁻¹ while the estimated annual amount of clay-sized fraction translocated by eluviation is between 0.08 and 1 t ha⁻¹ yr⁻¹. This is comparable to the annual loss of land by water erosion (between 1 and 5 t ha⁻¹ yr⁻¹) or by arable erosion (3.3 t ha⁻¹ yr⁻¹). Eluviation/illuviation is thus a discrete and active form of soil loss. With approximately 1,900 t.ha⁻¹ of clay-sized fraction, the amount of fine particles displaced at least once by bioturbation is higher than the one related to eluviation/illuviation. At first sight, it therefore seems possible for biological activity to compensate for vertical transfers of the clay-sized fraction by eluviation/illuviation. However, our study shows that a considerable amount of the clay-sized fraction will never be brought up by the bioturbation and will remain definitively lost for the surface horizons as bioturbation decreases non-linearly with depth. Consequently, a preventive management of the depletion of the clay-sized fraction in topsoil horizons by eluviation/illuviation should be preferred to the curative management of its consequences by bioturbation.

1. Introduction

The clay-sized fraction is a key compartment of the natural soil capital (Robinson et al., 2009). The clay-sized fraction is indeed linked with many of the functions and services rendered by soils (Adhikari and Hartemink, 2016) and is frequently used as an integrative indicator of soil quality (Bünemann et al., 2018). Issues with the clay-sized fraction are particularly problematic in topsoil horizons. There, a decrease in clay-sized fraction is generally accompanied by degradation of the soil architecture and subsequent increases in the risks of soil erosion and compaction (Kay, 1998) as well as by a lower carbon sequestration potential (Churchman et al., 2014; Hassink, 1997; Six et al., 2002), all of which combine to induce negative impacts on crop yields (King et al.,

2020).

In non-eroded temperate soils developed in a unique soil parent material, the distribution with depth of the clay-sized fraction is mainly controlled by two translocation processes: eluviation/illuviation and bioturbation (Bockheim et al., 2005; Phillips, 2007; Stockmann et al., 2011). Eluviation/illuviation consists of the redistribution of soil particles up to 10 μm in size from shallow eluviated E-horizons towards illuviated B-horizons by vertical or lateral translocation (Quenard et al., 2011). Eluviation/illuviation process involves the combination of several elementary mechanisms: 1/ mobilisation of clay-sized particles as a result of repeated wetting and drying cycles (Michel et al., 2010), changes in the ionic strength and pH of the soil solution (Van Den Bogaert et al., 2015), or freezing/thawing cycles (Worrall et al., 1999),

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and 2/ particle deposition (i.e., flocculation and filtration) (Goldberg and Forster, 1990; Jarvis et al., 1999; Quenard et al., 2011). The lumped effect of these processes can be measured through textural differentiation between the eluvial and illuvial horizons. In an attempt to quantify the intensity of eluviation and illuviation in 1 946 French Luvisols and Retisols, Quenard et al. (2011) however demonstrated that textural differentiation was a poor indicator of the eluviation/illuviation intensity in more than 90 % of the cases due to the co-occurrence of various factors or processes including parent material changes and heterogeneities, in-situ weathering, or bioturbation. To overcome this difficulty, various approaches have been developed to quantify the intensity of eluviation and illuviation independently from confounding processes among which the quantification of clay coatings (Miedema and Slager, 1972; Thompson et al., 1990), laboratory experiments (Cornu et al., 2014) or more recently multi-isotopic tracing (Jagercikova et al., 2017, 2014) or deterministic modelling (Finke and Hutson, 2008; Sauer et al., 2012). Quantifications remain however scarce in the literature and affected by limits such as lack of validation for clay coatings counting (Sauzet et al., 2017), consistency with field conditions for laboratory experiments (Cornu et al., 2014) or proper calibration for modelling (Finke et al., 2015; Opolot et al., 2015).

Bioturbation is the physical displacement of soil particles by living organisms. Although many agents contribute to bioturbation, especially plants through root growth and tree uprooting or burrowing animals, earthworms are considered to be the main agent in current temperate environments (Wilkinson et al., 2009). Bioturbation by earthworms has been frequently quantified using a large diversity of approaches including: i) the direct quantification of earthworms casts sampled either at the soil surface and/or within the soil profile (Gobat et al., 2010), ii) evidence of the burying of coarse fragments or other anthropic artefacts (Darwin, 1881), iii) the characterization of the earthworm community combined with measures or hypothesis of soil ingestion by individual earthworms (Pelosi, 2008), iv) laboratory studies (mesocosms and pollutants used as tracers) (Balseiro-Romero et al., 2020; Ferber et al., 2019; Zorn et al., 2005), or more recently, v) the fitting of optically-stimulated luminescence dates (Johnson et al., 2014) and/or isotopic tracers depth distributions (Bouché et al., 2014; Jagercikova et al., 2017; Tyler et al., 2001) with mathematical models. Reviewing bioturbation, Wilkinson et al. (2009) concluded that casting rates by earthworms range from 10 to 50 t ha⁻¹ y⁻¹ or more, particularly in tropical environments. Such data are however hardly comparable with eluviation as the origin of the mined soil particles remains largely unknown and since they do not take into account the redistribution of soil below the soil surface. Mixing rates, which are poorly quantified (Michel et al., 2022), are indeed far from being negligible (Wilkinson et al., 2009). Discrepancies between burial rates measured over years to decades and casting rates measured over months to years (Wilkinson et al., 2009) moreover highlight the difficulty associated with the extrapolation of casting rates over characteristic times of soil processes like eluviation.

The limited quantitative knowledge available at this stage concerning eluviation/illuviation and bioturbation rates makes it difficult to ascertain how these processes relate to each other. Some researchers have argued that they are synergistic in terms of the downward translocation of clay-sized particles, giving rise to texture contrasts in soils (Phillips, 2007, 2004). On the contrary, other researchers consider that the upward translocation of soil particles by bioturbation can partially (Thompson et al., 1990) or, in particular conditions, entirely cancel out (Langohr, 2001) a textural differentiation previously induced by eluviation/illuviation. From a quantitative point of view, recent attempts to model the vertical distribution of clay-sized particles through the description of various processes including bioturbation and eluviation show a tendency to overestimate the depletion of the clay-sized fraction in topsoil horizons as a result of unprecise rates of bioturbation (Opolot et al., 2015; Sauer et al., 2012). There is thus a need to better delimit the extent of eluviation/illuviation and bioturbation processes (Johnson

et al., 2014).

In this general context, the main goal of the research described in the present article was to take advantage of an image analysis procedure that was recently developed to quantify the porosity opened up by earthworms as well as the amount of illuvial clay (Sauzet et al., 2017), in order to quantify the intensity of illuviation and bioturbation cumulated over time in an agricultural soil. The key objectives of the research are i) to quantify the total intensity of illuviation and bioturbation and their depth distribution in a cultivated Luvisol, and ii) to assess the possibility for future bioturbation to limit or compensate the depletion of the clay-sized fraction in topsoil horizons due to eluviation in the light of the cumulative intensities over time of these two processes.

