

Article

Diversity and Micromorphology of Organic Matter in Riparian Forests on Carbonate-Rich Substrate (Switzerland)

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Abstract

The water level of Lake Neuchâtel (Switzerland) was lowered 150 years ago, initiating soil formation and colonization by riparian forests of the previously submerged areas. Although the soils of the whole area are young and have probably quite similar parent material (lacustrine sediments and moraine), the present soils show a large diversity of horizon structures and contents. The aim of this study is to describe the respective processes of accumulation, integration, and stabilization of organic matter and assess the soil variables influenced by these processes in the various types of riparian forests with different moisture levels. The investigation employed a semi-quantitative, holistic approach that combined field observations, laboratory analyses, and micromorphological examination of soil thin sections. The results indicate that the accumulation and stabilization of organic matter are primarily governed by physicochemical factors associated with the parent material, particularly soil texture and calcium cation saturation. Soil moisture and groundwater elevation were found to mainly influence biological activity and vegetation types. Additionally, the incorporation of organic matter is affected by both soil texture and bioturbation processes. Overall, this study underscores the complexity of the mechanisms regulating organic matter dynamics in young soils.

Keywords: pedogenesis; regulated lake; organic matter integration; soil thin section; calcium; forms of carbonate



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1. Introduction

Wetlands play a key role in the carbon cycle, as they contribute to the sustainable storage of organic carbon [1,2]. Although they cover only 3% to 4% of the Earth's surface, wetland soils are conducive to carbon sequestration and are estimated to store between 14% and 30% of soil carbon [3]. The capacity of these ecosystems to accumulate organic carbon varies with climate, soil properties, and water regime [4,5]. In addition, wetlands offer a multitude of ecosystem services and are of considerable ecological importance [6–8]. Unfortunately, these ecosystems are becoming increasingly rare and endangered in Central Europe, not only because of drainage but also because of climate change, which is forecasted to lead to more severe droughts [9,10]. As wetlands are variable [11], this study focuses on riparian forests on carbonate-rich substrate bordering a regulated lake on the Swiss Plateau. The soils of lakeside forests in carbonate environments have been little studied, particularly regarding their different forms of soil carbon, as well as the integration and storage of organic matter [12–14].

The processes involved in organic matter dynamics vary significantly in wetlands and carbonate environments and affect its stored quantity and form [15–17]. Large amounts of organic carbon in ecosystems come directly from vegetation through photosynthesis [18], and riparian forests are among the most productive habitats [19]. According to Cierjacks et al. [20], one of the primary factors influencing organic matter storage is the gradient of geomorphic floodplain dynamics, which can often be inferred from the vegetation structure. However, this relationship no longer holds in regulated riparian ecosystems, where flood dynamics are largely suppressed. Recent research by Siegfried et al. (submitted) demonstrates that ecosystem productivity in such environments shows only a weak correlation with the soil organic matter content.

Under the action of soil organisms, organic matter is consumed, decomposed, respired, and mineralized. All these terms are used to describe the way carbon from organic matter returns to the atmosphere in the form of CO₂ [18]. It has been shown that there is a positive correlation between the amount of litter brought into the ecosystem and the rate of decomposition [21,22]. It has also been observed that organic compounds with high nitrogen contents are degraded more rapidly [23]. When mineralization processes are less efficient, decomposition of organic matter remains limited, and the stock of organic carbon increases. This phenomenon occurs when the quantity of atmospheric CO₂ fixed by the ecosystem exceeds that produced by the consumption of available organic carbon by soil organisms [2]. In young forests, carbon is also stored each year in standing wood [24]. As mentioned above, the major factors influencing mineralization are, first, the amount of organic matter and nitrogen, as well as the temperature, oxygen concentration, soil texture, and pH and the inter-relationships between these parameters [25,26]. Oxygen concentration is usually negatively correlated with moisture, which results in the formation of anoxic zones within the soil when the water content is high. The primary consequence of low oxygen availability is a decrease in respiration, both microbial and root-based, because most organisms use oxygen as an electron acceptor in their metabolism [23]. Some anaerobic prokaryotes use alternative acceptors, but the degradation is slower due to reduced efficiency. However, the relationship between organic matter decomposition and soil water saturation remains complex, and our understanding of it is limited because of the involvement of water in numerous mechanisms and environmental factors that fluctuate across regions and temporal scales [25,27].

Another factor affecting the accumulation of organic carbon is the granulometry of the parental material. Indeed, a fine texture, composed of clay and fine silt, typically promotes stabilization of organic matter, reducing its accessibility to decomposers [28–30]. Moreover, soil texture is a primary determinant of soil porosity, which influences water infiltration and retention [23]. Weak interconnectivity between pores increases microbial diversity by providing more habitats but also reduces the accessibility of organic matter and limits oxygen diffusion [31].

Protection of organic matter in soil is also provided by organo-mineral bonds formed during pedogenic processes, favored by earthworms, which promote integration of organic matter into the mineral matrix by initiating soil structure in young soils [32]. These stabilization mechanisms include aggregation, sorption, and inclusion. In calcium-rich soils, calcium carbonate crystals envelop organic matter in a mineral matrix [33]. The inclusion may be of pedological origin [34] or of biological origin, i.e., due to living organisms [35,36]. However, water saturation can disrupt such mechanisms by destabilizing bonds between soil particles, causing deflocculation of clays and dissolution of cementing agents, such as carbonates [23].

However, living organisms can also be responsible for carbonate precipitation, and generally, bioformed calcium carbonate is less soluble than its physicochemical counterpart

and tends to accumulate in alkaline environments [37]. These calcium carbonate biocrystals can be induced by a biological matrix that promotes crystal nucleation outside cells, allowing organic matter to be included in a crystalline matrix [38] or biologically controlled inside cells, as in the case of mollusk shells [39]. This biomineralization process is common in bacteria and fungi and is also found in calcified spherulites of earthworms [40] and calcified root cells [41].

Pedogenesis in riparian soils is influenced by past and present waterlogging at varying depths [42]. The limitation of gas exchange between the soil and atmosphere can result in a prolonged deficit of oxygen, which not only reduces the biological activity of the soil, but also alters the mobility of certain soil constituents, such as iron, through oxidation-reduction processes [42]. A study conducted in riparian areas along a river in Switzerland revealed that regulation of these systems results in a loss of heterogeneity [12]. Indeed, under natural conditions, regular flooding strongly affects the spatial and temporal variability of carbon content in soils, creating high functional diversity in these ecosystems [12]. These processes have been much less studied in forests along lakes, whose soils have finer textures, than along braided rivers, characterized by coarser substrates.

Although our understanding of the mechanisms governing the dynamics of organic and inorganic carbon has advanced significantly in recent decades—especially concerning the influence of ecological conditions—some uncertainties persist [33]. In particular, the roles of carbonates and calcium in preserving organic matter in humid environments remain largely overlooked. Previous studies were mostly conducted in dry or humid conditions and emphasized the importance of the calcium ion to stabilize organic matter by ligand exchange, chelation, and cation bridging, all these processes being involved in organic matter occlusion and sorption [33]. But a similar influence of calcium was not addressed in wet or saturated soil conditions. In addition, edaphic processes occur at various spatial and temporal scales, from the landscape to the soil surface and across soil horizons [43–45]. Therefore, understanding the mechanisms responsible for organic matter dynamics requires a multiscale approach and the use of multiple methods. Micromorphology, the study of soil thin sections, allows for visualization of organic matter within the soil matrix, as well as its integration/relationship with mineral matter, various forms of inorganic carbon, and bioturbation. This method completes field descriptions and laboratory analyses by providing additional spatial and microscale information. Consequently, this study aims to provide a multifaceted approach to understanding riparian forest soils in carbonate-rich conditions. More specifically, it aims to better understand (i) how carbon accumulates in riparian forest soils along a lake; and (ii) what can be the variables explaining the variations observed in the quantity, stability, and integration of organic matter in such soils.

The study hypothesis suggests that there is greater organic matter accumulation in wetter forests, where soils are saturated with water for most of the year [46]. It can be tested as follows: in addition to waterlogging, the amount of nitrogen and calcium cations, as well as soil texture, must also influence the stability of organic matter by providing better stability in soils with low nitrogen, enriched in calcium cations, and with a more clayey texture [12]. The presence of ecosystem engineers, such as earthworms, can favor the construction of the organo-mineral complex, and thus the integration of organic matter into the mineral matrix [47]. To assess the hypothesis, laboratory analyses were associated with micromorphological observations to identify the different forms of organic and inorganic carbon. To conclude, this study attempts to fill a gap in the existing literature by providing an in-depth and multiscale analysis of organic and inorganic carbon associated with organic matter in riparian forests on a carbonate substrate.

2. Materials and Methods

2.1. Study Site

The Grande Cariçaie nature reserves are in Switzerland on the southern shore of Lake Neuchâtel at 430 m.a.s.l. (Figure 1). It is the largest lake swamp area in Switzerland (2532 ha), including 647 ha of riparian forests [48]. These forests are located on land that has emerged since 1878, following a large regulation project that lowered the lake level by 2.7 m [49]. The first forests appeared in the 1930s, but most of them began to develop from the 1950 to the 1960s, following a second phase of regulation, which reduced lake level variations [8,49]. The climate is temperate, with a mean annual precipitation of 854 mm and an average annual temperature of 9.8 °C (maximum monthly average in July of 19.3 °C and minimum of 0.9 °C in January; 1990–2020 average, data for Payerne, 490 m.a.s.l. 8 km from the lake; www.meteosuisse.ch).

