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ORIGINAL RESEARCH ARTICLE

From Leaf to Topsoil, a Semi-quantitative Assessment of the Organic Matter Variations in Riparian Forests on a Lake Shore

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Abstract

The water level of Lake Neuchâtel (Switzerland) was lowered 150 years ago, initiating soil formation and plant colonization on the previously submerged lands. Since then, four riparian forest types have been differentiated, with contrasted humidity and soil conditions. This study aimed to describe the processes underlying variations in organic matter (OM) composition and content, and to evaluate the importance of water level on soil development. This investigation was conducted in a semi-quantitative way, using a holistic approach. We measured OM production (wood, dead wood, and annual litter) and OM decomposition rate (tea bag index, soil respiration), and soil macrofauna was inventoried in parallel with descriptions of humus forms. Measured values varied with the plant composition of these forests and with water fluctuations. Two different organic matter pathways characterized the four forest types. Forests with waterlogged soils displayed fast decomposition, low soil respiration, low macrofauna biomass, and water-bound humus forms. Conversely, forests with a low water table showed slower decomposition rates, higher summer respiration rates, higher macrofauna biomass, and Mull-type terrestrial humus forms. Hence, there was a paradox between decomposition rate and respiration, where decomposition was more efficient in the most humid forests, although soil CO_2 emissions were lower than in drier forests.

Keywords Regulated lake · Litter · Decomposition rate · Soil respiration · Soil macrofauna · Water level

Résumé

Le niveau du lac de Neuchâtel (Suisse) a été abaissé il y a 150 ans, initiant la formation des sols et la colonisation des plantes sur les surfaces précédemment submergées. Depuis, quatre types de forêts riveraines se sont distingués, avec des conditions conditions d'humidité et de sol différentes. Cette étude vise à décrire les processus conduisant aux variations de la matière organique (MO) en termes de composition et de quantité, et aussi à évaluer l'importance de l'humidité sur le développement de ces sols. Cette recherche a été menée de manière semi-quantitative, en utilisant une approche holistique. La production de MO (bois sur pied, bois mort et production annuelle de litière) et le taux de décomposition de la MO (indice des sachets de thé, respiration du sol) ont été mesurés, et la macrofaune du sol a été inventoriée parallèlement à la description des formes d'humus. Les mesures ont montré des différences liées à la composition végétale de ces forêts et aux fluctuations hydriques. Les quatre types de forêts ont pemis de distinguer deux voies différentes d'évolution de la matière organique. Les forêts sur sol engorgé et très humide présentaient une décomposition rapide, une faible respiration du sol, une faible biomasse de macrofaune et des formes d'humus liées à l'eau. Inversement, les forêts à nappe phréatique plus profonde étaient caractérisées par un taux de décomposition plus lent, un taux de respiration estivale élevé, une biomasse de macrofaune plus importante et des formes d'humus terrestre de type Mull. Il existe donc un paradoxe entre le taux de décomposition et la respiration, où la décomposition est plus rapide dans les forêts les plus humides, bien que les émissions de CO_2 du sol soient plus faibles, que dans les forêts plus sèches.

Introduction

Wetlands are recognized as a critical link between the aquatic and terrestrial environments (Giese et al. 2000). They provide shelter for biodiversity, improve water quality,

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mitigate flooding, provide resources and regulate the climate (Nakamura 2022; Riis et al. 2020). Moreover, they are of major importance in the organic matter pathways, even though they represent only a tiny part of the Earth's surface (Trettin and Jurgensen 2002). The riparian forests are considered to be carbon sinks (Ofosu et al. 2022; Hanberry et al. 2015; Suchenwirth et al. 2012). Fluxes regarding the carbon cycle in wetlands have already been investigated (Trettin and Jurgensen 2002; Mitsch and Mander 2018), more particularly in riparian forests adjacent to braided streams under tropical climates (Giese et al. 2000; Wigginton et al. 2000; de Souza Rezende et al. 2016; Gonçalves and Callisto 2013). Strongly man-influenced or degraded riparian forests along rivers in Central Europe have also been the subject of concern (Pfadenhauer and Grootjans 1999), leading to restoration projects (Klimo et al. 2008; Hughes et al. 2012). However, riparian forests along the shores of regulated lakes have been scarcely studied (e.g. Wilcox et al. 2005; Siegfried et al. 2024), and the dynamics of their organic matter have been even less investigated. Giese et al. (2000) showed that forests along braided rivers with altered hydrology exhibited modified plant community succession with ecosystem functions converging toward those observable in mature riparian forests along lakes. Despite these previous studies, uncertainties persist (Trettin and Jurgensen 2002). Indeed, quantifying the organic matter compartments and fluxes is quite challenging to assess in its entirety, and even more so in wetlands, due to difficult access and the impossibility of some measurements on waterlogged soils (Suchenwirth et al. 2012; Cierjacks et al. 2011).

Organic matter dynamics in riparian forests proceed similarly to those in other wetland ecosystems, with significant constraints such as water-saturated soils, anaerobic microbial communities and adapted plant species (Trettin and Jurgensen 2002). These parameters modify the distribution and quantity of organic matter, as well as the pathways of vegetation-to-soil decomposition, compared to strictly vadose environments. The organic matter cycle begins with the production of biomass by vegetation. These environments are known to be highly productive and vary according to system hydrology (Mitsch et al. 1991). Riparian forests with flowing water (close to a dynamic stream) have higher net biomass production than those with stagnant water (Brinson et al. 1981). Soil organisms then fragment, transform, and decompose the organic matter. They also participate in its integration into the soil and influence its distribution in the soil profile (Frouz 2018). Macro- and mesofaunal activity is higher in the topsoil than in the subsoil (Brussaard 1998), and it is also higher in ecosystems in transition, e.g., those developing after disturbance (Frouz 2018). In Switzerland, a high density of Enchytraeidae was found in moist acidic soils with a large proportion of organic matter. In contrast, a high diversity of earthworms was observed in young riparian soils (Bullinger-Weber et al. 2007). Humus forms, which represente the habitat of soil decomposers, provide clues to the dynamics of organic matter mineralization and integration and are also considered a tool for investigating the primary interaction between organic matter and minerals (Bullinger-Weber et al. 2007; Le Bayon et al. 2024). This decomposition rate is often highly variable in these riparian ecosystems, even at small scales, and depends more on soil environmental conditions and forest structure than on organic matter composition (de Godoy Fernandes et al. 2021; Schmidt et al. 2011).

However, the influence of water is probably one of the predominant factors, and some studies have emphasized that litter decomposition is usually inhibited when soil water content is >80% (Mori et al. 2021; Petraglia et al. 2019). Several factors control the dynamics of water within soils in riparian forests, including the texture and mineralogy of soil sediments, proximity and fluctuations of the water table, climate (precipitation and temperature), microrelief, and finally vegetation cover and type (Prax et al. 2008). In water-saturated soils, oxygen limitation slows organic matter decomposition, leading to its accumulation (Sahrawat 2004). According to a review by Cunha-Santino and Bianchini Junior (2023), organic matter storage is a more prevalent process than mineralization in submerged soils. Soil respiration, i.e., the flux of CO_2 emitted from the soil, indicates the decomposition rate of organic matter (Brinson et al. 1981) because it partly originates from soil fauna and oxygen-dependent microbial respiration. Next to soil humidity, often related to soil water depth, temperature is also crucial, and decomposition can be slow in anaerobic conditions (Luo and Zhou 2006). However, soil respiration is partly emitted by plant root respiration and by carbonate soil weathering too (Ramnarine et al. 2012). Hence, soil respiration is not directly proportional to organic matter decomposition.

Finally, natural riparian forests exhibit considerable heterogeneity in their structure and soil properties, even at small spatial scales, influencing the dynamics of organic matter (de Godoy Fernandes et al. 2021). Most of the studies on organic matter dynamics focused on riparian areas along natural tropical rivers (e.g. Giese et al. 2000; Wigginton et al. 2000; Gonçalves and Callisto 2013) or in temperate regions (e.g. Trettin and Jurgensen 2002; Mitsch and Mander 2018), while others are based on models and remote sensing data (e.g. Hanberry et al. 2015; Suchenwirth et al. 2012). However, to our knowledge, none of these studies focused on riparian forests adjacent to a lake.

Our study aims to identify and measure the processes underlying organic matter dynamics in four types of riparian forests adjacent to a lowered-level lake 150 years ago. The objectives are (i) the quantification of the various organic matter compartments; (ii) the evaluation of the differences between the organic matter fluxes attached to the distinctive types of riparian forests; (iii) and the identification of the relationships between the variables.

The research hypotheses are as follows: biomass production, soil fauna, soil respiration and decomposition rate vary depending on forest type. These ecological variables are strongly influenced by hydrological conditions (groundwater table height and fluctuations) and tend to be lower in long-submerge riparian forests (Huylenbroeck et al. 2021; Djukic et al. 2018; Luo and Zhou 2006). Secondly, soil respiration is correlated with the rate of organic matter decomposition, which is indirectly inversely proportional to topsoil organic matter content (LaCroix et al. 2019).

Materials and Methods

Study Site: La Grande Cariçaie

The riparian forests of the Grande Cariçaie nature reserves in Switzerland are located on the southern shores of Lake Neuchâtel at 430 m.a.s.l (Fig. 1). This region was subjected to a major river correction 150 years ago (1868–1891). This lowered the lake level by 2.7 m, releasing new lands that had been submerged (Vischer 2003). These areas, still under the influence of the lake or small rivers, were rapidly colonized by wetland vegetation. The first forests emerged in the 1930s, but the majority developed between 1945 and 1970 (Siegfried et al. 2024). A second regulation project of the lake took place between 1962 and 1973 to reduce seasonal variations in lake level (Siegfried et al. 2024; Vischer 2003). Today, these areas are part of one of Switzerland's largest marshland complexes and are protected. They comprise 42 km of shoreline and 2532 ha of surface area, including 647 ha of riparian forests. The shores are mainly on Tertiary sandstones, whose material originates from the erosion of the young Alps (mainly freshwater Molasse from Aquitanian and Burdigalian; Swisstopo 2025; Buttler et al. 1995). Glacier and lake erosion produced cliffs 30–70 m high. Subsequent wave erosion contributed to the formation of the present wetland bed sediments, with grain sizes ranging from sand to silt (Buttler et al. 1995; Cornali 1992). A mix of glacier moraine (Würm) and limestone-rich lacustrine sediments enhances the system's complexity (Verrecchia 2007). Impermeable molasse bedrock lies less than 7 m beneath the sedimentary cover, which can be thin, down to just 30 cm (Buttler et al. 1995).

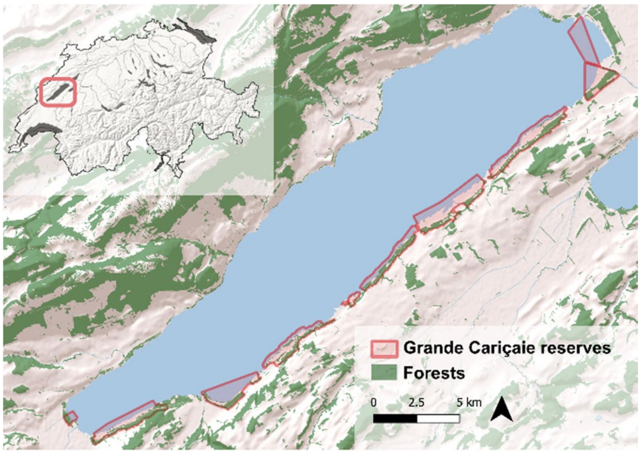

Fig. 1 Spatial distribution of the Grande Cariçaie reserves located along the shores of Lake Neuchâtel, Switzerland (background map: Esri Topo; forest: Swisstopo)

The climate is temperate, with a total annual rainfall of 854 mm, peaking in June (92 mm). The yearly average temperature is 9.8 °C, with a minimum monthly average of 0.9 °C in January and a maximum of 19.3 °C in July (data for Payerne, 8 km from Lake Neuchâtel at 490 m.a.s.l., 1990–2020 average; MeteoSwiss 2025).