2. Material and methods

2.1. Soil description and sampling

The soil under study is classified as a Luvisol (WRB, 2014) of approximately 1.5 m depth that has developed on quaternary loess deposits (more details in Sauzet et al. (2016)). This soil is under conventional agricultural management with a maize-wheat crop succession and is part of the QualiAgro long-term field experiment located on the Plateau des Alluets (Yvelines, France). It consists of the typical horizons of a Luvisol according to WRB (2014), namely: ApEBtC (Supplementary data 1). The plough layer contains 14 % clay, 79 % silt, and 7 % sand whereas the Bt horizon exhibits the diagnostic clay content increase and is composed of 31 % clay, 64 % silt, and 5 % sand. A field sampling of the earthworm community realized on this field and detailed in Ricci et al. (2015) showed the presence of three earthworm species: one anecic species (10.6 individuals m⁻², 20.6 g m⁻²), *Lumbricus terrestris*, and two endogeic species (51 individuals m⁻², 8.9 g m⁻²), *Aporrectodea caliginosa* and *Allolobophora rosea*. The endogeic *Aporrectodea caliginosa* was the most abundant taxon in the soil profile under study whereas *Lumbricus terrestris* constituted the bulk of the earthworm biomass.

Kubiena boxes (150 × 80 × 50 mm) were used to extract 8 undisturbed soil samples between 30 and 160 cm deep (Supplementary data 1). Each horizon containing clay coatings (Sauzet et al., 2016) was sampled at least once (Supplementary data 1). From each of these boxes, three thin sections 14 cm wide by 6 cm deep, spaced 3 to 5-cm apart, and around 25-µm thick were prepared following the procedures of Guilloré (1985). Illuvial features (clay coatings or infillings, and papules, i.e., redistributed and fragmented clay coatings disconnected from the porosity and of an equivalent diameter lower than 200 µm) and earthworm burrows (i.e. rounded voids of an equivalent pore diameter between 1 and 2 mm plus voids of an equivalent pore diameter above 2 mm) were quantified on these soil thin sections using the image analysis procedure developed and verified by Sauzet et al. (2017). The three measures for each Kubiena boxes were averaged in order to obtain representative measures for the sampled soil layers (Sauzet et al., 2017). The areal proportions of clay coatings, papules, and earthworm burrows were linearly extrapolated for the non-sampled soil layers, as for example between the 80 and 90 cm depths, in order to obtain their depth distributions with a constant depth increment of 10 cm. As a first approximation, the areal proportions quantified by image analysis were used to assess the volumetric proportion of clay coatings (V_{coat}), papules (V_{pap}), and earthworm burrows (V_{bur}).

2.2. Quantification of illuviation

The intensity of the eluviation/illuviation process was quantified by the mass of clay coatings and papules detected between 30 and 160 cm-depth per unit surface area of soil (kg/m⁻²). This mass was computed according to the following equation:

$$M_{ill} = \sum_{i=1}^n (V_{pap,i} + V_{coat,i}) \times \rho_{coat} \times Th_i \quad (1)$$

where $V_{pap,i}$ and $V_{coat,i}$ are the volumetric proportions of papules and coatings, respectively, measured by image analysis in the soil layer i expressed as a percentage of the volume of the soil layer, Th_i is the thickness of the i^{th} sampled layer (m), and n is the number of 10-cm thick soil layers in which illuvial features were identified, i.e., from 30 to 160 cm depth (Sauzet et al., 2016). The bulk density of the clay coatings (or papules), ρ_{coat} measured with the kerosene method on 21 manually sorted replicates of clay coatings was $1,750 \text{ kg m}^{-3}$ (Sauzet et al., 2016).

Clay coatings are thought to be permanent features in soils except in strongly hydromorphic soils (Kühn et al., 2010; Payton, 1993; Pedro et al., 1978). Clay coatings can however be fragmented and redistributed by various pedoturbation processes, especially bioturbation by earthworms giving rise to the so-called papules but they are supposed to be never reintegrated into the soil matrix. As a result, the total mass of illuviated clay-sized features, i.e. clays coatings plus papules, measured the intensity of the cumulative illuviation from the start of the illuviation process until today. In different Luvisols developed in the western European calcareous loess belt as the one under study, Finke and Hutson (2008) and Quenard et al. (2011) estimated that the total duration of illuviation ranged from 4000 to 14 000 years and from 1000 to 9000 years, respectively.

2.3. Quantification of bioturbation

The intensity of bioturbation (by earthworms) was quantified by first assessing the soil volume that was bioturbated by earthworms. Then, the mass of soil and the mass of clay-sized fraction, contained in the bioturbated soil volume before the soil displacement by earthworm activity were quantified. The bioturbated soil volume is composed of open burrows and of burrows infilled by surface material and by excretion of casts from earthworms (Fig. 1).

For each soil layer i , the volumetric proportion of open burrows ($V_{bur,i}$) was measured via image analysis by partitioning the porosity

generated by earthworms from the total macroporosity according to the size and shape of pores (Sauzet et al., 2017). In the studied soils, papules were mostly located into biological infillings and were consequently interpreted as fragments of clay coatings redistributed by bioturbation (Sauzet et al., 2016). The volumetric proportion of infilled burrows ($V_{inf,i}$) was accordingly estimated by assuming that it is equal to the ratio between the proportion of illuvial features fragmented by biological activity, the so-called papules ($V_{pap,i}$), and the total proportion of illuvial features ($V_{pap,i}$ plus $V_{coat,i}$) on thin sections (Miedema and Slager, 1972):

$$V_{inf,i} = \frac{V_{pap,i}}{V_{pap,i} + V_{coat,i}} \quad (2)$$

The mass of bioturbated soil per unit area of soil (M_{turb} in kg/m^{-2}) was computed according to the following equation:

$$M_{turb} = \sum_{i=1}^n (V_{bur,i} + V_{inf,i}) \times \rho_i \times Th_i \quad (3)$$

where $V_{bur,i}$ and $V_{inf,i}$ denote the volumetric proportions of open burrows and infilled burrows, respectively, in percent of the total volume of the soil layer i , ρ_i is the bulk density (kg m^{-3}) of the soil layer i , and Th_i is the thickness (m) of the soil layer i . As in Eq. (1), n is the number of 10-cm-thick soil layers from 30 to 160 cm depth. The assessment of $V_{inf,i}$ was impossible in the ploughed horizon due to the lack of illuvial features.

The mass of bioturbated clay-sized particles per unit area of soil ($M_{turb < 2\mu\text{m}}$ in kg/m^{-2}) was finally computed by multiplying for each soil layer i the total mass of bioturbated soil by the clay content in the layer.