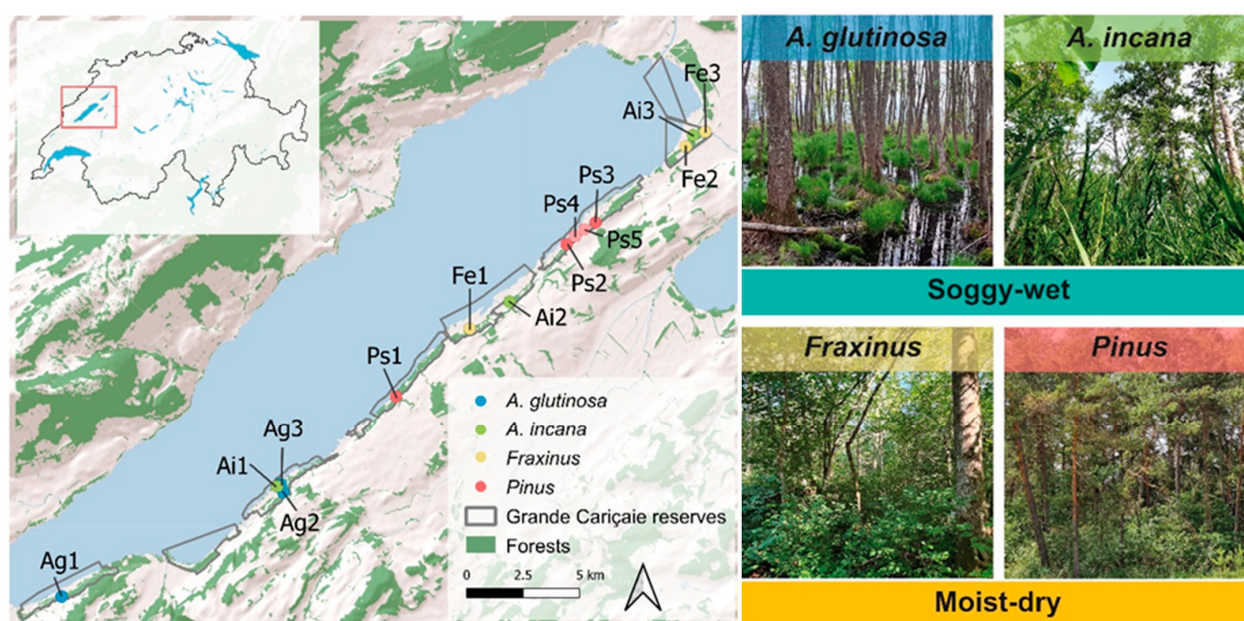


Figure 1. Spatial distribution of the Grande Cariçaie reserves located along the shores of Lake Neuchâtel (Switzerland; background map: Esri Topo; forest: Swisstopo) and the location of the stations. On the right, illustration of the plant communities, classified according to the species composition [8] and in two moisture classes (precise locations provided in the Supplementary Materials Section S1). Forest type abbreviations according to the dominant tree species: Ag, *A. glutinosa* forests; Ai, *A. incana* forests; Fe, *Fraxinus* forests; Ps, *Pinus* forests.

The southern shores of Lake Neuchâtel are mainly formed by Tertiary alluvial deposits from the Alps at the origin of the lower freshwater Molasse (Aquitanian and Burdigalian; map.geo.admin) [48]. This was eroded by glaciers in the Würm period, which created Lake Neuchâtel and left a thin moraine, attested to by some erratic blocks. These sediments were completed by the material that issued from erosion of the Molasse cliffs, still overhanging the alluvial zone. The parental material of the soils is now a mixture, with variable respective contributions of moraine and sediments liberated by molasse erosion, completed by loose, carbonate-rich lacustrine deposits [48].

The study site has a well-established historical timeline, with extensive information already available from previous research, particularly regarding vegetation and hydrology [8,48]. However, gaining a deeper understanding of the soils would provide a more comprehensive view of these ecosystems, especially in terms of how vegetation types may affect soil carbon accumulation.

2.2. Sampling Design, Forest Stand Conditions, and Soil Description

Twelve of the ninety-four stations previously described by Siegfried et al. [8] were selected to represent the diversity of wetland forests in Grand Caricaie. The stations selected were the most representative, based on vascular plant composition. They were classified as belonging to four different riparian forest alliances: three stations in black alder forests (*Alnus glutinosa* (L.) Gaertn.; *A. glutinosa* forests), three in grey alder forests (*Alnus incana* (L.) Moench; *A. incana* forests), three in ash forests (*Fraxinus excelsior* L.; *Fraxinus* forests), and three in pine forests (*Pinus sylvestris* L.; *Pinus* forests; Figure 1). Two supplementary stations of *Pinus* forests were added for some soil analyses (details in Supplementary Materials Section S1). Piezometric tubes (1 m long) with automatic sensors (Hobo® U20L Water Level Logger, Hobo Data Loggers, Bourne, MA 02532, USA) were installed to record water level variations in these twelve stations, from June 2020 up to April 2024. A soil profile was dug at each station. An auger probe was extracted instead of digging a pit at stations that were too wet. A description of profile horizons was completed in the field using the following parameters: structure, texture (skeleton and fine particle), color (according to the Munsell code), pH (Hellige), reactivity to HCl, proportion of roots, presence of organisms (e.g., earthworms), and depth of the groundwater table. Bulk soil samples were taken by soil horizon for laboratory analyses. Samples were also collected using Kubiëna boxes extracted from not-waterlogged dug soil profiles to produce thin sections for micromorphological analyses [45,50,51]. Soils were classified following the World Reference Base for soil resources [52], based on field observations and laboratory analyses.

2.3. Physicochemical Analyses

Forty-nine bulk soil samples from 12 soil pits (3 in each forest type) were dried at 40 °C and sieved at 2 mm for laboratory analyses. The laboratory analyses were duplicated to improve results. Analyses included (i) grain-size distributions, assessed using a laser Beckman Coulter grain-sizer, with a conventional pre-treatment, i.e., carbonate removal and organic matter oxidation using H₂O₂ [53]; (ii) dominant minerals (not on all samples), measured by X-ray diffraction (XRD; ARL Xtra Thermo); (iii) soil extraction using NH₃Cl to quantify exchangeable cations, and more precisely Ca²⁺ (CEC; protocol in Supplementary Materials Section S2) [54]; (iv) soil pH_{H2O}, measured using a pH meter (Metrohm) after suspension in a 1:2.5 soil:water ratio [53]; (v) total carbon (organic and inorganic) and nitrogen, measured using an Thermo Finnigan Flash EA 1112 elemental analyzer (CHN); (vi) calcium carbonate (CaCO₃), assessed by mass loss during decarbonation (addition of HCl) [53]; (vii) soil organic matter (SOM) content, measured by loss on ignition (450 °C); and (viii) SOM quality, measured by Rock Eval pyrolysis, which provided the amount of total organic carbon (TOC), as well as hydrogen and oxygen indices (HI and OI, respectively), and allowed the generation of two other indices [55] related to the proportion of immature organic matter (I-index) and to its thermoresistance (R-index) from various area parameters (A1 to A5). The horizons were separated according to their organic matter content: horizons were qualified as “organic horizons” when their content in organic matter was >20%, as “mineral horizons” when this content was <5%, and as “organo-mineral horizons” when it was between 5 and 20% (Supplementary Materials Section S3, variable MO-LBI).

2.4. Soil Micromorphology

Twenty-five soil thin sections were made from Kubiëna boxes by the Geology Service of Dr. Massimo Sbrana (Servizi per la geologia, Piombina, Italy). The objective was to target some specific features illustrating the various states of organic matter and forms of calcium carbonate, attesting to biological activity and the integration of organic and mineral

parts into the soil [45,56,57]. Observations were conducted using an Olympus BX54 microscope (objective magnification 20 $\times$, 40 $\times$, 100 $\times$, and 200 $\times$) coupled using an Olympus DP 72 digital camera. A five-point abundance visual scale was used to quantify selected variables in order to compare quantitative laboratory data with thin section observations (NO, not observed; 1, <1%; 2, 1%–10%; 3, 10%–25%; 4, 25%–50%; 5, >50%). Selected variables were used to differentiate the various forms of carbon in the soil, as well as pedoturbations. Organic matter (the largest organic carbon compartment) is found in the soil in recognizable (i.e., recognizable organic tissues) or amorphous form (unrecognizable tissues or organic gels), as well as integrated into the soil mineral matrix. Inorganic carbon is found mainly as carbonate minerals [58]. Carbonate minerals can be inherited from the soil parent material or from freshwater mussel shells or precipitated as pedogenic carbonate features [45]. These have been formed in situ in the soil and can be (i) biospheroids formed by earthworms during the digestion process [45], (ii) microsparite, which is carbonate grains between 5 and 20 μm , formed by cement precipitation or biospheroid shattering, or (iii) micrite, a crystal phase <4 μm [57]. Bioturbation can also be observed through the abundance of earthworm burrows, the passage of roots, and the presence and abundance of fecal pellets, representing the excrement of mesofauna. The integration of organic matter has been described according to four categories: no mineral (pure organic matter), side-by-side, integrated, and mostly mineral (Figure 2).