Four types of riparian forests were assessed (Siegfried et al. 2024; Fig. 2): (1) *Alnus glutinosa* forests, which are composed of pure stands of black alders (*Alnus glutinosa*) with hygrophilous species (like *Caltha palustris*) in understory; (2) *Alnus incana* forests, which are mainly composed of grey alders (*Alnus incana*) and other tree species such as poplars (*Populus* spp.) and birches (*Betula pendula* aggr.), with tall grasses (*Carex acutifomis* and *Carex riapria*) in understory; (3) *Fraxinus* excelsior forests, which are mixed stands with different tree species like *Fraxinus excelsior*, *Quercus robur*, *Ulmus glabra*, or *Prunus* sp., with a sparse understory with more mesophilic herbaceous species; and (4) *Pinus sylvestris* forests, which are dominated by pines (*Pinus sylvestris*), with *Carex flacca* and *Molinia arundinacea* in understory. Siegfried et al. (2024) provided a more detailed description of these four forest types. According to the phytosociological system, these communities can be classified as *Alnion glutinosae*, *Alnion incanae*, *Fraxino-Quercion roboris* and *Erico carneae-Pinion*, respectively (Mucina et al. 2016). The soil composition and physicochemical properties of these stations were presented in Siegfried et al. (2025).

Selection of the Stations

Three plots of 500 m^2 were selected in each of the four riparian forest types, for a total of 12 plots distributed along the entire southern shore of Lake Neuchâtel (Appendix I). Based on Siegfried et al. (2024) and Delarze et al. (2015),

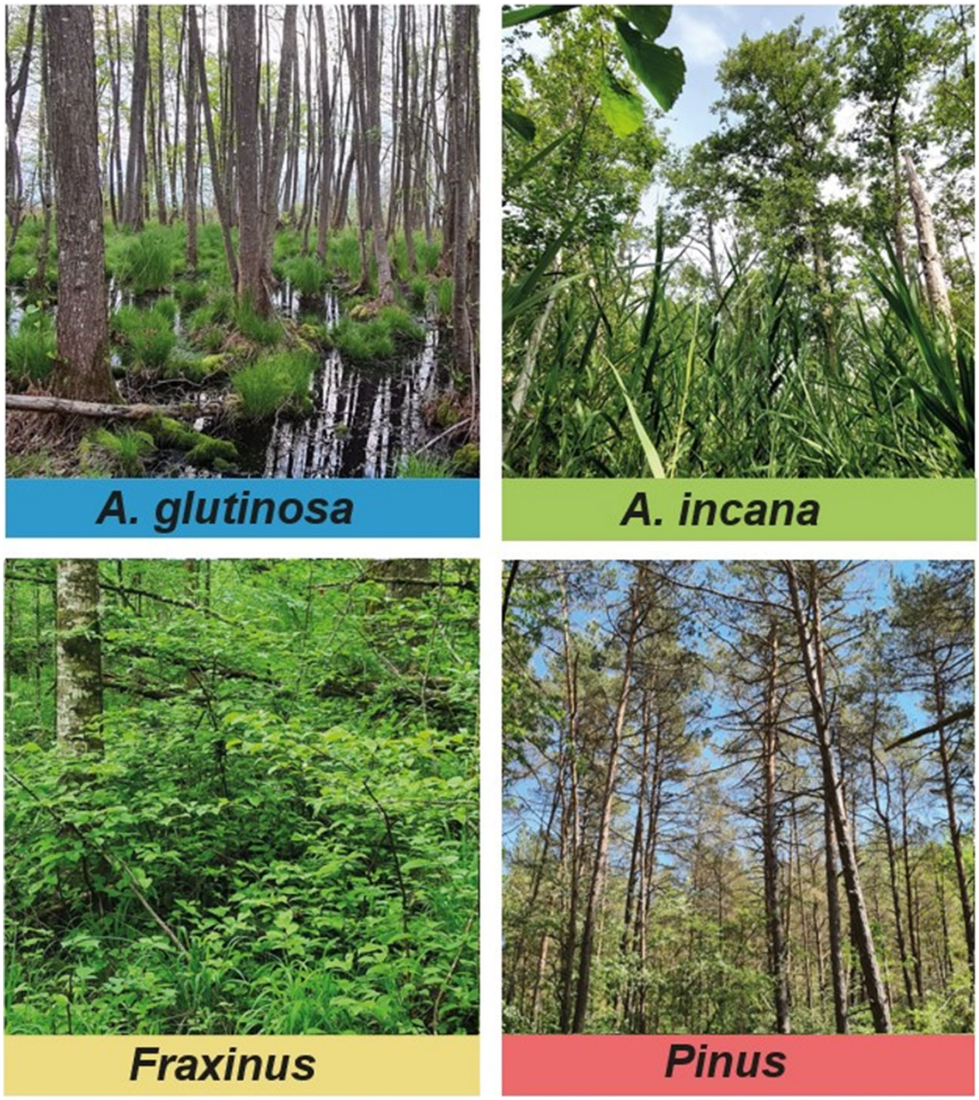

Fig. 2 Field photographs of the four types of riparian forests studied in the Grande Cariçaie reserves: *Alnus glutinosa*, *Alnus incana*, *Fraxinus excelsior* and *Pinus sylvestris* forests. These communities are described in Siegfried et al. (2024)

we selected the most representative stands in each forest type based on their structure and species composition.

Hydrology

The presence of water and its dynamics are among the main factors influencing the species composition in European riparian forests (Buttler et al. 1995; Klimo et al. 2008; Machar et al. 2020). To assess water table fluctuations, piezometric tubes (1 m long, one per station) with automatic sensors (Hobo® U20L Water Level Logger) were installed in June 2020 in three forest types and in March 2021 in *Pinus sylvestris* forests. These sensors recorded the temperature and pressure every two hours. The Hoboware®Pro software converted the measured pressure into water levels after correcting for variations in atmospheric pressure. A water index was calculated from the number of days with water level above a 10-cm depth from April 2021 to June 2023.

Organic Matter Input

The contribution of organic matter to the system was measured using two methods based on (1) the organic matter in place (living tree and dead wood) and (2) the annual production of organic matter that plants generate each year (e.g. leaf biomass).

A first set of measurements was based on the Swiss national forest inventory, which collects precise data on the volumes of wood and dead wood in forest stands (Brändli et al. 2020; Fischer and Traub 2019; Keller 2011). All trees with a diameter > 12 cm (DBH) were measured within a circle of 200 m^2 (8 m radius) around the centre of the plot. The basal area of all the living trees was summed and adjusted to the hectare.

The volume of deadwood was evaluated for dead standing trees (DBH > 12 cm) and for ground-deadwood. For a standing dead tree, the formula was (Bütler Sauvain 2003):

$$\frac{V}{ha} = \sum (basal\ area * height * shape\ index) * 50$$

The basal area and height are in square meters and meters, respectively. The shape index is a correction factor for tree shape. In our study, we used a shape index of 0.5 for all species (Bütler Sauvain 2003).

Lying deadwood > 7 cm in diameter was measured along three 15-meter transects (Appendix 1). The volume was calculated according to Silva et al. (2021):

$$\frac{V}{ha} = \frac{\pi^2}{8L} * \sum \left(diameter^2\right) * 1/T$$

L is the length of the transect (here 15 m), T is the number of transects (here 3), and the diameter is given in cm.

The measure of litter production generally provides information on above-ground carbon fluxes (Hoover 2008; Ukonmaanaho et al. 2016). Two methods were used to measure (a) the tree litter fall necromass (what falls from trees and bushes taller than 1 m) and (b) the herbaceous litter biomass (non-woody plants). (a) Leaves, fruits, and branches that fell from trees were collected at each station using three litter traps, set 8–11 m apart, from May to December 2021 and 2022. The surface collection of the litter trap was 0.5 m^2, at 1 m above the ground, with a mesh size of 1 mm (Cornali 1992; Hoover 2008; Ukonmaanaho et al. 2016). (b) Herbaceous litter was harvested at ground level over three 0.5 m2 areas in 2021. Because the herbaceous fraction is relatively small compared to the biomass produced by the trees, a single collection during the growing season was considered sufficient (Cornali 1992). The collected material was oven-dried at 40 °C to constant weight, then weighed (Ukonmaanaho et al. 2016). The values for *Pinus* forests were extracted from Cornali (1992), who used the same two methods to measure the litter. We used the data from this study because *Pinus* forests were not initially included in the project and were added later. Considering the low changes observed in these *Pinus* forests between 1984 and 2022, with a tree stratum structure and composition quite similar between the two periods (Siegfried et al. 2024), we are confident that temporal changes are not sufficient to bias comparisons between forest types.

Decomposition of Organic Matter

The assessment of the decomposition rate of organic matter is essential to understand its dynamics (Hoover 2008). The "tea bags index" method was applied (Keuskamp et al. 2013). In each station, nine green tea bags (EAN no. 87 22700 055525) and nine rooibos tea bags (EAN no. 87 22700 188438) were buried 8 cm deep during autumn 2021. Three of them were retrieved after 3, 6, and 9 months, respectively, dried at 40 °C and weighed. The percentage of mass loss was considered to correspond to the rate of organic matter decomposition.

Soil CO_2 emissions (respiration) were measured punctually once a month from April 2021 to April 2022, during and following a dry day (Grand et al. 2016). The measurements were carried out with a LICOR 8100a at the exact location in 12 plots (a plastic collar maintained in the soil between measurements) to ensure reliable data across sampling periods. Each measurement comprises 3 to 5 observations, including a 30-second pre-purge phase, a 90-second measurement phase, and a 30-second post-purge phase. Data on CO_2 emissions were correlated to monthly averages of rainfall (www.meteosuisse.ch), the lake level (FOEN, https://www.bafu.admin.ch/bafu/en/home/topics/water/info-specialists/state-of-waterbodies/state-of-lakes/water-levels-in-lakes.html), the soil temperature (measured simultaneously) and the water table depth (piezometric tubes).

Biological Activity

Soil fauna was appraised through various methods. The different species, biomass, ecological categories (epigeic, endogeic, anecic; Bouché 1977; Bottinelli et al. 2020), and abundance of earthworms (*Lumbricidae*) were extracted from an area of 30 × 30 cm using mustard flour (Lawrence and Bowers 2002) and hand-sorting (Bouché and Aliaga 1986). This procedure was repeated at three locations in each station in one day during autumn 2022. Earthworms were preserved in 4% formalin, individually weighed, and identified at the genus and species levels when possible using the keys of Bouché (1972), Sims and Gerard (1999), Sherlock (2018), and Csuzdi and Zicsi (2003). Echytraeids (*Enchytraeidae*), as well as earthworms, were extracted using the same methodology, and their biomass and abundance were also quantified. In addition, we sampled one soil core (4 cm in radius, 9 cm in height) at each station. The samples were then exposed to light and heat at the top, which caused arthropods to migrate from the topsoil to deeper layers, where they fell into a recipient containing ethanol for collection (Macfadyen-Bieri extractor; Bieri et al. 1987). Arthropods were counted and identified at the major group level (primarily at the order level).

Humus forms were identified according to Zanella et al. (2018a, b, c) by observing the decomposition of the litter from the above-ground to the first soil horizon depth, based on a precise description (state and type of organic matter, size of soil aggregates), i.e. between 0 and 7–25 cm (topsoil), depending on the location. For each station, topsoil was sampled, dried at 105 °C (to remove the residual humidity), and sieved. Their organic matter content was measured by loss-on-ignition, i.e., by calculating the mass difference after combustion at 450 °C (Sutherland 1998).