Infillings may represent either the recent passage of an earthworm, or an old and abandoned burrow (Wilkinson et al., 2009). The longevity in soils of such infillings is not precisely known. Given that a come back to the initial structure of the surrounding soils is unlikely, such infillings may however be viewed as permanent and then be used as indicators of bioturbation integrated over long time periods. Wilkinson et al. (2009)

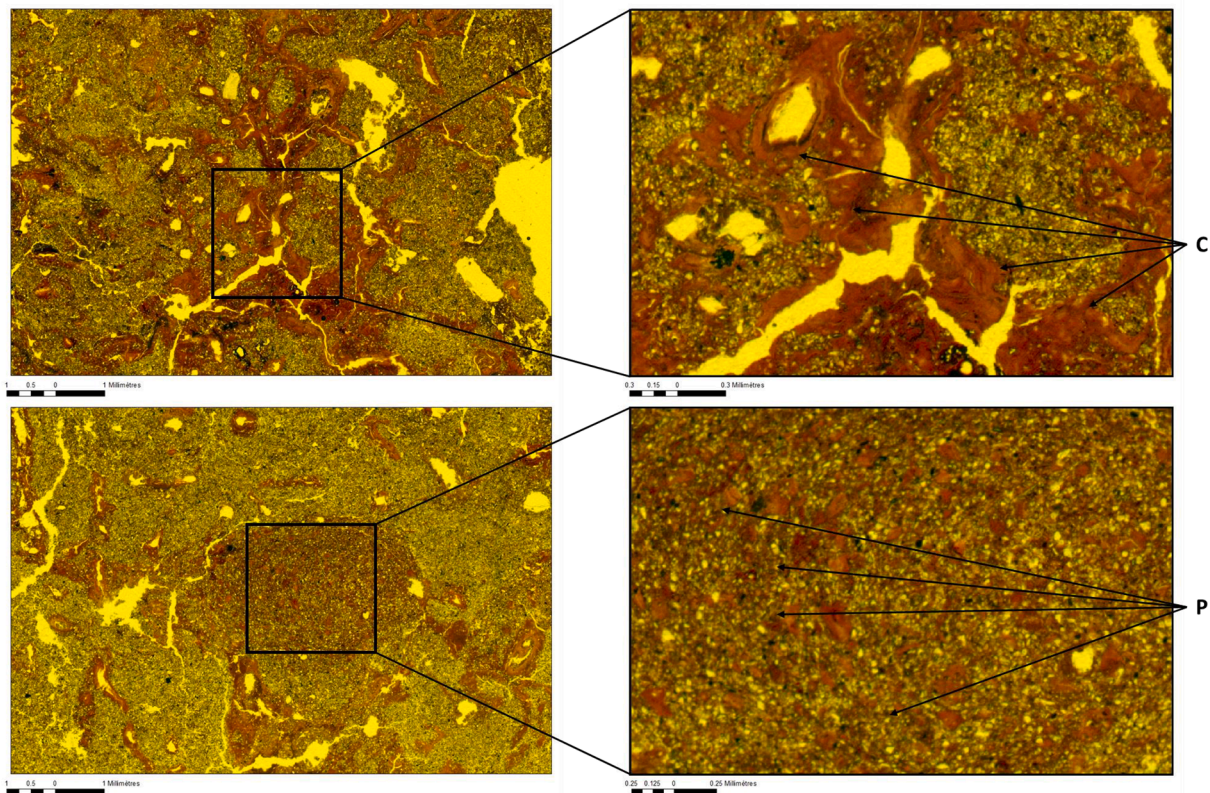


Fig. 1. Examples of illuvial clay features observed on thin sections between 90 and 100 cm depths in the Bt-horizon of a cultivated Luvisol (C = clay coating, P = papule).

indeed considered that these infillings “occupy the historical end of the spectrum of observable biofabrics”. According to the use of papules for quantifying the volume of infilled burrows, the quantified infilled burrows are necessarily more recent than the oldest clay coatings likely to be fragmented and redistributed by earthworms. According to the total duration of the eluviation/illuviation process, the volume of infilled burrows ($V_{inf,i}$) thus represents the cumulated volume of soil that has been reworked by earthworm at least once over the last 1000 to 14000 years. It is obvious that the intensity of bioturbation was not constant over time but varied with soil development, land use changes or, more recently, with the adoption of intensive practices. By contrast, open burrows are potentially younger and may be interpreted, at least in surface soil horizons, as a snapshot of the current earthworm activity (Wilkinson et al., 2009).

2.4. Bioturbation model fitting with depth

The depth-distribution of bioturbation was modelled with a constant ($V_{urb} = a$), a linear model ($V_{urb} = a \cdot depth + b$), and finally a logarithmic model ($\ln(V_{urb}) = a \cdot depth + b$) in which V_{urb} is the sum of V_{inf} and V_{bur} , i.e., the total bioturbated soil volume in percent, and a and b are two regression coefficients adjusted with the R software using the *lm* function (linear model).

A bioturbation rate constant with depth is frequently assumed by researchers (Elzein and Balesdent, 1995; Koven et al., 2013) whereas other studies invoke a non-linear depth-dependence of bioturbation rates (Jagercikova et al., 2014; Johnson et al., 2014; Keyvanshokouhi et al., 2019; Wilkinson et al., 2009). The performance of each of these models against measured data was evaluated on the basis of Pearson product moment correlation, p-value, and Residual Mean Square Errors (RMSE). Finally, to illustrate the spatial variability of the depth-dependence of bioturbation rates, the measured and modelled bioturbation rates in the studied temperate Luvisol were compared to those modelled by Wilkinson et al. (2009) in an Australian Regosol where bioturbation was dominated by ants and worms.

3. Results

3.1. Quantification of illuviation

Illuvial features are observed over the entire soil profile (Figs. 2 and 3). In the E horizon, illuvial features represent a very small proportion of the soil volume (Fig. 3) and are mostly present in the form of redistributed fragments (papules). In the Bt horizon, 9 % at most of the soil volume is occupied by clay coatings and clay infillings or, to a lower extent, by papules. Illuvial features are still observable in C horizons until a depth of 160 cm where they are mostly clay coatings and represent at least 2 % of the total soil volume (Figs. 2 and 3). The total surface area occupied by these illuvial features increases and then decreases with depth, passing through a maximum localized between 75 and 95 cm deep (Fig. 3).

Eluviation/illuviation resulted in a total transfer of clay-sized particles estimated for the whole soil profile at $1,133 \text{ t ha}^{-1}$ (M_{ill} , Fig. 4). Relatively negligible in the E horizon, transfers are maximal in the Bt-horizons where they reach 150 t ha^{-1} per 10 cm thick layer of soil and then decrease with increasing depth. However, transfers of clay-size fraction remain very significant up to a depth of 150 cm, where they still represent nearly 40 t ha^{-1} , i.e., values close to those quantified in the upper part of the Bt horizon.