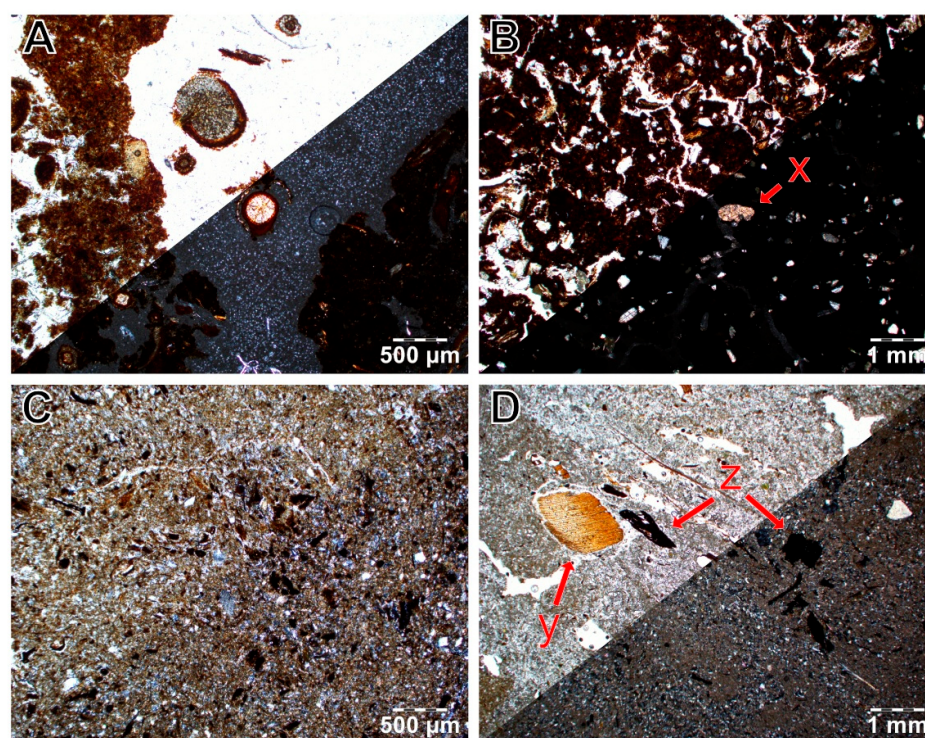


Figure 2. Illustration of the four classes of organic matter integration through micromorphological observations in soil thin sections. Each microphotograph was cut in half diagonally, with the top left section in plane-polarized light (PPL) and the bottom right in cross-polarized light (XPL). (A) No mineral: it is almost all organic matter, with root cross-sections and an amorphous organic phase (horizon Ag3.1). (B) Side-by-side: organic matter (dark patches) juxtaposed with minerals (bright spots). Most mineral grains are sand-sized quartz. There is a grain of inherited carbonate (x) in the middle (brown orange under XPL; horizon Ai1.1). (C) Integrated: organic matter mixed with mineral groundmass. In this horizon, the mineral matrix is silt loam (Ag1.1). (D) Mostly mineral: the scarce organic matter is often in a recognizable form, sometimes with small traces of an amorphous phase. In this thin section, there are fragments of plant cells (y) with pieces of charcoal (z) in a sandy loam-textured mineral groundmass (Fe2.4).

2.5. Data Processing

A moisture index and categories were created based on the median of the groundwater level (Supplementary Materials Section S4), calculated on the mean daily water level. The moisture index is the median value for each station over the entire measurement period. The stations were considered soggy-wet when the median of the water table was >-0.15 m and moist-dry when the median was <-0.25 m. The thermal stability of the organic matter was assessed using the I and R indices calculated from the pyrogram curves resulting from Rock Eval pyrolysis [59]. Total inorganic carbon (TIC) was calculated using total carbon (measured with the elemental analyzer, CHNS) minus TOC (Rock Eval; Supplementary Materials Section S5). Boxplots were generated using the `boxplot()` function from Borcard et al. [60] (associated with a Kruskal–Wallis test and its corresponding post hoc comparisons). A correlation matrix (Spearman) was used to identify relationships between variables (Supplementary Materials Section S6). Principal coordinate analysis (PCA function in FactoMineR library) with data imputation was used to illustrate links between environmental variables and soil characteristics. To determine whether there were differences among the different groups (i.e., moisture category, forest type, soil class, and horizon type), the Kruskal–Wallis test was applied, as well as the Dunn test as a post hoc test. Random forest analyses (`randomForest` function in `randomForest` library) were performed to determine the most important variables for organic carbon quantity (TOC) and organic matter stability (R-index). Finally, a second correlation matrix was built with laboratory data and micromorphology observations to explore how the physicochemical characteristics are reflected in the soil micromorphology. All the variables used in this study are listed in Supplementary Materials Section S3. Statistical analyses were performed with R software, version 4.3.2. (R Core Team 2017).

3. Results

3.1. Soil Diversity

The soils of the riparian forests in the Grande Cariçaie Reserves were strongly influenced by water. According to IUSS Working Group WRB [52], they were divided into classes of Gleysols (eight stations), Stagnosols (two stations), and Fluvisols (four stations; Table 1; Supplementary Materials Section S7). Gleysols are characterized by reducing conditions due to prolonged saturation by groundwater [52]. They were found in *Alnus* and *Fraxinus* forests. Stagnosols are defined by their stagnic properties due to saturation with water from the surface, which leads to reducing conditions during a part of the year [52]. In the Grande Cariçaie reserves, these soils were observed at stations with a high clay content ($>20\%$ of the fine fraction) and an impermeable rock layer at depth. They were found in both *A. glutinosa* (Ag1) and *Pinus* (Ps1) forests. Finally, Fluvisols were soils derived from fluvial materials that did not meet the criteria of the two other soil classes. Some qualifiers were applied to these soils, such as “Orthofluvic” (having fluvial material) and “Bathycalcaric” (having a high proportion of inorganic carbon at depth) [52]. Other qualifiers applied to some soils, such as “Humic” or “Histic” [52], indicate a significant amount of organic matter. The five soils in the *Pinus* forests had the qualifier “Leptic” due to an impermeable molasse layer at a depth of around 40 cm. This classification did not propose traits for some specific soils observed in the Grande Cariçaie, such as Paleosol in a *Pinus* forest (Ps1) and a drained Histic horizon in a *Fraxinus* forest (Fe3), due to the lowering of the lake. Therefore, the forest type and moisture categories did not directly correspond to the soil type, even at the level of qualifiers (Supplementary Materials Section S7).

Table 1. Soil properties according to their moisture content and the forest group, with their main quantitative characteristics by horizons. Mineral grain size distributions were not measured for organic horizons. All results from laboratory analyses are provided in Supplementary Materials Section S3.

Quantitative Range of Soil Values by Horizon Type												
	n	Gleysol	Stagnosol	Fluvisol	Horizon	pH	TOC	R Index	Nitrogen	Calcium Cation	TIC	Clay and Fine Silt
Soggy-wet	3	2	1		Organic	5.11–7.65	11.5–46.9	0.47–0.495	0.96–3.03	27.9–56	1–5.8	-
					Organo-mineral	7.68–9.15	4.6–5.2	0.526–0.56	0.32–1.01	29.7–31.1	1.2–2.2	17–71
					Mineral	8.11–9.12	0.1–1.3	0.617–0.665	0.01–0.48	9.2–17.7	1.7–2.8	25–95
	3	3			Organic	6.17	24.7	0.538	1.9	54.1	1.1	-
					Organo-mineral	7.57–8.16	2.6–6.6	0.492–0.745	0.17–0.43	21.9–36.6	0.3–1.1	19–64
					Mineral	8.38–8.92	0.1–0.5	0.659–0.683	0–0.03	7.5–17.7	2.6–4.2	5–26
Moist-dry	3	3			Organic	7.48	11.7	0.556	0.78	46.1	0.3	-
					Organo-mineral	8.09–8.34	1.3–2.7	0.515–0.693	0.14–0.27	19.5–22.7	0.3–2.6	30–65
					Mineral	8.33–8.83	0.1–1.9	0.569–0.669	0–0.16	10.2–20.4	2.6–4.4	29–32
	5	1	4		Organo-mineral	6.92–8.3	0.5–7.3	0.521–0.679	0.06–0.85	16.4–27	0.2–3	41–99
					Mineral	8.46–9.09	0–1.3	0.557–0.682	0.04–0.31	7.8–19.5	0.7–2.7	26–96
												0–56

Column explanations: n, number of stations; Gleysol, Stagnosol, Fluvisol, number of soil classified in each category; Horizon, type of horizon; pH, pH_{H2O}; TOC, Total organic carbon [%] measured with Rock Eval pyrolyzer; R index, indice from Sebag et al. [55], proportion of thermoresistant organic matter, measured with Rock Eval pyrolyzer; Nitrogen, Total nitrogen [%], measured with a CHNS analyzer; Calcium cation, Calcium cationic exchange capacity [cmol/kg], measured with an ICP-OES; TIC, Total inorganic carbon [%], calculate from total carbon excluding organic carbon; Clay and fine silt, Grain size between 0 µm and 20 µm, measured with a laser granulometry on fine soil [%]; Sand, Grain size between 50 µm and 2 mm, measured with a laser granulometry on fine soil [%].

Table 1 summarizes the main variables, listed by forest and horizon types (detailed in Supplementary Materials Section S3). The pH was lower in the surface horizons, with a minimum of 5.1 in an organic horizon from an *A. glutinosa* forest (Ag3), and was alkaline in deep mineral horizons (a maximum of 9.1 also in a *A. glutinosa* forest; Ag1). Organic matter, evaluated by total organic carbon (TOC), organic matter stability (R-index), and total inorganic carbon (TIC), was not significantly different among vegetation types, moisture categories, and soil classes (Supplementary Materials Section S8). Total nitrogen was strongly correlated with TOC (correlation coefficient, $r = 0.96$; Supplementary Materials Section S6). Regarding exchangeable ions, calcium was the most abundant, followed by manganese. The concentrations of potassium, sodium, phosphorus, iron, and aluminum were negligible (Supplementary Materials Section S3). Textures of organo-mineral and mineral horizons were highly variable, with horizons ranging from a clay fraction of 23% to a sand fraction of 92%. However, most of the soils had a texture between sandy loam and silty loam (according to the USDA; Supplementary Materials Section S9).