Data Processing of Variables

To visualize data, boxplots were created using the boxplerk function (using agricolae package) described in Borcard et al. (2018). The significance between forest types was assessed according to a Kruskal-Wallis test, and the significant difference between groups, with a post-hoc comparison (Borcard et al. 2018).

A principal component analysis (PCA; the PCA function in the FactoMineR library) was applied to identify linkages between forest types and environmental variables. All the variables used in this study are listed in Table 1. The statistical analyses were performed with R software, version 4.3.2 (R Core Team 2017).

Table 1 Abbreviation and description of the variables used in the PCA (Fig. 9)

Variable	Description
Quantitative variables used in PCA	
Tree	Basal area of living trees (DBH > 12 cm) $[m^2 \cdot ha^{-1}]$
DWood	Volume of standing and on the ground deadwood $[m^3 \cdot ha^{-1}]$
LitterFall[1]	Quantity of litter collected in litter traps (leaves, flowers, and fruits) $[g \cdot m^{-2} \cdot year^{-1}]$
HerbLitter[1]	Quantity of herbaceous biomass $[g \cdot m^{-2} \cdot year^{-1}]$
GTea	Decomposition index of green tea. Calculated using a decomposition rate from tea bags after 3, 6, and 9 months.
Rooibos	Decomposition index of rooibos. Calculated using a decomposition rate from tea bags after 3, 6, and 9 months.
SResp	Annual mean of CO_2 soil emission $[\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}]$
Arthro	Quantity of arthropods $[number \cdot m^{-3}]$
EWorm	Earthworms (*Lumbricina*) collected mass $[g \cdot m^{-2}]$
Enchy	Enchytraeids collected mass $[g \cdot m^{-2}]$
SOM	Organic matter [%] in the first soil horizon (Appendix IX)
Passively projected variables	
Forest	Forest type based on exhaustive plant inventories
Humus form	Simplified classification according to Zanella et al. (2018) (Appendix IX)
Water	Percentage frequency of the number of days per year with a water level at a soil depth < 10 cm. Index calculated with water levels measured from April 2021 to June 2023

[1] The quantity of litter from litter traps and of the herbaceous biomass were not included in the PCA (Fig. 9) because the data from the *Pinus* forests were measured in a previous study (Cornali 1992)

Results

Hydrology

Data from the piezometers provided a relevant indication of water levels and their variations at the stations over the three to five years of the study (Fig. 3; Appendix III). There was a significant difference in daily averages between the habitats (Kruskal-Wallis test; p-value < 0.0001). *A. glutinosa* forests had the highest water level, close to the soil surface and a soil submerged for almost half of the year (autumn-winter). *A. incana* forests were less wet, with a water table close to the surface in winter but dropping to 50 cm during the summer. The *Fraxinus* forests had deep soils, with a water table at 30–50 cm in winter and dropping below 80 cm during the summer. The *Pinus* forests had shallow soils, around 40 cm thick, just above a compact, hard, impermeable molasse rock. The groundwater level rose rapidly after rain, but the soil dried out during the summer due to evaporation and lack of precipitation. Recorded data showed a significant rise in the water level in July 2021 (Fig. 3). This flood event was exceptional, the largest since the second lake regulation (1962–1972), with a lake level 1.42 m above the 1980–2020 average. Some of the *Fraxinus* (3/3), *A. incana* (2/3) and *A. glutinosa* (1/3) stations were flooded by the lake between one and two weeks. None of the *Pinus* stations were affected by the rising lake water. In contrast, the 2022 and 2023 summers were dry, with low precipitation (www.meteosuisse.ch).

Organic Matter Input

The amount of living wood differed between forest types (Kruskal-Wallis test, p-value = 0.0499; Fig. 4A; Appendix IV). *A. glutinosa* and *Pinus* forests had the largest basal area, the former having a greater number of trees (between 15 and 32 per 200 m^2). Trees in *Pinus* forests were less numerous (between 9 and 25), but some had large DBH (maximum 76 cm). *A. incana* forests had a low basal area, with 3 to 7 trees over 12 cm per station. *Fraxinus* forests also had 5–6 trees/200 m^2, but the highest average of DBH per tree, i.e. 31 cm (against 20–23 cm in the other forest types). Deadwood values were not significantly different between habitats (p-value = 0.1963; Fig. 4B; Appendix IV). Regardless of the kind of forest, the amount of deadwood on the ground (mean = 72 m^3/ha) was often larger than the standing deadwood (mean = 41 m^3/ha; p-value 0.013).

Depending on the station, the litter falling from the trees and shrubs was between identical (*A. incana*) and 70 times larger (*Fraxinus*) than that from the annual production of the herbaceous layer (Fig. 5; Appendix V). Litter traps from *A. glutinosa* forests collected the highest litterfall input, while the *A. incana* forests had the lowest litter production

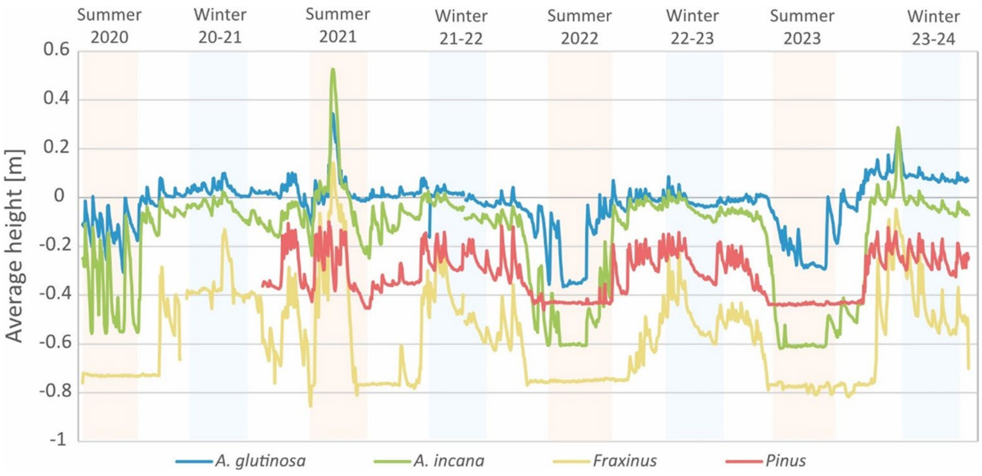

Fig. 3 Fluctuations of the water table depth in the four forest types in the Grande Cariçaie reserves. The daily average depth was measured from the soil surface (level 0) during three consecutive years (June 2020 to April 2024). Periods without variations (flat curve) corresponded to a water table level lower than the probe position (no measurement). This limit is around −0.45 m in *Alnus glutinosa* forests (never reached), -0.6 m in *Alnus incana* forests, -0.75 m in *Fraxinus* excelsior forests and −0.40 m for *Pinus sylvestris* forests, corresponding for *Pinus* forests to the impermeable sandstone bedrock. July 2021 was characterised by very important flood and the summers 2022 and 2023 were particularly dry

(Fig. 5A). Conversely, the *A. incana* forests had the highest leaf biomass in the herbaceous layer, and the *Fraxinus* forests were the lowest (Fig. 5B).

Decomposition of Organic Matter and Biological Activity

The results on tea bag decomposition emphasized a clear difference between the two types of tea, with green tea degrading faster than rooibos (Fig. 6). The green tea decomposition was significantly higher in wetter sites (*A. glutinosa* and *A. incana* forests) than in drier ones (*Fraxinus* and *Pinus* forests). The rooibos tea degraded more slowly in *Pinus* forests compared to all the others. The decomposition of the tea was very rapid during the first three months, then slowed down considerably (Appendix VI).

Monthly measurements of soil respiration (April 2021 to April 2022) indicated significant differences between wet (*Alnus*) and dry (*Fraxinus* and *Pinus*) forests (Kruskal-Wallis test, p-value = 0.0006; Fig. 7). The soil in *Fraxinus* forests had the highest CO_2 efflux in August with an average value of 8.31 (±1.21) $\mu mol \cdot m^{-2} \cdot s^{-1}$. The soil in *Pinus* forests showed high emissions in June (average 3.95 $\mu mol/m^2/s$) and August (average 3.92 $\mu mol \cdot m^{-2} \cdot s^{-1}$; Appendix VII). The soil of *A. glutinosa* forests emitted the lowest respiration rate of all forest types, with the highest value at 2.59 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in August. Soil temperature was a relevant parameter as soil respiration increased during the warmest months (June to Grand et al. 2016). Soil waterlogging also influenced CO_2 emissions, with lower fluxes from the wet forests and lower emissions in July 2021, during the major flood (Fig. 7).

The earthworm biomass and the abundance of arthropods were significantly higher in the *Fraxinus* and *Pinus* forests compared to the two *Alnus* forests. However, the enchytraeid biomass did not differ significantly between forest types (Fig. 8), as did the number of earthworms and enchytraeids (Appendix VIII). A high proportion of earthworms was not identified because individuals were either juveniles or cut. However, among classified individuals, anecic worms were more common in *Pinus* and *Fraxinus* forests than in the two *Alnus* forests (p-value = 0.035; Appendix VIII). For example, *Eiseniella* sp. occurred exclusively in *Alnus* forests, whereas *Allolobophora* sp. and *Aporrectodea* sp. were more abundant in drier forests (*Fraxinus* and *Pinus*; Appendix VIII). The number of arthropods was 2 to 8 times higher in the *Fraxinus* and *Pinus* forests than in the *Alnus* forests (Fig. 8). Most individuals belong to the *Acari* (Mites) subclass and were present in all forest types. The *Collembola* class was also present in all forests, but with around 5 times fewer individuals than *Acari* (Appendix VIII). Many *Hymenoptera* larvae were also recorded, but only in the *Fraxinus* forests.

The types of humus forms were simplified into four categories according to Zanella et al. (2018), i.e. Mull, Hydromull, Anmoor, and Histic (Appendix IX). Humus forms were highly variable in both types of *Alnus* forests, where Hydromull, Anmoor, and Histic forms were observed. Mull forms, i.e. terrestrial forms, with water influence shorter than 6 months per year, were only found in *Fraxinus* and

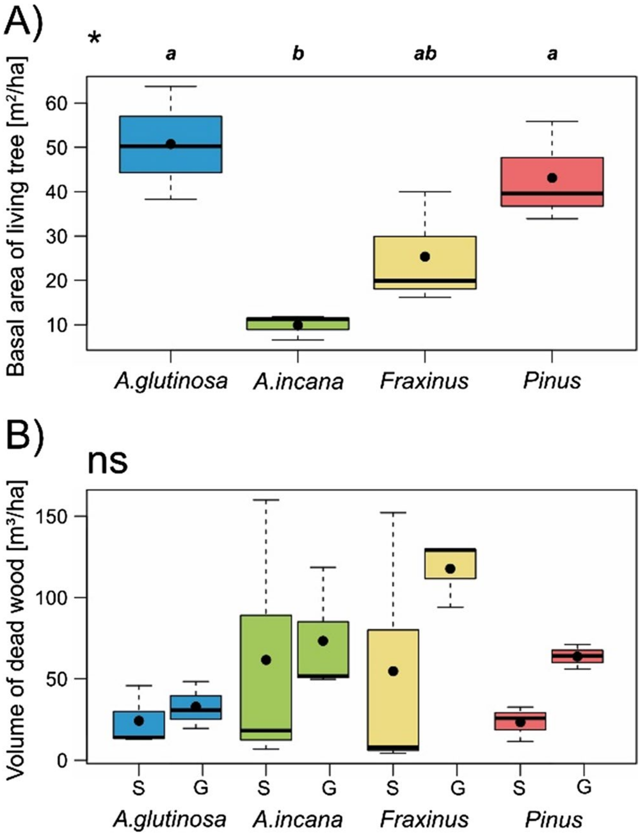

Fig. 4 **A**) Basal area of living trees; **B**) Volume of standing dead wood (S) and dead wood lying on the ground (G) in four forest types. Living trees and standing deadwood included trees on 200 m^2 with a DBH > 12 cm and dead wood on the ground included logs with a diameter > 7 cm encountered along three 15-m transects. The bold black line indicates the median and the boxes are limited by the first and third quartile. The stars indicate the significance of differences between habitats, according to a Kruskal-Wallis test (* p-value ≤ 0.05, ** $p \leq 0.01$ and *** $p \leq 0.001$). The different lowercase letters refer to significant differences between groups with a post-hoc comparison (Borcard et al. 2018)

Pinus forests (Fig. 9). The proportion of organic matter in the first soil horizon was highly variable in the *Alnus* forests (12–95% in *A. glutinosa* forests; 9–58% in *A. incana* forests). It decreased in quantity and variability in *Fraxinus* forests (23% in drained peat and around 6% in the other stations) and was uniform in the *Pinus* forests (10–12%; Appendix IX).

