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Ecosystem engineers' contribution to soil structure formation in floodplains

PhD thesis

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Preface

This dissertation originates from the FloodSTRESS project which was funded by the Swiss National Science Foundation (SNF), project no. FN 315230_153460, and CCES-project RECORD Catchment of the ETH domain within a period of four years. This thesis is conceptualised as a paper dissertation, meaning that all main chapters exclusively include articles being either already published in scientific journals or still under consideration for publication. Therefore, all rights to the main chapters are or will be on the respective journals.

Abstract

Soil structure formation constitutes an extremely important process in near-natural and restored floodplains. A stable soil structure protects riverbanks from erosion and contributes to the preservation of ecosystem services. However, developing a soil structure in alluvial soils is difficult for several reasons. Extensive alluvial dynamics cause periodic waterlogging and continuously rejuvenate soils by the deposition of unconsolidated sediments which affect soil macro-organisms acting as soil engineers. Plants and earthworms are highly successful soil engineering organisms being able to build up a stable soil structure through the formation of stable macro-aggregates. Macro-aggregates may contain significant amounts of organic matter which can be efficiently stabilised through associations to mineral particles thus contributing to the sequestration of organic matter in the soil. Despite its importance, the role of plants and earthworms in soil structure formation in floodplain soils and in organic matter stabilisation in macro-aggregates is still poorly investigated. In particular, the influence of the landscape hydrology and soil physicochemical parameters on plants and earthworms and their capacity to improve the structural stability of floodplain soils are widely unexplored. Moreover, the mechanisms of macro-aggregate formation and organic matter stabilisation by plants and earthworms including interaction effects in different alluvial sediments are poorly understood. Third, little is known about the efficiency of plants and earthworms to create a stable soil structure in the short term under extensive alluvial dynamics. For this purpose, a three stage experiment was designed: I) analysing the structural stability of soils as a function of plant and earthworm communities, the landscape hydrology and soil physicochemical parameters at the field scale, II) understanding the mechanisms of macro-aggregate formation and OM stabilisation in mesocosms by means of two selected soil engineers, e.g. the red canary grass *Phalaris arundinacea* and the endogeic earthworm *Allolobophora chlorotica*. This chapter was divided in two parts, IIa) testing Rock-Eval pyrolysis to discriminate macro-aggregates formed by *P. arundinacea* and *A. chlorotica* and IIb) analysing the mechanisms of macro-aggregate formation and OM stabilisation for a succession of different mineral and organic layers similar to alluvial soils reconstructed in mesocosms. In the third chapter III), the efficiency of *P. arundinacea* and earthworm communities to create a stable soil structure in the short term was determined in semi-controlled field plots exposed to natural alluvial dynamics. Soil structure was analysed using different traditional pedologic indicators combined with modern imaging techniques. Plant abundance was demonstrated to be crucially affected by fluctuating water levels, but

nevertheless strongly contributed to the stabilisation of the topsoils. Especially *P. arundinacea* was highly efficient to improve the soil structure in sandy alluvial deposits in the short term and to build up stable macro-aggregates within 8 weeks in mesocosms. Earthworm abundance neither correlated to the structural stability of topsoils nor responded to any soil physicochemical parameters or fluctuating water levels in the field. However, earthworm communities, including *A. chlorotica* increased the porosity in the short term, but the stability of their structures was neither increased mesocosms nor in semi-controlled field plots. Nevertheless, *A. chlorotica* efficiently increased the thermal stability of organic matter in macro-aggregates in silty alluvial layers. In the long term, earthworms including *A. chlorotica* contribute to soil structure formation and the sequestration of carbon when their structures gain in stability with aging. Based on the results, interactions between plants and earthworms in macro-aggregate formation and OM stabilisation was assumed, but could not be clearly demonstrated with the applied methods. The methods used to determine soil structure formation and OM stabilisation were highly useful, but standard procedures still need to be defined for data processing and sample preparation. Conclusively, plants and earthworms have great potential to increase the success of river restoration projects, whereby plants in the short term and earthworms in the long term.

Keywords: pioneer plants; earthworms; alluvial soils; aggregation; organic matter stabilisation; hydropedology; X-ray computed tomography; Rock-Eval pyrolysis

Résumé

La formation de la structure du sol est un processus primordial en zone alluviale semi-naturelle et revitalisée. Une structure du sol stable protège les berges de l'érosion et contribue à la préservation des services écosystémiques de ce type de milieux. Cependant, la mise en place de la structure des sols alluviaux est délicate pour plusieurs raisons. La dynamique alluviale très marquée engendre régulièrement des engorgements et rajeunit continuellement les sols au travers de dépôts de sédiments non consolidés, ce qui impacte les macroorganismes tels que les ingénieurs du sol. Les plantes et les vers de terre sont des organismes ingénieurs très performants capables de façonner une structure cohésive au moyen de macro-agrégats stables. Ces derniers peuvent contenir des teneurs conséquentes de matière organique, stabilisée par les particules minérales, ce qui contribue à sa séquestration dans le sol. Malgré son aspect crucial, le rôle des plantes et des vers de terre dans la mise en place de la structure du sol et la stabilisation de la matière organique au sein d'agréats reste peu méconnu en zones alluviales. Plus particulièrement, l'influence de l'hydrologie à l'échelle du paysage ainsi que celle des paramètres physico-chimiques sur les plantes et les vers de terre est encore peu étudié, et notamment leur capacité à améliorer la stabilité structurale des sols alluviaux. De plus, les mécanismes de formation des macro-agrégats ainsi que la stabilisation de la matière organique par les plantes et/ou les vers de terre selon le type de sédiment est encore mal connu. Enfin, les connaissances manquent sur l'efficacité de ces acteurs dans la réalisation d'une structure stable à court terme, et sous l'effet d'une dynamique fluviale intense. Pour toutes ces raisons, une expérimentation en trois étapes a été menée afin : I) d'analyser la stabilité structurale des sols en fonction des plantes et des communautés lombriciennes, de l'hydrologie du milieu et des paramètres physicochimiques à l'échelle du terrain, II) de comprendre les mécanismes de formation des macro-agrégats et de la stabilisation de la MO au travers d'une étude en mésocosmes, à l'échelle des processus, en sélectionnant des ingénieurs du sol, à savoir la baldingère faux-roseau *Phalaris arundinacea* et un ver de terre endogé *Allolobophora chlorotica*. Ce chapitre a été divisé en deux parties, IIa) tester la pyrolyse Rock Eval pour discriminer les macro-agrégats issus de *P. arundinacea* et *A. chlorotica*, IIb) analyser les mécanismes de formation des macro-agrégats et de stabilisation de la MO lors d'une superposition de couches de différents matériaux minéraux et organiques, en simulant ainsi des sols alluviaux reconstitués en mésocosmes. Dans le troisième chapitre, III) l'efficacité de *P. arundinacea* et des communautés lombriciennes à créer une structure du sol stable sur le

court terme a été déterminée au sein d'un système expérimental semi-contrôlé, exposé à la dynamique alluviale naturelle *in situ*. La structure du sol a été analysée au moyen des indicateurs pédologiques traditionnels combinés à des techniques modernes d'imagerie. L'abondance des plantes a été démontrée comme étant drastiquement impactée par la fluctuation des niveaux d'eau, mais elle contribue toutefois très fortement à la stabilisation des horizons de surface. *P. arundinacea* a largement amélioré la structure du sol dans les dépôts sableux sur le court terme et a contribué à la fabrication de macro-agrégats stables en 8 semaines en mésocosmes. Sur le terrain, l'abondance des vers de terre n'est ni corrélée à la stabilité structurale des horizons de surface, ni à aucun des paramètres physico-chimiques ou fluctuations des niveaux d'eau. Cependant, les communautés lombriciennes, incluant *A. chlorotica*, ont amélioré la porosité du sol sur le court terme, mais la stabilité de leurs structures biogéniques n'a jamais augmenté, que ce soit en mésocosmes ou en conditions semi-naturelles. Toutefois, *A. chlorotica* augmente de manière efficace la stabilité thermique de la matière organique dans les macro-agrégats formés à partir de sédiments limoneux. Sur le long terme, les vers de terre, dont *A. chlorotica*, contribuent à la formation de la structure du sol et à la séquestration du carbone quand leurs structures biogéniques gagnent en stabilité avec le temps. Ces résultats laissent supposer des interactions entre plantes et vers de terre dans la formation des macro-agrégats, mais celles-ci n'ont pas été clairement établies avec les techniques utilisées. Les méthodes, qui ont permis de déterminer la formation de la structure du sol et la stabilisation de la MO, ont été très utiles mais les procédures standards nécessitent encore d'être définies pour notamment la préparation des échantillons et le traitement des données. En conclusion, les plantes et les vers de terre possèdent un grand potentiel pour favoriser la réussite des projets de revitalisation en zone alluviale, les plantes sur le court terme et les vers de terre sur un plus long terme.

Mots-clés : plantes pionnières ; vers de terre ; sols alluviaux ; agrégat ; stabilisation de la matière organique ; tomographie par rayons X ; pyrolyse Rock Eval.

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General introduction

Soil structure formation and stabilisation

Soil structure is defined as the spatial arrangement of mineral and organic particles that form a stable soil fabric composed of soil aggregates and pore space (Tisdall and Oades, 1982; Brussard and Kooistra, 1993; Barrios, 2007). Soil aggregates are particularly built up around organic nuclei which are associated to mineral particles and stabilised by micro-organic and inorganic cementing agents (Tisdall and Oades, 1982; Tisdall, 1996; Guggenberger et al., 1996; Bronik and Lal, 2005). Soil aggregates are distinguished between micro-aggregates of 50 - 250 μm size and macro-aggregates of 250 - 2000 μm size (Fig. 1) (Tisdall and Oades, 1982; Six et al., 2004; Bossuyt et al., 2005). Micro-aggregates are formed through chemical adsorption of clay minerals to organic matter (OM) particles and through persistent organic cementing agents of bacterial and fungal origin (Oades, 1984; Angers et al., 1997). Macro-aggregates are composed of micro-aggregates that are rearranged and agglutinated by vegetation and soil macro-fauna (Fig. 1) (Six et al., 2000; 2002). In contrast to micro-aggregates that are more resistant to physical forces, macro-aggregates become more vulnerable to breakdown with increasing age (Barrios, 2007). Macro-aggregates disintegrate into micro-aggregates caused by the microbial decomposition of binding agents, but can also be rapidly reoriented into new macro-aggregates through the activity of soil macro-fauna (Six et al., 2004).

Soil structure formation, in particular the formation of stable aggregates, is a process which runs predominantly in the upper soil layers (Lavelle et al., 1997; Brown et al., 2000). This zone includes the interfaces between the five hotspots of enhanced physicochemical soil processes and high biological activity (Beare et al., 1995; Barrios, 2007): 1) the aggregatusphere characterised by a dense spatial arrangement of micro- and macro-aggregates, 2) the porosphere describing the void in between the aggregates filled by water and air, 3) the detritosphere denominating the zone of enhanced microbial decomposition of OM, 4) the rhizosphere and 5) the drilosphere designating the zones which are characterised by a high density and activity of plant roots and earthworms. Soil structure formation is controlled by a complex interplay of physical processes affecting the ecosystem, soil physicochemical parameters and soil organisms (Kay, 1998; Duiker et al., 2003; Bronik and Lal, 2005). Regarding physical processes, alternating desiccation and remoistening leads to hardening of soil aggregates, thus physically improving the structural stability of soils (Dalal and Bridge, 1996). The physicochemical parameters of soils either

directly affect aggregate formation and stability or promote microorganisms which, on their part, contribute to aggregate formation. The stability of aggregates is strongly influenced by the soil texture being positively correlated to the proportion of silt and clay and negatively correlated to the proportion of sand in soils (Duiker et al., 2003; Bronik and Lal, 2005; Kaiser et al., 2012). Additionally, the stability of aggregates shows a strong positive correlation to the amount of soil organic matter (SOM) and its bulk chemistry (e.g. the chemical quality), as easier decomposable OM can be transformed into organic substances agglutinating soil particles (Guggenberger et al., 1996; Kong et al., 2005; Jouquet et al., 2008). Physical cementation of mineral and organic particles is of particular importance in coarser textured soils, as sand grains have a low specific surface compared to clay minerals allowing a chemical adsorption of organic substances (Haynes and Beare, 1997; Kay, 1998). Regarding chemical properties of the soil, the calcium carbonate content promotes aggregation, as Ca^{2+} directly cements soil particles together or interacts with SOM (Duiker et al., 2003; Bronik and Lal, 2005). Other chemical properties can indirectly affect aggregation through promoting or suppressing microbial activity, such as pH values (Chorom et al., 1994; Haynes and Naidu, 1998) and the cation exchange capacity (CEC) which can decrease repulsive forces of negatively charged clay minerals (Tisdall, 1996). Soil organisms affect aggregate formation and stability among different biological scales. On the micro-scale, organic substances secreted by microorganisms represent the initial step for the formation of micro-aggregates (Tisdall and Oades, 1982). Additionally, arbuscular mycorrhizal fungi (AMF) excrete extracellular polysaccharides such as Glomalin which act as a binding agent (Ternan et al., 1996; Jastrow et al., 1998). On the macro-biological scale, soil engineering organisms as ecosystem engineers contribute significantly to the formation and stability of macro-aggregates (Blouin et al., 2013).

A well-developed soil structure can positively influence the soil functioning and improves the biodiversity in ecosystems (Bronik and Lal, 2005). Stable structural elements provide niches for the soil fauna, as well as for plants and associated above-ground organisms (Bronik and Lal, 2005). In addition, several ecosystem services can be promoted by a stable soil structure: the spatial arrangement of soil aggregates and the pore space (Fig. 1) positively affects the water storage capacity and water circulation in the soil which improves the water quality due to efficient adsorption of nutrients and pollutants to soil particles (Bronik and Lal, 2005). Furthermore, a stable soil structure increases the resistance to soil erosion caused by water and wind (Diaz-Zorita et al., 2002; Mardhiah et

al., 2014). Moreover, soil aggregates can make an important contribution to the carbon sink function of terrestrial ecosystems through the efficient sequestration of SOM into micro- and macro-aggregates (Fig. 1) (Martin, 1991; Bossuyt et al., 2005). The majority of these ecosystem services is poorly developed in ecosystems which are either relatively young, such as glacier forefields (van Leeuwen et al., 2017), or frequently affected by strong exogenous dynamics, such as savannah ecosystems by fire (McMullan-Fisher, 2011), or both in combination, such as floodplains, that are frequently flooded and affected by erosion and deposition of alluvial sediments (Junk and Welcomme, 1990; Naiman and Décamps, 1997).

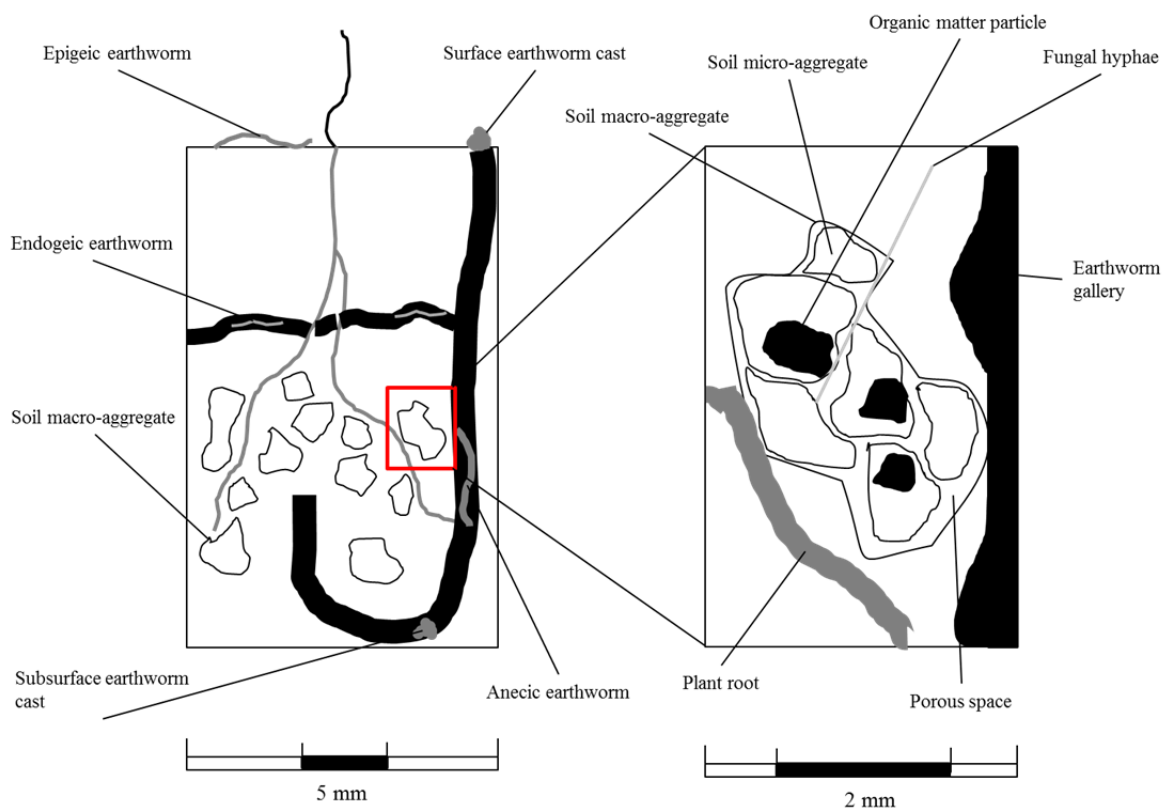


Fig. 1: The formation and composition of micro- and macro-aggregates in the soil by soil engineering organisms.

As mentioned above, soil structure formation and maintenance depends on numerous exogenous factors, on the physicochemical soil properties and on the activity of soil biota. For this reason, measuring or rating soil structure is difficult. So far, uniform standards and procedures for an exact method how to analyse soil structure have not yet been defined (Rabot et al., 2018). Generally, soil structure is analysed using a broad variety of tools and indicators either directly measuring the structural stability or indirectly analysing the void-

matrix ratio, the spatial arrangement and the connectivity of the porous system: traditionally, soil structure is measured via its structural stability using pedologic indicators, such as the physical appearance of soil aggregates in the field (IUSS Working Group WRB, 2006), their bulk density, their mean weight diameter and their physical stability against water (Kemper and Rosenau, 1986; Miedema, 1997). The proportion of water-stable macro-aggregates in relation to the total amount of aggregates within a soil sample is considered as the most pertinent pedologic indicator (Six et al., 2000). Indirect methods have developed to evaluate the macro- and micromorphology of the soil structure using different non-destructive imaging techniques, such as stereo- and light microscopy, transmission electron microscopy and nuclear magnetic resonance imaging (NMRI) (Vogel *et al.*, 2002; Vervoort and Cattle, 2003). Recently, X-ray computed tomography (X-ray CT) have become particularly popular for the evaluation of the spatial arrangement and the connectivity of the porous system (Capowiez et al., 2011; 2015; Helliwell et al., 2013; Amossé et al., 2015). The void-matrix ratio, the total number and length of the void segments and their connectivity can be calculated from image analyses and are useful indicators allowing conclusions about the development of a soil structure to be drawn (Capowiez et al., 2011).

Ecosystem engineers

Ecosystem engineers are defined as organisms being able to build up an ecosystem from the initial stage by causing significant physical changes in their environment and by controlling the resources of other subordinated organisms (Jones et al., 1994, 1997a, b). Ecosystem engineers can contribute to the creation, maintenance and modification of habitats by influencing the ecosystem itself and other species living in this ecosystem across large spatial and temporal scales (Jones et al., 1994, 1997a, b; Wright et al., 2004; Jouquet et al., 2006). The dimension of the engineering effect largely depends on the life cycle of the organisms, the persistence of physical structures they create and the habitat complexity (Jones et al., 1997a; Sueiro et al., 2011). Ecosystem engineers can be classified according to different criteria, e.g. by the functional structures they create (Jones et al., 1997a, b) or by means of their behaviour (Jouquet et al., 2006). Jones et al. (1997a, b) distinguished “autogenic engineers” influencing ecosystems through their own physical structure, such as trees or corals, and “allogenic engineers” which create physical structures using organic and inorganic materials to build up their habitats (e.g. beaver

dams, bird nests). An extended definition was provided by Jones et al. (2010) including biochemical (e.g. OM transformation), biological processes (e.g. food supply) and their feedback mechanisms. Based on this concept, Berke (2010) proposed a division into four categories, 1) structural engineers, 2) bioturbators, 3) light engineers and IV) chemical engineers. Jouquet et al. (2006) discriminated “extended phenotype engineers” which directly affect the fitness of other species through their physical structures or their effects and “accidental engineers” whose physical structures do not affect other organisms. The impact of ecosystem engineers is greatest in ecosystems whose physical structures may persist for long periods of time without being replaced, destroyed or reset, e.g. in forests, peatlands or coral reefs (Jones et al. 1997a). On the other hand, ecosystem engineers might be of particular importance for the creation and stabilisation of young, dynamic and rejuvenated ecosystems such as glacier forefields, savannahs, mangrove swamps or floodplains (Jones et al. 1997a; Le Bayon et al., 2013; 2017). In these types of ecosystems, soil structure formation is among the most important engineering effect promoted by soil engineering macro-organisms (Lavelle et al., 1997; Jouquet et al., 2006; Blouin et al., 2013). Soil engineers contribute to the formation of stable macro-aggregates, increase the porosity of the soil and stabilise SOM through its incorporation into macro-aggregates (Lavelle and Spain, 2001; Jouquet et al., 2006; Fonte et al., 2012). In soils of the temperate climate zone, plants and earthworms are among the most important soil engineering organisms (Lavelle et al., 1997; Tanner, 2001; Kong and Six, 2010; Blouin et al., 2013; Le Bayon et al., 2017).