3.2. Quantification and modelling of bioturbation

The sum of the volumes of burrows (V_{bur}) and infillings (V_{inf}), is between a low value of about 20 % and a high of 60 to 70 % (Fig. 5). Bioturbated volumes decrease with depth up to 1 m depth and tend to stabilize deeper in the profile, around a proportion of bioturbated soil of

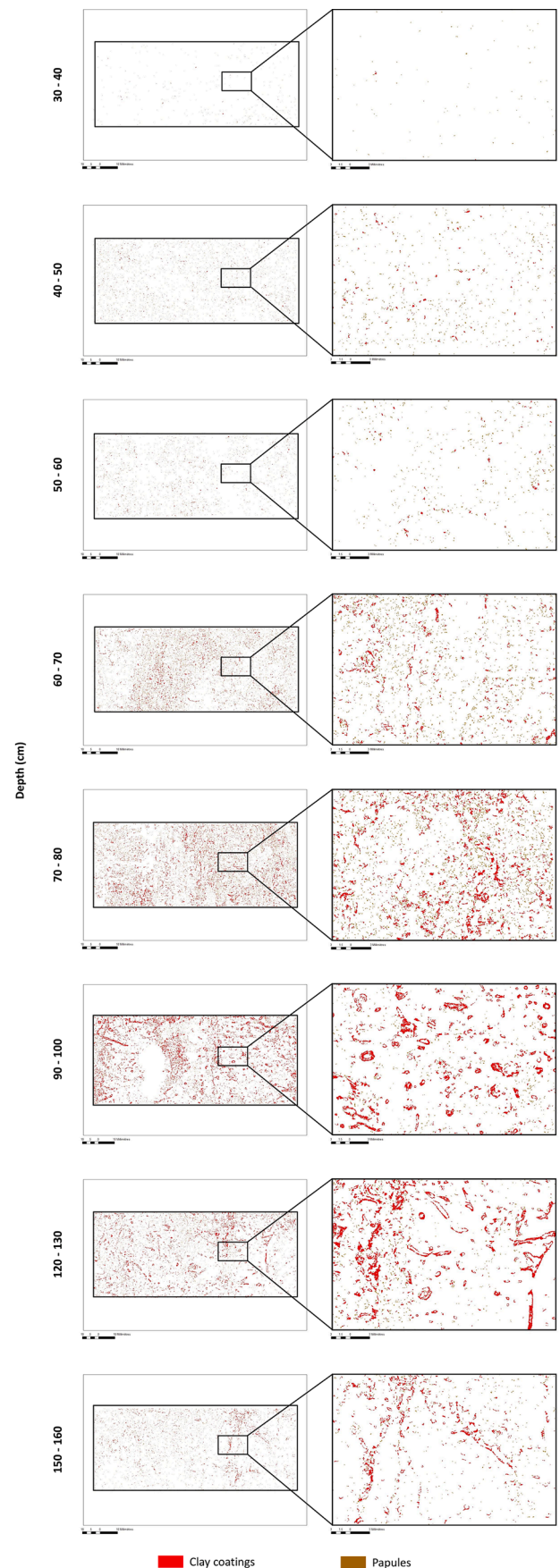


Fig. 2. Depth distribution of clay coatings (red) and papules (brown) in the cultivated Luvisol.

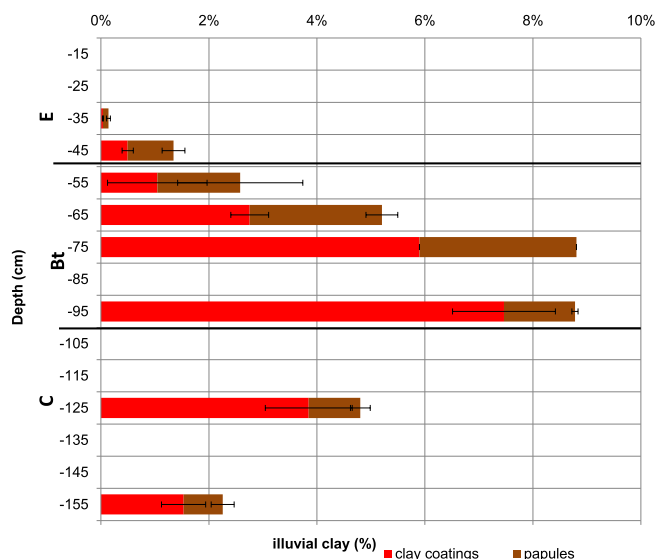


Fig. 3. Depth distribution of clay coatings and papules abundance (%) in a cultivated Luvisol.

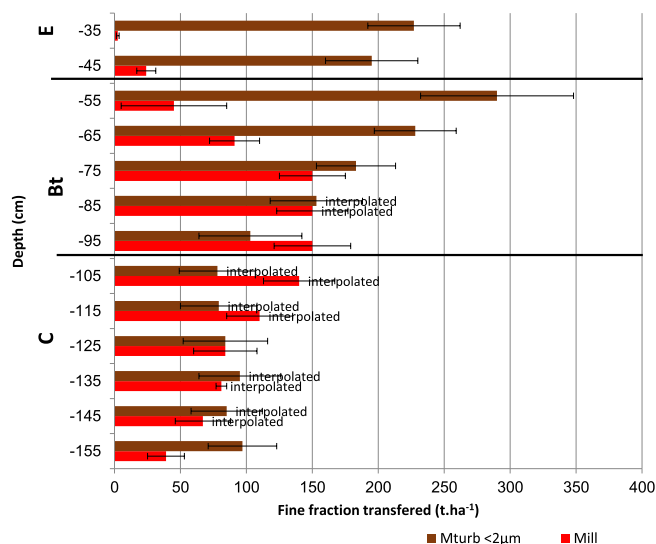


Fig. 4. Depth distribution of the fine fraction transferred (t/ha) due to illuviation or bioturbation in a cultivated Luvisol.

20 to 30 %. The bioturbation process, far from being limited to the surface horizons (not studied), modifies a significant proportion of the soil at any given depth without, however, affecting, for a given depth, the entire volume of soil.

The volume of burrows is systematically lower than the volume of infillings (Fig. 5). However, their relative abundance is relatively variable due to distinct depth distributions (Fig. 5). Whereas the volume of biological infillings is maximal at shallow depths, decreases very rapidly down to 1 m, and then increases again, the volume occupied by burrows shows an inverse distribution with values of only a few percent in the E and C horizons and maximum values in the Bt horizon at about 1 m depth. In any case, with earthworm porosity still representing about 1 % of the total surface analysed at 160 cm depth, it appears that soil fauna has explored the entire thickness of the soil.

Finally, by redistributing on average nearly 40 % of the total soil volume between the depths of 30 and 160 cm, earthworm activity is responsible for a material displacement of about $6,930 \text{ t ha}^{-1}$, i.e., about $1,900 \text{ t ha}^{-1}$ of clay-sized fraction (M_{turb} , Fig. 4) over the last 1000 to

14000 years. Given a soil density of around $1,500 \text{ kg m}^{-3}$, the total mass of soil bioturbated by earthworm activity is equivalent to the mass of soil contained in the first 45 cm of soil.