Relations between Variables

The x-axis of the principal component analysis referred to variables related to organic matter decomposition (e.g., earthworm biomass, green tea decomposition rate, organic matter proportion) and was correlated with water level. The y-axis pointed to the amount of organic matter entering the system (e.g., tree, dead wood, litter, biomass of herbaceous layer; Fig. 9; Appendix X).

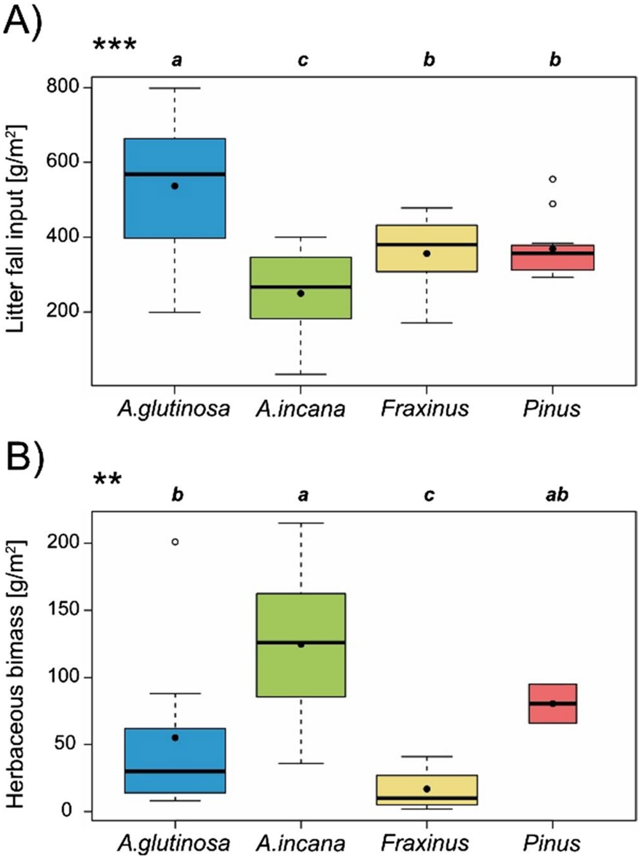

Fig. 5 **A**) Annual necromass collected in litter traps (tree leaves, fruits and branches) in 2021 and 2022 in the broadleaf forests and in 1983-86 in *Pinus* forests (data from Cornali 1992); **B**) Herbaceous biomass harvested in 2021 in the broadleaf forests and in 1984 in *Pinus* forests (data from Cornali 1992). The width of the boxplots is proportional to the number of measurements. Symbols as in Fig. 4

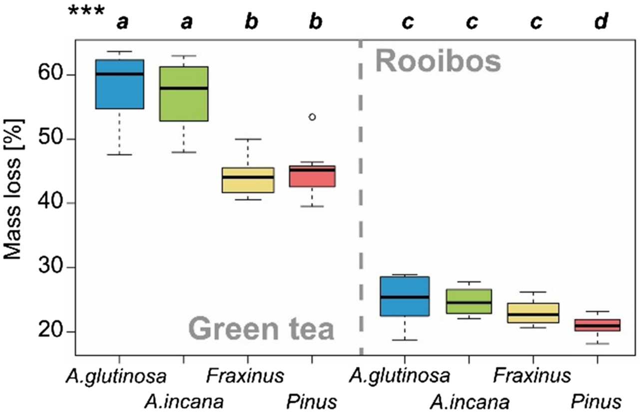

Fig. 6 Proportion of mass loss (%) in tea bags (green tea on the left and rooibos on the right) after three months, 8 cm deep inside the soils. Symbols as in Fig. 4

The *Fraxinus* and *Pinus* forests have similar environmental conditions for organic matter decomposition (Fig. 9). These stations were characterized by higher soil

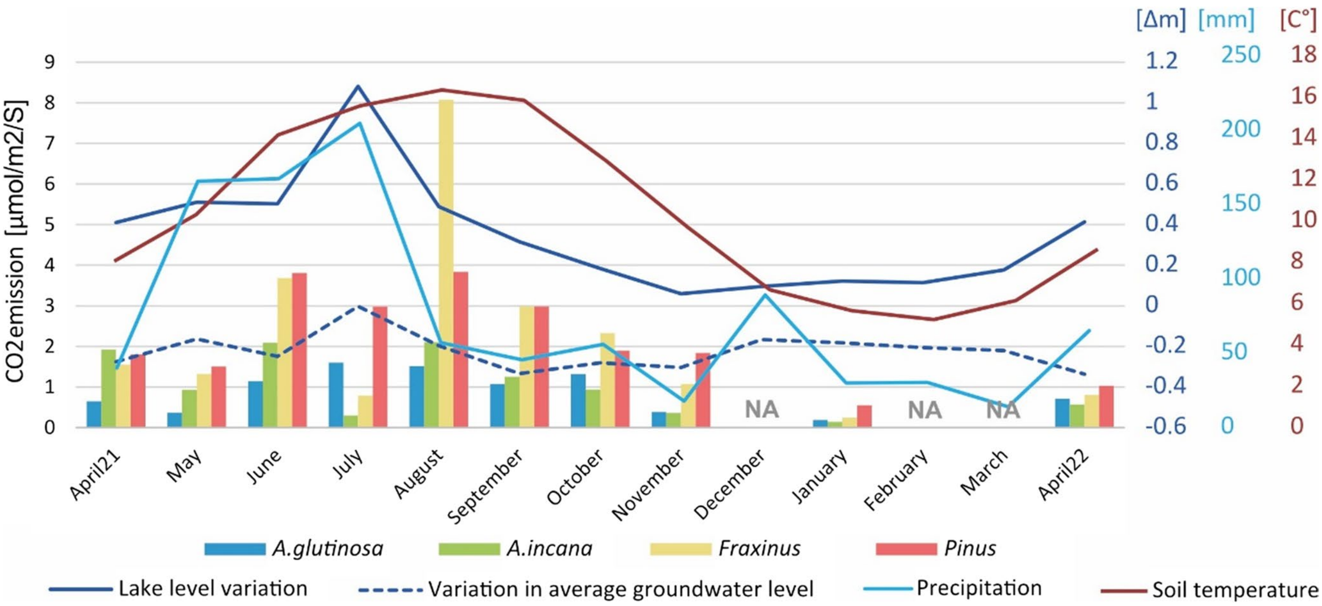

Fig. 7 CO_2 efflux from forest soils (bars), in relation to the lake level (Δm, measured relatively to the average lake level at 429.3 m.a.s.l.), groundwater level (Δm, measured relatively to the surface soil level), monthly precipitation (in mm, MeteoSwiss 2025) and soil temperature (in °C) during measurements

CO_2 emissions, significantly larger earthworm biomass and a higher number of arthropods than in the wet forests. Humus forms, exclusively terrestrial, belonged to the Mull class. Finally, these forests have a low water index value, which is anticorrelated with many variables (e.g., soil CO_2 emissions, earthworm biomass, arthropod numbers; Appendix XI).

Conversely, alder stands are more scattered on the plot (Fig. 9), distinguished from dry forests by the quicker decomposition of green tea and a greater proportion of organic matter in the topsoil. *A. glutinosa* forests had a higher above-ground biomass and basal area of living trees compared to *A. incana* forests, which contained a higher herbaceous biomass.

Discussion

According to our data, the four riparian forest types displayed differences in their pathways of organic matter, mainly due to water dynamics. Water remained a prominent factor influencing many variables, such as plant and faunal composition and diversity, soil respiration, decomposition rates (teabags), and the pathways for the degradation, integration and storage of organic matter into the soil. However, our initial hypotheses were not validated: biomass production in the different riparian forests did not appear to be influenced by water dynamics, and the rate of organic matter decomposition tended to be greater in forests with long periods of submergence.

Organic Matter Input

Organic matter input mainly originated from tree leaves (more than 80% on average). The average annual total litter input was 454 $g \cdot m^{-2} \cdot y^{-1}$ (ranging from 297 $g \cdot m^{-2} \cdot y^{-1}$ at an *A. incana* forest plot to 683 $g \cdot m^{-2} \cdot y^{-1}$ at an *A. glutinosa* forest plot; Fig. 5). These values were close to the range of 250–758 $g \cdot m^{-2} \cdot y^{-1}$ indicated by Trettin and Jurgensen (2002) for bottomland hardwoods in North America and to the range of 205–1334 $g \cdot m^{-2} \cdot y^{-1}$ reported by Mitsch et al. (1991) for forests along the Ohio River. This latest study showed a correlation between biomass production and water-level variation, with low productivity in stagnant semi-permanently flooded areas (Mitsch et al. 1991). However, our results showed little or no correlation between ecosystem production and water variations (Appendix XI). There was also no significant difference in total biomass production between forest types (p-value of 0.22). However, when considering in detail the origin of organic matter, *Fraxinus* forests had around 25 times more litter coming from tree leaves (392 $g \cdot m^{-2} \cdot y^{-1}$) than from the herbaceous layer (17 $g \cdot m^{-2} \cdot y^{-1}$). In comparison, *A. incana* forests differed by their low litterfall production (244 $g \cdot m^{-2} \cdot y^{-1}$) and a large proportion of herbaceous litter (124 $g \cdot m^{-2} \cdot y^{-1}$). This was explained by differences in canopy density, with a low number of large, living trees in *A. incana* forests (30 living trees per ha (DBH>12 cm) and 10 m^2/ha for the basal area average; Fig. 4 and Appendix IV). The resulting low foliage cover induced more light at ground level, allowing several large *Carex* species, such as *C. acutiformis*, *C.*