Plants

Plants are both “autogenic” and “allogenic engineers” according to Jones et al. (1997a) and “extended phenotype engineers” according to Jouquet et al. (2006). Depending on the type of ecosystem and influencing physical factors, plants can have various engineering effects in soils (Tanner, 2001; Kong and Six, 2010), such as peat accumulation in raised bogs (van Breemen, 1995), adsorption of heavy metals (Salt et al., 1995) and nitrogen and phosphorous cycling (Tanner, 2001; Graham and Vance, 2003). Soil structure formation is among the most important engineering effect of plants gained equally by trees, shrubs and herbaceous plants (Tanner, 2001; Gurnell and Petts, 2002; 2006; Gurnell, 2014). Plants create water-stable macro-aggregates and improve the porosity of soils by means of their root system in the rhizosphere (Caravaca et al., 2002). Macro-aggregate formation by roots

is a process involving different direct and indirect mechanisms. Roots directly contribute to macro-aggregate formation through physical penetration into the soil, while soil particles are entangled by fine roots (Rillig et al., 2002). Moreover, roots secrete organic exudates which are binding agents directly agglutinating soil particles or stimulate associated microorganisms and rhizobacteria which release organic substances contributing to aggregation on their part (Degens et al., 1994; Angers and Caron, 1998; Czarnes et al., 2000). Indirectly, alternating wet-dry cycles are increased in the rhizosphere due to water uptake by roots which can lead to physical aggregation (Angers and Caron, 1998). In young and dynamic ecosystems, such as floodplains, the engineering capacity of plants might be of particular importance. Recent findings indicated that roots trap sediments which need to be efficiently stabilised and structured to prevent river shore erosion (Nanko et al., 2008; Corenblit et al., 2009; Crouzy and Perona, 2012; Perona et al., 2012).

Earthworms

Similar to plants, earthworms can be classified as “allogenic engineers” according to Jones et al. (1997a) and as both “extended phenotype engineers” and “accidental engineers” according to Jouquet et al. (2006) depending on the species and the ecological category (see below). Earthworms are saprophagous macro-invertebrates living in the drilosphere being among the first macro-organisms to engineer soils (Lavelle et al., 1997; Ponge, 2013). Earthworms can be divided into three ecological categories defined by their behaviour, feeding ecology and ecological niches (Bouché, 1972; Edwards and Bohlen, 1996; Edwards, 2004): Epigeics live in the litter layer on top of the mineral soil decomposing and transforming litter into stabilised OM (Fragoso and Lavelle, 1995; Brown et al., 2000). Thus, epigeics do not directly contribute to soil structure formation, but supply transformed organic substances that are associated to the mineral fraction of the soil in a second stage (Bossuyt et al., 2005; Seeber et al., 2006). Endogeics and anecics are highly involved in the formation of macro-aggregates through their burrowing and casting activity (Zhang and Schrader, 1993; Blanchart et al., 1997; Brown et al., 2000; Lavelle and Spain, 2001). Endogeics live in organo-mineral subsurface horizons, feed on soil and digest OM of various chemical composition (Fragoso and Lavelle, 1995; Eisenhauer et al., 2009; Sanchez de Leon et al., 2014). Compared to endogeics, anecics produce a low number of galleries in which they move and selectively ingest OM (Fragoso and Lavelle, 1995). Although anecics particularly live in the topsoil which is enriched in OM, galleries

can occur up to a depth of 1.5 m in the soil (Brown et al., 2000; Jouquet et al., 2006; Eisenhauer et al., 2009). Endogeics and anecics produce stable macro-aggregates either in form of burrow walls along their galleries or in form of faecal excretions accumulated as casts (Shipitalo and Protz, 1988; Barrois et al., 1993; Lavelle et al., 1997; Brown et al., 2000). During burrowing, earthworms secrete external mucus over their skin which directly agglutinates soil particles along the burrow walls or enhances the activity of microbes secreting cementing substances on their part (Brown et al., 2000). During casting, mineral and organic particles are mixed and agglutinated with mucus and saliva in earthworms' digestive tract and defecated as casts which are deposited in the galleries (mostly for endogeics) or at the soil surface (mostly for anecics) (Lavelle et al., 1997; Brown et al., 2000). Besides the formation of stable macro-aggregates, earthworms have several other important engineering effects in the soil. The majority of earthworm species decrease the bulk density of soils, facilitate water infiltration through the creation of macro-pores (Ehlers, 1975; Pérès et al., 1998; Bottinelli et al., 2010) and improve the nitrogen cycling and phosphorus availability (Edwards and Bohlen, 1996; Le Bayon and Binet, 2006). A few earthworm species produce larger globular casts which increase the bulk density of the soil and decrease the aggregate stability and infiltration capacity (Blanchart et al., 1997; Milleret et al., 2009a; b; Kohler-Milleret et al., 2013). Thus, Blanchart et al. (1997) discriminated "compacting" and "decompacting" earthworm species. In general, earthworms are sensitive to high and low soil moisture contents and large proportions of coarse sand (Edwards and Bohlen, 1996; Henszey et al., 2004; Davis et al., 2006; Perrault and Whalen, 2006). Apart from that, earthworms were demonstrated to have a high tolerance against a broad range of soil physicochemical parameters (Eijsackers, 2010). Thus, earthworms are able to rapidly colonise new soils or soils which were threatened by anthropogenic activity in the past (Brown et al., 2000). Therefore, earthworms can play a key role in the restoration of ecosystems (Blouin et al., 2013; Frouz et al., 2014).

Organic matter stabilisation in soil aggregates

Apart from being the main components of a stable soil structure, soil aggregates can play a significant role in the terrestrial carbon cycle. The association of OM to the mineral soil matrix can make an important contribution to carbon sequestration in the soil (Martin, 1991; Bossuyt et al., 2005). For this purpose, OM needs to be efficiently stabilised in the

soil, in particular in soil aggregates (Christensen, 1996; Sollins et al., 1996). There are three important mechanisms of OM stabilisation in soil aggregates: OM can be physically stabilised through its occlusion into soil aggregates without the molecular structure being modified during this process. OM can be chemically stabilised by adsorption to clay minerals forming stable clay-humus complexes, and biogeochemically stabilised through its transformation into highly recalcitrant compounds that cannot be decomposed by microorganisms (Six et al., 2004; von Lützow et al., 2006; Jastrow et al., 2007; Jouquet et al., 2011). The latter processes simultaneously result in the increase of OM thermal stability in soil aggregates. Based on recent findings about OM stabilisation in the soil, Schmidt et al. (2011) proposed a paradigm change regarding OM dynamics in the soil. According to the traditional view on OM dynamics, the terrestrial carbon cycle is represented by one coherent process initiated by external litter inputs which are decomposed by the soil micro- and macro-fauna. OM is assigned to different pools from which the labile pool is consumed by soil organisms releasing CO₂ into the atmosphere. The recalcitrant fraction, which is indigestible for soil organisms, is enriched in the soil relative to the labile fraction and contributes to the carbon sink function in the soil. However, Schmidt et al. (2011) proposed two new perspectives which are in contrast to the traditional view on the soil carbon cycle: First, the authors suggested the existence of multiple carbon cycles running spatially and temporally decoupled from one another. For example, litter inputs can be decomposed at the soil surface without being incorporated into the soil matrix. On the other hand, OM directly introduced into the soil matrix from root exudates or from earthworms via mucus and saliva can be directly stabilised. Second, the authors proposed that the molecular structure of OM is not the predominant factor determining its residence time in an ecosystem. It is far more important to what extent OM is efficiently stabilised in soil aggregates. This implies that even the labile fraction of OM generally characterised by a rapid turnover rate can persist in the soil for millennia through physical protection. In this case, the labile OM fraction is inaccessible for soil organisms without being biogeochemically transformed. In conclusion, the persistence of SOM in the soil is controlled by physicochemical and biological factors and needs to be analysed at the ecosystem level (Schmidt et al., 2011).

Plants and earthworms can contribute significantly to the stabilisation of OM in macro-aggregates (Jouquet et al., 2006; Fonte et al., 2012). OM associated to macro-aggregates comes from different carbon pools in the soil: 1) free particular OM of different

decomposition stage, 2) OM from inputs of plants and earthworms and 3) OM from microorganisms stimulated by OM inputs from plants and earthworms. OM inputs provided by plant roots and earthworms differ in their chemistry, but can be both assigned to the labile OM fraction (Yavitt et al., 2015). Root exudates particularly consist of polysaccharides, as well as, to a lesser extent, of amino acids, carbohydrates and vitamins (Nardi et al., 2005; Shukla et al., 2011). Organic substances secreted by earthworms mainly contain proteins and conjugated saccharides (Zhang et al., 2016). Based on the different OM chemistry provided by plants and earthworms, macro-aggregates can be assigned to the soil engineer that contributed to their formation (Hedde et al., 2005; Velasquez et al., 2007; Zhang et al., 2009; Zangerlé et al., 2011). This approach allows for inferences on the mechanisms of macro-aggregate formation by plants and earthworms. Increasing the knowledge on these mechanisms is of crucial importance to better understand the development of a stable soil structure (Pulleman et al., 1995; Bossuyt et al., 2004; Velasquez et al., 2007; Zangerlé et al., 2011). In the recent past, near infrared reflectance spectroscopy (NIRS) was demonstrated to be promising to assign soil aggregates to plants and earthworms based on the chemical composition of incorporated OM (Hedde et al., 2005; Velasquez et al., 2007; Zhang et al., 2009; Huerta et al., 2013; Zangerlé et al., 2011; 2014). Additionally, OM signatures of both plants and earthworms in the same aggregate indicated interaction between soil engineers during macro-aggregate formation (Zangerlé et al., 2011). However, this general approach is restricted to experimental designs in which several conditions can be controlled. In micro- and mesocosms, the initial matrix, the treatments and the amount and bulk chemistry of OM can be standardised allowing OM signatures in soil aggregates to be analysed as the contribution of soil engineers to macro-aggregate formation. In the field, OM from the bulk soil is highly variable in space and time in terms of the quantity and bulk chemistry. In that case, modifications of the OM signatures in aggregates are very small relative to the variability of OM in the soil exceeding the effect of soil engineering organisms.

Floodplains

Floodplains are defined as lowland areas being frequently inundated by fluctuating water levels from adjacent river systems (Junk and Welcomme, 1990; Naiman and Décamps, 1997; Stanford et al., 2005). Floodplain soils can be periodically waterlogged in consequence of lateral inundation by surface water or rising groundwater levels (Salomé et

al., 2011). Inundation by surface water often leads to erosion of unconsolidated sediments or to the accumulation of fresh alluvial deposits, depending on the surface water discharge (Nanson and Croke, 1992; Marriot, 1998; Graf-Rosenfellner et al., 2016). Major flood periods locally cause strong soil erosion, but also the deposition of thick sediment layers burying and conserving former topsoils (Gurwick et al., 2008; Blazejewski et al., 2009; Bätz et al., 2015). Weaker inundation periods favour the accumulation of finer-textured alluvial sediments combined with the input of significant amounts of allochthonous OM (Cabezas and Comin, 2010; Cierjacks et al., 2011; Bätz et al., 2014). In many floodplain ecosystems, habitat succession follows a strong topographical gradient (Gurnell and Petts, 2002). Habitats on the riverbank are stronger affected by floods at higher frequency and duration, and by erosion and sediment deposition while habitats more distant to the river are only affected during major flood events (Bendix and Hupp, 2000; Cierjacks et al., 2011; Hayashi et al., 2011; Graf-Rosenfellner et al., 2016). Habitat succession often correlates with the succession stage of vegetation and soils: in close proximity to the river, habitats are settled by pioneer vegetation and softwood forests, and by hardwood forest further distant to the river (Francis, 2007; Francis et al., 2009; Gurnell et al., 2001; Moggridge and Gurnell, 2009). Soils in the active zone close to the river represent the initial stage of soil development and are characterised by a superimposition of many indistinguishable soil horizons (Guenat et al., 1999; De Vivo et al., 2001; Bullinger-Weber et al., 2007; Coppola et al., 2010). Depending on the thickness and the soil texture, these soils are classified as Leptosols (Fluvic), Fluvisols or Fluvic Arenosols (IUSS Working Group WRB, 2015). In these soil types, soil structure formation is an initial process running particularly in the topsoil and involving interactions between recent alluvial deposits, allochthonous OM and pioneer plant and earthworm species (Guenat et al., 1999). Alluvial soils under hardwood forests are pedologically more developed, as they are less affected by alluvial dynamics. These soils are mostly categorised as Fluvic Cambisols (IUSS Working Group WRB, 2015). However, micro-topographical landscape units can create different types of habitats in the same area along the topographical gradient. Alluvial dynamics can have a distinctive effect in local hollows compared to micro-topographical elevations nearby (Naiman and Décamps, 1997; Stanford et al., 2005; Clerici et al., 2011; Gurnell, 2014). This micro-topographical variability creates a mosaic of habitats on a small scale and is the main reason why floodplains are considered as hotspots of biodiversity (Malmqvist and Rundle, 2002; Tockner and Stanford, 2002). Apart from hosting an enormous faunal and floral diversity, floodplains fulfil a broad range of ecosystem services

having an economical value for humans (Palmer and Richardson, 2009; Tockner et al., 2011). Floodplains adjacent to large braided river systems can store significant amounts of water during flood periods. Water storage in floodplain soils significantly reduces the peak discharge which simultaneously mitigates the flood risk at anthropogenic settlements in lowland areas (Acreman et al., 2003). Furthermore, dissolved organic nutrients and pollutants can be adsorbed to the soil matrix during water circulation in the floodplain (Brooks and Shields, 1996). Due to this natural water purification mechanism, floodplains are widely used for drinking water enrichment (Alewell et al., 2008). Soil structure formation and stabilisation are key processes in floodplain ecosystems to accelerate habitat succession and to promote and maintain the ecosystem services (Guenat et al., 1999; Bullinger-Weber et al., 2007; Graf Rosenfellner et al., 2016).

River management in the past and river restoration

At present, floodplains are among those ecosystems being most severely affected by human activity in the world (Malmqvist and Rundle, 2002; Tockner and Stanford, 2002). In Europe, first river corrections were initiated 150 years ago, making the fertile floodplain soils favourable for intensive agricultural use (Acreman et al., 2003; Bundesamt für Umwelt BAFU, 2015). In the course of the industrialisation, rivers strongly gained in importance for energy production. Furthermore, settlements nearby rivers or in lowland areas needed to be better protected from floods (Bundesamt für Umwelt BAFU, 2008). For this purpose, rivers have been canalised and embanked until the late 80s of the 20th century (Boon et al., 2000). However, river embedding disconnected the river from the adjacent floodplain by interrupting the alluvial dynamics which are essential for the ecosystem functioning of floodplains (O’Hanley, 2011). Missing alluvial dynamics result in a strong decline of biodiversity and suspend the majority of the ecosystem services in floodplains. Furthermore, river embedding, initially intended to minimise the flood risk, rather intensifies the frequency and magnitude of flooding (Acreman et al., 2003; O’Hanley, 2011). Flood peaks are characterised by a sharp and sudden increase due to increased flow velocities in straight riverbeds and missing inundation areas reducing and delaying the arrival of the flood peak in settled areas (Acreman et al., 2003). Global annual costs of flood damages on anthropogenic infrastructure amount to more than 100 billion US dollars (United Nations Office for Disaster Risk Reduction, 2015) and to 270 million CHF on average in Switzerland (calculated from values provided in Andres and Badoux, 2018). In

the last two decades, the focus of river management has been set to the natural flood protection, the improvement of ecosystem services and ecological aspects of the rivers and floodplains (Palmer et al., 2010; Fournier et al., 2012). In consequence, numerous river restoration projects have been initiated all over the world (Palmer et al., 2010; Fournier et al., 2012; 2013). In Switzerland, about 4000 km of rivers are planned to be restored within the next 40 years (Bundesamt für Umwelt BAFU, 2015). The restoration goals in Switzerland were defined by the Bundesamt für Umwelt BAFU and aim to restore the biodiversity of rivers and floodplains and to improve flood protection by providing natural inundation areas (Bundesamt für Umwelt BAFU, 2008).

Remaining gaps to fill

The contribution of plants and earthworms to soil structure formation has already been analysed in several different ecosystems. For instance, recent studies highlighted positive effects of plants and earthworms to increase the structural stability of managed forest soils (Caro et al., 2014; Yavitt et al., 2015) and of soils in the humid tropics (Jouquet et al., 2008; 2011). Furthermore, plants and earthworms were shown to improve the physical soil properties in degraded peatlands (Johansen et al., 2017; Haapalehto et al., 2017) and former mining areas (Frouz et al., 2014). However, their contribution to soil structure formation in floodplain soils, despite considered as a key process, is still poorly understood (Guenat et al., 1999; Bullinger-Weber et al., 2007; Graf-Rosenfellner et al., 2016). Recently, pioneer plants and earthworms were already demonstrated to have a great potential of structuring alluvial soils (Gurnell and Petts, 2002; 2006; Bullinger-Weber et al., 2007; 2012; Graf-Rosenfellner et al., 2016; Le Bayon et al., 2013; 2017), but their abundance can be limited by alluvial dynamics (Ausden et al., 2001; Plum and Filser, 2005; Gurnell and Petts, 2002; 2006; Ivask et al., 2007; Zorn et al., 2006; 2008; Bätz et al., 2014; 2015). Plant and earthworm communities have already been investigated in floodplain transects as a function of soil physicochemical properties and the flood frequency assessing a decreasing effect with increasing distance to the river (Salomé et al., 2011; Fournier et al., 2015). The structural stability of floodplain soils was thereby assessed to increase gradually along a toposequence (Bullinger-Weber et al., 2012). However, the micro-topography of floodplains and the spatial and temporal characteristics of the landscape hydrology have never been considered in the analyses of soil structure formation and of plant and earthworm communities in floodplains. Multiple interactions

effects including plants and earthworms, the physicochemical soil parameters and water dynamics on the structural stability of floodplain soils have not yet been analysed in detail. As hydrologic processes, in general, are supposed to be a driving factor for the soil development in semi-terrestrial ecosystems, the landscape hydrology, in particular the inundation by surface water and the fluctuations of groundwater levels can be crucial for soil structure formation in floodplains (Lin et al., 2005; 2015; Bouma 2012; 2016; Ma et al., 2017).

The analysis of soil structure formation in floodplains also requires a better understanding of the mechanisms of macro-aggregate formation and the associated OM stabilisation induced by plants and earthworms in alluvial sediments at the mesocosm scale. For this purpose, *in vitro* experiments are useful, as treatments, physical conditions and soil physicochemical parameters including OM quantity and bulk chemistry can be controlled. This experimental design not only allows single effects of macro-aggregate formation and OM stabilisation, but also interaction effects of plants and earthworms to be analysed. Recently, aggregate formation and soil stabilisation by plants and earthworms including interaction effects were successfully investigated in micro- and mesocosms for different soil and sediment materials (e.g. Milleret et al., 2009a, b; Fonte et al., 2012; Kohler-Milleret et al., 2013; Amossé et al., 2015; Yavitt et al., 2015; Angst et al., 2017; Lubbers et al., 2017). The capacity of the selected organisms to improve the aggregate stability strongly depended on the sediment type, the selected organisms and species-specific interactions, whether positive or negative. Although alluvial soil material was already tested (Amossé et al., 2015), the specific characteristics of floodplain soils were thereby not considered. The superposition of mineral layers of different textural composition and of buried organo-mineral topsoil or litter layers is typical for floodplain soils (Kercheva et al., 2017). Creating an artificial superposition of layers similar to alluvial deposits in mesocosms, processes of macro-aggregate formation and OM stabilisation running in alluvial soils can be simulated in a more realistic way. Focusing on one typical pioneer herbaceous plant and one earthworm species allows mechanisms of macro-aggregate formation and OM stabilisation to be analysed at a basic level. Recently, NIRS has found successful application to describe the mechanisms of macro-aggregate formation by plants and earthworms through the analysis of the incorporated OM (Velasquez et al., 2007; Zangerlé et al., 2011, 2014). However, NIRS only provides information about the quantity and bulk chemistry of OM and does not provide any information on its stabilisation.

Furthermore, infrared signatures are difficult to interpret in calcium carbonate rich soils paired with low total OM contents which are typical for several floodplain soils (Dalal & Henry, 1986; Chodak, 2008). Associations of calcium carbonate to OM strongly affect the infrared spectra and complicate the interpretations of the data (Cozzolino and Moron, 2004; Chodak, 2008). Therefore, the analysis requires a holistic method which is robust for low total OM and high calcium carbonate contents. Rock-Eval pyrolysis is a promising method which was originally designed for the exploration of oil and gas reservoirs (Espitalité et al., 1985), but has recently found increased application in biogeochemical and pedologic topics (Albrecht et al., 2015; Saenger et al., 2013; 2015; Sebag et al., 2005; 2016; Matteodo et al., 2018). However, Rock-Eval pyrolysis has not yet been applied specifically to OM associated to aggregates. Thus, the applicability of Rock-Eval pyrolysis to distinguish soil macro-aggregates by their origin comparable to NIRS and additionally to provide information on the stability of OM in macro-aggregates is unclear.

Soil structure formation in the most active zone in close proximity to the river is among the most important, but also among the most difficult processes (Bätz et al., 2014; 2015). Alluvial dynamics are particularly distinctive on these “active surfaces” leading to either strong erosion or to the deposition of thick and mostly coarse textured alluvial sediments (Bätz et al., 2014; Corenblit et al., 2014; Gurnell, 2014). Therefore, this zone is only sparsely colonised by a few pioneer herbaceous plant species and few, mostly epigeic earthworms tolerating strong alluvial dynamics (Gurnell and Petts, 2002; 2006; Mardhiah et al., 2014). Despite the crucial importance of soil structure formation in this zone, only few investigations have already been conducted (Corenblit et al., 2014; Bätz et al., 2015; Graf-Rosenfellner et al., 2016). Time is a critical factor in this zone, especially the capacity of pioneer herbaceous plant and earthworm species to initiate the first steps to improve the structural stability of recent alluvial deposits in the short term. Long term chronosequences of 40 years indicated a gradual increase of the structural stability of floodplain soils (Pietrowski et al., 2008; Mardhiah et al., 2014). The short-term development of a soil structure has not yet been analysed in close proximity to a river considering strong alluvial dynamics resulting in river shore erosion and sediment deposition. To analyse the effect of pioneer herbaceous plants and earthworms separately, but under natural alluvial dynamics, semi-controlled plots installed in the field would be useful.