Principal component analysis (PCA; Figure 3) showed no significant difference between the two moisture categories (Figure 3A). Moreover, statistical relationships among soil, vegetation, and soil type variables remained weak (Figure 3C). Significant differences at the soil level were only observed in forest types between *Pinus* and *Fraxinus* forests (in Dim2, $p = 0.0095$). In terms of soil class, Gleysols were significantly different from Stagnosols (in Dim2, $p = 0.0048$) and marginally significantly different from Fluvisols (in Dim2, $p = 0.055$). Finally, in terms of horizon type, mineral horizons were significantly different from organic and organo-mineral horizons (both in dim1, $p < 0.001$). The organic and organo-mineral horizons were marginally significantly different (in Dim1, $p = 0.052$; Supplementary Materials Section S8).

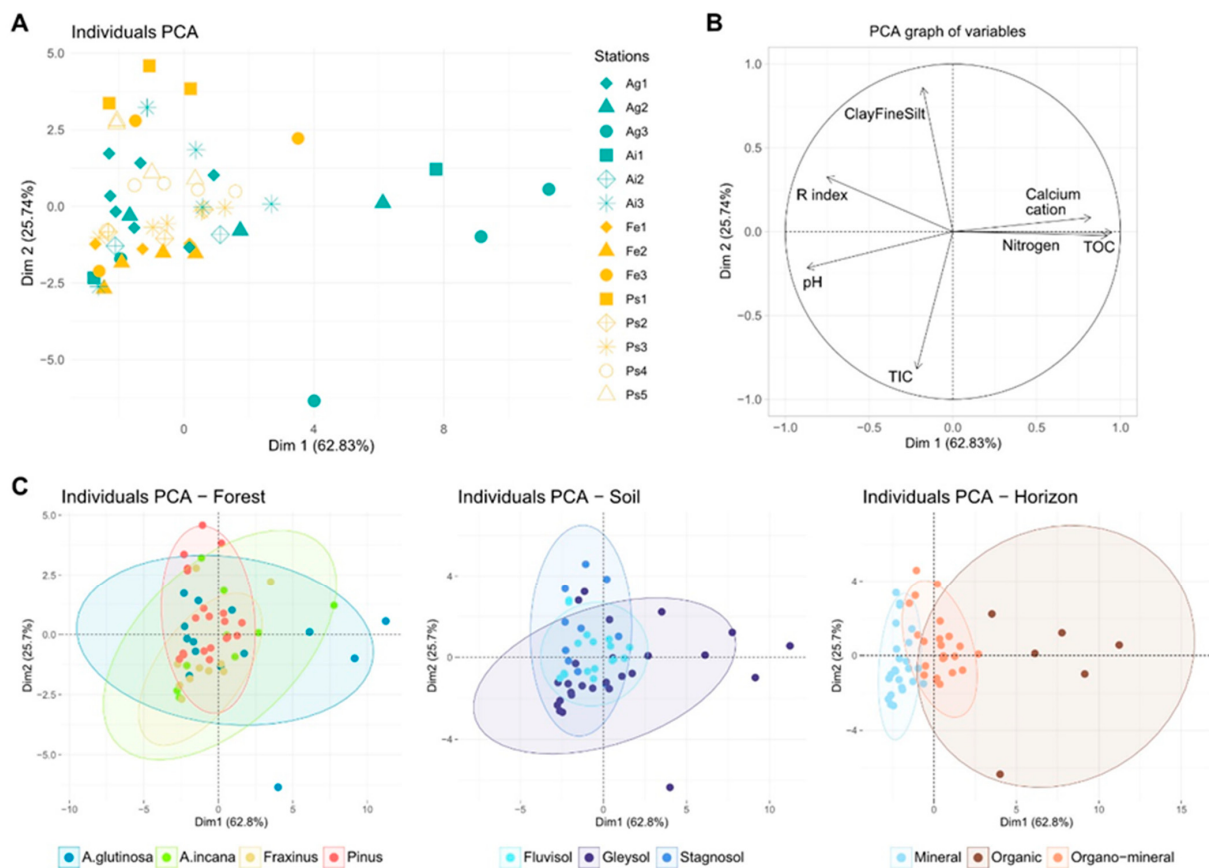


Figure 3. (A) Principal component analysis (PCA) based on physicochemical characteristics, with stations plotted using their moisture index (blue for soggy-wet, yellow for moist-dry) and station type (symbols; abbreviations as in Figure 1) and (B) variables plotted on the circle of correlation. (C) The three graphs below show the same PCA with the distribution and concentration of the stations according to vegetation, soil, and horizon type. The ellipses are of Student type.

Table 2 contains semi-quantitative observations of thin soil sections. Some variables differed according to forest type, such as the abundance of recognizable ($p = 0.021$) and amorphous ($p = 0.049$) organic matter and the abundance of fecal pellets ($p = 0.034$). *A. glutinosa* forests had the highest visual abundance of these three variables, whereas *Fraxinus* forests had the lowest. The visual abundances of micrite ($p < 0.001$) and earthworm burrows ($p < 0.001$) were higher in moist-dry forests than in soggy-wet forests (Supplementary Materials Section S10). There was a significant difference in visual abundance of organic matter (recognizable and amorphous), root passages, fecal pellets, shells, and micrite depending on horizon type. Mineral horizons had significantly less recognizable ($p = 0.004$) and amorphous ($p < 0.001$) organic matter, root passages ($p = 0.006$), and fecal pellets ($p = 0.002$). In contrast, they had a higher micrite abundance ($p = 0.044$). Organo-mineral horizons had significantly more shells ($p = 0.033$; Supplementary Materials Section S10). Additionally, some visual abundance variables were correlated. The main ones were earthworm burrows and micrite ($r = 0.770$), recognizable and amorphous organic matter ($r = 0.674$), microsparite and biospherulite ($r = 0.689$), and recognizable organic matter and fecal pellets ($r = 0.762$; Supplementary Materials Section S11).

Table 2. Results of the micromorphological observations of thin soil sections, according to a visual abundance scale from 1 to 5: NO, not observed; 1, $\leq 1\%$; 2, 1%–10%; 3, 10%–25%; 4, 25%–50%; 5, $\geq 50\%$. Stations are listed according to forest type (see abbreviations in Figure 1).

Station	Soil Type	Horizon Type	N°	Organic Matter		Carbonate					Bioturbation			MO Integration
				Recognizable	Amorphous	Pedogenic			Inherited		Earthworm Burrow	Root Passage	Faecal Pellets	
						Biospheroids	Microsparite	Micrite	Rock	Shell				
Ag1	Stagnosol	Organo-mineral	Ag1.1	3	4	NO	NO	4	5	2	NO	2	2	Integrated
Ag2	Gleysol	Organo-mineral	Ag2.2	5	4	NO	NO	1	1	NO	NO	3	1	Side-be-side and Integrated
Ag3	Gleysol	Organic	Ag3.1	5	4	NO	NO	NO	NO	1	NO	2	3	No Mineral
Ai1	Gleysol	Organic	Ai1.1	4	5	NO	1	NO	2	NO	NO	3	2	Side-by-side
		Mineral	Ai1.2	1	NO	NO	NO	NO	4	NO	NO	1	NO	Mostly Mineral
Ai2	Gleysol	Organo-mineral	Ai2.1	2	3	2	1	1	3	2	2	3	NO	Integrated
Ai3	Gleysol	Organo-mineral	Ai3.1	3	3	1	1	NO	2	3	NO	4	1	Side-by-side
		Organo-mineral	Ai3.2	2	3	1	1	NO	4	1	1	2	NO	Side-by-side
Fe1	Gleysol	Organo-mineral	Fe1.1	2	2	2	2	5	4	2	5	2	1	Integrated
		Organo-mineral	Fe1.2	1	2	2	2	5	4	1	3	2	NO	Integrated
Fe2	Gleysol	Mineral	Fe1.3	1	1	NO	3	4	4	1	4	2	NO	Mostly Mineral
		Organo-mineral	Fe2.1	2	2	3	3	5	3	2	4	2	1	Integrated
		Mineral	Fe2.2	2	1	3	2	5	3	2	5	3	1	Mostly Mineral
		Mineral	Fe2.3	1	1	2	3	5	3	2	4	2	NO	Mostly Mineral
		Mineral	Fe2.4	2	1	2	3	5	4	2	5	1	NO	Mostly Mineral
		Organic	Fe3.1	2	5	NO	NO	2	1	NO	3	3	1	Side-by-side and Integrated
Fe3	Gleysol	Organo-mineral	Fe3.2	1	2	NO	NO	5	2	NO	3	2	NO	Integrated
		Mineral	Fe3.3	2	2	NO	NO	5	4	NO	4	1	NO	Integrated
Ps1	Stagnosol	Organo-mineral	Ps1.1	3	3	NO	1	3	1	1	5	3	2	Integrated
		Organo-mineral	Ps1.2	2	2	NO	1	3	2	2	4	4	1	Integrated
Ps2	Fluvisol	Organo-mineral	Ps2.1	2	2	NO	NO	3	2	2	3	2	1	Integrated
		Mineral	Ps2.3	1	1	NO	NO	4	1	NO	2	NO	NO	Mostly Mineral
Ps3	Fluvisol	Organo-mineral	Ps3.1	4	2	2	1	3	3	1	4	2	2	Integrated
		Organo-mineral	Ps3.3	2	2	2	1	3	2	1	3	2	2	Integrated

3.2. Soil Organic Matter

Organic matter was higher at soggy-wet than moist-dry stations for organo-mineral horizons ($p < 0.02$). There was no significant difference in the mineral horizons (Figure 4). When only considering the topsoil horizons (organic and organo-mineral), *A. glutinosa* forests had the highest organic carbon content, and *Pinus* forests had the lowest ($p = 0.009$). The results from the random forest analysis showed that nitrogen, pH, and calcium cations were important explanatory variables to explain the organic matter content, whereas moisture index, calcite content, and TIC were moderately important explanatory variables (Supplementary Materials Section S8).