The constant model shows a higher RMSE than the linear and the logarithmic ones (Table 1). While the logarithmic model seems to better reproduce the depth distribution of bioturbation than the linear ones (Fig. 6), both of them show, in the studied soil, similar adjusted R^2 and RMSE (Table 1). The model from Wilkinson et al. (2009), characterized by a very rapid decline of bioturbation rates with depth (Fig. 6), poorly fits with the bioturbation rates measured in this study (Table 1).

4. Discussion

4.1. Validation of the quantitative approach and associated limits

Our methodological approach to quantify illuvial clay and earthworm porosity was validated in Sauzet et al. (2017) at the thin section (sample) scale thanks to an exhaustive accuracy assessment procedure.

At the profile scale, the quantification of illuvial features by image analysis successfully distinguishes the different horizons classically observed in Luvisols according to the abundance or the type of illuvial features. Whereas the illuviated Bt-horizons shows the highest abundances of illuvial features, only small amounts or traces of illuvial features are detected in, respectively, the C- and eluviated E-horizons (Figs. 2 and 3). In this last horizon, only fragments of clay coatings redistributed by earthworm activity are observed in good agreement with their definition as mineral horizons characterised by a loss of silicate clay, resulting in a relative concentration of sand and silt particles (Food and Agriculture Organization of the United Nations (FAO), 2006). The abundances of illuvial features and of clay coatings quantified by image analysis are moreover closely correlated with those quantified by point counting (Fig. 7) on the same samples (Sauzet et al., 2016). The amount of illuvial features and of clay coatings quantified by image analysis are however systematically lower than those quantified by point counting, the reverse being true for papules. Several factors likely contribute to these differences, among which: i) the micromorphological point-counting quantification can lead to an overestimation of the illuvial clay amounts due to edge effect as soil components are usually sloped at their borders with each other within the standard 25–30 μm (three-dimensional) thin sections (Murphy and Kemp, 1984), ii) the point-counting method is based on the use of a single grid partially adapted to the simultaneous quantification of papules of equivalent diameter less than 200 μm and of coatings of much larger size, which may lead to an underestimation of papules and an overestimation of clay coating (Ulery et al., 2008), iii) the image analysis procedure used in this study is prone to illuvial clay underestimation in comparison with manual outlining on thin sections by a micromorphologist (Sauzet et al., 2017). Whereas the quantitative approach tends to slightly underestimate the amount of total illuvial features and clay coatings with reference to more classical approaches by point counting, it is very likely more efficient in distinguishing and quantifying exhaustively small illuvial features like papules. This last benefit opens the way to an accurate quantification of the bioturbation in illuviated horizons.

Soil fauna explores the entire thickness of the profile, i.e., deeper than rooting depth that is sometimes thought to be a good proxy for parameterizing bioturbation (Johnson et al., 2014). Such exploration depth is in accordance with results of Bouché et al. (2014) or Le Bayon et al. (2017) that reported exploration depths as high as 200 cm. The higher volume of infillings than that of open burrows has also been observed by Wilkinson et al. (2009) or Piron et al. (2012). Open burrows are indeed the most recent changes in soil structure resulting from earthworm activity (Wilkinson et al., 2009). Their longevity in soils is supposed to be short due to their infilling by fallen surface or pore wall materials or to the excretion of casts by earthworms (Capowiez et al., 2014b, 2014a; Jangorzo et al., 2015; Wilkinson et al., 2009).

With one percent in deep soil horizons to slightly above 5 percent in

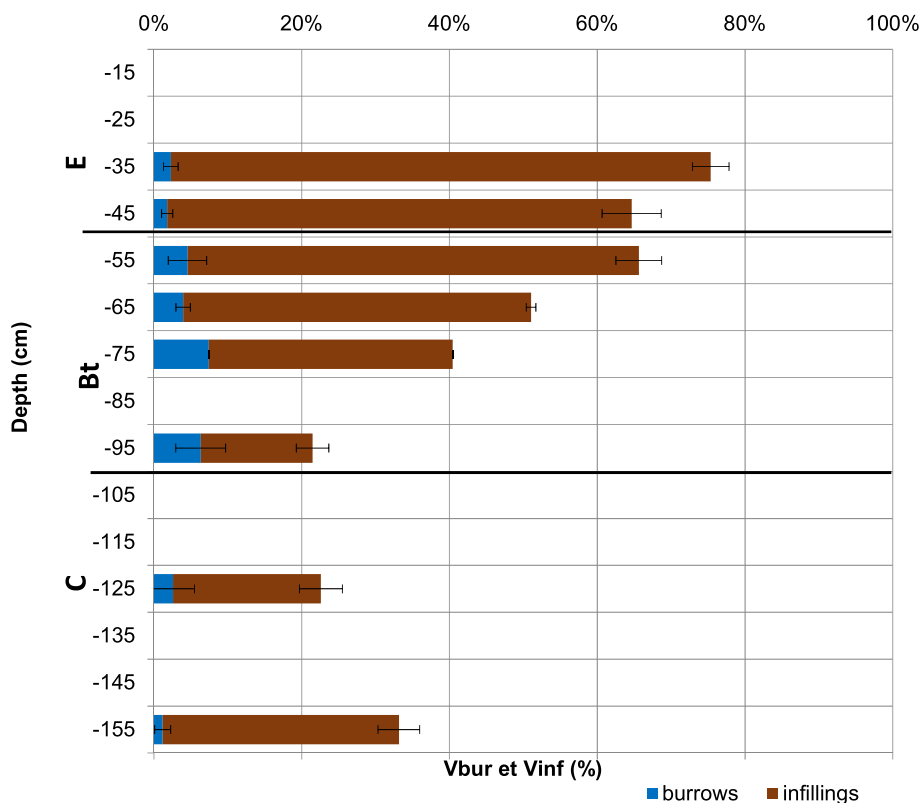


Fig. 5. Depth distribution of burrows (in blue) and infillings (in brown) abundance (%) in a cultivated Luvisol.

Table 1

Reliability of the constant, linear and logarithmic modellings of the bioturbation and comparison with that by Wilkinson et al. (2009).