Aims and hypotheses

In the framework of this dissertation, the contribution of plants and earthworms to soil structure formation in alluvial soils was analysed. This analysis was divided in three sections, each focussing on soil structure formation at a different spatial and temporal scale (Table 1): at the field scale, (I) influencing parameters of soil structure formation were analysed focusing on the landscape hydrology. At the mesocosm scale (II), mechanisms of macro-aggregate formation and OM stabilisation were analysed. At the field plot scale (III), short-term soil structure formation under strong alluvial dynamics was evaluated. Thereby, soil structure formation was analysed using traditional pedologic indicators as well as modern imaging techniques.

At the field scale (main chapter I), the topsoil structure stability in different field sites was analysed as a function of multiple interactions between distribution patterns of plant and earthworm communities (Six et al., 2002; Blouin et al., 2013), soil physicochemical parameters (Bronik and Lal, 2005) and the landscape hydrology (Lin et al., 2015; Ma et al., 2017). It was hypothesised that the structural stability of the topsoils were positively affected by plant and earthworm communities, finer textured and nutrient rich soil sites. On the other hand, negative linear and interaction effects of inundations by surface water and fluctuating groundwater levels on the structural stability of the topsoil were expected.

At the mesocosm scale (main chapter II), soil physicochemical properties and physical parameters were controlled in mesocosms enabling mechanisms of macro-aggregate formation and OM stabilisation to be analysed. Each one typical pioneer plant species, *Phalaris arundinacea* and one earthworm species *Allolobophora chlorotica* were selected as model organisms. This analysis was performed in two steps. In the first part (main chapter IIa), the applicability of Rock-Eval pyrolysis to identify signatures of OM from the plant and earthworm species in macro-aggregates was tested. It was hypothesised that Rock-Eval pyrolysis was able to distinguish macro-aggregates formed by plants from those formed by earthworms and to provide information about the stabilisation mechanisms of OM during its incorporation into macro-aggregates. In the second part (main chapter IIb), different textured mineral and a buried litter layer similar to alluvial soils were superimposed. Using Rock-Eval pyrolysis and X-ray CT, it was hypothesised that the type of engineer, the composition of the layer and its position within the mesocosm drive soil

structuration patterns of *P. arundinacea* and *A. chlorotica*, the stability of macro-aggregates and the thermal stability of incorporated OM.

Table 1: Summary of the observed engineers, the indicators and the respective methods used to measure soil structure and the influencing factors considered for the respective analyses. Each of the three experimental stages is represented by one main chapter in the dissertation. WSA denominated water stable aggregates.

Main Chapter considered	observed soil engineers	measured indicator of soil structure	measurement method of soil structure	influencing factor
I) Field scale	Plant and earthworm communities	Structural stability of the topsoil (upper 20 cm)	% WSA	landscape hydrology physicochemical soil properties
II) Mesocosm scale	<i>P. arundinacea</i> <i>A. chlorotica</i>	Macro-aggregate stability Total segment length Porosity Pore connectivity OM stabilisation	% WSA X-ray CT Rock-Eval pyrolysis	soil texture superimposition of different layers
III) Field plot scale	<i>P. arundinacea</i> Earthworm communities	Macro-aggregate stability Field saturated hydraulic conductivity Total segment Length Porosity Pore connectivity	% WSA Guelph Permeameter X-ray CT	alluvial dynamics soil depth

At the field plot scale (main chapter III), the strengths of field and *in vitro* experiments were combined to analyse the capacity of pioneer soil engineers to structure recent alluvial deposits in the short term. Field plots allowed treatments to be controlled and exposed to

natural alluvial dynamics for a defined period. Hydrologic measurements and X-ray CT were combined with freeze coring which was found out to be suitable for the analysis of soil structure formation in fine-grained low-cohesive soils within the framework of this dissertation (Liernur et al., 2017). It was hypothesised that pioneer herbaceous plants and earthworms were capable to contribute significantly to soil structure formation in the short-term despite strong alluvial dynamics.

The study site

All field experiments as well as the sampling of sediments and organisms for the *in vitro* experiments were performed at the restored floodplain site “Schafftäli” which is located in NE Switzerland close to Niederneunforn, Thurgau Canton (8°77’12” E, 47°59’10” N) (Schirmer et al., 2014) (Fig. 2). The “Schafftäli” site adjacent to the Thur River is currently part of the largest river restoration project in Switzerland which includes the restoration of the river and the floodplain along a section of 1.5 km (Bullinger-Weber et al., 2014; Schirmer et al., 2014). The Thur River is among the most dynamic rivers in Switzerland regarding its alluvial dynamics, as the river is not regulated by any artificial basins along its course (Fournier et al., 2013). The source of the river is located in the limestone-dominated Säntis massif at 2500 m a.s.l. After crossing the Swiss Plateau over a course length of 130 km, the river flows into the Rhine at 345 m a.s.l. (Samaritani et al., 2011; Fournier et al., 2012; 2013). In total, the river includes a catchment area of 1750 km² from its source to its mouth (Horat & Scherrer AG Hydrologie und Hochwasserschutz, 1999). The hydrologic regime is nivo-pluvial inducing an increased probability of flood occurrence in spring after snow melting or in late summer after an intense thunderstorm in the catchment area (Fournier et al., 2013). The discharge varies between 3 and 1190 m³ s⁻¹ having a mean annual discharge of 46.8 m³ s⁻¹ measured at the Niederneunforn gauging station (NIE, F2900, coordinates 8°46’57.78” E, 47°35’20.76” N, altitude 372 m a.s.l.) between 1910 – 1999 (Horat & Scherrer AG Hydrologie und Hochwasserschutz, 1999). Extreme flood events have a statistical return period of 25 years (HQ₂₅) and were measured in 1910 (1190 m³ s⁻¹), in 1978 (1060 m³ s⁻¹), in 1999 (1150 m³ s⁻¹) and in 2013 (1017 m³ s⁻¹) (hydrodaten.admin.ch). The latest extreme flood event in 2013

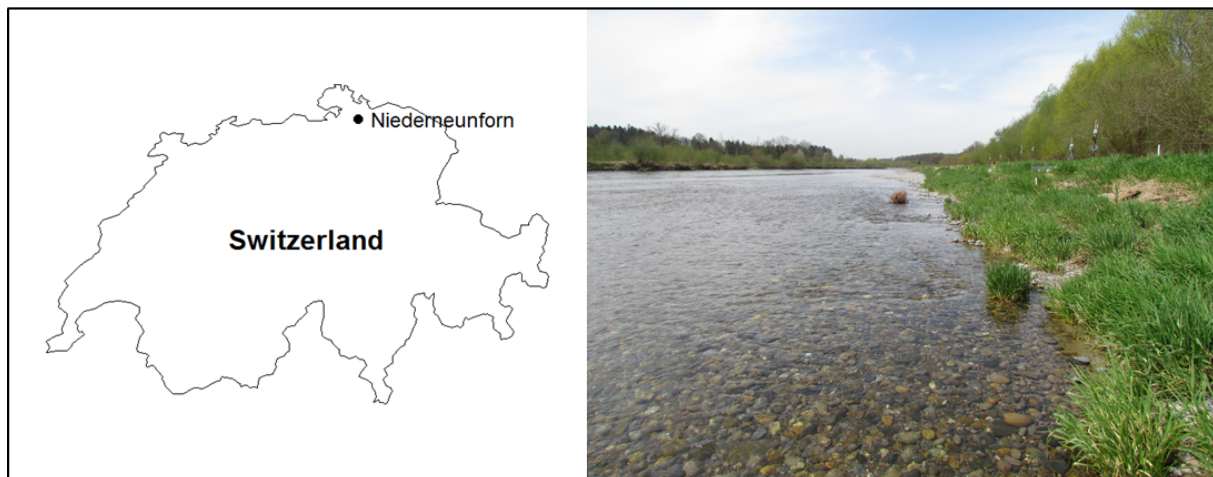


Fig. 2: Position and image of the Thur River floodplain in Thurgau Canton, NE Switzerland.

caused a sediment accumulation of up to 30 cm throughout the entire “Schaffäuli” site (Fournier et al., 2015). Similar to other former braided rivers in Switzerland, the Thur River has strongly been modified following different river and floodplain management strategies in the past 150 years. Management strategies can be divided into three phases: the first correction of the Thur River took place from 1878 until the 1960s in which the strong meandering river was canalised and embanked (Horat & Scherrer AG Hydrologie und Hochwasserschutz, 1999). The aim of this correction was to gain new agricultural land and to protect the Thur valley from inundations (Amt für Umwelt Kanton Thurgau, 2004). The first river training started in 1979 and aimed to shore up the existing river infrastructure and to increase the discharge capacity in the river bed. This occurred on the back of several severe flood events in the recent past. The extreme flood in 1999 caused heavy damage on the embankments close to Niederneunforn. As a result, the 2nd river training was initiated in 2002 including at the reconstruction of the damaged river infrastructure and at the restoration of the “Schaffäuli” site aiming to increase the biodiversity (Bullinger-Weber et al., 2014; Fournier et al., 2015). By doing so, the embankments on the northern side of the river were completely removed and the river shore was stabilised by willows (*Salix viminalis*) (Bullinger-Weber et al., 2014). This “natural” restoration resulted in the development of new habitats colonised by pioneer vegetation close to the river and the reconnection of the pre-existing hardwood forest to natural alluvial dynamics (Fournier et al., 2012; 2013). The “Schaffäuli” site was equipped with measurement devices immediately after its restoration within the framework of the “RECORD” project of the ETH domain. Vegetation succession, modification of

groundwater flow paths and geomorphological changes of the river bed and the floodplain have been monitored (Schneider et al., 2011; Schirmer, 2013). The post-restoration monitoring ended in 2016 after 14 years.

Main Chapter I): The field scale

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Topsoil structure stability in a restored floodplain: Impacts of fluctuating water levels, soil parameters and ecosystem engineers

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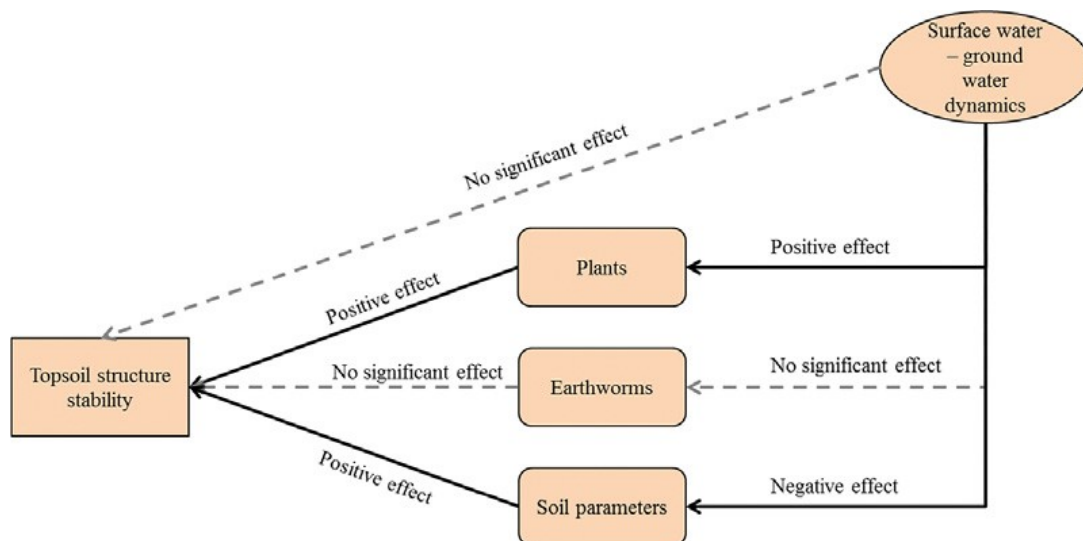
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Graphical Abstract



Abstract

Ecosystem services provided by floodplains are strongly controlled by the structural stability of the floodplain soils. The development of a stable structure in floodplain soils is affected by a complex and poorly understood interplay of hydrological, pedological and biological processes. This paper aims at analysing relations between fluctuating groundwater levels, soil engineering organisms and soil physico-chemical parameters on soil structure stability in a restored floodplain. Water level fluctuations in soil are modelled using a numerical surface-water – groundwater flow model and correlated to soil physico-chemical parameters and abundances of plants and earthworms. Causal relations and multiple interactions between the investigated parameters are tested through structural equation modelling (SEM). Fluctuating water levels in soil did not directly affect the topsoil structure stability, but indirectly through affecting plant roots and soil parameters that in turn determine topsoil structure stability. These relations remain significant for mean annual days of complete and partial (> 25 %) water saturation. Ecosystem functioning of a restored floodplain might already be affected by the fluctuation of groundwater levels alone, and not only through complete flooding by surface water during a flood period. Surprisingly, abundances of earthworms did not show any relation to other variables in the SEM. These findings emphasize that earthworms have efficiently adapted to periodic stress and harsh environmental conditions. Variability of the topsoil structure stability is thus stronger driven by the influence of environmental factors on plants than by the abundance of earthworms. This knowledge about the functional network of soil engineering organisms, soil parameters and fluctuating water levels and how they affect soil structural stability is of fundamental importance to define management strategies of near-natural or restored floodplains in the future.

Keywords: Soil aggregate; Structural equation modelling, Earthworm; Pioneer Plant; Flood; Surface water – groundwater modelling

1. Introduction

The development and preservation of a stable soil structure are fundamental aspects to ensure the functioning of an ecosystem (Bronik and Lal, 2005). The soil structure of young and dynamic or recently restored ecosystems, such as floodplains, is highly susceptible to external interferences. Regular flooding, erosion and sediment deposition can result in the decrease of soil structural stability or reset initial soil stabilisation processes (Junk and Welcomme, 1990; Bätz et al., 2015; Graf-Rosenfellner et al., 2016). However, the conservation of biodiversity in floodplains is directly linked to the structural stability of the floodplain soil, developing a mosaic of various floodplain habitats (Malmqvist and Rundle, 2002). Ecosystem services such as nutrient and pollutant recycling, flood and erosion control, carbon storage as well as surface and groundwater purification are promoted by stable conditions in floodplains (Brooks and Shields, 1996; Diaz-Zorita et al., 2002; Acreman et al., 2003; Bronik and Lal, 2005). Soil structure stability has been shown to be improved mainly by soil organisms' activities. In floodplain ecosystems, physical processes such as the alternation of desiccation and remoistening of the soil matrix are an additional factor driving its structural stability (Angers and Caron, 1998; Bronik and Lal, 2005). Furthermore, soil structure stability is directly influenced by various soil physico-chemical parameters, such as the soil texture (Tisdall and Oades, 1982; Sollins et al., 1996; Bullinger-Weber et al., 2007), carbonate and organic matter contents (Tisdall and Oades, 1982; Chorom et al., 1994; Haynes and Naidu, 1998; Kong et al., 2005). To a large extent, soil physico-chemical parameters can also influence soil organisms structuring the soil, especially through pH values (Ivask et al., 2007) and soil texture (Bullinger-Weber et al., 2007; Fournier et al., 2012). On the macro-biological scale, plants and earthworms are among the most successful soil ecosystem engineers in temperate ecosystems, being able to efficiently improve soil structure stability through the formation of water-stable macro-aggregates (Brown et al., 2000; Kong and Six, 2010). Plants physically enmesh soil particles or provide inputs of organic matter through root exudates that cement particles and/or stimulate the production of bonding agents by soil microbes (Degens et al., 1994; Angers and Caron, 1998). Earthworms build up soil aggregates through burrowing and casting as they move into the soil, and agglutinate organic and mineral particles with mucus and saliva produced in their

digestive system (Blanchart et al., 1997; Brown et al., 2000; Lavelle and Spain, 2001). Both plants and earthworms are considered as particularly efficient in floodplains due to their wide-ranging strategies to tolerate harsh environmental conditions (Gurnell and Petts, 2002, 2006; Thonon and Klok, 2007; Crouzy and Perona, 2012; Perona et al., 2012). Nevertheless, plant abundance and earthworm populations generally tend to be reduced in habitats frequently threatened by floods (Plum and Filser, 2005). So far, the effect of flood frequency on plants and earthworms has been described indirectly through sampling at varying distances to the river (Salomé et al., 2011; Bullinger-Weber et al., 2012; Fournier et al., 2015), or by monitoring and counting the number of flood events impacting the studied habitats (Ausden et al., 2001; Zorn et al., 2005; Gurnell and Petts, 2006; Ivask et al., 2007; Corenblit et al., 2009). With the methods applied so far, information concerning the response of ecosystem engineers towards floods is restricted to conditions in which soils are completely submerged. However, soil moisture contents below full saturation have also been shown to affect ecosystem engineers, as presented by Wever et al. (2001) and Davis et al. (2006) for earthworms and for plants (Henszey et al., 2004). Given that the degree of saturation in the soil is heavily influenced by the depth to groundwater, water table fluctuations could be an important control on the development of soils. A shallow depth to groundwater is likely to occur far more frequently than a flood event submerging the surface (Fig. 1). As ecosystem engineers are most widespread in the upper 20 cm of soil, representing the major part of the drilosphere and the rhizosphere (Lavelle et al., 1997; Tanner, 2001), water saturation through rising groundwater in this zone might already have a significant impact on their abundance and their capacity to improve the topsoil structure stability. To our best knowledge, there have not been any investigations analysing the relations between fluctuating groundwater levels, ecosystem engineers and soil parameters with regard to the stability of the topsoil structure. As the occurrence of ecosystem engineers and the development of the topsoil structure in a floodplain might be the result of the high temporal variability of groundwater fluctuations over seasons and years, groundwater- and soil moisture monitoring needs to be carried out over a time span of several years in order to estimate its mean impact at an intermediate time scale. For a number of reasons, numerical models simulating the spatial and temporal dynamics of surface water (SW)–groundwater (GW)

interactions in the river, the underlying aquifer and the floodplain can provide crucial information in this endeavour: I) a well calibrated flow model is a physically-based interpolator that allows quantifying groundwater fluctuations in space and time. Consequently, II) profiles of water saturation can be analysed at any point within the simulated floodplain. Numerical models can therefore complement the available observation data to a degree which is not possible employing additional monitoring equipment. However, the uncertainties of the numerical model need to be considered. A modelling approach to link the different variables to soil stability is further required. Structural equation modelling (SEM) has been described as a pertinent statistical method for the identification of causal effects among variables as well as direct and indirect linear relations (Bollen, 1989). More recently, SEM were improved for the analyses of more complex causal relations and multiple interactions (Grace and Bollen, 2006, 2008; Shipley, 2016). Using SEM, causal relations of biological factors and soil structure have been demonstrated for different ecosystems by Rillig et al. (2002) and Chaudhary et al. (2009). In this study, we aim to identify the relations between fluctuating water levels, plants, earthworms, soil parameters, and their combining effects on soil structural stability through SW-GW flow modelling and SEM. We hypothesise that (I) water level fluctuations in soils can explain the degree of topsoil structure stability through the distribution patterns of ecosystem engineers and/or the soil physico-chemical parameters. We assume concomitantly that (II) partial and complete water saturation might directly impact topsoil structure stability and indirectly ecosystem engineers' abundance. We furthermore expect to identify (III) direct effects of ecosystem engineers and soil parameters on the topsoil structure stability, including interactions between them.

2. Material and methods

2.1. Study site

The study was conducted at the “Schaffäuli” floodplain site along the restored section of the Thur River close to Niederneunforn (NNF, 8°77'12" E, 47°59'10" N) in the Canton Thurgau, Switzerland (Fig. 2; Schirmer et al., 2014). The Thur River is the longest river in Switzerland without any regulation by artificial reservoirs or natural lakes over the entire water course length of approximately 130 km (Fournier et al., 2013). However, the river is canalised and embanked

along most of its course. The source of the river is located in the limestone-dominated Säntis massif at 2500 m a.s.l. with a catchment area of 1750 km² (Samaritani et al., 2011). The hydrologic regime is nivo-pluvial. For the period 1910–1999 discharge at the Neunforn gauging station (Canton Thurgau river gauging station no: F2900, coordinates: 8°46'57.78" E, 47°35'20.76" N, altitude: 372 m a.s.l.) was between 3 and 1100 m³ s⁻¹ with a mean annual discharge of 46.8 m³ s⁻¹ (Horat and Scherrer AG Hydrologie und Hochwasserschutz, 1999). Flood events frequently occur during the snow melt period in spring and after intense rainfall events in autumn leading to inundations of the floodplain (Fournier et al., 2013). Maximum discharges at the Andelfingen gauging station, 10 km downstream of NNF (Swiss Federal Office for the Environment river gauging station no: 2044, coordinates: 8°40'55.08" E, 47°35'47.46" N, altitude: 770 m a.s.l.) were measured in 1910 (1190 m³ s⁻¹), in 1978 (1060 m³ s⁻¹) and in 1999 (1150 m³ s⁻¹) (Horat and Scherrer AG Hydrologie und Hochwasserschutz, 1999). The last large flood event measured at the station Neunforn occurred in 2013 and peaked at 1017 m³ s⁻¹, leading to sediment accumulations of up to 30 cm. As a result of the flood in 1999, the “Schaffäuli” site was restored by removing the embankments of the right river bank over a section of 1.5 km (Fig. 2). Since then, the adjacent floodplain has been equipped and systematically monitored for surface water and groundwater flow as well as for vegetation developments (e.g. Vogt et al., 2009; Schirmer et al., 2014). Since the restoration, the dynamics of both erosion and sedimentation increased strongly, and a gravel bank of temporally and spatially varying extent formed downstream of the embanked zone. Diem et al. (2014) identified four zones (K1 to K4) of distinct hydraulic conductivities within the “Schaffäuli” study site:

- (1) The highly permeable alluvial gravel island/riverbank section that is located along the restored section (K1=6×10⁻²ms⁻¹),
- (2) slightly less permeable sediments in the alluvial forest and riverbed surrounding the alluvial gravel island (K2=2×10⁻²ms⁻¹) (reduction of 66% compared to K1),
- (3) equally permeable alluvial sediments encompassing the alluvial forest along the embanked section (K3=1 × 10⁻² m s⁻¹) (reduction of 85% compared to K1), and

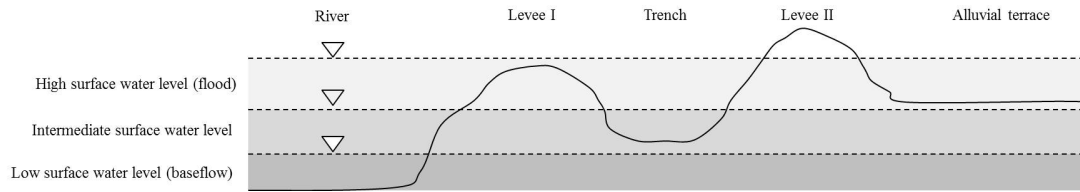


Fig. 1. Example of surface water–groundwater interactions in a floodplain. The white triangles represent the water level relative to water discharge. During intermediate surface water level, groundwater submerges the trench and saturates the topsoil of the alluvial terrace, without surface water directly inundating the trench and the alluvial terrace, as it is blocked by levee I and II. Only at high surface water level (flood), the trench is directly flooded by surface water; the alluvial terrace is inundated through rising groundwater.