The level of stability of organic matter can be assessed using the R-index [59] from various area parameters (A1 to A5; Supplementary Materials Sections S3 and S12). Because Rock Eval pyrolysis cannot analyze samples containing $<0.2\%$ organic matter, some samples were excluded from direct measurement. To retain these data, R-indices of these samples were instead modelled using TOC values (see Supplementary Materials Section S13). There was no significant difference between the type of moisture category or forest type and R-index (Figure 4). However, the R-index was significantly higher in mineral horizons ($p = 0.022$). The random forest analysis retained TOC, nitrogen content, and pH as important explanatory variables for the R-index, whereas TIC, fine sediments (clay and fine silt), and calcium cation content were considered moderately important explanatory variables (Supplementary Materials Section S8).

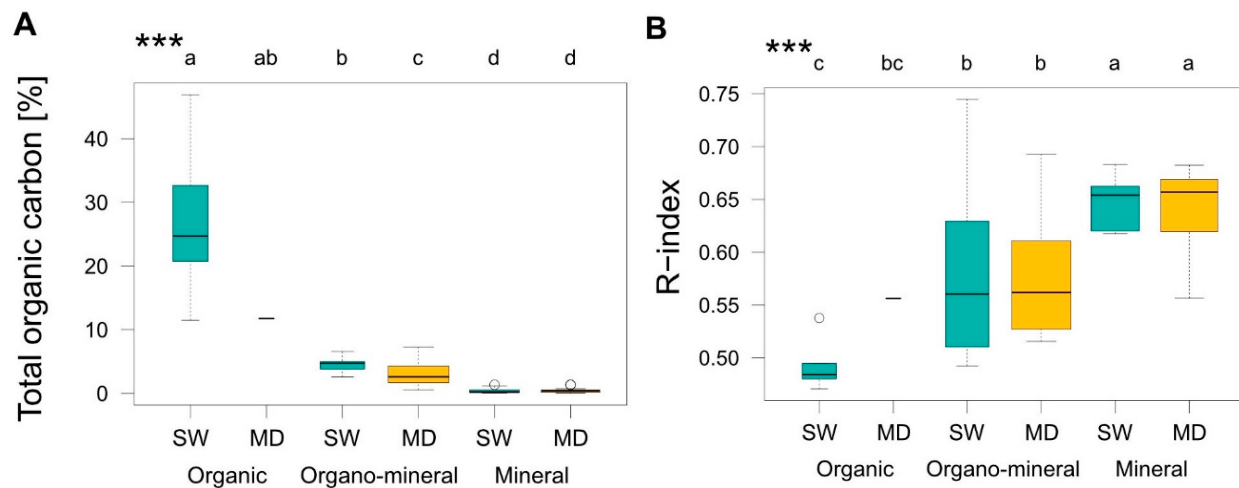


Figure 4. (A) Distributions of total organic carbon (TOC %) and (B) R-index from Rock Eval pyrolysis (characterizing the importance of thermoresistant organic matter), according to the type of horizon and to the moisture class (soggy-wet in blue, moist-dry in yellow). According to the Kruskal–Wallis test, the statistics of the TOC and the R-index are significantly different in the three horizon types (p -value < 0.001), as well as according to the moisture class for the TOC in the organo-mineral horizons (p -value < 0.001). The boxplot width was proportional to the number of samples: 5, 1, 8, 16, 10, or 14. The black line indicates the median, whereas the limits of the boxes refer to the first and third quartiles. The stars indicate the significance of the differences among groups for each environmental variable (***) if p -value is < 0.001. Letters indicate which group means are significantly different, with post hoc comparison, with an alpha threshold of 0.05 [60].

3.3. Integration of Organic Matter into the Soil

Four types of cohabitation between organic and mineral matter were observed in thin sections (Table 2). Two are the extremities of the organic matter gradient, i.e., when one of the two components is missing: the “no mineral” type (Figure 2A), when only organic matter is present in the soil surface, and the “mostly mineral” type, predominantly observed in the deep horizons, with only rare inclusions of organic matter, usually recognizable tissues, such as roots or charcoal (Figure 2D). In addition, there are two other types of structural interactions: “side-by-side”, with mineral grains randomly distributed in a groundmass of amorphous organic matter (Figure 2B), and full integration of organic matter into the mineral soil groundmass, forming a organo-mineral complex (Figure 2C). A significant difference exists between the soil texture and the type of integration. For example, organic and mineral matters remain juxtaposed (“side-by-side”) when the sand fraction reached or exceeded 70% ($p = 0.013$) or are integrated into one another when the texture is finer ($p = 0.009$). The saturation in calcium cation ($p < 0.001$) and pH ($p = 0.002$) also influenced the type of integration, while moisture type had no significant effect.

Micromorphology also highlights the effects of bioturbation in these soils. For example, earthworm burrows (as well as underground casts; Figure 5A–C), passage of roots (Figure 5D), and the presence of fecal pellets (Figure 5E,F) were signs of bioturbation. This is clearly illustrated in Figure 5C, where an earthworm brought some soil fragments from a surface horizon to a deep horizon. Earthworm traces are less present in the horizons with “side-by-side” interaction than in “integrated” and “mostly mineral” interaction ($p = 0.016$). Fecal pellets were less observed in mineral horizons than in organic-rich horizons ($p = 0.017$). Moreover, the root passages were moderately significant. They were rarer in the deep horizons, which were predominantly mineral, than in the organo-mineral horizons ($p = 0.05$).

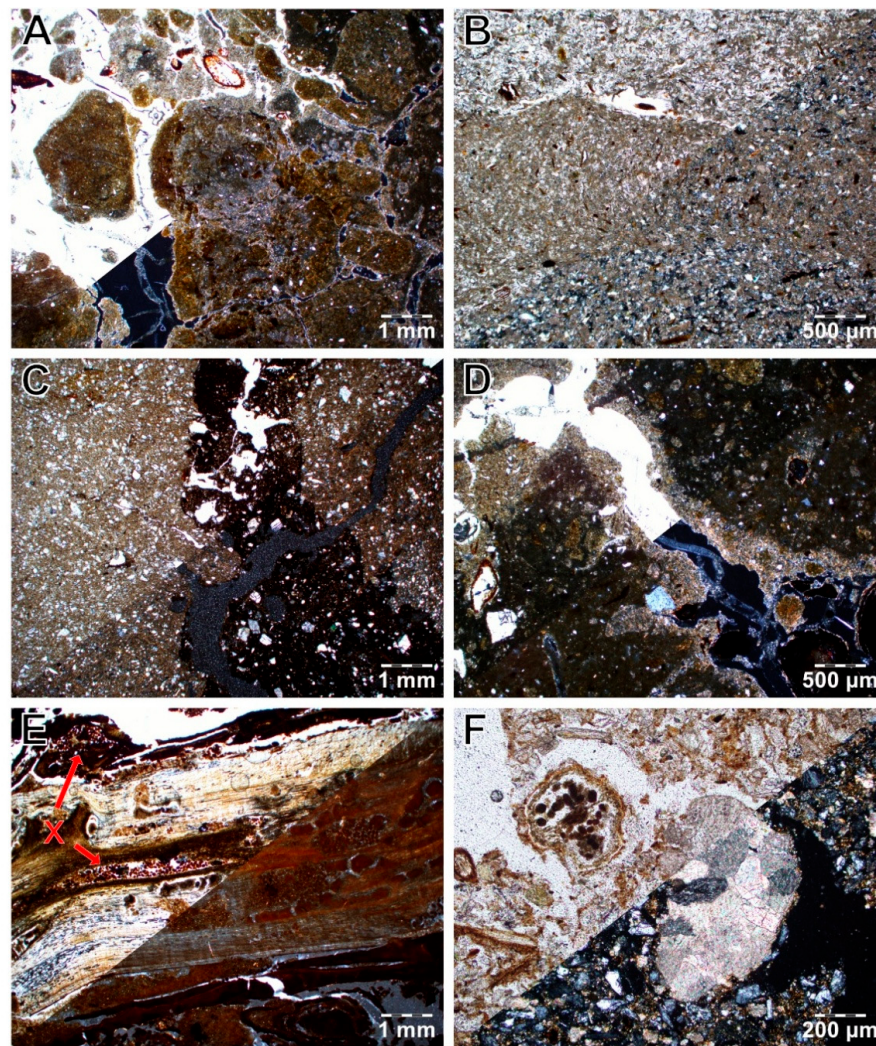


Figure 5. Micromorphological illustrations of bioturbation features. Each microphotograph was cut in half diagonally, with the top left section in plane-polarized light (PPL) and in the bottom right in cross-polarized light (XPL). (A) Earthworm casts (Ps1.2). (B) Earthworm burrow in a mineral horizon (Fe2.4). (C) Vertical earthworm burrow, filled with soil groundmass from the overlying organic horizon (Fe3.2). (D) Former root passage, surrounded by a depleted hypocoting. This pedoturbation is linked to water infiltration, depletion of iron oxides, and clay shrinkage, favored by root passage (Ps1.2). (E) Fecal pellets (arrows x) inside a longitudinal section of a root (Ag3.1). (F) On the left, fecal pellets inside a cross-section of a root and, on the right, a calcitic biospheroid from an earthworm (Fe2.1).