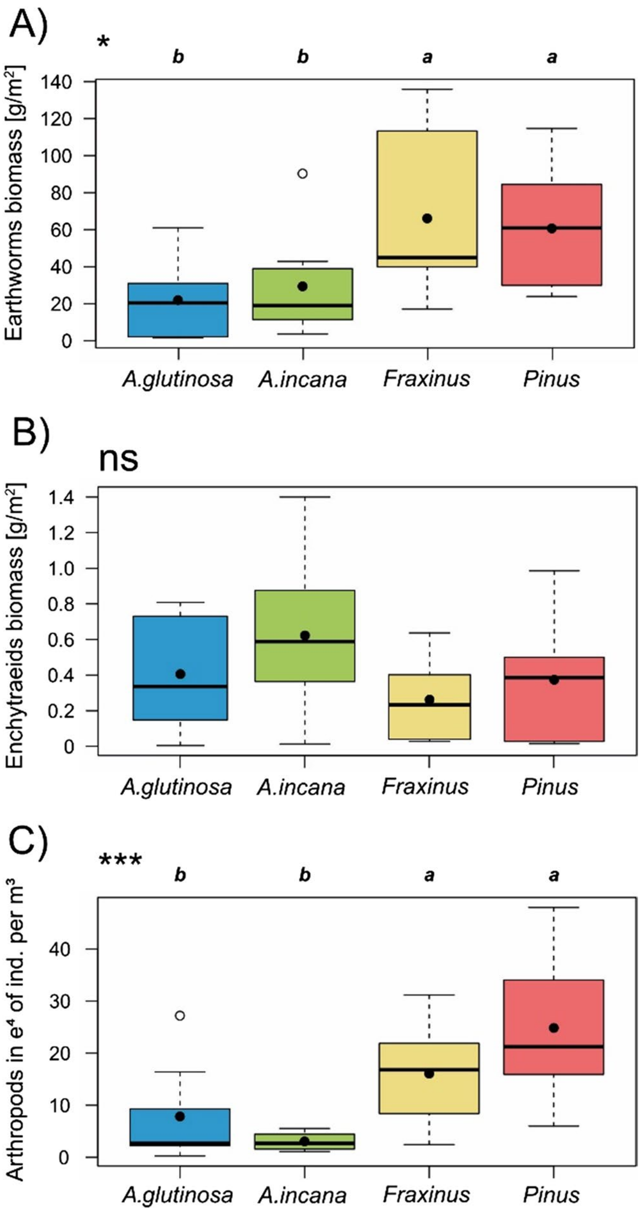

Fig. 8 **A**) Biomass of earthworms (*Lumbricina*) per m^2 (p-value = 0.0124); **B**) Quantity of individuals of enchytraeids (*Enchytraeidae*) per m^2 (p-value = 0.36); **C**) Number in thousands of arthropods (*Arthropoda)* individuals per m^3 of soil (p-value < 0.001). Symbols as in Fig. 4

riparia and *C. elata*, to form a high, dense herb layer. The reduced tree productivity likely results from the substantial amount of dead wood (Fig. 4B), predominantly dying poplars, indicative of a transition phase in *A. incana* forests. This transition was observed in a previous study, in which many *A. incana* stands shifted to *Fraxinus* forests in the last decades (Siegfried et al. 2024). Although both alder species have similar average lifespans (60–160 years; San-Miguel-Ayanz et al. 2016), *A. glutinosa* forests established a little later on the shores and had a more stable tree layer over the last decades (Siegfried et al. 2024). On the other hand, the high deadwood proportion in *Fraxinus* forests was probably related to the recent colonization of the stands by the invasive fungus *Hymenoscyphus fraxineus*, an Asian species that kills most *Fraxinus* trees (Pautasso et al. 2013). In the Grande Cariçaie, it is likely that not only humidity varied between stations, but also soil depth and station history, complexifying the relationships among variables (Siegfried et al. 2024).

Average dead wood in European primary and natural forests is evaluated at around 110 m^3·ha^{-1} (for example, between 27 and 255 m^3·ha^{-1} in beech forests in the Ukrainian Carpathians; Böhl and Brändli 2007). Forests in the Grande Cariçaie provided similar values, with an average of 57 m^3·ha^{-1} for *A. glutinosa* and 172 m^3·ha^{-1} for *Fraxinus* forests (Fig. 4B), with an average from 30 to 118 m^3·ha^{-1} of lying deadwood and 4 to 159 m^3·ha^{-1} of standing deadwood. This amount is well above the Swiss average of 24 m^3·ha^{-1} in lowland forests (Böhl and Brändli 2007), indicating the potentially high value of these forests for the xylophagous beetles and lignicolous fungi.

Decomposition of Organic Matter

The rates of organic matter decomposition varied among stands, with the highest rates in the wettest forests (Fig. 6). The differences between green tea and rooibos corresponded to previous observations (Djukic et al. 2018): green tea decomposes faster than rooibos due to its higher water-soluble compound content (Didion et al. 2016). The rate of decomposition was the fastest during the first three months and decreased thereafter (Appendix VI). A seasonal bias cannot explain this rate decrease, as the tea bags were installed in Autumn (November 9th and 10th, 2021), with the first three months in winter and the months 6–9 in spring and summer. Consequently, it can be assumed that the most labile compounds rapidly decayed during the first three months, leaving the more recalcitrant compounds, which degraded more slowly (Didion et al. 2016). In a previous article (Siegfried et al. 2025) in the same stands, the quality of organic matter was measured. It concluded that this quality varies greatly across soil horizons (organic, organo-mineral, or mineral), rather than by forest type. However, a slightly higher proportion of labile compounds was observed in *Alnus* forests. When comparing our results with Djukic et al. (2018), the values for green tea in *Alnus* forests were similar to those reported for the temperate biome. In contrast, those in *Fraxinus* and *Pinus* forests were much lower, comparable to those reported for the Mediterranean biome. Although using similar tea bags as litter allows stations to be compared with each other, it is essential to note that this approach does not necessarily reflect the actual decomposition rate of native litter (Didion et al. 2016). However,

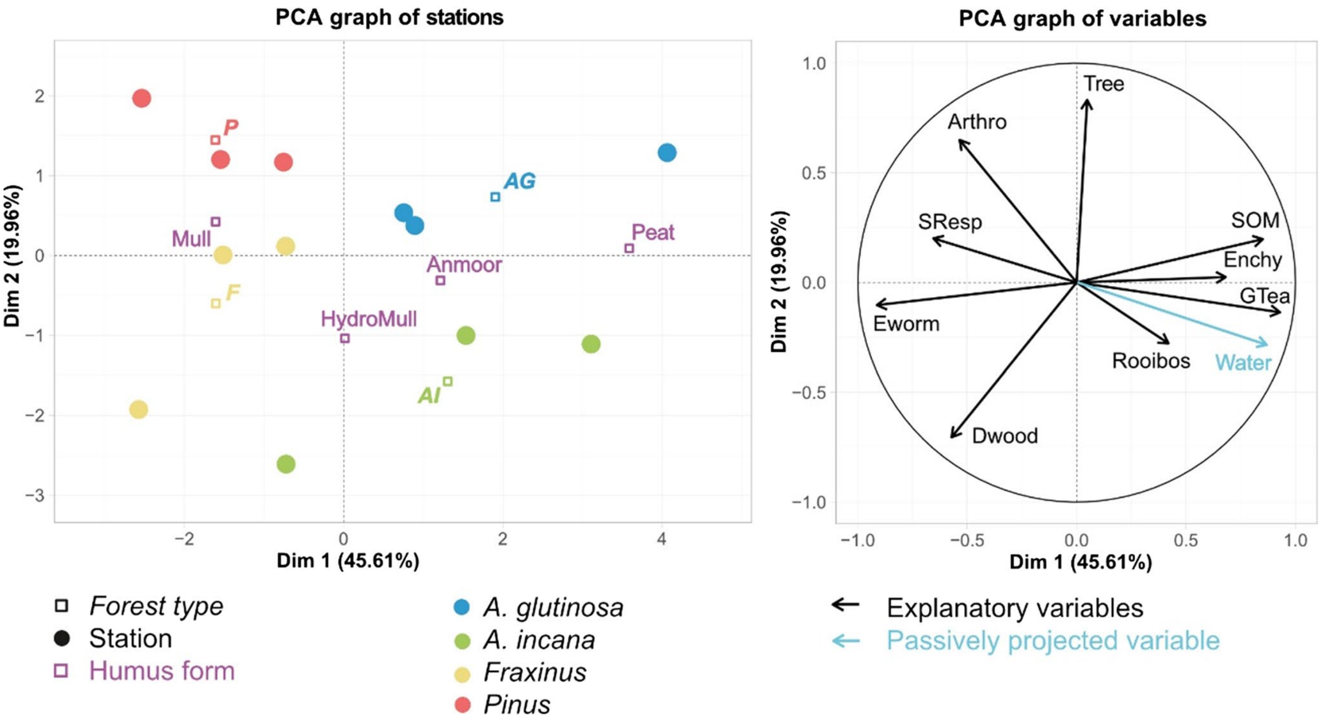

Fig. 9 Principal component analysis (PCA) of the stations based on environmental variables (see Table 1 for abbreviations). The x-axis (Dim 1) explained 45.61% of the total variance and the y-axis (Dim 2) 19.96%. The graph on the left represents the stations coloured according to the forest types and the passive projection of categorical variables. The graph on the right represents the environmental variables measured in the stations. Due to its high correlation with other variables (Appendix XI), water level (Water, in blue) passively projected based on the Pearson correlation coefficient of the values with the axis coordinates: -0.78 with Dim 1 and −0.31 with Dim 2. An alternative of this PCA, with two supplementary variables (litter and herbaceous biomass), partly measured in *Pinus* forests in a previous study (Cornali 1992), is available in Appendix X

based on a study by Ferreira et al. (2022), we can assume that the decomposition rate of green tea is similar to that of alder leaves in wet environments. The similarity is less evident for leaves from other tree species, such as *Fraxinus* or *Pinus*.

According to de Godoy Fernandes et al. (2021), higher decomposition rates are correlated with higher litter production and microbial activity in riparian forests in southeastern Brazil. In the Grande Cariçaie reserves, we found the highest decomposition rates in both *Alnus* forests. Hence, this correlation with litter production is verified in the *A. glutinosa* forests, which had the highest litter production, but not in the *A. incana* forests, with the lowest litter production (Fig. 5). *Alnus* forests were also the wettest habitats. This result contradicts our hypothesis that decomposition is slower in flooded areas. Consequently, the periods with sufficiently dry soil to allow organisms' respiration are probably long enough for a rapid decomposition in the upper soil layers (Mori et al. 2021; Petraglia et al. 2019). It is also possible that alder's roots aerate the soil, leading to accelerated mineralization (Pokorný et al. 2000).

A comparison with CO_2 emissions from specific biomes reported by Luo and Zhou (2006) emphasizes values similar to those in marshes (413 g C $m^{-2} \cdot y^{-1}$) and *Alnus* forests in the Grande Cariçaie (339–402 g C $m^{-2} \cdot y^{-1}$). However, soil respiration in *Fraxinus* and *Pinus* forests was higher (842–865 C $m^{-2} \cdot y^{-1}$) than average values in temperate forests (deciduous forests: 647 C $m^{-2} \cdot y^{-1}$, coniferous forest: 681 C $m^{-2} \cdot y^{-1}$). Measurements from an undisturbed riparian forest in North America provided values close to ours, with 718 C $m^{-2} \cdot y^{-1}$ (Oelbermann and Raimbault 2015). Variations observed between the vegetation types mainly originated from the water parameter. Silvola et al. (1996) showed that lower CO_2 emissions are measured when the water table is close to the soil surface. This result corresponds to our data on *Alnus* forests, which had the water table above or near the soil surface and also displayed lower CO_2 emissions than *Fraxinus* forests, which had a much deeper water table (Fig. 7). Soil CO_2 efflux was finally more sensitive to soil water content than to soil temperature (Bremer et al. 1998).

Humus Forms Reveal Organic Matter Dynamics

Humus forms at the interface between vegetation and mineral soil layers provide useful information on the distribution and temporal patterns of organic matter biodegradation, recycling, and possible accumulation. When water rarely or never reaches the soil surface, the soil is well oxygenated, and a Mull, the most efficient form of humus for degrading organic matter, is present (Zanella et al. 2018a; Le Bayon et al. 2024). Soil organisms mineralize the entire fallen litter or quickly integrate it into the soil. Maximal CO_2 emissions translated this high fauna and microbial activity in Summer. Consequently, the forest age does not influence the humus form in riparian systems (Bullinger-Weber et al. 2007). As water levels rise, the humus form changes and becomes more closely linked to the amount of accumulated organic matter. Indeed, the duration of soil waterlogging is negatively correlated with oxygen availability and, consequently, with the mineralization and integration of organic matter (Zanella et al. 2018c). Histic forms, corresponding to an important accumulation of organic matter, were found in the wettest conditions, where the water was close to the soil surface and stagnant (Fig. 9). Hydromulls were similarly observed at high water levels, but along small creeks that brought oxygenated water after flowing through waterfalls. This suggests that a higher oxygen content in water partly compensates for the low direct diffusion from the atmosphere and allows more efficient microbial activity than in stagnant waterlogged soils. Finally, Anmoors characterized the intermediate conditions between the last two. A gradient in humus forms related to water availability was observed, but not according to the duration of soil waterlogging, as described by Zanella et al. (2018c); rather, it appeared to be driven by soil oxygenation. The integration of organic matter into soil is discussed in greater detail in a previous article (Siegfried et al. 2025).