(4) less permeable sediments of the embankment all along the left river bank ($K_4 = 4 \times 10^{-3} \text{ m s}^{-1}$) (reduction of 95% compared to K_1).

2.2. Field sampling design and soil sampling

Nine sampling plots were selected in the restored floodplain section with varying distances to the river (12–53 m). The surface area of each plot was adapted to the local extent of the vegetation and subsequently normalised to a square-shaped standard area of 25 m^2 . The locations of sampling plots are illustrated in Fig. 2. The vegetation and soils were described and sampled in each plot in July 2015, including five replicates that were randomly taken within each plot. Soil types were described as Calcaric Fluvisols, Calcaric Fluvisols or Calcaric Fluvisols Cambisols (IUSS Working Group WRB, 2015). Vegetation was recorded in relevés according to the method of Braun-Blanquet (1964). The percentage of herbs and shrubs covering the soil surface was estimated and subsequently used for the calculation of the root size and root abundance factors (see Section 2.3). During soil description, composite soil samples and macro-aggregates $> 250 \mu\text{m}$ (Tisdall and Oades, 1982; Six et al., 2004) were uniformly taken from each replicate individually due to numerous soil layers originating from past flood events. Topsoil layers represented an alternation of A(k) and C(k) horizons for Fluvisols and Arenosols and of A(k) and Bw(k) for Cambisols. The thickness of the A(k) horizons was limited to maximally 3 cm, so representative sampling could not be performed on horizons separately. The depth of all samples was limited to the upper 20 cm of soil representing the major part of the drilosphere and the rhizosphere. Soil samples and macroaggregates were dried at 40°C in an oven for 72 h, homogenised and sieved at 2 mm.

2.3. Sampling of ecosystem engineers

Plant roots and earthworms were sampled in October 2015 and described at the same sites at which soil sampling was performed. Plant root size and abundance were used as indicators in the upper 20 cm of soil and described according to the guidelines for soil description (IUSS Working Group WRB, 2006). Digits between 1 (predominantly very fine roots $< 0.5 \text{ mm}$ in diameter) and 4 (predominantly coarse roots of $\geq 5 \text{ mm}$ in diameter) were assigned for the root size. Digits between 0 (no roots) and 4 (with ≥ 200 in the total number of roots smaller than 2 mm or with ≥ 20 in the total number of roots larger than 2 mm) were assigned for the root abundance (IUSS Working Group WRB, 2006). Obtained digits were subsequently normalised by the proportions of shrub and herbaceous plant roots that were determined during the vegetation relevé. The normalised values represent root size and root abundance factors, and were used as explanatory variables in the subsequent statistical analysis. Earthworms were extracted in autumn 2015 using the hot mustard extraction on a $0.5 \times 0.5 \text{ m}$ square combined with the hand-sorting method on a soil cube of $0.2 \times 0.2 \times 0.2 \text{ m}$ dug out in the center of the plot (Bouché and Aliaga, 1986; Lawrence and Bowers, 2002). The extracted earthworms were stored in 70% ethanol. Adult earthworms were weighed, identified to species level according to the identification key of Blakemore (2008) and classified according to their ecological categories (Bouché, 1972). Juveniles were just grouped and weighed. Total and mean earthworm abundance (individuals per m^2) was calculated for each sampling site.

2.4. Analysis of soil physico-chemical parameters

Soil texture was determined using the pipette Robinson method. For soil chemical parameters,

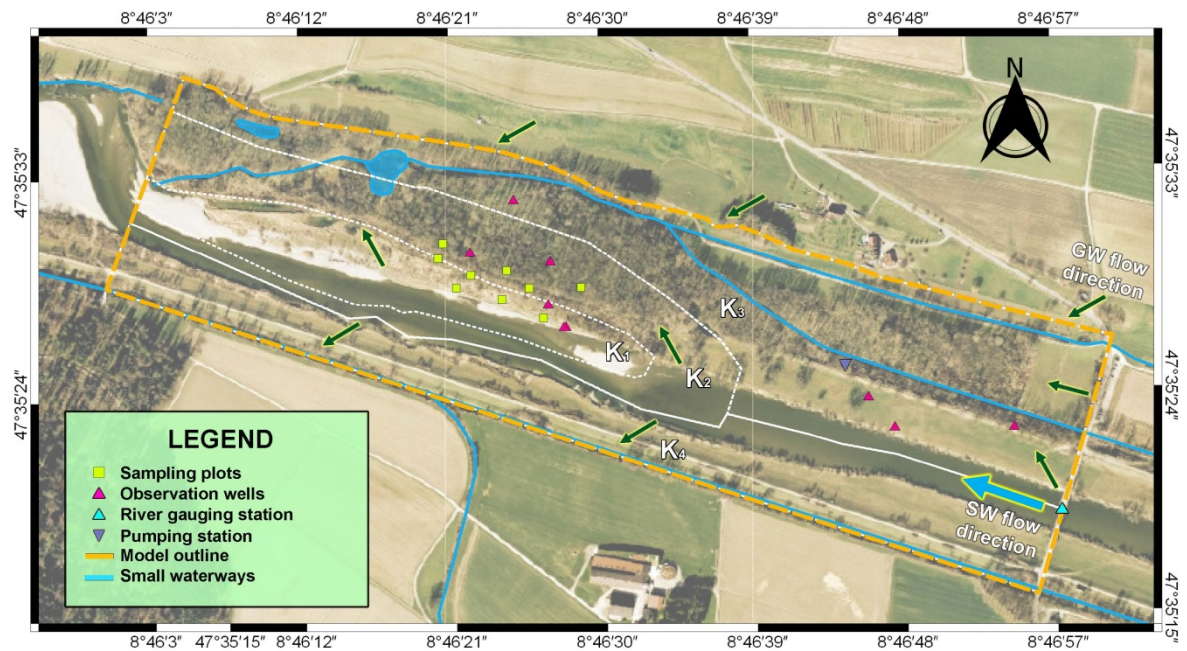


Fig. 2. Map of the different sampling locations. The flow direction of the Thur River is indicated by the big arrow within the river, GW flow directions are indicated by the smaller arrows. The embanked river section is located on the right border of the river upstream of the K2 zone, and the restored river section starts between the upstream limits of the K1 and the K2 zones. K-zones are separated by the dotted lines. The spatial extent of the numerical flow model is indicated by the dashed orange line. Coordinate system: WGS84. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) Orthophotos reproduced with permission of swisstopo (BA17095).

pH was measured using a combined pH Meter/conductometer (914 pH Meter/conductometer, Metrohm, Herisau) with the soil/water ratio of 1:2.5. Cation exchange capacity (CEC) and base saturation (Bs) were analysed using a buffered barium chloride solution (pH 8.5) that was further diluted 500 times and analysed for K, Mg, Ca and Na using an Inductively Coupled Plasma–Optical Emission spectrometer (ICP-OES Optima 2100 DV, Perkin Elmer). Total carbonate content ($\text{CaCO}_3 \text{ tot}$) was measured using a Bernard Calcimeter described in Vatan (1967). The amount of active carbonates ($\text{CaCO}_3 \text{ act}$) was determined according to the method of Drouineau (1942). Organic carbon and total nitrogen contents were measured using a CHN analyser (CHN-O Analyzer, Flash 2000, Thermo Scientific). 2.5. Soil structure stability analysis The degree of topsoil structure stability was identified by the analysis of aggregate stability which is used as the main indicator for soil structure stability (Six et al., 2000). The percentage of water-stable aggregates was determined for macro-aggregates of 250–2000 μm size according to the method described in Kemper and Rosenau (1986). A modified automatic diving apparatus equipped with sieves of 250 μm mesh size was applied for this analysis (Murer et al., 1993).

2.6. Hydrological flow model

2.6.1. Model setup

As a typical example of a surface water-groundwater system, SW and GW are characterised by dynamic exchange fluxes at the NNF site. The potential for flooding is therefore not only controlled by river flow and riverbed topography, but also by GW levels and the hydraulic conductivity (K [L/T]) of the riverbed and the underlying aquifer (Winter et al., 1998; Brunner et al., 2009; Schilling et al., 2017b). As exchange fluxes cannot be easily measured, physically-based, fully-coupled simulations of SW and GW were useful for the dynamic computation of exchange fluxes and flooding under consideration of all the relevant hydrological and physical parameters. For this purpose, the physically based and fully-coupled SW-GW flow model HydroGeoSphere (HGS) (Therrien et al., 2010; Brunner and Simmons, 2011; Kurtz et al., 2017) that has been successfully applied to simulate complex river-aquifer systems (e.g., Banks et al., 2011; Karan et al., 2014; Schilling et al., 2014, 2017a, 2017b; Tang et al., 2015, 2017), was used to simulate the NNF site. HGS allows the coupled simulation of SW flow based on the diffusion-wave approximation of the 2-D Saint Venant equation and of variably-saturated GW flow based on the

Richards equation and the van Genuchten parametrisation. Specific details on the underlying equations and parameters can be found in the HGS manual (Aquanty Inc., 2016). The spatial extent of the simulated area is 0.37 km². The aquifer in NNF is approximately 6 m thick and consists of glacio-fluvial sandy gravels (Vogt et al., 2009; Vogt et al., 2010; Diem et al., 2014). The aquitard is composed of a lacustrine clay and its vertical limits were estimated by Diem et al. (2014). Following the procedure described by Käser et al. (2014), the horizontal numerical grid for the NNF site was generated using AlgoMesh (HydroAlgorithmics Pty. Ltd.) and GridBuilder (McLaren, 2011), and consisted of 8642 approximately equilateral finite elements. Within the river, the elements had an average side length of 7m, in the alluvial forest of the restored section 15m and in the alluvial forest of the embanked section 25 m. Vertically, the model was discretised into 10 grid layers with proportional thicknesses: 1.3% of the total vertical extent for each of the four topmost layers, 13% for each of the following four layers, and 23.8% for the bottom two layers. The fine vertical discretisation close to the surface was employed to guarantee numerical integrity in solving the highly non-linear Richards equations for unsaturated flow in the soil. Compared to embanked river sections, both the riverbed topography and its hydraulic conductivity can be highly transient in the natural and restored river sections. This is due to the pronounced erosion and deposition processes in these sections (Gianni et al., 2016; Partington et al., 2017). The riverbed topography of such systems is thus associated with structural uncertainties which, however, can be reduced using approaches such as high-resolution through-water photogrammetry (Feurer et al., 2008; Brunner et al., 2017; Schilling et al., 2017a). At the NNF site, a digital elevation model (DEM) dating from 01 Feb. 2015 with a horizontal resolution of 0.5 m was available for the floodplain and the embanked section from the Amt für Raumentwicklung Kanton Zürich (<http://www.geolion.zh.ch/geodatensatz/show?gdsid=298>, accessed 03 Aug. 2017). However, for the restored river section, no high-resolution riverbed DEM was available. The topography of the riverbed for that section was therefore linearly interpolated between measured cross-sections.

2.6.2. Boundary and initial conditions

Transient simulations of four years (2013, 2014, 2015 and 2016) were carried out based on daily changing boundary conditions (Fig. 3). The Thur

River was implemented as a second-type (specified flux) boundary condition using discharge measurements from the Neunforn gauging station (Fig. 3b). The small existing data gaps were bridged based on discharge data from the nearby Andelfingen gauging station. River outflow was simulated using a critical depth boundary condition. Precipitation was conceptualised as a specified nodal flux boundary condition using measurements from the NNF rain gauge (MeteoSchweiz, station: NIE, coordinates: 8°47' E, 47°36' N, altitude = 440 m a.s.l., Fig. 3a). Evapotranspiration was not simulated. During flood events it is not important (see Diem et al., 2014).

Table 1: Parameter values used for the numerical flow model.

Parameter	Value	Source
Saturated hydraulic conductivity (K)	$K_1 = 6 \times 10^{-2} \text{ m} \cdot \text{s}^{-1}$ $K_2 = 2 \times 10^{-2} \text{ m} \cdot \text{s}^{-1}$ $K_3 = 1 \times 10^{-2} \text{ m} \cdot \text{s}^{-1}$ $K_4 = 4 \times 10^{-3} \text{ m} \cdot \text{s}^{-1}$	Diem et al. (2014)
Porosity (n)	0.2	Diem et al. (2014)
van Genuchten α	$3.48 \cdot \text{m}^{-1}$	Li et al. (2008)
van Genuchten β	1.75	Li et al. (2008)
Rill storage height	0.1 m	Calibrated
Manning's coefficient	$0.0525 \cdot \text{s} \cdot \text{m}^{1/3}$	Calibrated

Nevertheless, during shallow groundwater conditions evapotranspiration could constitute a noteworthy flux. However, given the good hydraulic connection with the river, water leaving the system through evapotranspiration will be immediately replaced by infiltrating river water. Inflow of GW on the upstream model boundary (South-East) was implemented as a specified head boundary condition using hydraulic head measurements (Fig. 3c) from the most upstream piezometer (see Fig. 2). Closely following the conceptualisation of Diem et al. (2014), outflow of GW on the downstream model boundary (North-East) was implemented as a fixed-head boundary condition of 370.2 m a.s.l., and GW outflow on the lateral model boundaries (South-West and North-East) was defined as a specified flux boundary condition (nodal volumetric flux of $-10 \text{ m}^3 \text{ day}^{-1}$). The inflow of river water to the restored river section was monitored at the

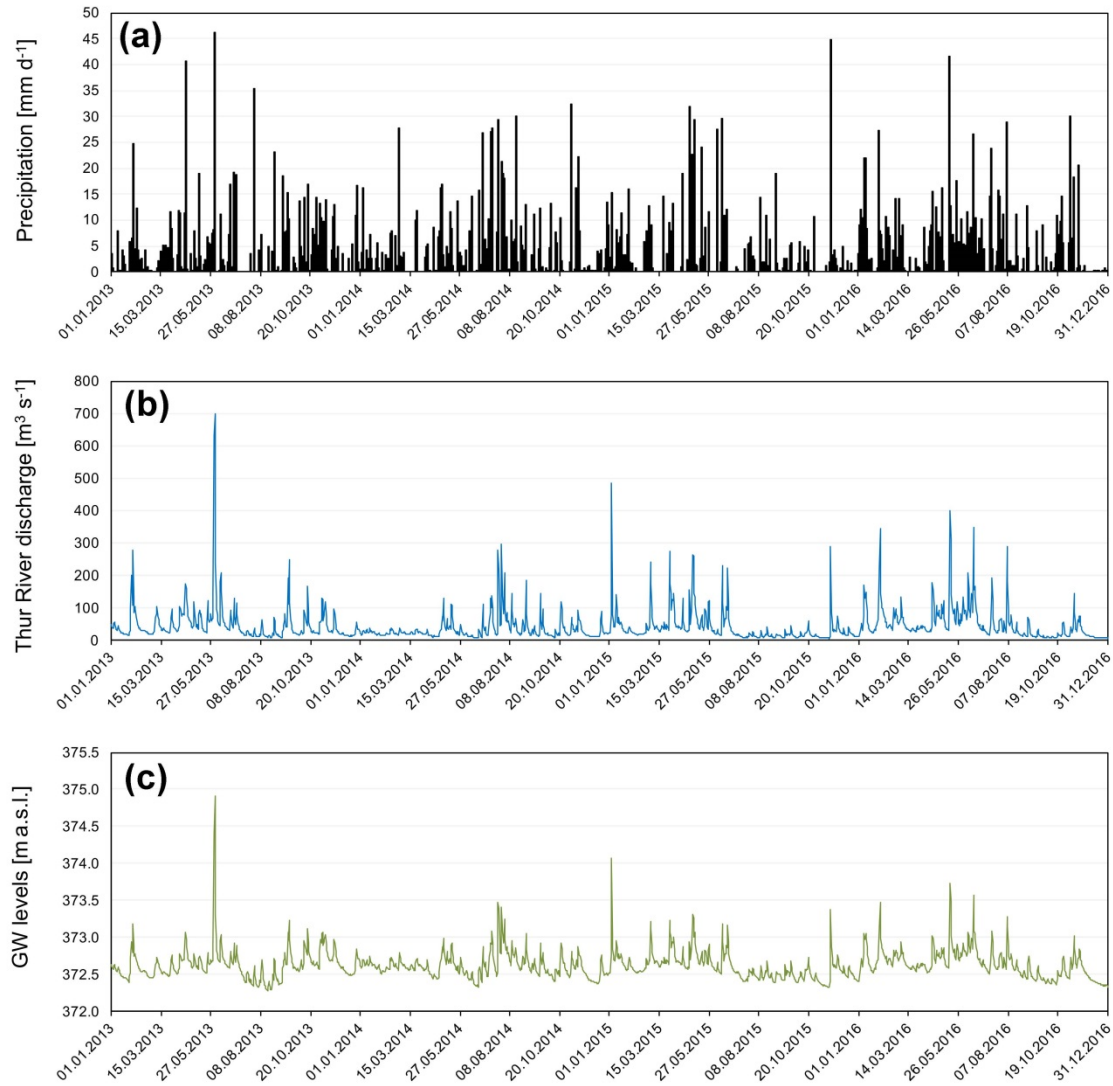


Fig. 3. Time series of (a) precipitation (daily sums, MeteoSchweiz, station: NIE), (b) River Thur discharge (daily averages, Canton Thur, station F2900) and (c) GW levels of the most upstream piezometer (daily averages, Canton Thur, station: G2905). These time series were used to define the boundary conditions of the numerical flow model.

Neunforn river gauging station with a 5-minute interval. Groundwater levels within the floodplain were monitored along two transects and multiple additional piezometers scattered throughout the floodplain at a 15-minute interval (see Fig. 2 for the detailed locations of the different observation points). The value of the different hydraulic parameters used for the numerical flow simulations of the NNF site are listed in Table 1. The two surface flow parameters “rill storage height” and “Manning's coefficient” were calibrated to reduce the residual between the simulated and measured surface water depth at the Neunforn gauging station.

2.7. Mean annual days of water saturation (MADOWS)

For each sampling plot, vertical water saturation profiles were extracted from the numerical flow model and used as an indicator for groundwater level fluctuations. The water saturation was averaged to one daily value for the upper 20 cm of the soil (i.e., the topsoil). For each year, the number of days with complete water saturation (100%) and partial water saturation (>85%, >70%, >55%, >40%, >25%) were counted. Complete water saturation can be either a result of a direct inundation by surface water or of groundwater saturation through rising surface

water levels (Fig. 1). Based on these counts per year, one average value for the mean annual days of water saturation per saturation level (MADOWS100, MADOWS85, MADOWS70, MADOWS55, MADOWS40 and MADOWS25) was calculated for the period 2013–2016.

2.8. Statistical analysis

2.8.1. Variance analysis

Differences between the water saturation levels were analysed with a one-way analysis of variance (ANOVA). Requirements for ANOVA application (normal distribution and variance homogeneity) were tested in advance using the Shapiro-Wilk test and the Levene test, respectively. Group specific differences were subsequently determined using Tukey's HSD posthoc analysis. Differences were considered significant at a $P < 0.001$ level.