The total organic carbon was strongly correlated with the observation of amorphous organic matter ($r = 0.692$) and much less with recognizable organic matter ($r = 0.457$). This is partly because recognizable organic matter elements > 2 mm were removed when the samples were sieved before analysis. Amorphous organic matter was also strongly correlated with the amount of calcium cations (0.852) and nitrogen (0.617). It was also negatively correlated with pH (-0.678) and TIC (-0.552 ; Supplementary Materials Section S11). There was more organic matter in the side-by-side integration type than when the organic matter was integrated into the organo-mineral complex. The forms of inorganic carbon were correlated with the observations of micrite (0.527; Figure 6E–H) and, to a lesser extent, with inherited carbonate minerals (0.459; Table 2). The abundances of biospheroids ($r = 0.223$; Figures 5F and 6C), microsparite (0.235; Figure 6D), and shells (0.055; Figure 6A) did not seem to have a significant influence on the amount of total inorganic carbon. The

moisture index negatively influenced the abundance of earthworm burrows (-0.754) and micrite (-0.712 ; Supplementary Materials Section S11).

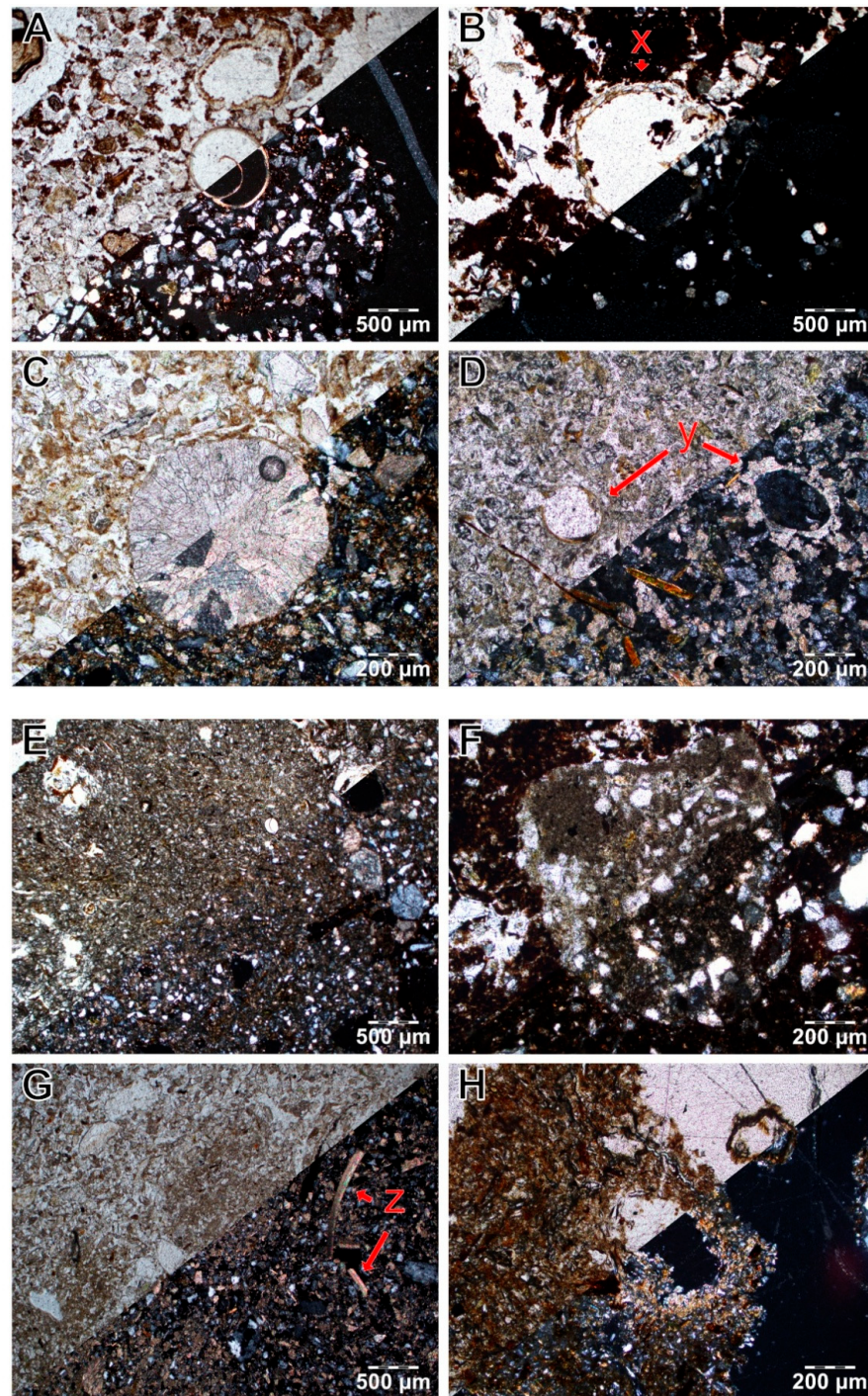


Figure 6. Micromorphological illustrations of the different forms of carbonate. Each microphotograph was cut in half diagonally, with the top left section in plane-polarized light (PPL) and in the bottom right in cross-polarized light (XPL). (A) Shell of a mollusk, probably from the Planorbidae family (Ai3.1). (B) Section of root with calcified cells (arrow x; Ai3.1). (C) Calcitic biospheroid from an earthworm (Fe2.1). (D) Microsparite rich matrix, with two sections of shell on which calcite has crystallized (arrows y; Fe1.3). (E) Brown-grey micritic micromass under XPL (Fe3.3). (F) Pedogenic carbonate nodule formed by micritic aggregates (Fe3.1). (G) Impregnation of the groundmass by secondary calcium carbonate. On the right, under XPL, fragments of mollusk shell (arrows z; Fe2.3). (H) Carbonate coating (Ps3.1).

4. Discussion

On one hand, the soils of the riparian forests of the Grande Cariçaie were characterized by a strong influence of water, which determines both biological activity and vegetation [8,21]. On the other hand, the parental material strongly influenced the accumulation, integration, and stabilization of organic matter (Figure 3C).

Therefore, the discussion section is organized as follows. It begins by exploring soil diversity within these forests to set the context for subsequent analysis. Next, it examines the primary mechanisms that regulate organic matter—specifically its accumulation, integration, and stability in the soil. The discussion then considers how time and parent material influence pedogenesis, emphasizing their significance in soil development. Finally, the section concludes with a critical assessment of the study's limitations, providing perspective on the findings.

4.1. Evolving Patterns of Soil Diversity

Soils differ because of their local history, sometimes with pedogenic processes that have changed over time. For example, the soil at station Fe3, Gleysol, had a highly rich organic first horizon that formed in a calm waterlogged environment before the lake level was lowered. Consequently, this first organic horizon is a relic of the marshy history of the region. The input of organic matter now occurs in a completely unsaturated (vadose) and oxic environment. In contrast, the soil at station Ag3, also a Gleysol that was completely waterlogged for most of the year, showed different organic matter accumulation processes. In the past, the soil at station Fe3 must have been similar to that at Ag3.

The soil at Ps2 station, a Fluvisol that appeared after the lowering of the lake in 1878, reflects even older past conditions. This was particularly obvious in thin sections, with the presence of clays resulting from advanced stages of weathering, inherited from a tropical climatic period [61], and incorporating nanocrystals of iron oxide (presumably hematite/goethite) that color clays bright red. The microstructure was also distinctive, with hollow aggregates and significant water movement that led to significant iron redistribution (Figure 7). With these characteristics, one can consider this soil a “Paleosol” [62], with inherited characteristics from previous soil processes.

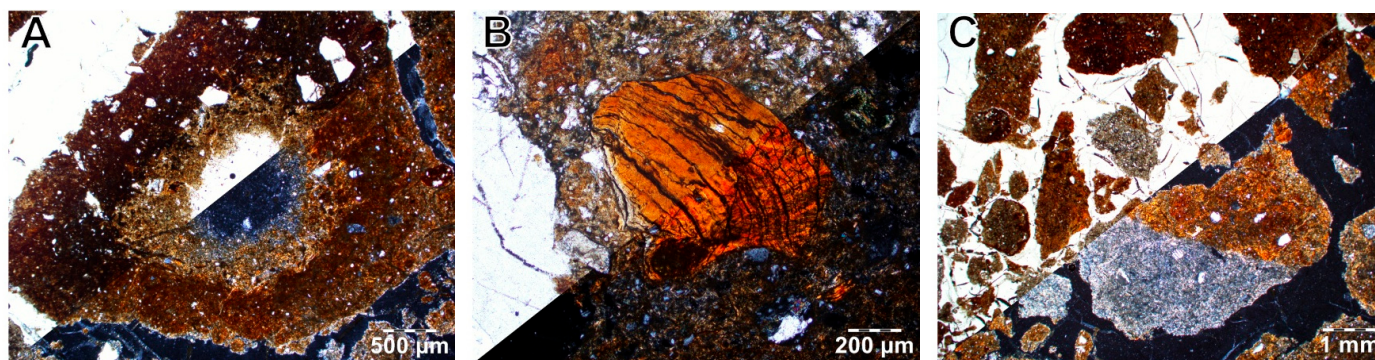


Figure 7. Micromorphological illustration of the Ps2 station “Paleosol”. Each microphotograph was cut in half diagonally, with the top left section in plane-polarized light (PPL) and in the bottom right in cross-polarized light (XPL). (A) Hollow aggregate. (B) Fragment of laminated mineral clay coating, also called “papula”. (C) Only part of the aggregate had been subjected to intensive leaching (white elements, rich in quartz). The other half, orange, is still rich in iron oxide.