Model used for prediction of V_{tot}	Equation	p-value	cor	RMSE
Constant model (this study)	$V_{tot} = 47.37$	–	–	20.2
Linear model (this study)	$V_{tot} = 81.13 - 0.43 \cdot \text{depth}$	$2.57 \cdot 10^{-6}$	0.82	11.5
Logarithmic model (this study)	$V_{tot} = \exp(4.52 - 0.0094 \cdot \text{depth})$	$4.89 \cdot 10^{-8}$	0.88	10.1
Logarithmic model (Wilkinson et al., 2009)	$V_{tot} = \exp(5.97 - 0.13 \cdot \text{depth})$	0.0004	0.69	50.4

less deep soil horizons, the volume of open burrows is in the range classically reported, at least in temperate cultivated soils (Thompson et al., 1990). Relatively few studies have quantified the volume of infilled burrows with depth. In sandy Australian soils, the bioturbated volume represents 20 % of the total soil volume at 10 cm depth, 5 % at 30 cm depth and about 1 % at 70 cm depth (Wilkinson et al., 2009). The volume of bioturbated soil in loamy soils in what was turned into the Dutch polders between the 17th and 18th centuries is between a maximum of 51 % in the surface horizons and a minimum of 7 % between 20 and 30 cm deep (Jongmans et al., 2003). Finally, in a polluted silty-sandy cultivated soil in northern France (Fernandez et al., 2010), 8 %, 16 % and 0 % of the total soil volume was bioturbated respectively at the surface, between 25 and 50 cm deep and between 50 and 75 cm deep. The slightly lower volumes of bioturbated soil volume reported for a given depth in these studies may be linked to more adverse soil conditions for earthworm burrowing such as a sandy texture (Baker et al., 1992), soil pollution (Edwards and Bohlen, 1996), or, for the polderised soils, to the quantification of the cumulated bioturbation over a shorter time period.

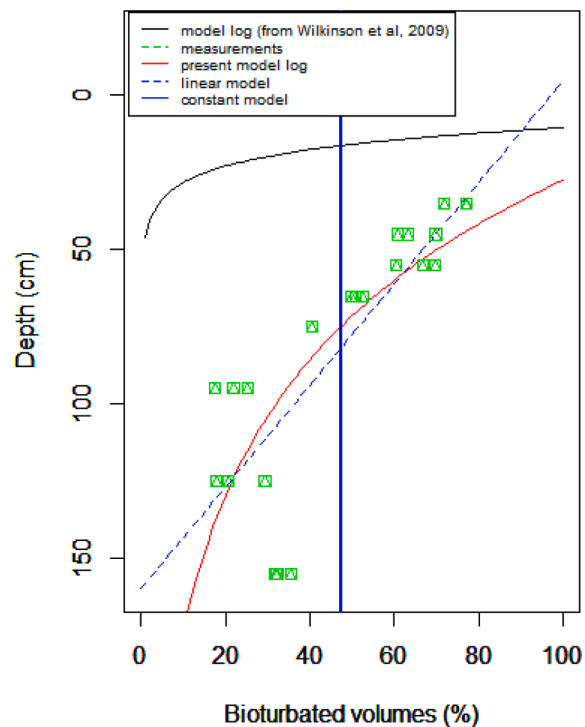


Fig. 6. Constant, linear and logarithmic fitting of the bioturbated soil volumes with depth in a cultivated Luvisol and comparison with the modelling by Wilkinson et al. (2009).

Finally, as we also observe in our fitting with depth, Jagercikova et al. (2014), Wilkinson et al. (2009) and Johnson et al. (2014) found that the best-fit mixing rate decreases non-linearly with increasing soil

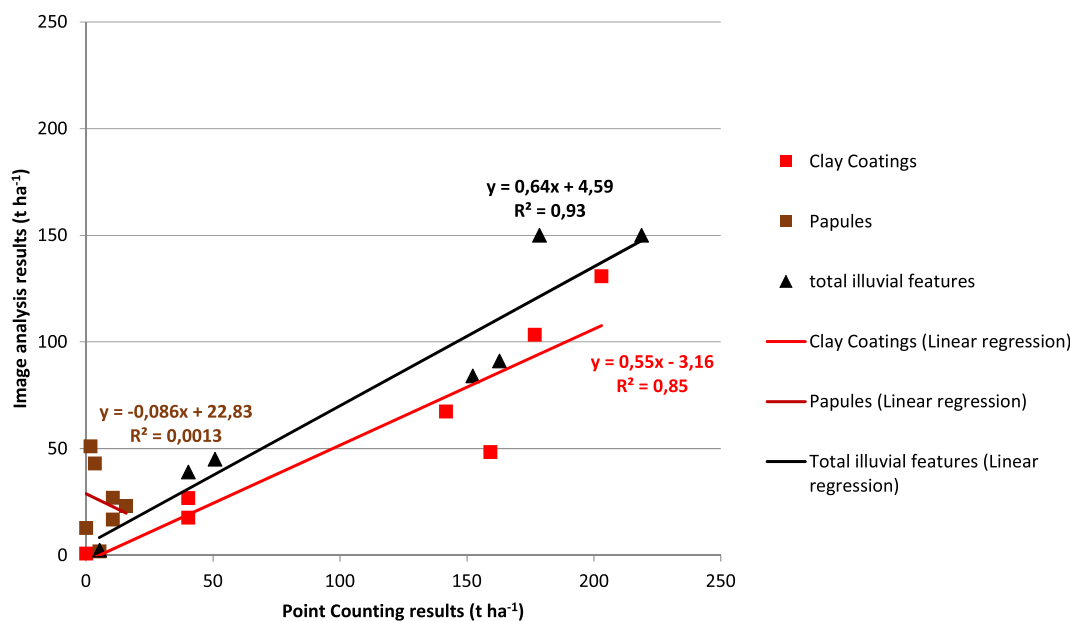


Fig. 7. Comparison of the masses in clay coatings, papules and total illuvial features quantified by image analysis and by point counting (Sauzet et al., 2016) in a cultivated Luvisol.

depth. The decrease in bioturbation intensity with depth thus clearly appears to be a common observation in all these studies.

The quantification of bioturbation using the relative proportion of papules as an indicator of soil reworking provides coherent depth-distribution of bioturbation, relative abundance of open and infilled burrows as well as total volume of bioturbated soil. Such an approach, although indirect, consequently appears particularly interesting to quantify long term soil reworking by soil fauna. This type of quantification is all the more important since contrasted pedoclimatic contexts, land uses and land management, or changes in earthworms communities and populations induced large discrepancies between bioturbation rates.

4.2. Intensity of matter transfers by eluviation/illuviation and bioturbation

4.2.1. Eluviation/illuviation: A significant form of clay-sized particles depletion from surface soil horizon

The few available data regarding the quantification of eluviation/illuviation intensity were obtained either from experimental laboratory measurements of the amounts of particles eluviated from undisturbed soil columns coupled with estimates of the formation times of Bt horizons (Cornu et al., 2014; Quenard et al., 2011), or from multi-isotopic modelling of matter transfers (Jagercikova et al., 2015, 2014). The transfer in clay-sized soil particles measured in the profile ($1,133 \text{ t ha}^{-1}$) is in the upper range of the estimates proposed by Quenard et al. (2011), i.e., between 1 and $1,150 \text{ t ha}^{-1}$, and higher than the estimates proposed by Duchaufour et al. (2018), i.e., between 600 and 750 t ha^{-1} .