2.8.2. Structural equation modelling (SEM)

Full structural equation models (SEMs) were set up in two steps to estimate direct and indirect effects of variables on the degree of soil structure and to determine complex causal relations among these variables (Bollen, 1989; Grace and Bollen, 2006; Shipley, 2016). A priori, conceptual models in form of two directed acyclic graphs (DAGs, Shipley, 2016) were established under consideration of biologically plausible and relevant hypotheses and pathways (Fig. 4a, b). The direction separation (d-separation) method was then applied to verify the plausibility of the pathways drawn in the DAGs based on Fischer's C test and the corrected Akaike information criterion (AICc) (Shipley, 2016). Topsoil structure stability (labelled by “y”, Fig. 4a, b) was determined as the response variable in all models with regard to the hypotheses (see Section 1). Six models were run with MADOWS as the main predictor variable separated according to complete (MADOWS100) and partial water saturation (MADOWS85, MADOWS70, MADOWS55, MADOWS40, MADOWS25) (labelled by x1). Observations for soil physico-chemical properties and ecosystem engineers were assembled as composite variables (Grace and Bollen, 2006, 2008). Composite variables are endogenous variables that are statistically similar to a predictor variable in multiple regressions. They represent a weighed combination of their associated variables and neglect variables that are not statistically significant. Soil physico-chemical properties were assembled as the composite

variable “soil parameters” (labelled by η_3), root size and root abundance factors for herbaceous and shrub roots were assembled as the composite variable “plants” (labelled by η_1), and abundances of earthworms of different ecological categories were assembled as the composite variable “earthworms” (labelled by η_2). For soil texture, which was assembled into “soil parameters”, clay content was neglected in order to avoid statistical dependencies among predictor variables. Path analyses of the relations suggested in the conceptual models (i.e., in the DAGs) were performed using SEM with maximum likelihood estimation for Chi-squared analysis (Shipley, 2016). Path coefficients were calculated for each predicted relation in order to define each relation's individual strength. Path coefficients are labelled with the letters β , γ , ι , κ and λ and grouped according to their associated variable or composite variable (Fig. 4a, b). SEM was performed using the “lavaan” package (Rosseel, 2012) in R (R Development Core Team, 2017). Providing specific details on the mathematics involved in the SEM method and the “lavaan” package is beyond the scope of this article. For a more detailed description of the SEM method and the “lavaan” package, see Bollen (1989), Grace and Bollen (2006, 2008), Rosseel (2012) and Shipley (2016). An initial analysis of the SEMs did not indicate a good model fit when including the composite variables “plants” and “earthworms” in a DAG simultaneously. Therefore, the influence of MADOWS, soil parameters, plants and earthworms on topsoil structure stability was tested in two separate models for the composite variables “plants” and “earthworms”. The analysis of causal relations and path coefficients of soil parameters and MADOWS on topsoil structure stability is not restricted when running two separate models for the analysis of the influence of plants and earthworms.

3. Results

3.1. Topsoil structure stability and soil parameters

The mean percentage of water-stable aggregates was around 30% in the floodplain, but ranged between values of 8 and 62% (Table 2). The percentages of silt and sand, and the base saturation show high standard deviations indicating a large variability within the plots. Standard deviations for CEC, total and active carbonates, TOC contents and pH values do not show a large variability between the sampling plots (Table 2).

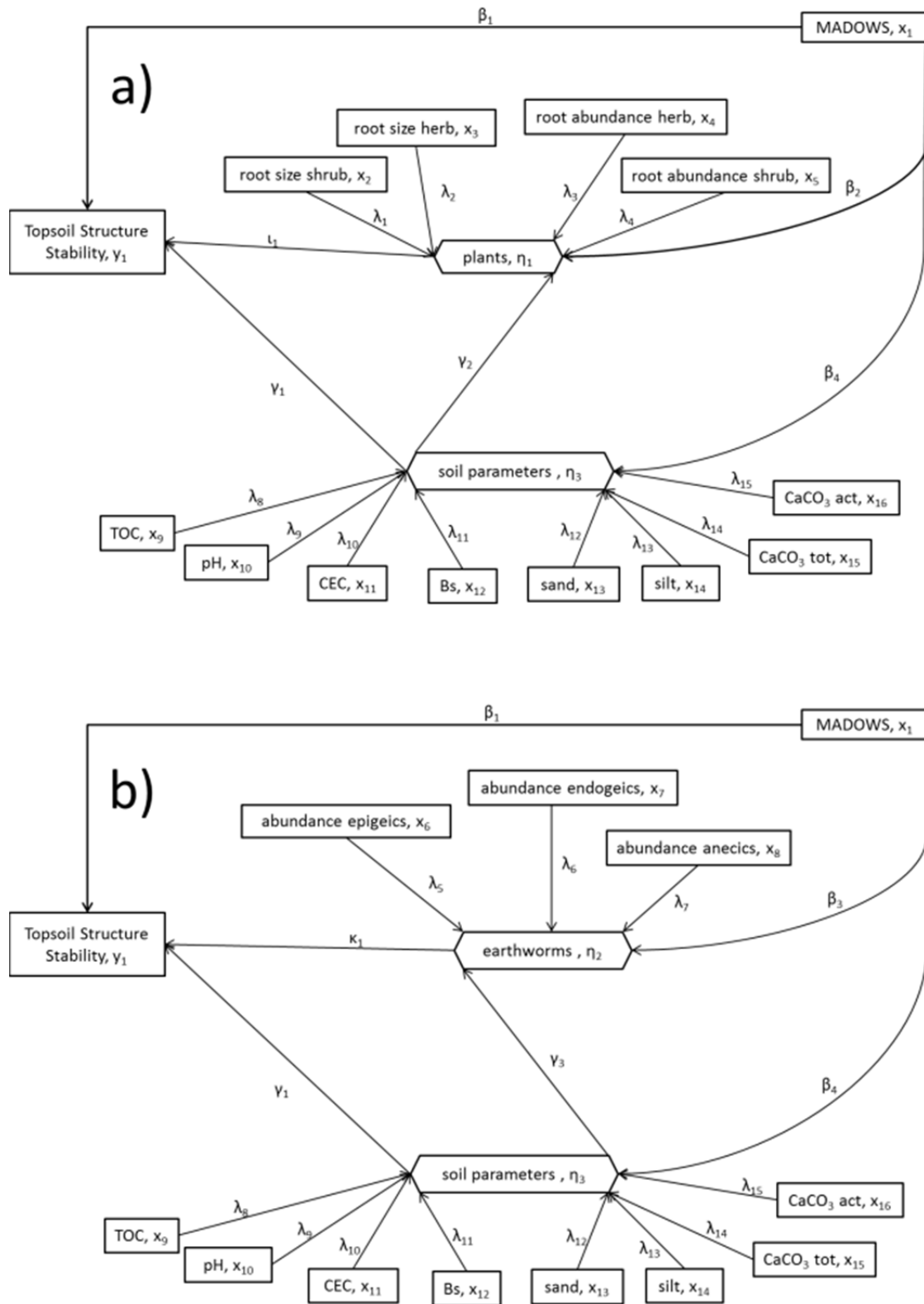


Fig. 4. The two directed acyclic graphs (DAGs) which were proposed as hypotheses for direct or indirect relations testing by structural equation modelling (SEM). The two DAGs differ by the composite variables a) “plants, η_1 ” and b) “earthworms, η_2 ”. All observed variables are illustrated in boxes, while x illustrates the state as predictor variable and y as the response variable. Associated composite variables are bordered by a hexagonal shape and marked by η . Arrows mark pathways of hypothesised effects. Path coefficients are marked by β , γ , ι , κ and λ , and grouped according to predictor variables. MADOWS stands for mean annual days of water saturation, CEC for cation exchange capacity and Bs for base saturation.

Table 2: Descriptive statistical values for topsoil structure stability, plants, earthworms and soil parameters with n = 45 observations. “ind” stands for individuals and “CEC” for cation exchange capacity.

Parameters	Mean	min	max	Standard deviation
Water stable aggregates (%)	29.91	8.53	62.20	12.64
pH	7.97	7.53	8.35	0.18
Silt content (%)	31.54	3.80	71.10	22.95
Sand content (%)	63.16	27	94.10	23.65
CEC (cmolc kg ⁻¹)	16.36	8.31	29.62	4.87
Base saturation (%)	70.89	42.79	94.69	12.08
Total CaCO ₃ (%)	28.94	27.10	30.09	0.64
Root size factor herbs	0.53	0.03	1.00	0.36
Root size factor shrubs	0.12	0.00	0.30	0.11
Root abundance factor herbs	0.62	0.09	1.75	0.47
Root abundance factor shrubs	0.29	0.00	2.40	0.75
Abundance epigeics (ind m ⁻²)	10.21	0.00	123.80	27.47
Abundance endogeics (ind m ⁻²)	73.66	0.00	503.04	114.00
Abundance anecics (ind m ⁻²)	60.39	0.00	414.00	77.52

3.2. Mean annual days of water saturation (MADOWS)

Simulated mean water saturation in the topsoil, averaged over the simulated 4 years (2013–2016), ranged from 25 to 30%. Average annual values were slightly increased for 2013 and 2014 compared to 2015 and 2016 (data not shown). The mean annual days with complete water saturation (MADOWS100) was <10 averaged over all plots, and ranged between 0 and 25 days for the individual plots (Fig. 5). The mean number of days with partial water saturation tended to be increased stepwise by the factors 1.5 for MADOWS85 and MADOWS70, but was not statistically significant. The mean annual days N55% water saturation (MADOWS55) was significantly higher than for MADOWS100 ($P < 0.001$), but not for MADOWS85 and MADOWS70. MADOWS40 was almost 3 times higher compared to MADOWS55, but only differed significantly from MADOWS70, MADOWS85 and MADOWS100 ($P < 0.001$). MADOWS25 was N350 days for all plots during the entire modelling period and differed significantly from MADOWS100 – MADOWS40 ($P < 0.001$).

3.3. Ecosystem engineers

Mean values for root size and root abundance factors (see Section 2.3) were greater for herbs than for bushes (Table 2). Root size and root abundance factors indicated a strong variation for both herbs and bushes. Both factors could not be calculated for shrubs in three sampling plots, as no bushes were recorded in the corresponding relevés. Mean earthworm abundance of all ecological categories was 157 individuals (ind)

m⁻². Total abundances of earthworms showed a broad range of variation, ranging from 0 ind m⁻² to > 750 ind m⁻². Endogeics showed the highest mean abundance in all plots followed by anecics and epigeics. Epigeics and anecics were completely absent in several sampling plots, but contributed to almost 30% (epigeics) and 50% (anecics) to the total abundance of earthworms in others. Percentage of endogeics tended to be equally distributed in all sampling plots.

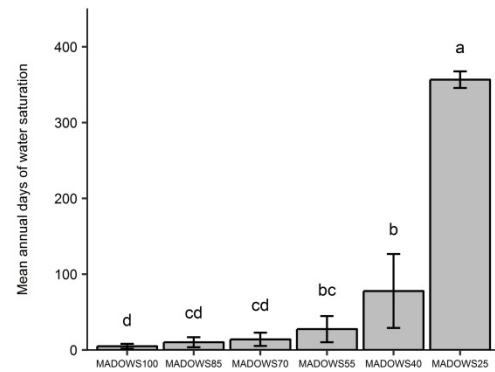


Fig. 5. Barplots showing modelled values for the mean annual days of water saturation (MADOWS) in the first 20 cm of soil for 100% (MADOWS100), for > 85% (MADOWS85), for > 70% (MADOWS70), for > 55% (MADOWS55), for > 40% (MADOWS40) and for > 25% (MADOWS25) water saturation. Error bars represent standard deviations of values for n = 45 observations. Letters a, b, c and d represent results from Tukey's HSD tests for one way ANOVA at significance level $P < 0.001$.

3.4. Structural equation modelling SEM

Full structural equation models could be fitted for complete and partial water saturation, as presented in Fig. 6a, b for MADOWS100. Path coefficients for partial water saturation are presented in Table 3. According to the SEM, the composite variables “soil parameters” and “plants” have a significant positive effect on the topsoil structure stability with path coefficients of 0.68 and 0.31. The silt content has the strongest positive impact on the composite variable “soil parameters” (path coefficient of 0.98), followed by CEC and TOC. Sand content and the pH value have strong negative impacts (path coefficients of -0.81 and -0.40). The remaining observed soil physico-chemical properties did not contribute significantly to “soil parameters”. The root size and root abundance factors for both shrubs and herbaceous plants have strong effects on the composite variable “plants”, with positive path coefficients for shrubs and negative ones for

herbs. No significant influence of the composite variable “earthworms” on the topsoil structure stability was found. While MADOWS100 did not show a significant direct influence on topsoil structure stability, it did on “plants” (path coefficient of 0.33) and on “soil parameters” (path coefficient of -0.50). MADOWS100 thus had an indirect effect on topsoil structure stability by positively influencing “plants” and negatively influencing “soil parameters”, which in turn both showed a positive impact on topsoil structure stability. Significance levels of causal relations and values of path coefficients did not show large variations when running the model with MADOWS85, MADOWS70, MADOWS55 and MADOWS40 (Table 3). Significant effects of mean annual days of partial water saturation on “soil parameters” and “plants” disappeared only for MADOWS25, indicating that the average water saturation during a year (see Section 3.2) in the topsoil neither controlled topsoil structure stability nor explained occurrence of soil parameters and distribution patterns of ecosystem engineers.

Table 3: Values for path coefficients for partial water saturation in the topsoil. MADOWS stands for mean annual days of water saturation. Path coefficients correspond to the pathways presented in Fig. 2. Non-significant path coefficients are indicated by n.s.

Path coefficient	MADOWS				
	>85%	>70%	>55%	>40%	>25%
β_1	n.s.	n.s.	n.s.	n.s.	n.s.
β_2	0.43	0.47	0.44	0.47	n.s.
β_3	n.s.	n.s.	n.s.	n.s.	n.s.
β_4	-0.49	-0.43	-0.47	-0.48	n.s.
γ_1	0.63	0.64	0.63	0.65	0.47
γ_2	n.s.	n.s.	n.s.	n.s.	n.s.
γ_3	n.s.	n.s.	n.s.	n.s.	n.s.
ι_1	0.26	0.25	0.25	0.24	0.26
κ_1	n.s.	n.s.	n.s.	n.s.	n.s.

4. Discussion

4.1. Applicability of the SW-GW model

In many respects, the application of a SW–GW flow model was suitable to analyse the influence of fluctuating water levels on topsoil structure stability, ecosystem engineers and soil parameters. Over the simulated period (2013–2016), for example, two sampling plots were visually submerged only once in four years by a flood event and only considering SW would thus have led to the assumption that these plots are not regularly and often influenced by alluvial dynamics. However, based on our SW-GW flow simulations, it was revealed that in all sampling plots, GW often rose within the upper 20 cm of

soil, which impacted ecosystem engineers similar to flooding by SW. The SW-GW simulations thus allowed reproducing the influence of fluctuating water levels much more holistically than pure flood observations or SW simulations, which would have clearly underestimated the effects of water level fluctuations on the topsoil structure stability. However, numerical SW-GW flow simulations are themselves subject of uncertainty due to the heterogeneous, and often unknown nature of the subsurface. In our current study, uncertainties in groundwater levels of up to 20 cm were observed, but the simulated water levels corresponded well with the observed ones during the crucial periods of low and average river water discharge. Higher uncertainties were observed during high and extreme discharge periods, e.g., during floods. As the water levels during high- and extreme-flow periods can rise up to 1 m above terrain, the investigated topsoil would be fully saturated even under consideration of 20 cm of uncertainty. The impacts of these flow model uncertainties are therefore minimal for the purpose of our analysis. Evapotranspiration was not included in the model simulation. In this particular configuration of boundary conditions and hydraulic properties, the explicit simulation of evapotranspiration would not have significantly changed the water table dynamics and thus the subsequent statistical analysis: there is a direct hydraulic connection between the floodplain and the river, so evapotranspired water would have been replaced by river water. Given that the hydraulic conductivity of the site is very high and the spatial scales small, evapotranspiration would immediately be compensated by the increased inflow from the river, thus having minimal influence on water table dynamics. The last major flood event at NNF in early 2013 dramatically changed the riverbed morphology, and information on the morphology of the floodplain before this event are not available. As the morphology of the river and the floodplain is a critical factor for flooding and for the exchange flow dynamics between SW and GW, sufficiently accurate flow simulations of years prior to 2013 could not be carried out. During the simulated period (2013–2016), only smaller flooding events occurred, which did not significantly modify the river morphology. For the simulated period, the SW-GW flow model was nevertheless an appropriate approach to determine more specifically groundwater level fluctuations in soil. To the best of our knowledge, this study is the first of its kind which analyses the relations between fluctuating groundwater levels, ecosystem engineers and soil parameters with regard to the stability of the topsoil structure.

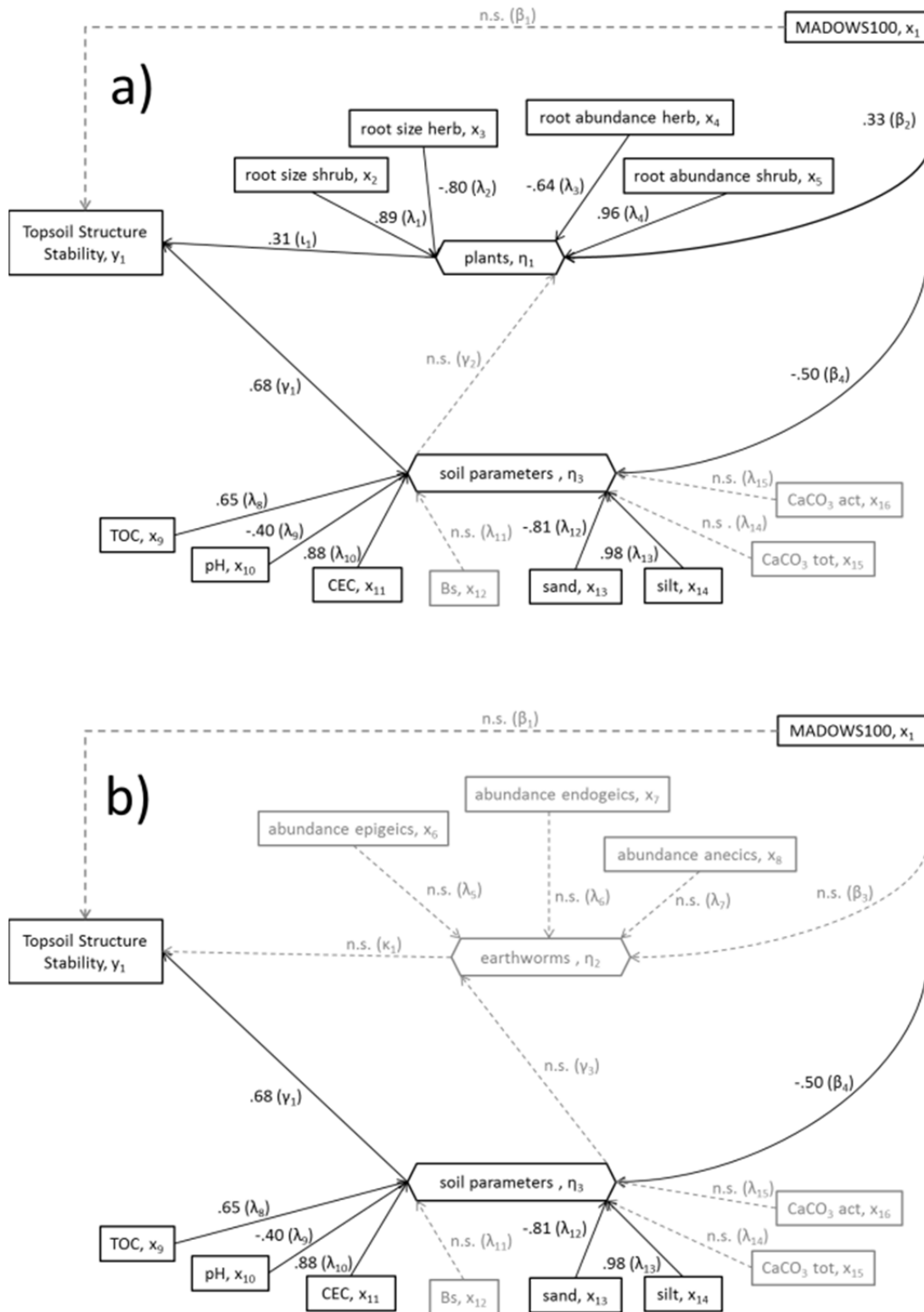


Fig. 6. Results obtained from SEM for mean annual days of water saturation (MADOWS)=100% printed as directed acyclic graph (DAG) for a) plants and b) earthworms including path coefficients for significant relations at $P < 0.05$ level. Paths showing no significant effects (n.s.) are dashed and grey-coloured. Letters x and y represent vectors of observed predictor and response variables, η are vectors containing composite variables. Path coefficients are marked by β , γ , ι , κ and λ , and grouped according to predictor variables CEC stands for cation exchange capacity and Bs for base saturation.

4.2. Effect of fluctuating groundwater levels on topsoil structure stability

The results from the SEMs indicated that neither the number of days with complete, nor the number of days with partial water saturation in the upper 20 cm of soil directly influenced topsoil structure stability. However, both scenarios indicated strong influences on soil parameters and plants that, in turn, influence topsoil structure stability. Complete and partial water saturation thus showed no direct, but a strong indirect effect on topsoil structure stability. As reported by Bullinger-Weber et al. (2014), the percentage of water-stable macro-aggregates decreases with increasing flood frequency. However, in our study, a direct relation between SW-GW interaction and the topsoil structure stability was not significant, neither for the number of days with complete, nor with partial water saturation. Floods usually have a destructive impact on soil structural stability, as scour forces at the soil surface lead to topsoil erosion (Cierjacks et al., 2011). In our study, the number of days with complete water saturation partly corresponding to floods was low during the modelled period and thus might not have affected the topsoil structure stability. Occurring more frequently than full inundations, GW table fluctuations partly saturating the topsoil did, however, not influence its structural stability either. The fluctuation of groundwater levels is smooth and physical forces do not have a destructive effect on soil structure stability compared to floods. Conversely, desiccation and remoistening of soil aggregates were even shown to improve their structural stability (Shipitalo and Protz 1988; Decaëns, 2000; Shipitalo and Le Bayon, 2004). Fluctuating GW levels thus can also have an overall effect of improving structural stability in topsoil. Against our expectations, even a relatively low partial water saturation (i.e., MADOWS40) exerted a significant negative influence for soil parameters and positive influence for plants. The effect disappeared only at MADOWS25, which ranged slightly below the average water saturation of 25–30%. Low rates of water saturation were expected for the plot with sandy soils, but not for soils that contain larger proportions of finer soil texture. The floodplain soils thus appear to be efficiently drained, independent of the amount of finer soil particles, which allows them to rapidly dewater after a high-water event. This reasoning is supported by Liernur (2016) and Liernur et al. (2017), who, in the same sampling plots, measured extraordinary high water infiltration rates that were linked to a well-structured macro-

porous system extending to a depth of 50 cm and thus favouring drainage capacity of the topsoil. This draining pathway likely explains the low mean contents of annual water saturation (i.e., below 30% for all sampling plots).