Not only did their history point to the special characteristics of these soils, but also their texture. For example, the two Stagnosols were rich in clay, but not enough to be classified as Vertisol [52]. Nevertheless, these clay-rich soils prevent good infiltration of surface water into the soil. Their horizons were easily identifiable by their mottled appearance due to the

reduced and oxidized forms of iron, as the water mainly percolated from the top. At Ps1, as in the other *Pinus* forests, the soil was thin because of the presence of a hard, impermeable molassic bedrock at 27 cm. Rainwater infiltrated the soil, and when it reached the bedrock, it temporarily waterlogged the soil before evaporating or slowly draining it away (the area was very flat). Because the Fluvisols were coarser in texture, the water flowed easily, whereas on Ps1 it flowed very slowly owing to the clay-rich soil. The same phenomenon occurred at station Ag1, except that a small river and runoff from the hinterland delivered the surface water. As a result, the soil was saturated from the surface most of the year but could be damp to almost dry in its deepest layers (field observation).

4.2. Organic Matter Accumulation

The accumulation of organic matter in soils first depends on the amount of organic matter provided to the system through photosynthesis, which is influenced by vegetation type and ecosystem production [17,21]. However, in the forests of the Grande Cariçaie reserves, the relationship between the quantity of litter reaching the soil and the accumulation of organic matter was not very significant [21]. Second, the accumulation of organic matter also depended on what was consumed by soil organisms through their metabolism and what was accessible to them, which influenced the quantity that accumulated in the ecosystem [18]. The distance from the surface influenced the amount of TOC [63]. The further away from the surface and the main source of organic matter, the less there was, resulting in increasing mineral horizons, despite the contribution of organic matter by the roots, as in most soils (Figure 4). According to Schmidt et al. [30], the mechanisms that regulate the rate of organic carbon turnover differ with depth. In organic horizons, it is the recalcitrant nature of organic matter (i.e., its composition) that influences its stabilization, while in deeper horizons, it is more the ecosystem properties. This second point would better explain the variation among forest moisture categories in the topsoil horizons.

In addition to horizon type, it was thus ecosystem conditions that influenced the amount of soil TOC in these forests, namely nitrogen, pH, calcium cation, and moisture. The results showed that the TOC was mainly influenced by the amount of nitrogen. Nitrogen enters the soil in two ways. The first is through recycling of organic matter, since nitrogen is an essential component of plant metabolism, and it returns to the soil during vegetation decay [64]. The second source of nitrogen in the soil is provided by nitrogen-fixing bacteria found in these systems, mainly in symbiosis with alder roots [65]. The last point explains the high amounts of nitrogen present in *A. glutinosa* forests in the topsoil horizons (Table 1). However, this was not observed in *A. incana* forests, which had a nitrogen content in the topsoil horizons like that of moist-dry forests. This could perhaps be explained by the youth of the trees and hence symbiosis, but few studies exist on this subject. Nitrogen can significantly increase the accumulation of soil organic matter by stabilizing soil aggregates within the soil ecosystem, mostly in temperate zones with appropriate rainfall [64,66]. However, this correlation between nitrogen and TOC can also be a co-occurrence, as nitrogen is also a component of organic matter. When organic decomposition is slow, some nitrogen also accumulates in the soil, but a part of it remains inaccessible to organisms because it is trapped within organic matter. Soils with neutral or alkaline pH have the largest and most diverse bacterial populations [23]. However, the activity of soil organisms is highest at neutral pH and decreases above pH 7 [67]. pH influences organic matter accumulation by affecting microbial activity, enzyme function, and stabilization mechanisms. However, in the case of the carbonate soils of Grande Cariçaie, with little difference in pH at the level of the parent material, it seems that the residues of organic matter decomposition would lower the pH and not vice versa (Table 1) [68]. Saturation with calcium also plays an important role in the protection of organic matter through aggregation, sorption, and inclusion [33,69].

As the concentration of calcium cations did not correlate with the amount of inorganic carbon (-0.272 ; Supplementary Materials Section S6), it was probably through aggregation and sorption mechanisms that calcium played its protective role. These calcium cations could come from the groundwater, either from the lake or the hinterland, as well as from the parent material [23,70]. Considering only the surface horizons, moisture influenced the quantity of organic carbon. Indeed, waterlogging of soils induces zones of anoxia that are inaccessible to aerobic decomposers, leading to slower decomposition/oxidation of organic matter [18].

4.3. Organic Matter Integration

Recognizable organic matter is usually transformed by soil organisms over time. Some are mineralized through organism respiration, and some are released as amorphous organic matter when degraded and/or recombined. It is the latter that is integrated into the mineral part of the soil [71]. Integration itself was observed in two of the four categories: either as side-by-side (salt-and-pepper structure) or by integration per se (Figure 2). The differences between these two categories were mainly driven by two variables: texture and bioturbation. Indeed, the texture not only influenced water infiltration, but also the integration of organic matter. Quartz sands favored the juxtaposition of organic matter and mineral phases, while silt-rich textures, with more specific surface areas and more reactive sites, favored the integration of organic matter into the soil mineral matrix [17]. The second variable, bioturbation, referred to soil living organisms, but also to vascular plants through their root activity. This bioturbation depended on moisture, with more macroinvertebrate activity in moist-dry forests (Table 2) [21]. Thin section observations showed that fecal pellets were often found among recognizable organic matter, very often inside roots, independent of the type of moisture (Figure 5E,F). These pellets were produced by soil arthropods that fragment organic matter [56,57]. On the other hand, earthworm burrows were absent or at least less present in the side-by-side class but much more current in the integrated class. They were found at all depths and demonstrated the ability of earthworms to bring organic matter deep into the soil (Figure 5C; observation of earthworms just above the groundwater table at a depth of approximately 70 cm in *Fraxinus* forests). Earthworms were negatively correlated with soil moisture ($r = -0.754$); they preferred moist-dry conditions that did not reduce their respiratory capacity and sandy soils, which affect gallery stability ($r = -0.444$). These results agree with those obtained by extracting earthworms from the same soils [21] and previously in the laboratory [47,72].

4.4. Organic Matter Stability

The R-index was strongly anti-correlated with the TOC. Indeed, the TOC was higher at the surface, where there was the freshest and most labile organic matter [59]. The TOC decreased with depth, where more stable organic matter was found, corresponding to organic compounds that could not be easily decomposed by biological activity [26]. These recalcitrant compounds were found in samples with lower nitrogen and calcium cations, which are two elements that normally protect soil organic matter [33,66]. In addition, soil organisms are less active in soils depleted of these elements, allowing the more thermally stable compounds to persist longer [17].

According to several studies, texture also plays a role in the stability of organic matter and aggregates. Indeed, fine textures have a high specific surface area, which adsorbs organic compounds, offering physical protection by surrounding them, and enhancing aggregate formation [29,69,73,74]. Contrary to previous results, we found no correlation between R-Index and texture (ClayFineSilt $r = 0.277$; Sand $r = -0.196$; Supplementary Materials Section S6), and although random forest considered this

variable as explanatory, it explained only a very small proportion of the variance (Supplementary Materials Section S8).

The I- vs. R-index diagram showed that some organo-mineral horizons had typical characteristics of the organic horizons, meaning that organic matter in these horizons was very labile (Figure 8) [59]. This could be due to the chemical structure of organic molecules and their diversity. Lehmann et al. [26] highlighted the importance of the diversity of organic compounds in the soil, rather than their individual composition. Soil organic matter is formed from a variety of carbon molecules that are sources of energy for soil organisms. These organisms have evolved to exploit these sources with optimal energy efficiency. The diversity of energy sources is susceptible to an increase in decomposition rate, but energy investment also increases with the rarity of the compounds used. Rare compounds are often more concentrated at depth, not because of their chemical composition, but because of their lower concentration at the surface, and therefore the lack of organisms specializing in their degradation. Decomposition of soil organic matter is then no longer just a question of the recalcitrant nature of the compounds; it is more likely a probability that decomposers and substrates can join in the same place and at the same time [26]. In the soils of the Grande Cariçaie, our results showed that the thermal stability of organic matter depends more on its intrinsic chemical composition (low nitrogen content) than on environmental conditions such as moisture (Figure 4B). Although this project did not consider them, other factors such as redox fluctuations and changes in the microbial community may also play a role and cannot be completely excluded as influences.

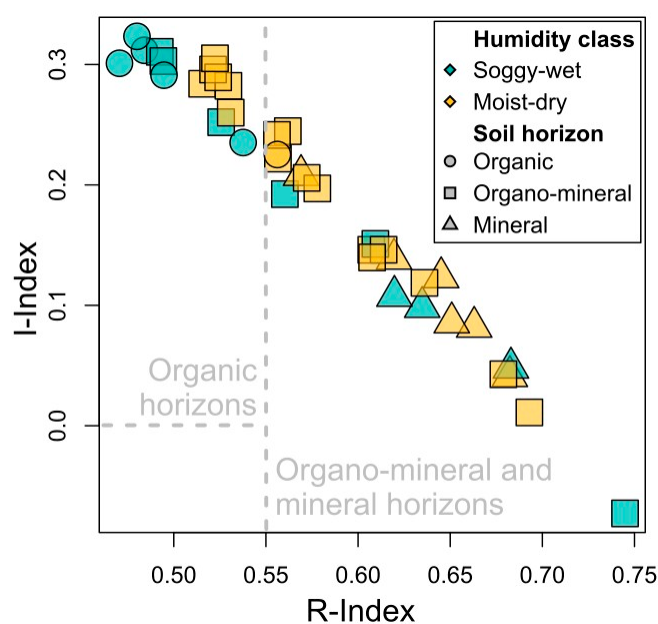


Figure 8. I- vs. R-index plot according to horizon types and moisture classes. Due to machine limitations, indices could not be calculated for samples with a TOC of less than 0.2%, and they do not appear in this graph. Dashed grey lines indicate horizon type boundaries according to Sebag et al. [59].