Soil Fauna

Even if fungi and bacteria are mainly responsible for the mineralization of the litter, soil macro- and mesofauna have a significant impact on the transformation, fragmentation, and integration of organic matter (Zanella et al. 2018a; Le Bayon et al. 2024). Arthropods physically break down organic matter using their mouthparts, thereby increasing the surface area available for bacteria and fungi to attack (Neher and Barbercheck 2019). Earthworms play a significant role in burying organic matter in the soil, and mixing it with mineral particles in their digestive systems, thus creating aggregates (Le Bayon and Shipitalo 2004; Le Bayon et al. 2021a).

As commonly described in the literature, the soil fauna was not uniformly distributed in the riparian forests we studied. Earthworms and arthropods were more prevalent in the dry *Fraxinus* and *Pinus* forests (Fig. 8; Appendix VIII; Siegfried et al. 2025) than in the wet forests. This result is consistent with the Mulls found in these forests, confirming that soil fauna contribute to the formation and maintenance of these dynamic humus systems. Moreover, water-saturated conditions in *Alnus* forests are probably constraining for earthworms due to anoxia, which drives them away (Edwards and Arancon 2022). The relationship with humus forms in these areas is clear, as earthworms are rarely found in Anmoors (sometimes in Summer, when the water level decreases, thus unsaturating the topsoil) and are most of the time absent in Histic systems (Zanella et al. 2018b, c). As with earthworms, soil moisture, plant communities, and soil conditions may also influence arthropod abundance (Wang et al. 2019; Kernecker et al. 2015).

The biomass of earthworms found in riparian buffer strips in forests from Central Europe is $< 50\ \mathrm{g{\cdot}m^{-2}}$ (Cameron et al. 2021), but $116\ \mathrm{g{\cdot}m^{-2}}$, with 220 individuals, were found in European, humus-rich beech forests (Bullinger-Weber et al. 2007). In the Grande Cariçaie, we observed lower biomass in *Alnus* forests ($22\text{–}29\ \mathrm{g{\cdot}m^{-2}}$) and intermediate values in *Pinus* and *Fraxinus* forests ($61\text{–}66\ \mathrm{g{\cdot}m^{-2}}$; Fig. 8). This difference can be explained in part by the fact that over 80% of the earthworms sampled were juveniles, despite the suitable sampling season (Appendix VIII). When specifically looking at the number of individuals, the values were closer to those reported by Bullinger-Weber et al. (2007), ranging from 169 to 298 individuals per m^2 (Appendix VIII). However, these numbers remain well below the 460 individuals per m2 reported in a forest with regular flooding in southern Quebec (Kernecker et al. 2015). Complementary surveys in Spring and Autumn would be necessary to get a better overview of earthworm communities and their variation.

We identified 13 earthworm species and subspecies, corresponding to approximately 25% of the 53 species present in Switzerland (Salomé et al. 2011; taxo.drilobase.org ; Appendix VIII). Other studies of riparian ecosystems in Switzerland at similar elevations reported 15 to 19 species (Le Bayon et al. 2013; Glasstetter 2012; Fournier et al. 2012; Salomé et al. 2011), indicating that earthworm diversity in the Grande Cariçaie is within the same range. However, this diversity may be underestimated due to the high amount of juveniles that are impossible to identify solely on morphological features.

Focusing on ecological categories, we observed higher proportions of epigeic earthworms and enchytraeids in the two wet *Alnus* forests. Epigeics live at the very soil surface; they can escape anoxic conditions in the mineral soil layers and thus can find a suitable habitat in the leaf litter. According to Bullinger-Weber (2007) and Schomburg et al. (2018a, b, 2019), epigeic earthworms and plant roots are pioneer engineers that produce soil structure through short-term casting and burrowing, especially in sandy environments. Enchytreids are mainly involved in the decomposition and recycling of organic matter (Pelosi and Capowiez 2022).

On the other hand, endogeics and anecics dominate the drier *Fraxinus* and *Pinus* forests, where they can dig deeper into the soil. When the texture is more suitable, loamy or silty, endogeics are known to actively improve the soil structural stability, while anecics are mainly recovered in deeper soils (Le Bayon et al. 2021a; Bayon et al. 2021b; Amossé et al. 2015).

A Paradoxical High Decomposition Rate in Wet Conditions

Our investigation at the Grande Cariçaie highlighted the importance of the water parameter, but also raised a paradox. Indeed, the rate of organic matter decomposition is often assumed to be positively associated with soil fauna activity and soil respiration, which were higher in the less humid forests (Luo and Zhou 2006). However, the results showed the opposite for the mass loss assessed with tea bags (Figs. 6 and 9). Moreover, this high decomposition rate was observed in soils with the highest organic matter content (Fig. 9).

The first possible explanation relies on a temporal bias. Indeed, tea bags were placed in November 2022, and soil fauna was inventoried in October 2022, following a major summer drought. However, this explanation seems unlikely, as another bait-based method (Bait lamina test) was carried out simultaneously to fauna inventories and provided the same results as the green tea decomposition, i.e. a higher consumption of the organic baits in *Alnus* forests than in the *Pinus* and *Fraxinus* forests (unpublished data; Appendix XII). A second explanation lies in the differing temporal scales of the two methods. Decomposition rate integrates processes over extended periods (months), whereas soil respiration is captured via brief, monthly one-off basis (minutes). To strengthen the link between soil respiration and organic matter decomposition, future research should employ continuous monitoring, thereby reducing the risk of overlooking “hot moments”, i.e. intervals of optimal decomposition conditions (Briones 2018). A third explanation involves decomposition caused by specific microfauna or microflora that were not measured in this study. Dissolved organic carbon (DOC) or methane (CH_4) could have formed an escape route of carbon from the system. Some anaerobic decomposition remains possible, as methane emissions were not measured, but such a process is less efficient than the aerobic one (Greenwood 1961; Mitsch and Mander 2018). However, carbon leakage in the form of DOC is more convincing in these riparian forests (Laudon et al. 2012). A final explanation is that specialized decomposers of nitrogen-rich compounds in *Alnus* forests rapidly consume the nitrogen-rich part of the organic matter. That is possible because alder litter is rich in nitrogen (due to *Frankia* fixation; Bocock 1964; Weber 1990) and has a degradation rate similar to that of green tea (Ferreira 2022). Wu et al. (2025) also found that decomposition rates are higher in wetlands. They suggested that this is due to microbial communities specialized to these environments, capable of efficiently decomposing organic matter under anaerobic or fluctuating conditions. Similar measurements to those of the tea bags, but with native litter, would be a good way to test this hypothesis, rather than standardized substrates (tea bags), which limit our ability to capture the full diversity of in situ decomposition processes.

This study showed that decomposition rates in wetlands are linked to the interaction between the local climate, timescales, substrate quality, and soil biology. So, it may not be so paradoxical to have significant mass loss associated to low CO_2 efflux. The specific environmental conditions of these riparian forests show that the pathways of organic matter decomposition are much more complex than assumed.

According to de Godoy Fernandes et al. (2021), the rate of decomposition in tropical forests is influenced by ecosystem productivity, suggesting that greater photosynthesis would lead to more root exudates, greater microorganism activity, and thus increasing soil respiration. We did not observe this phenomenon in the Grande Cariçaie, as the two *Alnus* forests had different productivities (Fig. 5), whereas CO_2 emissions (Fig. 7) and organic matter decomposition rates (Fig. 6) were similar.

Limits in Studies of Riparian Environments

Precisely quantifying pathways of organic matter in the studied riparian forests was complex. Indeed, several limitations could not be avoided. We originally planned to use litterbags with 1 and 4 mm mesh sizes, placed with native litter at the soil surface and 8 cm in depth (Huang et al. 2020). However, fine sediments were deposited on the litter during a flood, and it was impossible to remove them without losing dead leaf fragments. The finer mesh of the tea bags prevented sediment deposition but also prevented macrofauna from accessing the organic matter. Similarly, we collected earthworms’ castings (Le Bayon et al. 2002; Bayon et al. 2022) to measure their activity. However, the high soil humidity made their field identification difficult, and not all earthworm species produce visible castings (Le Bayon and Binet 1999). Finally, these forests are regularly disturbed by mammals. Although it may positively affect the ecosystem functioning, it also influences data collection. For example, a new beaver dam flooded large areas of two *Alnus* forests, changing the soil water regime. Additionally, some of the tea bags were lost due to wild boars and foxes digging, and litter traps were lost due to tree falls or visits from an inquisitive animal.

Conclusion and Perspectives

Our study demonstrated, through a holistic approach, that there were clear and significant differences in the pathways of organic matter observed in the different riparian forests. As expected, the water level and its associated fluctuations are undoubtedly a preeminent parameter, influencing ecosystem production, soil fauna, the rate of organic matter decomposition, the soil respiration, and the humus forms. Nevertheless, numerous questions remain, notably concerning the decomposition rate of organic matter, which clearly anticorrelates with soil respiration.

Given their history, these riparian forests offer a rare opportunity to study soil and vegetation dynamics in parallel under different water conditions. Indeed, their substrate was probably very similar 150 years ago, when they emerged after lowering the lake level (old glacial moraine with lacustrine sediments). Since then, differences in water conditions have led to contrasting soils, rich in organic matter, with low faunal biomass, low soil respiration, and high decomposition rates in the wetter conditions, and the opposite characteristics in the drier sites. Interestingly, the plant communities are even more sensitive to ecological conditions, as each of these two categories is further differentiated into two forest types based on water level and/or soil depth (Siegfried et al. 2024, 2025).

Although this study already considered many parameters, complementary measurements could improve our understanding of these ecosystems. For example, measurements of methane emissions, dissolved organic carbon in water and evaluation of microbial pathways involving bacteria and fungi would help assess the importance and seasonality of the anaerobic decomposition of organic matter in these soils. Data on dissolved oxygen in water could more precisely explain the distribution of soil fauna, even in waterlogged soils, especially if a finer identification of the collected arthropods complements it. Finally, a second inventory of soil fauna would be useful for evaluating the effects of adverse meteorological events. Indeed, the Grande Cariçaie reserves were impacted by a historic flood in 2021 and a severe drought in 2022, which may have influenced our data.