4.3. The effect of soil parameters on topsoil structure stability

According to the SEMs, topsoil structure stability was strongly influenced by soil parameters, mainly by the soil texture, pH and TOC values, as well as cation exchange capacities. Several studies have already shown a positive correlation between the fine soil fraction and the soil structure stability (Sollins et al., 1996; Bronik and Lal, 2005; Bullinger-Weber et al., 2007). On the other hand, aggregates composed of coarser material are considered less stable than those composed of finer material (Guenat et al., 1999; Kaiser et al., 2012). In the latter case, the interaction between the fine sand fraction and organic matter is of great importance for soil aggregate formation (Bronik and Lal, 2005). It is therefore not surprising that the TOC content showed a significant positive effect on soil aggregation in this study. Organic matter which is incorporated into soil aggregates chemically binds to mineral particles or is occluded into soil aggregates and improves the structural stability of soils (Tisdall and Oades, 1982; Chorom et al., 1994; Tisdall, 1996; Haynes and Naidu, 1998; Kong et al., 2005). The importance of pH values and cation exchange capacity found in this study has also been found in previous studies, whereby the effect on soil structure stability is rather indirect: increased pH values can enhance microbial activity and clay dispersion (Haynes and Naidu, 1998; Chorom et al., 1994), whereas cation exchange capacity can reduce repulsive forces of negatively charged fine soil particles (Tisdall, 1996). Calcium carbonates did not show any effect on soil aggregates in this study, although they usually act as a cementing agent which agglutinates soil particles (Bronik and Lal, 2005). The influence of carbonates was likely not significant as neither total nor active carbonate values indicated any variation between the sampling plots (data not shown). The majority of the soil physico-chemical parameters are mutually interrelated: for example, an increased silt content usually causes a higher cation exchange capacity compared to a sandy soil. This could be a reason for the extraordinary strong relation between MADOWS and soil parameters found in this study. Especially during flood events, alluvial sediments are deposited in the

floodplain area, whose texture usually depends on the flow velocity (Cierjacks et al., 2011; Graf-Rosenfellner et al., 2016).

4.4. The effect of plants on topsoil structure stability

Root size and root abundance factors (see Section 2.3) showed a significant positive effect on topsoil structure stability, and were positively affected by MADOWS. “Herbs” had a negative effect on the composite “plants” in contrast to “shrubs”, whose effect was strongly positive. As already highlighted in several studies, plants highly contribute to soil aggregation through their root system and thus improve the structural stability in soils: on one hand, soil particles are physically enmeshed during the extension of the root system in the rhizosphere. On the other hand, plant roots release root exudates that directly agglutinate soil particles or stimulate rhizospheric microorganisms, improving the structural stability of soils (Degens et al., 1994; Angers and Caron, 1998; Blanchart et al., 2004; Fonte et al., 2012). However, MADOWS had a positive effect on “plants”, particularly on shrubs. Pioneer shrubs, such as willows, are well adapted to periodic water saturation and to recurring floods over their branched root system (Crouzy and Perona, 2012; Perona et al., 2012; Bätz et al., 2014). In close proximity to the river, plots were dominated by pioneer herbaceous plants whose root system is similar to those of shrubs in terms of functioning. However, SEM results indicated that the proportion of herbs decreased with increasing flood frequency. In plots more distant to the river, pioneer herbaceous plant species are replaced by other herbaceous plants assembled to an alluvial forest alliance. There, especially the abundance of shrubs decreases. This can be explained by the almost closed canopy in the post-pioneer riparian forest which established under a decreasing effect of flood frequency allowing a development of more stabilized habitats with less frequent disturbances (Corenblit et al., 2009).

4.5. The effect of earthworms on topsoil structure stability

In the SEMs, earthworm abundance surprisingly did not show any influence on topsoil structure stability and was not explained by MADOWS or soil parameters. These results are somewhat contradictory to the current state of the literature, as many earthworms, especially endogeics and anecics, are known to efficiently structure soils

(Schäfer and Schauerermann, 1990; Brown et al., 2000; Kong and Six, 2010) and show large dependencies on soil properties and variable soil moisture contents. Anecics are less tolerant to frequent disturbances and prefer habitats with more stable environmental conditions, larger soil depth and a finer soil texture (Guenat et al., 1999; Bullinger-Weber et al., 2012; Le Bayon et al., 2017). However, the abundance of anecics is not restricted to the upper 20 cm of soils in which the generally low water content increases the risk of desiccation. This fact might be one explanation why soil properties of the upper 20 cm did not have a significant influence on their abundance, and why the topsoil structure stability was not affected by anecics. Surprisingly similar, SEMs did not show any significant relations of endogeics and epigeics on topsoil structure stability or interferences through soil parameters and MADOWS either. Especially endogeics are considered to be very important for soil aggregation (Brown et al., 2000). A potential reason for the absence of a significant influence according to SEM could be the fact that the occurrence of endogeics did not show large variability between the sampling plots, which could be a result of their higher tolerance to varying environmental conditions (Ivask et al., 2007). Epigeics are to a lesser extent affected by soil properties because they do not get directly in touch with the soil. Epigeics rather live on top of the soil feeding on litter rather than rummage the soil matrix or contribute to topsoil structure stability (Shipitalo and Protz, 1988; Bullinger-Weber et al., 2007; Eijsackers, 2010; Salomé et al., 2011). Water saturated soils, in general, have a negative impact on earthworms' abundance (Plum and Filser, 2005; Zorn et al., 2008). However, the mean annual water saturation in the topsoil was only around 25–30%, and days with higher water saturations were low due to the efficient drainage of the soils (Liernur, 2016). The period during which earthworms were stressed by rising water levels in the soil over the measurement period was thus low over considering the course of a year. Furthermore, earthworms have developed efficient strategies to avoid water saturated conditions in soil or survive in water saturated soils for a short time: anecics try to escape the habitat as they are less tolerant to water saturated soils (Plum and Filser, 2005). Endogeics can tolerate water-saturated conditions up to several weeks through physiological adaptations: *A. chlorotica* and *A. caliginosa* for example stay in diapause by reducing metabolic activities during a flood period and recover as soon as a flood period has ended (Plum and Filser, 2005; Zorn et al., 2008). During water saturated conditions in soil,

the population of epigeics almost entirely collapses, but recovers rapidly due to their high re-succession rate and their cocoons that can outlast water saturated conditions for several months (Roots, 1956; Plum and Filser, 2005). Water saturated conditions thus have a strong direct impact on abundance of epigeics – but this effect could not be reproduced by the SEMs due to their extraordinary high and rapid recolonisation rate.

4.6. Scopes and limitations of SEM to our experimental design

The application of SEM was suitable for the analysis of direct relations and complex multiple interactions of different variables in this study. The indirect effect of fluctuating groundwater levels on topsoil structure stability over plants and soil parameters could be highlighted, but would have been remained concealed with regression modelling only. SEM was thus an appropriate way to analyse the data and visualize complex causal relations between the variables in our study. The relations of the composite variables “plants” and “earthworms” could not be implemented in the same SEMs due to the insufficient model fit, which resulted most likely from the limited number of samples. Equally a result of the low number of replicates, the predictor variables were not enlarged with additional parameters, such as the biomass of earthworms (Grace and Bollen, 2008; Shipley, 2016). Furthermore, the different time scales of the variables made it complicated to implement the variables in the same SEMs at first glance. The characteristic timescale associated with soil parameters, for example, are significantly longer compared to the population dynamics of earthworms. However, soil development in floodplains is a continuous process, as major flood events periodically burrow former topsoils and superpose them with thick layers of alluvial sediments. The last major flood event impacting all habitats dates back to 2013, shortly before the beginning of our simulation period. As only a handful of smaller flood events but no further major one influenced the habitats, it can be assumed that topsoil structure and parameter development sampled and analysed in this study has developed rather smoothly from 2013 on forward. The same applies to plants and earthworms that have recolonised the topsoil after this event. The relatively calm period between 2013 and 2016 has enabled the development of rather stable plant and earthworm populations that fluctuate between seasons and years, but have not

completely collapsed since 2013. The populations at the moment of sampling thus reflected the result of community dynamics of the past years. Therefore, it can be considered as a decisive factor for the modelling outcome that all predictor variables were shifted to a similar time scale during the investigated time period. The SEM thus properly describes relations and functions for the simulated time period between 2013 and 2016. However, one cannot infer whether the found relations also hold true for a different period or another floodplain ecosystem with stronger or weaker alluvial dynamics. Nevertheless, our results strongly suggest that the found relations are assignable to similar alluvial systems unless soil development is reset or communities of ecosystem engineers collapse due to major flood events.

5. Conclusions

The combination of numerical flow simulations using a physically based, fully-coupled SW-GW model with SEM allowed identifying causal relations and multiple interactions between the topsoil structure stability, ecosystem engineers, and soil properties under complete and partial water saturation of the topsoil. Neither complete nor partial water saturation had a direct influence on topsoil structure stability, but an indirect influence by affecting distribution patterns of plant roots and soil parameters that had, in turn, a significant effect on topsoil structure stability. The distribution of earthworm populations was neither significant for topsoil structure stability nor affected by soil parameters and fluctuating GW levels. Fluctuating GW levels thus control abiotic factors in the plots as well as the distribution patterns of plants and their capability to structure the topsoil in our study. However, earthworm populations are much more independent from fluctuating GW levels and abiotic conditions of their habitats compared to plants, as they developed adaptation strategies which allow them tolerating harsh environmental conditions. Analysing GW levels in soil was more appropriate than purely observing flood frequencies, as partial water saturation in soil already had an effect on soil properties, plants and indirectly on topsoil structure stability. These effects would have been underestimated if only complete water saturation of the soil had been considered. The modelled period between 2013 and 2016 was a convenient period to study topsoil parameters and ecosystem engineers, without any major flood event burrowing the topsoil or extinguishing populations of ecosystem

engineers. Therefore, the question remains open whether our results are specific for the modelled period and the floodplain at NNF. However, it is very likely that the influences of the different predictor variables on topsoil structure stability as found in our study are also applicable to comparable near-natural or restored floodplain systems. It can generally be stated that analysing relations between SW-GW dynamics and soil engineering organisms in floodplains is of crucial importance to evaluate the maintenance of ecosystem services for improving management strategies for near-natural floodplains and the success of floodplain restoration projects.

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Main Chapter IIa): The mesocosm scale I

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Rock-Eval pyrolysis discriminates soil macro-aggregates formed by plants and earthworms

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Abstract

Plants and earthworms, as soil ecosystem engineers, play a crucial role during stabilisation of organic matter in soil through its incorporation into soil aggregates. It is therefore essential to better understand the mechanisms and interactions of soil engineering organisms regarding soil organic matter stabilisation. Several methods have already been successfully applied to differentiate soil aggregates by their origin, but they cannot specify the degree of organic matter stability within soil aggregates. Rock-Eval pyrolysis has already been proved to be pertinent for analyses of soil organic matter bulk chemistry and thermal stability, but it has not yet been directly applied to identify biogenic organic matter signatures within soil aggregates. In this study, Rock-Eval pyrolysis was used for the identification of the soil aggregate origin as well as for the determination of the soil organic matter bulk chemistry and thermal stability in a controlled experiment. Mesocosms were set up, containing treatments with a plant, an earthworm species, or both. Water stable soil macro-aggregates >250 µm were sampled and tested with Rock-Eval pyrolysis after a two-month incubation period. Rock-Eval pyrolysis was able to differentiate soil macro-aggregates by their origin, and to identify a specific signature for each treatment. Macro-aggregates from the plant and earthworm treatment were characterized by a mixed signature incoming from the two soil engineers, indicating that both engineers contribute concomitantly to soil aggregate formation. Organic matter thermal stability was not positively affected by earthworms and even tends to decrease for the plant treatment, emphasising that organic matter was mainly physically protected during the incubation period, but not stabilised. However, future research is required to test if signatures for the tested organisms are species specific or generally assignable to other plant and earthworm species.

Keywords: soil organic matter; ecosystem engineers; Rock-Eval pyrolysis; mesocosm; soil aggregates; thermal stability

1. Introduction

Earthworms and plants are essential soil ecosystem engineers in temperate systems due to their ability to structure soils through the formation of water-stable soil macro-aggregates. Plants form soil macro-aggregates either through mechanical enmeshment of soil particles by roots or through the secretion of root exudates cementing soil particles together (Degens et al., 1994; Angers and Caron, 1998). Earthworms fractionate soil organic matter (SOM) and build up a stable soil structure through SOM incorporation into soil macro-aggregates (Lavelle et al., 1997; Brown et al., 2000; Tanner, 2001). They combine mineral and organic matter by feeding on soil and glue selected soil particles together with saliva and mucus as they pass through the digestive tract (Blanchart et al., 1997; Brown et al., 2000; Lavelle and Spain, 2001). These biological processes combined with SOM biogeochemical stabilisation mechanisms determine the residence time of SOM in the pedosphere (Schmidt et al., 2011). A changing paradigm was presented by Schmidt et al. (2011), indicating that SOM stability is driven through biological and physicochemical influences from the surrounding environment rather than by its molecular structure. Labile organic matter (OM) can thus persist for decades if it is protected against microbial decay through adsorption to mineral surfaces or occlusion into soil aggregates (Christensen, 1996; Sollins et al., 1996; von Lützow et al., 2006; Jastrow et al., 2007). According to this, processes of SOM turnover rates have to be investigated not only at the molecular scale, but must be extended to the scale of the ecosystem functioning (Schmidt et al., 2011). This primarily concerns the mechanisms of how ecosystem engineers incorporate SOM into soil aggregates, e.g. using plant root exudates or mucus from earthworms' digestive tracts. However, the identification of the soil aggregates' origin according to the biological fingerprints from their respective engineers remains challenging. Aggregates from field samples are not only characterized by fresh biogenic OM through its modification of plants and earthworms, but also contain previously incorporated OM from the bulk soil, either found as particulate organic matter or as organic matter associated to the fine soil fraction. Using controlled laboratory experiments (i.e. equal initial organic matter content and bulk chemistry, no external litter input, introduction of specific plants or earthworms), differences in SOM signatures in aggregates can be discriminated and thus assigned to the activity of each specific soil engineer. Near infrared spectroscopy (NIRS)

has been successfully applied to the differentiation of the soil aggregate origin in several microcosm experiments under controlled conditions (Hedde et al., 2005; Velasquez et al., 2007; Zhang et al., 2009; Huerta et al., 2013; Zangerlé et al., 2011, 2014). This method allows the quantitative determination of biogenic structures of soil aggregates based on the identification of functional OM groups at specific infrared wavelengths. This analysis draws a specific OM fingerprint that can be assigned to one specific ecosystem engineer. However, previous studies indicate that certain requirements for the soil substrate have to be fulfilled in order to obtain optimum data accuracy (Chodak, 2008). Assessment of total C and N values were imprecise in soils with low TOC contents (i.e. 0.3%) (Dalal and Henry, 1986), when calibrating NIRS data. Furthermore, C-O bounds of carbonates were shown to affect NIRS results in soils containing extraordinary high carbonate contents (Cozzolino and Moron, 2004; Chodak, 2008). An alternative method is thus required in order to distinguish soil aggregates even under unfavourable soil conditions for measurements. Rock-Eval pyrolysis has been described as a low-cost and a technically less demanding method for the characterization and quantification of soil carbon, as it does not require any previous treatment of the sample (Lafargue et al., 1998; Disnar et al., 2003). Compounds of organic and inorganic matter are identified through a stepwise pyrolysis of a sample in an inert/oxygen atmosphere by which SOM and carbonbearing minerals are broken down according to its thermal stability (Lafargue et al., 1998; Behar et al., 2001). Initially developed for the exploration of oil and gas reservoirs (Espitalité et al., 1985), this method has already proved pertinent for the evaluation of several biogeochemical problems, such as for the exploration of contaminated sites (Lafargue et al., 1998) or for the estimation of OM decay and transformation rates in soil and sediments (Sebag et al., 2006; Marchand et al., 2008; Carrie et al., 2009; Hare et al., 2014; Albrecht et al., 2015). Recently, the method was applied to the identification of SOM thermal stability in soil horizons from soils around the world based on more than 1000 samples (Sebag et al., 2016). This approach has not yet been performed on OM identification in soil aggregates formed by plants and earthworms. We thus aim to test the applicability of Rock-Eval pyrolysis for the first time on water stable soil macro-aggregates created by ecosystem engineers, coupled with controlled sediment and OM inputs. In doing so, we attempt to distinguish these aggregates according to their origin from either plants,

earthworms or both. Based on the technical features offered by Rock-Eval pyrolysis, our study was conducted using a three step analysis including (i) a quantitative OM analysis through the determination of organic and mineral carbon contents, (ii) a qualitative OM analysis through the calculation of standard Rock-Eval parameters and, (iii) a thermal stability analysis of the OM using new indices, as proposed in Sebag et al. (2016). Considering these analyses, we developed the following hypotheses: (i) the composition of organic matter in soil macro-aggregates can be discriminated and thus assigned to engineering effects of plants and earthworms, respectively, and, (ii) the ecosystem engineers affect the OM bulk chemistry during the aggregation process. We furthermore expect (iii) that thermal stability of OM in macro-aggregates is improved if soil engineers contribute to aggregate formation.

2. Material and methods

2.1. Incubation experiment

A mesocosm experiment was set up and incubated in pots over 8 weeks in a climatic chamber under controlled conditions. Twenty pots (10 cm in height, 7 cm in diameter at the bottom increasing to 11 cm at the top) were prepared and allocated to four different treatments with five replicates each, containing plants (P), earthworms (EW), and both plants and earthworms (P + EW). The remaining five pots were kept as a control (CT) but treated under the same conditions. Pots were wrapped in an aluminium foil and covered with a net of 1 mm mesh size at the bottom to allow drainage and prevent anoxic conditions. A transparent plastic cylinder was installed on top to prevent earthworms from escaping. The pots were filled with a silty alluvial sediment composed of 3% clay, 67% silt, and 30% sand content, a pH_{water} value of 7.95, and 30% total carbonates. This sediment was collected at the restored section of the Thur River floodplain at Niederneunforn (8°77'12" E, 47°59'10" N), Thurgau canton, Switzerland. It is a recent deposit, overlying a Calcaric Fluvisol (Siltic) (IUSS Working Group WRB, 2015). The sediment fraction was oven-dried at 40 °C for 72 h in order to preserve the SOM fraction, and sieved by hand at 2 mm. In the field, seedlings of the pioneer plant species *Phalaris arundinacea*, weighing between 5 and 7 g were sampled, and adult earthworms of the endogeic species *Allolobophora chlorotica* were collected using the "hot" mustard extraction method (Lawrence and Bowers, 2002). Dead leaves from the willow tree *Salix viminalis* were air-dried and crushed by hand to provide food for earthworms during the incubation experiment. Pots were filled with

600 g of sediment mixed with 1 g of *Salix viminalis* leaves, rewetting the sediment after each 2 cm of filling. One seedling of *Phalaris arundinacea* was planted in the pots for P and P + EW treatments. A group of three adult earthworms of similar total biomass was added to each pot for EW and P + EW treatments. Pots were incubated for 8 weeks at 18 ± 3 °C, 65% humidity, and a 16/8 h day-night time rhythm simulated in a climate chamber. Humidity in the pots was controlled once a week over the total weight of the pots and rewetted, if necessary, to keep the soil moisture content at field capacity. Irrigation was performed using a fog irrigation nozzle in order to preserve new macro-aggregates built at the soil surface. Pots were randomly arranged under the artificial lights after each humidity control to avoid a potential position effect inside the climate chamber.

2.2. Aggregate sampling

Macro-aggregates of 0.250–2 mm size were sampled after 8 weeks of incubation using two sieves arranged on top of each other. Aggregates larger than 2 mm and smaller than 0.250 mm were neglected, whereas those remaining on the 0.250 mm sieve were carefully plunged into demineralized water at 25 °C for 5 min (Murer et al., 1993). This treatment preserves macro-aggregates that have an increased stability compared to aggregates formed by desiccation and remoistening (Tisdall and Oades, 1982; Jastrow and Miller, 1991; Six et al., 2000). These water-stable macro-aggregates are formed by a combination of biogeochemical processes, to which plants and earthworms contribute to a large extent (Shipitalo and Le Bayon, 2004; Milleret et al., 2009b; Fonte et al., 2012). Macro-aggregates were then air-dried over an entire week and finely crushed for further analyses. Soil material from the CT pots was only sampled and air-dried before being crushed.