4.5. Importance of Time and Parental Material on Pedogenesis

The soils in carbonate wetlands are complex, resulting from the interactions among many factors during pedogenesis. Among these, time is one, because pedological processes occur over long periods. It influences soil pedogenesis through a combination of rapid and slow processes that alter soil properties, structure, and chemistry [75]. From this point of view, the soils of the Grande Cariçaie reserves are extremely young, as pedogenesis began at the earliest after the emersion of the former lake beds, approximately 150 years ago [8].

Weak evidence of weathering processes, the supersaturation of calcium cations throughout the soil profile, and the low presence of pedogenic clays confirm the youthfulness of these soils [75]. The clays present in these soils were mostly inherited (Supplementary Materials Section S3). In fact, in particles smaller than 2 μm , kaolinite, smectite, chlorite, and serpentine cannot form pedogenically under temperate condition and in so short a time. However, this is less certain for illite-vermiculite clays, which are the first clays to be formed in temperate and alkaline environments and could already start to form in soils 100–150 years old [23]. This would have to be verified by scanning electron microscopy or dating, but the presence of altered mica fragments in some thin sections suggests that at least some may be pedogenic (Figure 9).

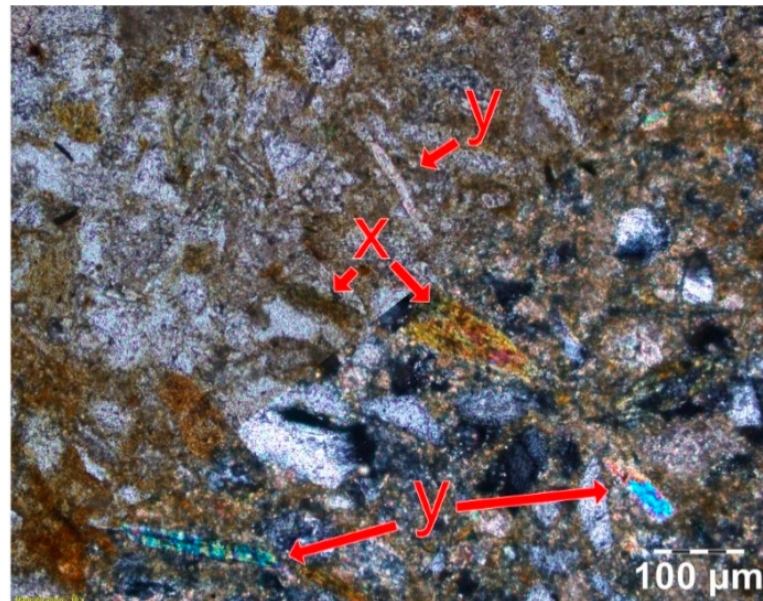


Figure 9. Micromorphological illustration of mica alteration. Each microphotograph was cut in half diagonally, with the top left section in plane-polarized light (PPL) and in the bottom right in cross-polarized light (XPL). Highly altered biotite, brown in PPL and brown-green in XPL (arrows x), and three muscovite, translucent in PPL and bright pink-blue in XPL (arrows y), are visible (Fe1.3; photograph by C. Lugt and C. McMackin).

Despite the recent emersion of lake sediments, there was already significant accumulation of organic matter at some stations, e.g., with a 16 cm thick organic horizon at station Ai1. Similarly, pedogenesis was already pronounced at some stations, especially the moist-dry ones, as organic matter was finely integrated with mineral matter (Table 2). This was made possible by the fine texture of the mineral matrix, which came from the silts and clays of the lake sediments (Supplementary Materials Section S3), as well as efficient bioturbation in these environments (Table 2; Supplementary Materials Section S10) [50,76].

Parental material is also recognized as an important factor affecting pedogenesis and organic matter fate in soils [77]. Parental materials were mainly of fluvial origin [52] and could be highly variable in texture, differently sorted due to the various phases of deposition and reworking by the lake, e.g., through the formation of sand dunes (station Ai1). They were also highly variable in their composition, owing to their diverse origins. Indeed, most of the parental material was transported by water or glaciers and may have come from molasse cliffs overlooking the lake, from the moraine of the Rhône glacier during the last ice age, or from sediments carried by rivers from the Northern Alps or the Jura Mountains [48]. Some soils also contain lacustrine carbonates with shells of freshwater mollusks such as Planorbidae (Figure 6A), Lymnaeidae, and Unionidae [78]. This represents

the inherited part of the carbonate fraction. However, pedogenic carbonates were also present, as secondary phases that precipitated inside these soils. They can be found in the form of biospheroids, microsparite, and micrite, which can be observed as nodules, impregnations, or coatings (Figure 6B–H). Calcium carbonates were omnipresent in various parental materials and were reinforced by lake sediments, providing the necessary primary physicochemical conditions for its precipitation. The vegetation has not yet had time to influence pedogenesis in a decisive way, and it was still parental material that influenced the vegetation, as can be seen in the *Pinus* forests found on the thinnest soils (Supplementary Materials Section S7). Texture also influenced moisture, which is ubiquitous in all these riparian forests, especially in winter, and was well represented by the classification of these soils. The Gleysols were mainly on coarse sandy substrates and were influenced by groundwater close to the surface. Conversely, the Stagnosols were found on soils rich in fine elements, which prevented good water circulation and maintained surface water. Finally, the Fluvisols of these forests had a texture that allowed good water drainage, but as they were shallow on a rock slab, they could undergo periods of waterlogging followed by dry periods, with the water being evaporated, used by plants, or run off at the surface of the impermeable rock (Supplementary Materials Section S4).

4.6. Study Limitations

A major limitation of this study was the difficulty of sampling waterlogged soil. Digging soil pits was challenging due to tree roots, soil collapse, and groundwater-induced mixing horizons. An auger was useful, but it may have compacted some horizons and only provided an estimate of horizon thickness and depth, although the real depth was measured after each extracted sample to situate it at its right location in the reconstituted core. This potential bias can be problematic for soil classification, especially when adding qualifiers. In addition, some horizons were difficult to extract, such as sandy horizons, which had very little cohesion. Furthermore, it was not possible to extract Kubiana boxes from the auger samples, resulting in missing thin sections from more than half of the horizons of the soggy-wet stations. The second important point is the limited number of stations, which reduced the statistical robustness of data processing, impaired by missing values for some variables, such as the texture for highly organic horizons or the R-index for horizons with too low organic matter content. Finally, soil pits were all dug in 2018 for *Pinus* forests and 2021 for the other forests. Even if we assume that soils did not significantly change from one year to another, as pedogenic processes take time to settle [71,75], the water level strongly differed (quite dry in 2018, very high level in 2021), which can lead to changes in features such as iron ion distribution. In addition to this, some processes were practically impossible to identify when the soils were saturated, like aggregate formation and soil structure. Despite these limitations, we are confident that most of the presented processes were correctly described and that the observed differences corresponded to the reality of the soil conditions.

5. Conclusions

This study highlighted the complex aspect of these ecosystems in terms of carbon dynamics. In the context of very young soils (~150 years), pedogenesis is already, and surprisingly, pronounced. The chemical and physical properties of the parent material provide the best explanation for the accumulation and stability of the organic matter. Water has a major influence on these environments, influencing forest type as well as soil organisms (especially earthworms), involving a greater amount of organic matter at soggy-wet stations. On the other hand, humidity seems to have little influence on the thermal stability of organic matter and its integration.

Micromorphology showed that texture and bioturbation were the main elements influencing the integration of organic matter, as well as the presence of multiphased soils. This method provided a structural approach to the soil, which would have not been possible to assess solely with physicochemical analyses. The combination of visual and destructive methods was essential for understanding soils as a multiscale system.

There remain many research opportunities to explore and better understand these complex ecosystems. For instance, studies using carbon isotopes could provide a better understanding of the evolution of the deep organic matter, e.g., by dating it with ^{14}C or by using the fact that, as soil organic matter decomposes and matures, $\delta^{13}\text{C}$ values typically become less negative. Such studies would help to assess soil organic matter turnover and stabilization. The combined measurement of $\delta^{13}\text{C}$ in both organic matter and secondary carbonates would enable clear identification of the carbon source, whether it originates from soil respiration, dissolved inorganic carbon in the water table, or the geological substratum. Moreover, a better detailed analyses of clays and mineral phases would provide supportive appreciation of the role of mineral weathering in organic matter integration processes, leading to the pedogenic evolution of soils in such environments.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f16081203/s1>: Section S1. Station information; Section S2 [79–81]. Protocol for exchangeable cations (CECs); Section S3. Variables; Section S4. Groundwater table variations and moisture categories; Section S5. Comparison of organic and inorganic carbon measurement methods; Section S6. Correlation matrix of the various laboratory variables; Section S7 [82,83]. Soil description; Section S8. Statistical tests; Section S9. Soil texture; Section S10. Statistical analysis of micromorphology data; Section S11. Matrix of correlations with some laboratory and micromorphology data; Section S12. A1 to A5 area contributions; Section S13. Modelling of the NA R-index.

Author Contributions: Conceptualization, L.S., P.V., and E.V.; methodology, L.S.; material preparation, L.S.; data collection, L.S.; formal analysis, L.S.; writing—original draft preparation, L.S.; writing—review and editing, L.S., P.V., and E.V.; visualization, L.S., P.V., and E.V.; supervision, P.V. and E.V. All authors have read and agreed to the published version of the manuscript.

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