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Author Contributions All authors contributed to the study conception and design. Material preparation, data collection, and analyses were performed by Lila Siegfried. The first draft of the manuscript was written by Lila Siegfried. Renée-Claire Le Bayon, Eric Verrecchia and Pascal Vittoz commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and analyzed during the current study are available in the supplementary material.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

References

Amossé J, Turberg P, Kohler-Milleret R, Gobat JM, Le Bayon RC (2015) Effects of endogeic earthworms on the soil organic matter dynamics and the soil structure in urban and alluvial soil materials. Geoderma 243:50–57. https://doi.org/10.1016/j.geoderma.2014.12.007

Bieri M, Delucchi V, Stadler M (1987) Optimization of extraction conditions in the air-conditioned Macfadyen funnel extractor for soil arthropods. Pedobiologia 30(2):127–136 ISSN 0031-4056

Bocock KL (1964) Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J Ecol 52(2):273–284. https://doi.org/10.2307/2257595

Böhl J, Brändli UB (2007) Deadwood volume assessment in the third Swiss National forest inventory: methods and first results. Eur J for Res 126:449–457. https://doi.org/10.1007/s10342-007-0169-3

Borcard D, Gillet F, Legendre P (2018) Numerical ecology with R. Use R! (2e ed.). Springer, New York. p. 435. ISBN 978-1-4419-7976-6

Bottinelli N, Hedde M, Jouquet P, Capowiez Y (2020) An explicit definition of earthworm ecological categories–Marcel Bouché's triangle revisited. Geoderma 372:114361

Bouché MB (1972) Lombriciens de France, Ecologie et Systématique. Paris: INRA. Annales de Zoologie-Ecologie animale. vol 72, no HS, p 671

Bouché MB (1977) Strategies lombriciennes. Soil Organismes as Components of Ecosystems, Ecological Bulletins, Stockholm 25:122–132

Bouché MB, Aliaga R (1986) Contre Une dégradation physique et chimique des sols et pour leur optimisation économique, l'échantillonnage des lombriciens: Une urgente nécessité. Defense-des-Vegetaux (France) V 40(242):30–36

Brändli UB, Abegg M, Allgaier Leuch B (réd (2020) Inventaire forestier national suisse. Résultats du quatrième inventaire 2009–2017. Birmensdorf, Institut fédéral de recherches sur la forêt, la neige et le paysage WSL; Berne, Office fédéral de l'environnement. p. 341. https://doi.org/10.16904/ENVIDAT.147

Bremer DJ, Ham JM, Owensby CE, Knapp AK (1998) Responses of soil respiration to clipping and grazing in a tallgrass prairie. J Environ Qual (Vol 27(6):1539–1548. https://doi.org/10.2134/jeq1998.00472425002700060034x

Brinson MM, Lugo AE, Brown S (1981) Primary productivity, decomposition and consumer activity in freshwater wetlands. Annu Rev

Ecol Syst 12(1):123–161. https://doi.org/10.1146/annurev.es.12.110181.001011

Briones MJ (2018) The serendipitous value of soil fauna in ecosystem functioning: the unexplained explained. Front Environ Sci 6:149. https://doi.org/10.3389/fenvs.2018.00149

Brussaard L (1998) Soil fauna, guilds, functional groups and ecosystem processes. Appl Soil Ecol 9(1–3):123–135. https://doi.org/10.1016/S0929-1393(98)00066−3

Bullinger-Weber G, Le Bayon RC, Guenat C, Gobat JM (2007) Influence of some physicochemical and biological parameters on soil structure formation in alluvial soils. Eur J Soil Biol 43(1):57–70. https://doi.org/10.1016/j.ejsobi.2006.05.003

Bütler Sauvain R (2003) Dead wood in managed forests: how much and how much is enough? Development of a snag-quantification method by remote sensing and GIS and snag targets based on Three-toed woodpeckers' habitat requirements. PhD thesis No. 2761. EPFL, Lausanne

Buttler A, Cornali P, Bueche M (1995) Etude des effets de la régulation des lacs subjurassiens sur la végétation et le milieu. Université de Neuchâtel, sur mandat de l'Office fédéral de l'environnement, des forêts et du paysage (OFEFP), Neuchâtel

Cameron A, Boilard G, Dubois R, Bradley R, Benetkova P, Jozefowska A, Thevathasan N, Whalen J, Šimek M (2021) Distribution of earthworm communities in agroecosystems with forested riparian buffer strips: A multiscale study. Appl Soil Ecol 167:104035. https://doi.org/10.1016/j.apsoil.2021.104035

Cierjacks A, Kleinschmit B, Kowarik I, Graf M, Lang F (2011) Organic matter distribution in floodplains can be predicted using Spatial and vegetation structure data. River Res Appl 27(8):1048–1057. https://doi.org/10.1002/rra.1409

Cornali P (1992) Ecologie des pinèdes (*Pinus silvestris*) de la rive sud du lac de Neuchâtel (Suisse): Phytosociologie, pédologie, hydrodynamique, hydrochimie, phytomasse et productivité, minéralomasse et cycles biogéochimiques. PhD Thesis. Faculté des Sciences de l'Université de Neuchâtel, Neuchâtel

Csuzdi C, Zicsi A (2003) Earthworms of Hungary (Annelida: Oligochaeta, Lumbricidae). Hungarian Natural History Museum, Budapest, p 271. https://doi.org/10.5281/zenodo.4309820

Cunha-Santino MBD, Bianchini I (2023) Reviewing the organic matter processing by wetlands. Acta Limnol Bras 35:e19. https://doi.org/10.1590/S2179-975X3423

de Godoy Fernandes PH, de Souza ALT, Tanaka MO, Sebastiani R (2021) Decomposition and stabilization of organic matter in an old-growth tropical riparian forest: effects of soil properties and vegetation structure. For Ecosyst 8:1–9. https://doi.org/10.1186/s40663-021-00293-0

de Souza Rezende R, Graça MAS, dos Santos AM, Medeiros AO, Santos PF, Nunes YR, Goncalves JJF (2016) Organic matter dynamics in a tropical gallery forest in a grassland landscape. Biotropica 48(3):301–310. https://doi.org/10.1111/btp.12308

Delarze R, Gonseth Y, Galland P (2015) Guide des milieux naturels de Suisse: écologie, menaces, espèces caractéristiques. 3^{e} ed. Bussigny: Rossolis, p. 440. ISBN 978-2-940365-90-6

Didion M, Repo A, Liski J, Forsius M, Bierbaumer M, Djukic I (2016) Towards harmonizing leaf litter decomposition studies using standard tea bags—a field study and model application. Forests 7(8):167. https://doi.org/10.3390/f7080167

Djukic I, Kepfer-Rojas S, Schmidt IK, Larsen KS, Beier C, Berg B, Alatalo J (2018) Early stage litter decomposition across biomes. Sci Total Environ 628:1369–1394. https://doi.org/10.1016/j.scitotenv.2018.01.012

Edwards CA, Arancon N (2022) Biology and ecology of earthworms (ed. 4). Springer Science+Business Media, LLC, part of Springer Nature. p.567. https://doi.org/10.1007/978-0-387-74943-3

Ferreira V, Silva J, Cornut J, Graça MA (2022) Microbial colonization and decomposition of commercial tea and native alder leaf litter in temperate streams. Aquat Sci 84(1):4. https://doi.org/10.1007/s00027-021-00834-3

Fischer C, Traub B (2019) Swiss National Forest Inventory-methods and models of the fourth assessment. Berlin, Heidelberg: Springer. ISBN 978-3-030-19292-1 978-3-030-19293-8

Fournier B, Samaritani E, Shrestha J, Mitchell EA, Le Bayon RC (2012) Patterns of earthworm communities and species traits in relation to the perturbation gradient of a restored floodplain. Appl Soil Ecol 59:87–95

Frouz J (2018) Effects of soil macro-and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma 332:161–172. https://doi.org/10.1016/j.geoderma.2017.08.039

Giese LA, Aust WM, Trettin CC, Kolka RK (2000) Spatial and Temporal patterns of carbon storage and species richness in three South Carolina coastal plain riparian forests. Ecol Eng 15:S157–S170. https://doi.org/10.1016/S0925-8574(99)00081−6

Glasstetter M (2012) Earthworm diversity in urban habitats of Basel (Northwestern Switzerland) (Oligochaeta: Lumbricidae). Zool Middle East 58(sup4):95–102. https://doi.org/10.1080/09397140.2012.10648989

Gonçalves JJF, Callisto M (2013) Organic-matter dynamics in the riparian zone of a tropical headwater stream in Southern Brasil. Aquat Bot 109:8–13. https://doi.org/10.1016/j.aquabot.2013.03.005

Grand S, Rubin A, Verrecchia E, Vittoz P (2016) Variation in soil respiration across soil and vegetation types in an alpine Valley. PLoS ONE 11(9):e0163968. https://doi.org/10.1371/journal.pone.0163968

Greenwood DJ (1961) The effect of oxygen concentration on the decomposition of organic materials in soil. Plant Soil 14(4):360–376. https://doi.org/10.1007/BF01666294

Hanberry BB, Kabrick JM, He HS (2015) Potential tree and soil carbon storage in a major historical floodplain forest with disrupted ecological function. Perspectives in plant ecology. Evol Syst 17(1):17–23. https://doi.org/10.1016/j.ppees.2014.12.002

Hoover CM (ed) (2008) Field measurements for forest carbon monitoring: a landscape-scale approach. Springer Science and Business Media: Durham, USA. ISBN 978-1-4020-8505-5

Huang W, González G, Zou X (2020) Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global meta-analysis. Appl Soil Ecol 150:103473. https://doi.org/10.1016/j.apsoil.2019.103473

Hughes FM, del Tánago MG, Mountford JO (2012) Restoring floodplain forests in Europe. In: Stanturf J, Madsen P, Lamb D (eds) A goal-oriented approach to forest landscape restoration. World Forests, vol 16. Springer, Dordrecht.DOI10.1007/978-94-007-5338-9_15

Huylenbroeck L, Latte N, Lejeune P, Georges B, Claessens H, Michez A (2021) What factors shape Spatial distribution of biomass in riparian forests? Insights from a lidar survey over a large area. Forests 12(3):371. https://doi.org/10.3390/f12030371

Keller M (ed) (2011) Swiss National Forest Inventory. Manual of the Field Survey 2004–2007. Birmensdorf, Swiss Federal Research Institute WSL, 269 pp. http://www.wsl.ch/publikationen/pdf/10919.pdf

Kernecker M, Whalen JK, Bradley RL (2015) Agricultural management and flooding shape habitats for non-native earthworms in Southern Quebec. Can Appl Soil Ecol 96:240–250. https://doi.org/10.1016/j.apsoil.2015.08.011

Keuskamp JA, Dingemans BJ, Lehtinen T, Sarneel JM, Hefting MM (2013) Tea bag index: a novel approach to collect uniform decomposition data across ecosystems. Methods Ecol Evol 4(11):1070–1075. https://doi.org/10.1111/2041-210X.12097

Klimo E, Hager H, Machar I, Bucek A, Schmalfuss R, Klasz G, Schume H (2008) Revitalization and protection of Floodplain forests. In: Klimo E (ed) Floodplain forests of the temperate zone of Europe. Lesnická Práce, Publishing House for Forestry, pp 301–323. ISBN 978-80-87154-16-8

LaCroix RE, Tfaily MM, McCreight M, Jones ME, Spokas L, Keiluweit M (2019) Shifting mineral and redox controls on carbon cycling in seasonally flooded mineral soils. Biogeosciences 16(13):2573–2589. https://doi.org/10.5194/bg-16-2573-2019

Laudon H, Buttle J, Carey SK, McDonnell J, McGuire K, Seibert J, Tetzlaff D (2012) Cross-regional prediction of long-term trajectory of stream water DOC response to climate change. Geophys Res Lett 39(18):L18404

Lawrence AP, Bowers MA (2002) A test of the 'hot' mustard extraction method of sampling earthworms. Soil Biol Biochem 34:549–552. https://doi.org/10.1016/S0038-0717(01)00211-5

Le Bayon RC, Binet F (1999) Rainfall effects on erosion of earthworm casts and phosphorus transfers by water runoff. Biol Fertil Soils 30:7–13. https://doi.org/10.1007/s003740050580

Le Bayon RC, Moreau S, Gascuel-Odoux C, Binet F (2002) Annual variations in earthworm surface-casting activity and soil transport by water runoff under a temperate maize agroecosytem. Geoderma 106(1–2):121–135. https://doi.org/10.1016/S0016-7061(01)00121-5

Le Bayon RC, Bullinger G, Gobat JM, Guenat C (2013) Earthworm communities as ndicators for evaluating floodplain restoration success. Floodplains - Environmental Management, restoration and ecological applications. 3, Nova Science, Chapter, pp 47–68