Considering that the current stock of clay-sized particles in the eluviated Ap- and E/Bt-horizons horizons is around $1,000 \text{ t ha}^{-1}$, the eluviation/illuviation process almost halved the content in the clay sized fraction of these horizons over time. If one accepts with Quenard et al. (2011) that the duration of eluviation/illuviation ranged between $1,000$ and $14,000$ years, the annual amount of the clay-sized fraction exported by eluviation is between 0.08 and $1.1 \text{ t ha}^{-1} \text{ yr}^{-1}$, that is an annual decrease of the clay-sized fraction in the eluviated horizons by 0.008 to 0.1% . This value is in the lower range of the annual loss of land by water erosion ranging between 1 and $5 \text{ t ha}^{-1} \text{ yr}^{-1}$ (Cerdan et al., 2010) or by arable erosion estimated at $3.3 \text{ t ha}^{-1} \text{ yr}^{-1}$ (Van Oost et al., 2009). According to Schwartz et al. (2005), the eluviated surface horizon is

currently presenting a surface dispersion index of 2.7 and consequently a “very high” risk of soil crusting. Hypothesising no change in the volume of the ploughed horizon nor in its stocks of organic matter, silt, and sand, decreasing the risk of soil crusting to “high” risk (surface dispersion index lower than 2) or to “moderate” risk (surface dispersion index lower than 1.8) would require the addition in the ploughed horizon of respectively around 350 t ha^{-1} and 500 t ha^{-1} of clay sized soil particles corresponding to a content in clay sized particles around 230 and 250 g kg^{-1} . The long term sustainability of agricultural cropping in such soils thus requires, at least, to decrease the intensity of the eluviation/illuviation process or, better yet, to compensate it.

4.2.2. Bioturbation: The influence of re-bioturbation

Considering the estimate we have obtained of the soil volume that has been bioturbated, at least once, during the last $1,000$ to $14,000$ years, between 6.9 and $0.5 \text{ t ha}^{-1} \text{ yr}^{-1}$ of soil appears to be displaced in the profile due to earthworm activity, which is a very low number according to literature data. Indeed, Peres et al. (2009) estimated that the quantity of annual subsurface casts was $240 \text{ t ha}^{-1} \text{ yr}^{-1}$. This underestimation is not surprising as surface casting activity is not taken into account in our study. According to Müller-Lemans and van Dorp (1996), the turnover of ingested and redeposited soil represents $200 \text{ t ha}^{-1} \text{ yr}^{-1}$. They moreover estimated that among the $60 \text{ t ha}^{-1} \text{ yr}^{-1}$ of surface casts, only $20 \text{ t ha}^{-1} \text{ yr}^{-1}$ of dry matter comes from the deep soil (i.e., deeper than 20 cm). These results thus suggest that we missed the greatest part of the total bioturbation. re-bioturbation by earthworms is also not considered. Such re-bioturbation is a well-known phenomenon (Bouché et al., 2014; Bruneau et al., 2004; Wilkinson et al., 2009). It is perfectly consistent with the genesis of specific soil features of re-bioturbation (Humphreys, 1993; Wilkinson et al., 2009), or with the greater clay content of the biological infillings compared to non-bioturbated volumes (Edwards, 2004; Van Groenigen et al., 2019). Finally, the preservation of undisturbed clay coatings clearly highlights the juxtaposition of two types of structure in soils: under and without bioturbation control. We quantify here that $1,000$ to $14,000$ years of earthworms' activity resulted in the reworking of almost 40% of the soil volume between 30 and 160 cm -depth. It is thus unlikely that bioturbation completely obliterated for such depths the legacy of other soil processes (clay coatings, mottling,...) as it is sometimes postulated in soils with a considerably higher intensity of bioturbation (Langohr, 2001;

Thompson et al., 1990).

4.3. Competition between the two processes: antagonism or synergism?

4.3.1. Depth of equilibrium

At the scale of the profile, the amount of the clay-sized fraction transferred by bioturbation ($1,900 \text{ t ha}^{-1}$) is higher than the one transferred by eluviation/illuviation ($1,133 \text{ t ha}^{-1}$). This is not surprising as Humphreys (1993) and Paton et al. (1996) underlined the importance of particle transfers due to animals compared to physico-chemical ones. At first glance, therefore, it seems possible for biological activity to compensate for vertical transfers due to eluviation/illuviation. However, three very different situations can be distinguished according to depth (Fig. 4):

1. up to a depth of 70 cm, i.e., in the E horizon and in the upper part of the Bt horizon, transfers of the clay-sized fraction by bioturbation exceed those associated with the eluviation/illuviation process;
2. Between 70 and 90 cm deep and beyond 120 cm deep, the transfers linked to the two processes are in equilibrium;
3. Finally, between 90 cm and 120 cm in depth, i.e., in the lower part of the Bt horizon and in the upper part of the C horizon, the eluviation/illuviation process causes transfers of the clay-sized fraction of higher amplitude than the bioturbation process;

As a result of these contrasting evolutions, the quantity of the clay-sized fraction displaced by bioturbation is much greater than the one transferred by eluviation/illuviation up to an equilibrium depth (70 cm), then the ratio reverses for higher depths. Among all the clay-sized particles that cross this equilibrium depth, a part remains definitively lost for the surface horizons. Such losses toward the deepest soil layers is for example explicitly taken into account by Bunzl (2002) in his modelling of bioturbation. Earthworms are moreover essentially foraging the surface horizon (see discussion above) and secondarily the less deep soil horizons, i.e., above 70 cm (Fig. 5). These horizons are less enriched in clay-sized fraction than deeper horizons (the highest content in the clay-sized fraction and in the volume of illuvial features are observed between 80 and 100 cm-depth, Fig. 3 and Supplementary data 1), which limits the likelihood of any upward movement of soil matter due to earthworm casting to compensate the downward movement of clay-sized particles due to eluviation.

4.3.2. Transfer directions

Consequences of fine fraction transfers on the state and functioning of soils depend not only on the quantities of fine fraction transferred but also on the direction and distance of these transfers. Eluviation/illuviation process induces over time inter-horizon transfers from the eluviated horizon to the illuviated horizon with multiple consequences: aggravation of the sensitivity to compaction and erosion for the eluviated horizons, aggravation of hydromorphy in the illuviated horizons and even potential net losses of clay for the soil profile (eluviation out of the root zone) (Buurman et al., 1998; Montagne et al., 2016; Ogg et al., 2022). At first sight, the upward transfer due to bioturbation is very well established by numerous observations including the burial of coarse fragments or historical artefacts (Wilkinson et al., 2009), the formation of biomantles (Faivre and Chamorro, 1995), or the recontamination of cleaned surface soil layers by materials from underlying contaminated soil (Ferber et al., 2019), among others.

In the studied soil, the lack of papules in E-horizon can result from two different reasons. First, bioturbated soil materials, eventually deposited in the E-horizon, are not originating from deep illuviated horizons but from surface or subsurface soil horizons that do not contain clay coatings. Müller-Lemans and van Dorp (1996) indeed estimated that among the $6 \text{ kg m}^{-2} \text{ yr}^{-1}$ of casts deposited on the surface, only one third comes from soil depths higher than 20 cm and may thus be considered as an upward transfer.