2.3. Rock-Eval pyrolysis

The organic matter associated with the macro-aggregates was investigated with a sample of about 50–60 mg of fine crushed aggregates using a Rock-Eval 6 pyrolyser (Vinci Technologies) described in Lafargue et al. (1998) and Behar et al. (2001). The method is based on a stepwise pyrolysis and combustion of OM, releasing CO and CO₂ gases monitored by a flame ionisation detector (FID) for pyrolysis and an infrared detector (IR) for combustion under an artificial air supply (N₂O₂ 20/80). Released hydrocarbons monitored by

FID are graphed by two curves (S1 and S2). The S1 curve is ignored due to its occurrence as a pseudo-peak because soil samples usually do not contain thermovaporised free hydrocarbons, whereas the S2 curve represents the sum of all hydrocarbons. The TpS2 reflects the temperature at which the S2 peak reaches its maximum. The S3 curves represent the amount of CO and CO₂ released during pyrolysis in an inert atmosphere. The S4 and S5 curves are formed during the combustion of residual carbon under artificial air supply and detected by the IR detector (Behar et al., 2001; Disnar et al., 2003; Hetényi et al., 2005). Quantitative OM analysis was performed through the determination of the mineral carbon content (MINC), consisting of CaCO₃ and refractory organic carbon (CorgR) to a small extent. Furthermore, total organic carbon (TOC) is calculated using the sum of all released carbon components representing pyrolysable carbon (PC) and residual carbon (RC), which is only released during the combustion (Behar et al., 2001; Disnar et al., 2003). Further elemental analysis of SOM was not performed in this study due to the high conformity of TOC values in soil obtained from the Rock-Eval 6 pyrolyser and the Leco CNS-2000 ($R^2 = 0.998$, Disnar et al., 2003) and a Flash 2000 NC Analyzer ($R^2 = 0.987$, Saenger et al., 2013). Information on the OM bulk chemistry was provided by the Hydrogen index (HI), which summarizes the total amount of hydrocarbons appearing as the S2 peak normalized to TOC content, and the Oxygen index (OI), which includes the total amount of oxygen released during the CO and CO₂ production normalized to TOC content. Larger amounts of hydrocarbons are synonymous with easy decayable OM, whereas the amount of more mature OM is increased if more oxygen is released during CO and CO₂ production (Hetényi et al., 2005; 2006; Disnar et al., 2003; Carrie et al., 2012). SOM thermal stability was analysed through the calculation of the refractory OM index (R-index) and immature OM index (I-index) proposed by Sebag et al. (2016). These indices are calculated using relationships between five subdivided areas under the S2 curve according to predefined temperature thresholds ranging from the A1 area (for the lowest temperatures) to the A5 (for the highest ones) (Sebag et al., 2016). Higher temperature areas representing more thermally refractory OM compounds are used for the R-index calculation according to the following equation:

$$R\text{-index} = (A3+A4+A5) / 100 \quad (1)$$

whereas, the I-index is calculated using lower temperature areas representing thermally more labile OM compounds (Albrecht et al., 2015)

following:

$$I\text{-index} = \log_{10} ((A1+A2)/A3) \quad (2)$$

Referring only to the signal of the S2 curve, R-Index and I-Index are independent from the CaCO₃ content. Furthermore, the HI-index was additionally used as an indicator for SOM thermal stability analysis (Gregorich et al., 2015; Barré et al., 2016).

2.4. Carbonate content analysis

Subsequent carbonate analyses were performed on macro-aggregates in order to better interpret the values obtained from the Rock-Eval pyrolysis. Total carbonate content (CaCO₃ total) was determined using a Bernard Calcimeter with a readout scale precision of 0.1 ml (Vatan, 1967). The proportion of bioavailable carbonate (CaCO₃ active) was measured according to the method of Drouineau-Galet (Drouineau, 1942) using a Metrohm 702 SM Titrimetric titration apparatus.

2.5. Statistics

As the incubation experiment was set up as a 2×2 factorial design, two-way ANOVAs were conducted testing three omnibus effects: the main effect of each engineer P and EW and the interaction effect between these two engineers. All three effects were tested on Rock-Eval standard parameters (TOC, MINC, PC and RC), values from carbonate analyses, and calculated HI, OI, R- and I-indices. In case where an interaction effect could be found, the specific differences in treatments were subsequently identified with Tukey's HSD post-hoc test. If necessary, data were square-rooted in advance to meet the requirements for normal distribution and variance homogeneity. All statistics and data visualizations were performed with R version 3.3.2 (R Development Core Team, 2016) using "ggplot2" and "Cowplot" packages.

3. Results

3.1. Quantitative SOM and carbonate analysis

Results for quantitative SOM analysis indicated low values for all treatments ranging between 1.07 and 1.36% for TOC, between 0.86 and 1.08% for RC and between 0.2 and 0.29% for PC. Mean MINC values were less than 5.2% for all treatments (Table 1). Standard deviations of TOC, PC and RC values were, except for EW, weak for all treatments due to their range below the sampling and analytical error of the Rock-

Table 1

Average values with standard deviation from the Rock-Eval pyrolysis device according to the mesocosm treatments. “P” stays for plants, “EW” for Earthworms, “P + EW” for plants and earthworms, “CT” for control, “PC” for pyrolysable carbon, “RC” for residual carbon, “TOC” for total organic carbon, “MINC” for mineral carbon, “HI” for hydrogen index, “OI” for oxygen index, “R-index” for refractory index, “I-index” for immature index, “CaCO₃ tot” for total carbonates and “CaCO₃ act” for active carbonates. p-values represent results from Tukey's HSD tests for the two-way ANOVAs indicating main effects of “Plants” and “Earthworms” and interaction effects of “Plants:Earthworms”.

Parameters	Treatments				Omnibus effects		
	P	EW	P + EW	CT	Plant	Earthworm	Plant:Earthworm
PC (%)	0.28 ± 0.01	0.21 ± 0.01	0.26 ± 0.01	0.23 ± 0.00	p < 0.001	p < 0.01	n.s.
RC (%)	1.06 ± 0.02	0.93 ± 0.05	1.02 ± 0.03	0.88 ± 0.02	p < 0.001	n.s.	p < 0.01
TOC (%)	1.34 ± 0.02	1.14 ± 0.06	1.28 ± 0.04	1.10 ± 0.03	p < 0.001	n.s.	n.s.
PC/TOC ratio	0.21 ± 0.00	0.18 ± 0.01	0.20 ± 0.00	0.21 ± 0.01	p < 0.01	p < 0.001	p < 0.01
RC/TOC ratio	0.79 ± 0.01	0.81 ± 0.01	0.80 ± 0.01	0.80 ± 0.01	p < 0.01	p < 0.01	n.s.
PC/RC ratio	0.26 ± 0.01	0.23 ± 0.01	0.25 ± 0.01	0.26 ± 0.01	p < 0.05	p < 0.001	p < 0.01
MINC (%)	0.16 ± 0.01	5.18 ± 0.06	5.19 ± 0.03	5.19 ± 0.03	n.s.	n.s.	n.s.
HI (mg HC)	169 ± 5.05	143 ± 4.84	156 ± 3.20	160 ± 2.38	p < 0.001	p < 0.001	n.s.
OI (mg)	243 ± 3.61	252 ± 9.73	269 ± 4.37	260 ± 13.5	n.s.	n.s.	n.s.
R-index	0.58 ± 0.01	0.61 ± 0.01	0.60 ± 0.00	0.60 ± 0.01	p < 0.01	p < 0.05	n.s.
I-index	0.20 ± 0.01	0.17 ± 0.02	0.18 ± 0.00	0.16 ± 0.02	p < 0.01	n.s.	n.s.
CaCO ₃ tot (%)	29.03 ± 0.21	28.78 ± 0.65	29.30 ± 0.33	29.58 ± 0.25	n.s.	n.s.	n.s.
CaCO ₃ act (%)	22.25 ± 1.40	23.00 ± 2.48	24.16 ± 2.49	22.00 ± 2.07	n.s.	n.s.	n.s.

Eval machine (Behar et al., 2001). Values for TOC, PC, RC and MINC tended to be higher for two EW replicates than for the three others. A main effect of plants was found for most of Rock-Eval standard values, increasing significantly the values of TOC, RC, PC (p-value < 0.001) including the ratios of PC/TOC (p-value < 0.01) and PC/RC (p-value < 0.05), and decreasing the ratio of RC/TOC (p-value < 0.01). The main effects of earthworms indicated a significant decrease for PC values (p-value < 0.001), the PC/TOC ratio (p-value < 0.001) and the PC/RC ratio (p-value < 0.001). However this main effect of earthworms also led to a significant increase of the RC/TOC ratio (p-value < 0.01). Interaction effects were observed in RC values (P < 0.01) when testing relations from P to EW treatment and EW to P + EW treatment. Further interaction effects were found in PC/TOC and PC/RC ratios (p-value < 0.01) with earthworms as the strongest parameter. No main or interaction effects were found for MINC, the total carbonate content and the active carbonate content (Table 1). However, mean values of active CaCO₃ increased somewhat in treatments where earthworms were present.

3.2. Analysis of SOM bulk chemistry

The mean HI value of CT treatment remained around 160 ± 2.38 mg HC g⁻¹ TOC⁻¹ (Fig. 1a). A significant main effect of plants was to increase HI values (p-value < 0.001) and of earthworms was to decrease HI values (p-value < 0.001). No interaction effect was found for HI values (Table 1). According to Fig. 1a, P + EW treatment values ranged in between the values for P and EW treatment. The mean OI value for CT treatment was 408 ± 3.72 mg OC g⁻¹ TOC (Fig. 1b). No main or interaction effects for OI

values were statistically significant. Standard deviations were for both HI and OI indices, except for EW treatment, below the analytical error of the Rock-Eval machine (Behar et al., 2001).

3.3. OM thermal stability analysis

HI values already presented in section 3.2 are directly transferable to OM thermal stability and are not described here again. The mean R-index value of all macro-aggregates produced (resulting from all the treatments) in this study was 0.60 ± 0.01, and the mean I-index value is 0.18 ± 0.02. Plants affected both R-index and I-index (p-value < 0.01), showing decreasing values for R-index and increasing values for I-index. Earthworms only influenced R-index with increased values (p-value < 0.05) (Table 1). No interaction effects were detectable neither for R-index nor for I-index. Fig. 2 indicates that EW treatment data were in the same range of CT treatment, whereas data of P treatment was shifted towards more fresh OM. Values for P + EW treatment ranged in between the data of P treatment and the EW and CT treatment.

4. Discussion

4.1. Applicability of Rock-Eval pyrolysis to soil aggregates

In our experimental study, HI, OI, R- and I-indices of the sediment ranged within values from A and B horizons that are based on a dataset comprising more than 1000 samples from soil horizons worldwide (Sebag et al., 2016). Deposited floodplain sediments usually consist of topsoil material eroded from the

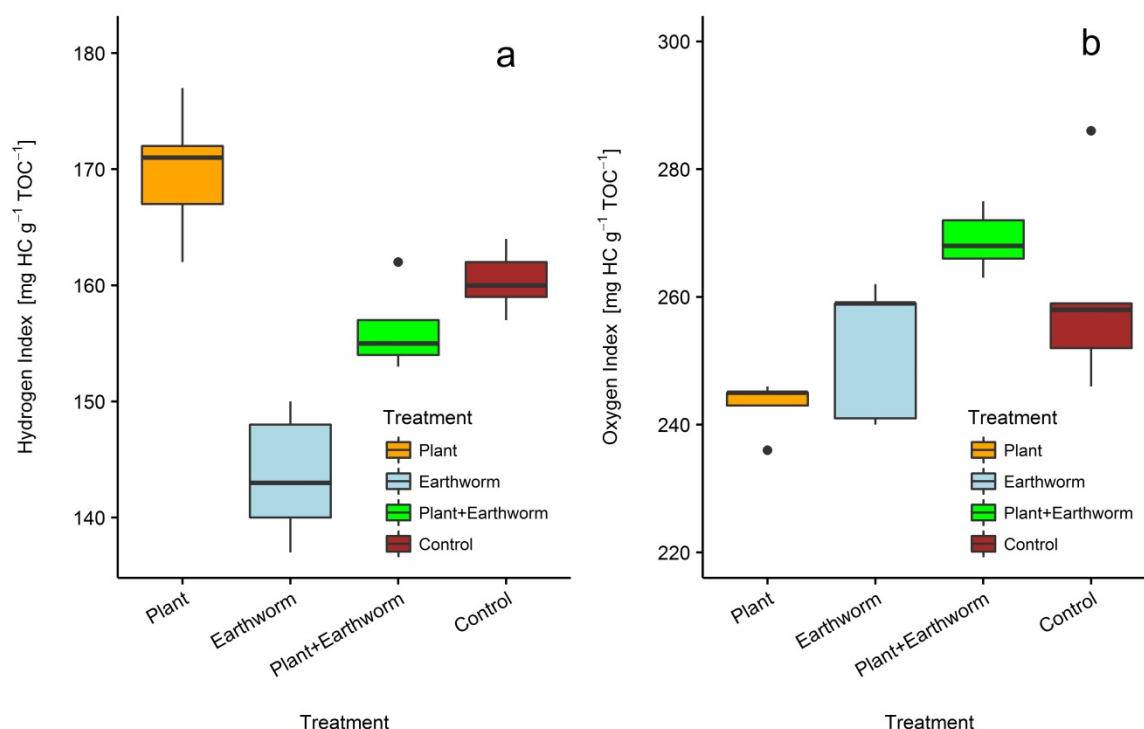


Fig. 1. Two indices used for SOM bulk chemistry analysis: a) Hydrogen Index according to the mesocosm treatments, b) Oxygen Index according to the mesocosm treatments, with $n = 5$ for all treatments.

catchment area upstream of a river system and deposited in floodplain ecosystems in lowland areas during flooding events (Nanson & Croke, 1992; Marriot, 1998). We observed that sediment was combined with OM and integrated into soil macro-aggregates by ecosystem engineers during the incubation experiment. Moreover, as the sediment was sieved at 2 mm, smaller pre-existing aggregates were re-arranged by soil engineers at the same time. Results showed modifications of Rock-Eval standard parameters and calculated indices in treatments containing soil engineers. As the presence of an engineer was the only modification during the incubation experiment, it can be assumed that these modifications can be assigned to the contributions of plants and earthworms to soil aggregation. Therefore, it seems possible to determine biological impacts on soil structuration processes based on the technical possibilities of Rock-Eval pyrolysis. The results for standard Rock-Eval parameters and calculated indices were furthermore grouped according to the mesocosm treatments and differed significantly from each other. Although these modifications were low in terms of their absolute number Rock-Eval pyrolysis was shown to be able to precisely measure the distinctive features of biogenic structures, i.e. plant root exudates and mucus or rather saliva from earthworms' digestive tract, to distinguish them according to their origin. Moreover, analyses of SOM quantity, bulk chemistry, and

thermal stability in each treatment emphasize specific ranges of values for each analysis that differ statistically. Therefore, Rock-Eval pyrolysis is able to identify a characterising signature for each treatment through the combination of results obtained with the three-step analysis. This procedure has never been performed on soil macro-aggregates so far and delivers promising results for the identification of soil macro-aggregate origin, and additionally for the quantity, bulk chemistry, and thermal stability of SOM in aggregates, whatever the soil type.

4.2. Plant signature

The OM signature in aggregates stemming from plants was characterized by increased TOC contents, higher HI-index and I-Index values, whereas R-Index values were lower compared to CT treatments. This indicates that fresh and easy decomposable OM compounds were incorporated into the macro-aggregates. Plants provide inputs of labile OM compounds such as root exudates or dead roots (Czarnes et al., 2000; Sebag et al., 2016), which can act as bonding agents for soil particles or may stimulate microbial activity in the surrounding bulk soil (Angers and Caron, 1998; Fonte et al., 2012). This plant signature on macro-aggregates thus reflects the direct influence of the plant itself, as well as the potential effect of

biogenic signatures of rhizospheric microorganisms that are stimulated indirectly through the presence of plant roots. Some compounds released by roots, such as carbohydrates and phenols, promote interaction with heterotrophic bacteria and are suspected to be responsible for the colonisation of roots by arbuscular mycorrhizal fungi (AMF) (Becard et al., 1995; Narula et al., 2009). Fine roots that remain in the soil aggregates and are colonised with mycorrhizal fungi may also contribute to the plant's characteristic signature. Root exudates can also affect soil aggregates through the modification of chemical components in the soil. The presence of organic acids in the rhizosphere can lead to the dissolution of CaCO_3 , which might be a possible explanation for the slight decrease of MINC values observed in the P treatment. However, this effect did not statistically characterise the plant signature. To sum up, plant signature can be understood as a combination of fresh OM residues directly incorporated into soil macroaggregates and OM products released from interacting organisms in the rhizosphere.

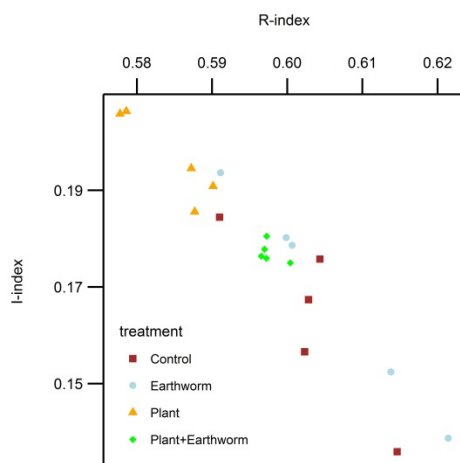


Fig. 2. R-Index plotted against I-index as an indicator for the SOM stability in aggregates, with $n = 5$ for all treatments.

4.3. Earthworm signature

Low HI values make the earthworm signature distinct, as well as its relative enrichment of RC and depletion of PC in relationship to TOC, compared to control treatments. Earthworms were shown to have a preferential feeding behaviour (Curry and Schmidt, 2007), whereby lighter OM fraction containing easier decayable compounds (reflected by PC) are selectively ingested. During the gut transit, OM compounds and mineral matter are mixed and agglutinated with mucus and saliva in the digestive tract (Brown et al., 2000). It can be

assumed that these substances, acting as bonding agents, are predominant factors explaining the specific earthworm signature. The ingested OM from bulk soil was recently shown to be occluded into the soil matrix rather than being chemically modified while passing the digestive tract (Angst et al., 2017). Contrary tendencies can be observed regarding the values for MINC. Three MINC values were lower, the remaining two even higher than the MINC values in the CT treatments. It seems likely that two different mechanisms proceed in EW treatments although the setup was equal for all replicates. Groups of earthworms in three of the replicates might alter the CorgR included into the MINC pool, thus leading to its reduction. MINC is increased in the two other treatments that might be explained by the increase of CaCO_3 into the MINC pool. These assumptions are strengthened through constant values of TOC, which are usually reduced parallel to the PC preferentially consumed by earthworms. The existing imbalance between a shift of a partial pool in proportion to the overall pool has thus to be offset otherwise. Moreover, it seems unlikely that the Corg pool is a source for MINC pool increase in the earthworm treatments because TOC contents in earthworm macroaggregates do not differ from the TOC values found in CT treatments. Therefore, the increase in the MINC pool seems to be controlled by an external source. Many earthworm species, including *A. chlorotica*, are known to produce calcium carbonate granules by their calciferous glands ranging from 0.125 mm to single CaCO_3 crystals (Becze-Deák et al., 1997; Canti, 1998; Canti and Pearce, 2003). The slight increase in active CaCO_3 found in EW and P + EW treatments indicates that earthworms might ingest Ca^{2+} and/or CaCO_3 from the bulk soil, produce calcium carbonate granules and incorporate them into the soil aggregates. Similar results have already been reported in Canti (2009) and Garcia-Montero et al. (2013). The reasons for the excretion of calcium carbonate have not been clarified, so far. Recent discussions focus on a mechanism that might regulate the pH of blood and tissue fluids or incidentally neutralizes the gut system (Canti and Pierce, 2003; Coleman et al., 2004; Briones et al., 2008).

4.4. Plant + Earthworm signature

In the P + EW treatment, TOC content slightly increased whereas MINC did not show any significant changes compared to the CT treatments. HI, I-Index and R-Index values ranged exactly between the values of P and EW treatments. These findings represent the combined signature of plants and earthworms

on the macro-aggregates that might be either a mixed signature of sampled aggregates or indicate interaction of both ecosystem engineers during the formation of soil macroaggregates. Previous studies have already shown that earthworms have a preferential feeding behaviour by consuming the C_{org} produced by plants through root exudates, as root exudates are more easily consumable by earthworms (Decaëns et al., 2001; Curry and Schmidt, 2007). Recent investigations emphasize that earthworms consume significant amounts of root derived OM that is incorporated into soil aggregates (Gilbert et al., 2014; Sanchez-de Leon et al., 2014). Beneficial effects are however reciprocal since plants take advantage of the earthworms' activity in the soil in the same way (Le Bayon et al., 2017). Earthworms are known to mobilise nitrogen, phosphorus, and exchangeable nutrients that are easier accessible for plants (Brown et al., 2000; Shipitalo and Le Bayon, 2004; Le Bayon & Binet et al., 2006; Le Bayon et al., 2011). Therefore, plants roots preferentially colonise earthworm structures (casts, burrow linings) to get access to the nutrient hotspot (Spiers et al., 1986; Zaller and Arnone, 1999). As a consequence, our results are an indicator that the interactions of both studied soil engineers, not only have positive effects on their growth or survival rate but also contribute concomitantly to the formation of soil macro-aggregates. Similar results were shown by Zangerlé et al. (2011), who recovered NIRS signatures of these two soil engineers in aggregates.