Le Bayon RC, Bullinger G, Schomburg A, Turberg P, Brunner P, Schlaepfer R, Guenat C (2021a) Earthworms, plants, and soils. In Hunt A, Egli M, Faybishenko F (eds) Hydrogeology, chemical weathering, and soil formation, 81–103. https://doi.org/10.1002/9781119563952.ch4

Le Bayon RC, Guenat C, Schlaepfer R, Fischer F, Luiset A, Schomburg A, Turberg P (2021b) Use of X-ray microcomputed tomography for characterizing earthworm-derived belowground soil aggregates. Eur J Soil Sci 72(3):1113–1127. https://doi.org/10.1111/ejss.12950

Le Bayon RC, Campiche S, Gerber V, Fietier A, Scherrer L, Turberg P (2022) Outils d'évaluation de La diversité et de l'activité des vers de terre: de La science participative à La recherche fondamentale. Étude Et Gestion Des Sols 29:99–116

Le Bayon RC, Ponge JF, Zanella A (2024) Earthworms and humus forms. In: Kooch Y, Kuzyakov Y (eds) Earthworms and ecological processes. Springer, Cham, pp 189–217. DOI https://doi.org/10.1007/978-3-031-64510-5_6

Luo Y, Zhou X (2006) Soil respiration and the environment. Elsevier, Academic Press, Burlington

Machar I, Hager H, Pechanec V, Kulhavy J, Mindas J (2020) Floodplain forests—key forest ecosystems for maintaining and sustainable management of water resources in alluvial landscape. Assessment and Protection of Water Resources in the Czech Republic, pp 249–274. Springer Water. Springer, Cham. ISBN 978-3-030-18363-9

MeteoSwiss (2025) Federal Office of Meteorology and Climatology MeteoSwiss. https://www.meteoswiss.admin.ch. Accessed 30 July 2025

Mitsch WJ, Mander Ü (2018) Wetlands and carbon revisited. Ecol Eng 114:1–6. https://doi.org/10.1016/j.ecoleng.2017.12.027

Mitsch WJ, Taylor JR, Benson KB (1991) Estimating primary productivity of forested wetland communities in different hydrologic landscapes. Landscape Ecol 5:75–92. https://doi.org/10.1007/BF00124662

Mori T, Aoyagi R, Taga H, Sakai Y (2021) Effects of water content and mesh size on tea bag decomposition. Ecologies 2(1):175–186. https://doi.org/10.1101/2020.11.15.384016

Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Tichý L (2016) Vegetation of europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl Veg Sci 19:3–264. https://doi.org/10.1111/avsc.12257

Nakamura F (2022) Green infrastructure and climate change adaptation: function, implementation and governance. Springer Nat Saporo(506 pp). ISBN 9789811667909 9789811667916

Neher DA, Barbercheck ME (2019) Soil microarthropods and soil health: intersection of decomposition and pest suppression in agroecosystems. Insects 10(12):414. https://doi.org/10.3390/insects10120414

Oelbermann M, Raimbault BA (2015) Riparian land-use and rehabilitation: impact on organic matter input and soil respiration. Environ Manage 55:496–507. https://doi.org/10.1007/s00267-014-0410-z

Ofosu E, Bazrgar A, Coleman B, Deen B, Gordon A, Voroney P, Thevathasan N (2022) Diverse temperate riparian buffer types promote system-level carbon sequestration in Southern Ontario. Can Forestry Chron 98(1):103–118. https://doi.org/10.5558/tfc2022-012

Pautasso M, Aas G, Queloz V, Holdenrieder O (2013) European Ash (Fraxinus excelsior) dieback – A conservation biology challenge. Biol Conserv 158:37–49. https://doi.org/10.1016/j.biocon.2012.08.026

Pelosi C, Capowiez Y (2022) Les enchytréides, Mieux les connaître pour Mieux les utiliser. Étude Et Gestion Des Sols 29:59–67

Petraglia A, Cacciatori C, Chelli S, Fenu G, Calderisi G, Gargano D, Carbognani M (2019) Litter decomposition: effects of temperature driven by soil moisture and vegetation type. Plant Soil 435:187–200. https://doi.org/10.1007/s11104-018-3889-x

Pfadenhauer J, Grootjans A (1999) Wetland restoration in central europe: aims and methods. Appl Veg Sci 2(1):95–106. https://doi.org/10.2307/1478886

Pokorný P, Klimešová J, Klimeš L (2000) Late holocene history and vegetation dynamics of a floodplain alder carr: a case study from Eastern Bohemia. Czech Repub Folia Geobotanica 35:43–58. https://doi.org/10.1007/BF02803086

Prax A, Richter W, Čermák J, Hybler V (2008) The hydrological and moisture regime of soils in floodplain forests. In: Klimo E (ed) Floodplain forests of the temperate zone of Europe. Lesnická Práce, Publishing House for Forestry, pp 75–101

Ramnarine R, Wagner-Riddle C, Dunfield KE, Voroney RP (2012) Contributions of carbonates to soil CO2 emissions. Can J Soil Sci 92(4):599–607. https://doi.org/10.4141/cjss2011-025

R Core Team (2017) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Riis T, Kelly-Quinn M, Aguiar FC, Manolaki P, Bruno D, Bejarano MD, Dufour S (2020) Global overview of ecosystem services provided by riparian vegetation. Bioscience 70(6):501–514. https://doi.org/10.1093/biosci/biaa041

Sahrawat KL (2004) Organic matter accumulation in submerged soils. Adv Agron 81:169–201. https://doi.org/10.1016/S0065-2113(03)81004-0

Salomé C, Guenat C, Bullinger-Weber G, Gobat JM, Le Bayon RC (2011) Earthworm communities in alluvial forests: influence of altitude, vegetation stages and soil parameters. Pedobiologia 54:S89–S98. https://doi.org/10.1016/j.pedobi.2011.09.012

San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) 2016 European atlas of forest tree species. Publication Office of the European Union, Luxembourg, 202 pp

Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478(7367):49–56. https://doi.org/10.1038/nature10386

Schomburg A, Verrecchia EP, Guenat C, Brunner P, Sebag D, Le Bayon RC (2018a) Rock-Eval pyrolysis discriminates soil macroaggregates formed by plants and earthworms. Soil Biol Biochem 117:117–124

Schomburg A, Schilling OS, Guenat C, Schirmer M, Le Bayon RC, Brunner P (2018b) Topsoil structure stability in a restored floodplain: impacts of fluctuating water levels, soil parameters and ecosystem engineers. Sci Total Environ 639:1610–1622

Schomburg A, Brunner P, Turberg P, Guenat C, Riaz M, Le Bayon RC, Luster J (2019) Pioneer plant phalaris arundinacea and earthworms promote initial soil structure formation despite strong alluvial dynamics in a semi-controlled field experiment. CATENA 180:41–54

Sherlock E (2018) Key to the earthworms of Britain and Ireland. 2nd ed. Field Studies Council, Shrewsbury. ISBN-10: 1908819405

Shipitalo MJ, Le Bayon RC (2004) Quantifying the effects of earthworms on soil aggregation and porosity. In: Edwards CA, (eds) Earthworm ecology. CRC, pp 183–200 https://doi.org/10.1201/9781420039719

Siegfried L, Beuvier S, Vittoz P (2024) Decadal riparian forest evolution beside a regulated lake: a case study in the Swiss lowlands. Folia Geobotanica 59(2):111–128. https://doi.org/10.1007/s12224-024-09456-7

Siegfried L, Verrecchia E, Vittoz P (2025) Diversity and micromorphology of organic matter in riparian forests on carbonate-rich substrate (Switzerland). Forests 16(8):1203. https://doi.org/10.3390/f16081203

Silva MA, Drollinger F, Morard E, Bütler R (2021) Évolution du bois mort dans les forêts de Montricher. Mémoire de la Société Vaudoise des Sciences Naturelles, 29, 47–61. ISSN: 0037-9603

Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ (1996) CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J Ecol 84:219–228. https://doi.org/10.2307/2261357

Sims RW, Gerard BM (1999) Earthworms: notes for the identification of British Species. London: Linnean Society of London and the Estuarine and Coastal Sciences Association. 171p. ISBN 90 04 07582 8

Suchenwirth L, Förster M, Cierjacks A, Lang F, Kleinschmit B (2012) Knowledge-based classification of remote sensing data for the Estimation of below-and above-ground organic carbon stocks in riparian forests. Wetlands Ecol Manage 20:151–163. https://doi.org/10.1007/s11273-012-9252-8

Sutherland RA (1998) Loss-on-ignition estimates of organic matter and relationships to organic carbon in fluvial bed sediments. Hydrobiologia 389:153–167. https://doi.org/10.1023/A:1003570219018

Swisstopo (2025) The federal geoportal. https://map.geo.admin.ch. Accessed 30 July 2025

Trettin CC, Jurgensen MF (2002) Carbon cycling in wetland forest soils. The potential of US forest soils to sequester carbon and mitigate the greenhouse effect. CRC, Boca Raton, pp 311–331

Ukonmaanaho L, Pitman R, Bastrup-Birk A, Breda N, Rautio P (2016) Part XIII: Sampling and Analysis of Litterfall. In: UNECE ICP Forests Programme Co-ordinating Centre (ed.): Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. Thünen Institute for Forests Ecosystems, Eberswalde, Germany, 14 p. ISBN: 978-3-86576-162-0

Verrecchia EP (2007) Lacustrine and palustrine geochemical sediments. In: Nash DJ, McLaren SJ (ed) Geochemical sediments and landscapes. Oxford: Blackwell Publishing Ltd, pp. 298–329. ISBN 978-0-470-71291-7 978-1-4051-2519-2

Vischer DL (2003) Histoire de la protection contre les crues en Suisse. Rapports de l'OFEG, Série Eaux, 5. Bern: OFEG. 208 p. ISSN 1660 – 0746

Wang K, Yuan X, Zhang G, Liu S, Wang F, Liu H, Zhou L (2019) Diversity and distribution of riparian arthropods in the drawdown zone of china's three Gorges reservoir. Environ Entomol 48(6):1340–1348. https://doi.org/10.1093/ee/nvz104

Weber A (1990) Host specificity and efficiency of nitrogenase activity of Fronkia strains from alnus Incana and alnus glutinosa. Symbiosis 8:47–60. https://doi.org/10.1007/BF02377079

Wigginton JD, Lockaby BG, Trettin CC (2000) Soil organic matter formation and sequestration across a forested floodplain chronosequence. Ecol Eng 15:S141–S155. https://doi.org/10.1016/S0925-8574(99)00080 – 4

Wilcox DA, Ingram JW, Kowalski KP, Meeker JE, Carlson ML, Xie Y, Patterson NJ (2005) Evaluation of water level regulation influences on lake Ontario and upper St. Lawrence river coastal wetland plant communities. Final Project Rep. 78p

Wu Q, Ni X, Sun X, Chen Z, Hong S, Berg B, Wu F (2025) Substrate and climate determine terrestrial litter decomposition. Proc Natl Acad Sci 122(7):e2420664122

Zanella A, Berg B, Ponge JF, Kemmers RH (2018a) Humusica 1, Article 2: essential bases—Functional considerations. Appl Soil Ecol 122:22–41. https://doi.org/10.1016/j.apsoil.2017.07.010

Zanella A, Ponge JF, Jabiol B, Sartori G, Kolb E, Gobat JM, Viola F (2018b) Humusica 1, Article 4: terrestrial humus systems and forms—Specific terms and diagnostic horizons. Appl Soil Ecol 122:56–74. https://doi.org/10.1016/j.apsoil.2017.07.005

Zanella A, Ponge JF, De Waal R, Van Delft B, De Nobili M, Ferronato C, Jabiol B (2018c) Humusica 2, Article 11: histic humus systems and forms–Epihisto intergrades and dynamics. Appl Soil Ecol 122:162–169. https://doi.org/10.1016/j.apsoil.2017.03.001

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