Secondly, bioturbated soil materials originating from deep illuvial horizons, and containing clay coatings, are not deposited in the E-horizon but either in the same deep horizon or directly brought to the soil surface. For depths higher than 75 cm, the depth distributions of clay coatings and papules are very similar (Fig. 3), suggesting that the abundance of papules is related to the amount of clay coatings rather than stemming from the vertical transfer of papules between horizons.

Whatever the reason, the apparent movement of soil particles is less an upward transfer of soil materials from deep soil horizons to surface horizons as is commonly imagined than an intra-horizon transfer over short distances, the latter resulting from either actual horizontal transfers or from the combination of an upward transfer with a downward one (Zorn et al., 2005). Finally, whereas the eluviation/illuviation process clearly induces a downward vertical transfer on several tens of centimeters, bioturbation simultaneously induces upward, horizontal, or downward movements of soil particles over distances ranging from a few millimeters for the displacement of non-ingested soil materials to several tens of centimeters for the transfer of ingested soil materials (Capowiez et al., 2021; Rogasik et al., 2014) for an overall apparent transfer that is likely variable with the composition of earthworms' communities or with the soil depth. However, much remains to be done to better distinguish between intra-horizon bioturbation and inter-horizon bioturbation, particularly its upward component, since it has the greatest impact on the state and functioning of soils as it may counterbalance the impact of the eluviation/illuviation process.

4.4. Toward a preventive or curative management of fine fraction transfer

According to the results presented above, the competition over the last 10,000 years between the downward transfer of clay-sized particles by eluviation/illuviation and their transfer by bioturbation, partly upward, has turned to the advantage of eluviation/illuviation.

However, it seems possible to increase future bioturbation, at least with reference to the current soil conditions and management, in order to promote the curative management of the consequences of the loss of clay-sized particles from the surface horizons via eluviation. It is clear that the diversity, abundance, and biomass of earthworms are rather low in the studied soil as is also frequently observed in large plains that are intensively managed on the basis of short cereal rotations (wheat/maize), conventional ploughing, and a regular use of pesticides (Ricci et al., 2015). There is thus a possibility to promote a soil management that is more favourable to earthworm communities and especially to anecics, which should ultimately result in an increasing intensity of bioturbation. Indeed, Müller-Lemans and van Dorp (1996) pointed out that there is a proportional relationship between the upward transfer of solid matter and the anecic biomass. In a study of the production of surface casts by different species of earthworms, Scullion and Ramshaw (1988) also obtained a positive correlation between the abundance of earthworms and the number of surface casts produced. In addition, a positive linear relationship between biomass and excretion rate has been reported by several authors (Scheu, 1987; Buck et al., 1999; Capowiez et al., 2010).

In the studied soil or in other Luvisols, Ricci et al. (2015) demonstrated that organic matter inputs, particularly manure, minimum soil disturbance, and permanent soil cover are helpful to increase anecic biomass. The impact on such practices on the activity of anecic earthworm however still needs to be precisely quantified since the relationships between abundances or biomasses of earthworms and their activity are not straightforward (Peres et al., 2010). On the other hand, increasing the activity of anecic earthworms should result in increasing not only casting activity but also their burrowing activity. Such earthworm burrows are not only preferential pathways for soil particles downward transfer (Jarvis et al., 1999; Michel et al., 2010; Oygarden et al., 1997) but also new interfaces that are not yet depleted in clay-sized particles (Phillips, 2007) from which mobilisation of clay-sized particles can occur as a result of repeated wetting and drying cycles

(Michel et al., 2010) or changes in the ionic strength and pH of the soil solution (Van Den Bogaert et al., 2015). This may have an indirect, but so far largely unaccounted for, effect up to the enhancement of the eluviation/illuviation process as suggested by Phillips (2004 and 2007).

Due to the remaining uncertainties regarding the practical ways to increase or maintain on the long-term a high intensity of bioturbation, it may be argued that a preventive management of the eluviation/illuviation soil process should be preferred to the curative management of its consequences by bioturbation. Several complementary agricultural practices may be mobilized to try to reduce the intensity of the eluviation/illuviation process: i) regular liming aiming at maintaining soil pH above the pH range favorable to clay-sized particles mobilization and dispersion, i.e., above 6.5 (Quenard et al., 2011), even if significant eluviation is still observed in neutral to alkaline soils (Montagne et al., 2016, 2013); ii) organic matter spreading or reducing soil tillage with the aim to increase organic matter contents in the surface soil horizon, increase the soil hydro-structural stability (Boivin et al., 2009), and ultimately decrease the mobilization of clay-sized particles (Annabi et al., 2011; Dupla et al., 2021); iii) covering the soil in order to protect the soil surface from raindrop impact and reduce splash mobilization of clay-sized particles (Adetunji et al., 2020). Some of these practices, potentially helpful to manage preventively the intensity of the eluviation/illuviation process, should additionally contribute to the curative management of its consequences by bioturbation. Their adoptions in soils suffering from severe eluviation are then particularly interesting.

5. Conclusion

To our knowledge, this research is the first exhaustive quantification of illuvial features at the soil profile scale using an image analysis procedure on large soil thin sections. This approach is consistent with the more traditional point-counting methods. By providing access to a precise quantification of morphological and topological characteristics of individual illuvial features, the perspective of quantitative micromorphology is furthermore particularly effective at quantifying the relative abundance of papules from which it is ultimately possible to infer the long-term soil reworking by earthworms, at least in illuviated soil horizons.

In the studied cultivated Luvisol, eluviation/illuviation and bioturbation processes have transferred 1,133 and 1,900 t ha⁻¹ of fine fraction respectively (30–160 cm depth) over the past 1,000 to 14,000 years. With a mean annual eluviation/illuviation rate for the past 10,000 years ranging from 0.08 to 1 t ha⁻¹ year⁻¹, eluviation/illuviation appeared to be a significant process of soil loss quantitatively, almost as important as water or tillage erosion. Even if bioturbation seemed to be quantitatively underestimated in this study, bioturbation and eluviation/illuviation were not as much in competition as initially thought. The clay-sized fraction beneath 70 cm depth seemed to be definitively lost. Furthermore, relatively small amounts of the clay-sized soil fraction are transferred upward through bioturbation as revealed by the very low abundance of papules in the E horizon. For that reason, curatively managing the loss of clay-sized particles from surface horizons through eluviation with bioturbation viewed as an ecological engineering solution is limited, at least in intensively managed cultivated soils like in the studied Luvisol. However, farmers could help limit eluviation and/or maximize bioturbation through alternative agricultural practices among which OM inputs, reduced tillage, or permanent soil cover seem particularly promising. Further research is still needed to accurately quantify the effects of these practices on the intensity of the eluviation/illuviation and bioturbation processes. A similar study assessing the bioturbation versus eluviation/illuviation balance in uncultivated soils of similar age to see what agriculture did in addition to natural soil development is thus expected.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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