4.5. OM thermal stability

The R-index and I-index have been proved to be powerful indicators for the assessment of the thermal stability of soil organic matter. These indices point to functional allocations of field samples corresponding to specific soil horizons (Sebag et al., 2016). Additionally, the HI was proposed as another indicator for the analysis of OM thermal stability (Gregorich et al., 2015; Barré et al., 2016). Results for the thermal stability obtained by the R-index and HI in this study are indeed comparable. However, HI values have a tendency to show greater differences between the signatures of the treatments and make them statistically significant. Compared to the R-index, HI is strongly controlled by the chemical composition of OM leading to increasing variances of the obtained values (Gregorich et al., 2015; Barré et al., 2016). Differences in the values of treatments in this study also suggest that these indices are suitable to assess thermal stability of OM in soil macro-aggregates. Thus, the values found in the CT treatments represent the Rock-

Eval signature of the transported sediment layer, which can be used as an initial value for the mesocosm experiment. CT treatments showed a certain variation, despite a thorough mixing of sediment with added plant leaves. Once a plant is added to the system, the thermal stability of organic matter in soil macro-aggregates decreases with a simultaneous increase of the degree of preservation of fresh organic matter. Plant root exudates consist of easily decomposable organic matter, belonging to labile OM pools in soil due to the rapid turnover rate. However, even thermally labile OM can be efficiently protected by mineral matter against microbial decay through occlusion into aggregates that can extend its residence time in soil (Schmidt et al., 2011). SOM thermal stability does not seem to be improved regarding EW and P + W except when using HI values. In general, the association of mineral and organic compounds is facilitated while passing through earthworms' digestive tract (Lavelle, 1988). As already mentioned above, recent findings indicate that, during this process, SOM is rather physically protected than modified regarding its chemical composition (Angst et al., 2017). Mechanical or biological breakdown and re-formation of aggregates hinder an effective stabilisation of OM in soil aggregates and thus decrease its long-term persistence. In a short term (20 days of incubation), Bossuyt et al. (2005) found that organic carbon was not protected in macro-aggregates in the presence of earthworms. During longer periods, the endogeic earthworm *A. caliginosa* was shown to stabilise significant amounts of organic carbon in micro-aggregates agglutinated to macro-aggregates (Bossuyt et al., 2005). Considering only the HI values, our studied species *A. chlorotica* might increase the thermal stability of OM in macro-aggregates even over short periods. On the other hand, *A. chlorotica* is in fact considered as a pioneer species in young dynamic ecosystems such as floodplains, but was shown to decrease the structural stability and increase soil compaction in a microcosm experiment (Milleret et al., 2009a). The signature must therefore be considered as a species-specific signature for *A. chlorotica* and thus cannot be readily projected to other earthworm species. However, Milleret et al. (2009a) highlighted that the effect of *A. chlorotica* was reversed when adding arbuscular mycorrhizal fungi and turned positive when also adding plants to their mesocosms. Nevertheless, the combination of plants and earthworms did not improve OM thermal stability of macro-aggregates in our study, regardless of whether the OM signature obtained from R-index and HI represents a mixture or a combined effect of both engineers. In contrast, according to Schmidt et al. (2011),

the incorporation and sequestration of SOM is a combination of interacting physical, chemical, and biological parameters within an ecosystem. Therefore, it was actually expected that the interaction between plants and earthworms would have positive effects on soil structuration and improve the thermal stability SOM.

4.6. Limitations

This study highlights the applicability of Rock-Eval pyrolysis to identify soil macro-aggregates according to their biological origin, based on specially selected parameters for the experimental setup. It is important to mention that the absolute numbers obtained from Rock-Eval analyses depend on initial conditions characterizing bulk soil or sediment and thus cannot be generalized or directly compared to other studies. The results obtained in our study thus reflect a mixture of pre-existing macro-aggregates and aggregates that were modified or newly formed by ecosystem engineers during the incubation experiment. The amount and stabilisation degree of SOM determines the starting conditions from which modifications of ecosystem engineers can be considered as relative deviations and may vary from strong to weak. Therefore, a general valid factor describing the degree of modification of organic signatures in soil macro-aggregates cannot be defined. In our study, the initial range of OM values is provided by the sediment mixed with litter in CT treatment because the sediment was not subject to any (macro-)biological modifications during the incubation period. Biogenic signatures led only to slight changes of absolute OM values in aggregates, but were grouped according to their respective treatments with low deviations leading to distinct OM signatures. Low initial OM contents in the bulk sediment might have been advantageous in order to allow visualisation of biogenic modifications in aggregates. Slight changes in OM composition in treatments could disappear with a strong OM signal of the bulk sediment. The use of OM poor sediments might be more appropriate to test biogenic modifications in soil aggregates, despite the fact that no application of OM rich sediments has been evaluated in this context so far. Although the signatures for each treatment seem to be comprehensible regarding the behaviour of plants and earthworms during soil aggregation, it should be noted that only one specific plant and earthworm species was tested in this study. It can be assumed that signatures for different plant and earthworm species might show certain variability due to the varying composition of root exudates or digestive flora. The P + EW signature is especially suspected to vary on a

larger scale because different earthworm species allocated to other ecological categories were shown to interact to a lesser extent with plants or contribute less to SOM incorporation and to soil aggregation (Bouché, 1972; Fragoso and Lavelle, 1995; Lavelle et al., 1997). Endogeics including the studied species *A. chlorotica* are most efficient in soil structuration and show high interaction with plants (Milleret et al., 2009a; Fonte et al., 2012). Epigeic earthworms primarily feed on OM in the topsoil whereas anecic earthworm burrowing activity is limited to a few galleries in deeper soils. The P + EW signature might therefore be less marked by earthworms when testing epigeics or anecics with plants in a mesocosm treatment. Further tests with different species are therefore mandatory in order to validate the signatures presented in this study.

5. Conclusions

This study presents the first application of Rock-Eval pyrolysis to aggregates formed by soil engineering organisms under controlled conditions. Our results show the potential of Rock-Eval pyrolysis to identify organismal-specific OM signatures and thus to distinguish soil macro-aggregates by their origin. In contrast to the methods applied for the identification of aggregate origin so far, Rock-Eval pyrolysis provides further information on SOM bulk chemistry. Using standard values and calculated indices, quantitative and qualitative assumptions can be formulated regarding SOM in aggregates. Indices for refractory and immature OM have shown their potential for the determination of SOM thermal stability in aggregates. During a short incubation period, our studied organisms did not significantly improve SOM thermal stability in soil macro-aggregates. SOM might be physically protected in soil aggregates rather than chemically bonded in short term. However, only one single plant and earthworm species was tested in this study, so signatures must be considered as species-specific. In order to validate and generalise the results, further experiments including different plant and earthworm species are required.

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Main Chapter IIb): The mesocosm scale II

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Composition and superposition of alluvial deposits drive macro-biological soil engineering and organic matter dynamics in floodplains

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Abstract

Soil structure formation in alluvial soils is a fundamental process in near-natural floodplains. Plants and earthworms are successful soil engineering organisms that improve the soil structural stability through the incorporation of mineral and organic matter into soil aggregates. However, the heterogeneous succession of different textured mineral and buried organic matter layers impedes the development of a stable soil structure. Our study aims at investigating the effects of soil engineering organisms, the composition, and the superimposition of different alluvial deposits on the structuration patterns, the aggregate stability, and organic matter dynamics in *in vitro* soil columns, recreating sediment deposition in alluvial soils. Two successions of three different deposits, silt – buried litter – sand, and the inverse, were set up in mesocosms and allocated to four different treatments, i.e. plants, earthworms, plants + earthworms, and a control. X-ray computed tomography was used to identify structuration patterns generated by ecosystem engineers. Organic matter dynamics were investigated by means of the R- and the I-indices, calculated from measurements obtained by Rock-Eval pyrolysis. Structuration patterns of plants were identified only in the top layers, whereas earthworms preferentially selected the buried litter and the silt layers. Aggregate stability increased in the presence of plants and in aggregates recovered in the buried litter layer. Organic matter dynamics were controlled by a complex interplay between the type of engineer, the composition, and the succession of the deposit in the mesocosm. Our results strongly indicate that the progress and efficiency of soil structure formation in alluvial soils strongly depends on interactions between soil engineering organisms and the composition of the soil, e.g. the thicknesses, textures, and superimposition of alluvial deposits.

Keywords: soil structure; Fluvisol; Earthworms; Pioneer plant; Rock Eval pyrolysis; X-ray analysis

1. Introduction

Soils of near natural floodplains constitute an important pillar to the preservation of biodiversity in floodplain ecosystems. At small spatial scales, floodplain soils differ considerably in their physicochemical properties, forming a large variety of terrestrial habitats (Malmqvist and Rundle, 2002). Besides, floodplain soils fulfil a broad range of ecosystem services, ranging from carbon sequestration, nutrient and pollutant cycling, up to flood and erosion control (Diaz-Zorita et al., 2002; Acreman et al., 2003; Bronik and Lal, 2005). Floodplain soils, such as Fluvisols or Fluvic Arenosols (IUSS Working Group WRB, 2015), are composed of different alluvial sediments that are superimposed due to recurring flood events (Nanson and Croke, 1992; Marriot, 1998). Alluvial deposits may differ considerably in their thickness and composition, e.g. in their texture, as well as in their organic matter (OM) content and bulk chemistry, depending on the flood magnitude and the sediment origin (De Vivo et al., 2001; Coppola et al., 2010). Soil physicochemical parameters can thus abruptly change in a soil profile, whenever a previous topsoil horizon is overlaid by a more recent alluvial deposit (Kercheva et al., 2017). Moreover, litter overtopping topsoil horizons can be buried before being incorporated into the soil matrix depending on the season, OM decomposition rates, and soil biota activity. Species dynamics and ecosystem services are positively correlated to stable conditions in the soil, which can be promoted by its structural stability and by the extension of the soils' belowground macro-porous system (Bronik and Lal, 2005). However, stabilisation of floodplain soils is a slow and complex process, due to the organisation and regular superimposition of different alluvial deposits and buried litter layers. Furthermore, the structural stability can be favoured or mediated by a complex interplay between soil physicochemical parameters, soil engineering organisms, and surface-water – groundwater dynamics (Guenat et al., 1999; Plum and Filser, 2005; Bullinger-Weber et al., 2007, 2012; Fournier et al., 2012; Schomburg et al., 2018b). Plants and earthworms are among the most successful soil engineering organisms at the macro-biological scale in temperate ecosystems (Lavelle et al., 1997; Tanner, 2001; Blouin et al., 2013; Le Bayon et al., 2017). They incorporate mineral particles and soil organic matter (SOM) into soil macro-aggregates, which significantly improve soil's structural stability (Brown et al., 2000; Six et al., 2002; Kong and Six, 2010). Plants physically entangle mineral and organic soil particles through rooting, release root exudates,

which act as a glue, or stimulate rhizobacteria (Degens et al., 1994; Angers and Caron, 1998; Czarnes et al., 2000). Earthworms agglutinate soil particles along the walls of their burrows or in casts, as they select organic and mineral components and enrich ingested material with mucus and saliva produced in their digestive system (Blanchart, 1997; Brown et al., 2000; Lavelle & Spain, 2001; Curry and Schmidt, 2007). Both plants and earthworms also have great potential for improving the structural stability in floodplain soils, as they rapidly colonise young soils and tolerate periodic flood events (Gurnell and Petts, 2002, 2006; Thonon and Klok, 2007; Le Bayon et al., 2013, 2017; Schomburg et al., 2018b). However, the soil structuration patterns created through plant rooting and through earthworms' burrowing and casting activity are still rarely investigated and poorly understood in floodplain soils. In particular, to our best knowledge, the superposition of alluvial deposits differing in their texture, and of buried litter layers, have not yet been considered in the analyses of the soil structure formation. In the field, structuration patterns are difficult to appraise due to spatial heterogeneity of superimposed alluvial deposits. Standardising these parameters by setting up *in vitro* experiments with a controlled and monitored superposition of mineral and litter layers comparable to floodplain soils, is useful for the analysis of the structuration patterns induced by plants and earthworms. Root galleries and earthworm tunnels in micro- and mesocosms can be visualised and analysed using X-ray computed tomography (X-ray CT; Pierret et al., 1999; 2002; Capowiez et al., 2011, 2015; Amossé et al., 2015). X-ray CT is a non-destructive tool used to create a 3D structure of a scanned matrix, and thus, analyses its macro-porous network (Helliwell et al., 2013; Turberg et al., 2014). By doing so, X-ray CT has emerged as a contemporary method to indirectly assess soil structure formation (Vogel et al., 2002; Vervoort and Cattle, 2003; Lin et al., 2005). Similarly to structuration patterns, OM dynamics, and in particular the mechanisms of OM incorporation into soil aggregates, might be strongly controlled by the heterogeneous composition of floodplain soils. In a recent study, Schomburg et al. (2018a) tested the effects and interactions of a pioneer plant and an earthworm species on OM dynamics and aggregation using Rock-Eval pyrolysis in a controlled mesocosm experiment. Through the analysis of OM signatures, soil aggregates were distinguished by their origin. Furthermore, OM thermal stability was analysed and used as an indicator for OM sequestration into soil aggregates. For this purpose, recently developed indices representing immature OM (I-Index)

and OM thermal stability (R-Index) were applied (Albrecht et al., 2015; Sebag et al., 2016; Matteodo et al., 2018). However, Schomburg et al. (2018a) considered one uniform alluvial sediment in the soil column. OM thermal stability analyses could thus be performed on a simple design focusing on the macro-biological processes, while neglecting the functional level of near-natural alluvial soils. In the present study, we aim to investigate the combined effects of different alluvial deposits, their superimposition, and the presence of soil engineering organisms on the structuration patterns and OM dynamics during its incorporation into soil aggregates. We use a mesocosm approach and simulate a natural floodplain soil through the superposition of two alluvial sediments strongly differing in their texture, which are separated by a layer of buried litter material. By doing so, we hypothesise that the type of soil engineer, the composition of the deposits, and their superimposition strongly control the structuration patterns, the degree of aggregate stability, and OM dynamics during its incorporation into soil aggregates.

2. Material and methods

2.1 Experimental design

An in-vitro experimental design based on Schomburg et al. (2018a) was set up in mesocosms to better understand the effects of soil engineers, the composition and superimposition of the sediment deposits on structuration patterns, the aggregate stability and OM dynamics in alluvial soils. Two alluvial sediment deposits (a silty and a sandy one) were superposed and separated by a layer of litter material (LOM layer) following two different superimpositions (Fig. 1): i) the silty sediment overtopping the sandy one (TopSi configuration with silt.top, LOM, sand.bottom) and ii) vice versa (TopSa configuration with sand.top, LOM, silt.bottom). Both configurations were allocated to four different treatments with five replicates each: i) the plant treatment (P), ii) the earthworm treatment (EW), iii) the combined plant and earthworm treatment (P + EW), and iv) the control (NT). This experimental design generated two different layouts for the data analysis: i) a one-factor design for the data that were available at the mesocosm level (plant biomass and weight gain of earthworms, see chapter 2.4). The studied factor was the “treatment” with four levels (P, EW, P + EW, NT). ii) a split-plot design for the data measured at the split plot level. The main unit factor was represented by the “treatments” and the split-plot factors were the three sediment deposits within the mesocosms. In addition, the position of each sediment deposit within the mesocosm

was considered with each sediment deposit defined by its “layer”: silt.top, silt.bottom, sand.top, sand.bottom, LOM (which is always the second layer; Fig. 1). Using this definition, the split-plot factor had five levels. The response variables measured at the split-plot levels were the total segment length (see chapter 2.3), the percentage of water-stable macro-aggregates (%WSA, see chapter 2.4), and the R-index (see chapter 2.5).

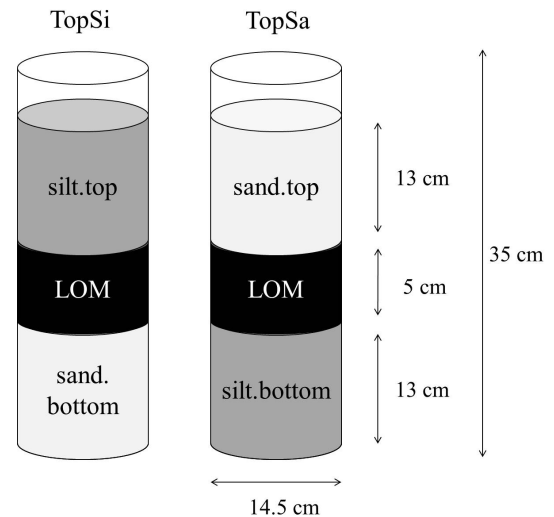


Fig. 1. The two mesocosms’ experimental designs with silt (silt.top), overlying an organic matter layer (LOM) and a sand layer (sand.bottom) (TopSi) and sand (sand.top), overlying an organic matter layer (LOM) and a silt layer (silt.bottom) (TopSa).

2.2 Mesocosm construction

Mesocosms were set up in cylindric PVC tubes of 35 cm in height and 14.5 cm in diameter. Sediment deposits, as well as litter and small branches of willow trees (*Salix viminalis*) for the LOM layer were sampled in the willow bush zone (Fournier et al., 2012) in the restored section of the Thur River in Niederneunforn (8°77’12” E, 47°59’10” N), Thurgau Canton, Switzerland. Both sediments were recent alluvial deposits of a (i) Calcaric Fluvisol and a (ii) Calcaric Fluvic Arenosol (IUSS Working Group WRB, 2015). Soil physicochemical parameters and the methods used for their respective analysis are listed in Table 1. Before filling the tubes, sediments and litter material were dried at 40°C for 72 h in order to preserve the SOM fraction. Sediments were sieved mechanically at 1 mm using a vibrating sieving apparatus. The fraction between 1 and 2 mm was neglected in order to remove the coarse sand fraction that may cause intestinal damage to earthworms’ digestive tracts (Shipitalo and

Protz, 1988). Sampling of ecosystem engineers and preparation of PVC tubes were performed similar to the design presented by Schomburg et al. (2018a). Each PVC tube was filled up with 2.5 kg of both sediments, which were mixed with 1.5 g of dried and shredded catgrass (*Zyperus zumula*) in order to supply food to earthworms during the experiment. The first sediment was filled stepwise into the tube and rewetted after each 2 cm of filling. This sediment was superposed by a mixed layer of 5 cm of willow tree branches and leaves. This layer was again covered by the other sediment and vice versa. For the plant treatment (P), a seedling of *Phalaris arundinacea* (8 – 10 g initial weight) was planted. For the earthworm treatment (EW), five adult individuals of *Allolobophora chlorotica* were placed in the LOM layer to allow them to choose their “preferred” sediment. The total weight of earthworms was checked to be similar for all treatments containing earthworms. Combined treatments were prepared, containing both plants and earthworms (P + EW). Treatments without any soil engineer represented the control (NT). Mesocosms were incubated over a period of 8 weeks and kept in similar conditions as those described in Schomburg et al. (2018a).

Table 1: Initial soil physicochemical parameters measured in silty and sandy alluvial sediments before starting the incubation experiment. Grain size distributions were obtained using a LS 13 320 Laser Diffraction Particle Size Analyzer equipped with an APS Auto Prep Station (Beckman Coulter); pH values were measured using a combined pH meter/conductometer (914 pH Meter/conductometer, Metrohm, Herisau) with a soil/water ratio of 1:2.5; TOC contents are calculated from Rock-Eval pyrolysis and total carbonate contents were obtained using a Bernard Calcimeter described by Vatan (1967).

Soil parameter	Silty Sediment	Sandy Sediment
Silt content (%)	56.00	4.50
Sand content (%)	34.50	92.50
Clay content (%)	9.50	3.00
pH _{water}	7.45	8.25
TOC content (%)	1.48	0.32
Total carbonate content (%)	37.00	30.00

2.3 X-ray Computed Tomography (X-ray CT)

2.3.1 Mesocosm scanning

After eight weeks of incubation, mesocosms were prepared for X-ray CT analysis. Plant stems were cut off at the edge and mesocosms closed at both ends. The remaining space between the closure cap and the sediment was filled up with styrofoam chips, in order to prevent movement of the sediment layers during the scanning process. Mesocosms were

scanned using a LightSpeed VCT (GE Medicalm Systems) medical scanner. The device was equipped with a rotating scanner emitting X-ray beams on a 1.2 mm focal spot with a peak energy of 120 KeV and a tube current of 500 mA. Data acquisition was based on a 64 channel detector and an axial pitch of 0.625 mm. These settings were already predefined for the analysis of soil and peat samples in recent studies (Turberg et al., 2014; Amossé et al., 2015; Liernur et al., 2017). Each image of the sequence was projected on a 512 x 512 pixel grid and adapted to the transaxial field of view, defining a cubic voxel size of 0.3 x 0.3 x 0.3 mm on all 2D reconstructed CT images. On average, 1200 CT images were generated per mesocosm.

2.3.2 Image Analysis

Raw images were treated using imageJ (open source software) (Schneider et al., 2012) and Avizo, version 9.3.0 (FEI, 2016). Raw images of each mesocosm were imported in imageJ and converted into one image sequence. Substacks were created individually for each image sequence and contact zones between the sediments and the PVC tubes were cut out. Image sequences were subsequently implemented in Avizo. Binarisation was performed in order to separate the mineral and organic matrix from the void representing plant root galleries, earthworm burrows, pores and cracks. Interactive thresholding was used, as the provided algorithms for automatic thresholdings did not accurately represent the features of interest (i.e. voids related to macro-biological engineering activity). Automatic thresholding using factorisation tended to overestimate root galleries in some image sequences, but did not vary significantly from interactive thresholding levels when considering all image sequences (Appendix 1c, d). In a first step, a specific threshold value was defined for each image sequence. The arithmetic mean of all individual threshold values applied on each image sequence was then calculated. Binarisation was performed again on each image sequence using the arithmetic mean of the threshold levels. Since all scans were conducted with exactly the same measuring configuration, mean values did not lead to a significant over- or under-estimation of the voids (Appendix 1c). Porosity was calculated on the ratio of the thresholded void and the remaining soil material. Skeletonisation of the voids was subsequently performed on the binarised 3D images using the auto-skeleton function with a smoothing coefficient of 0.5 and 10 iterations (Fig. 2). The total number of segments and nodes and the total segment length, calculated through skeletonisation, were used as an indicator for

macro-biological structuring activity in each material. All indicators were normalised per dm³ due to a slight variation in the total volume of each material.

2.4 Sampling of aggregates and soil engineers

Mesocosms were opened after CT scanning. Plant roots were sampled by hand, carefully washed with tap water, oven-dried for 48 hours and weighed. Earthworms were collected and

weighed after gut defection. Aggregate sampling was performed individually on each sediment using the same method applied by Schomburg et al. (2018a). Aggregates found in the LOM were carefully submerged into demineralised water. Mineral material deposited at the bottom of the column was subsequently sampled. Aggregate stability was determined according to the method described in Kemper and Rosenau (1986), using a modified automatic sieve-diving apparatus (Murer et al.,

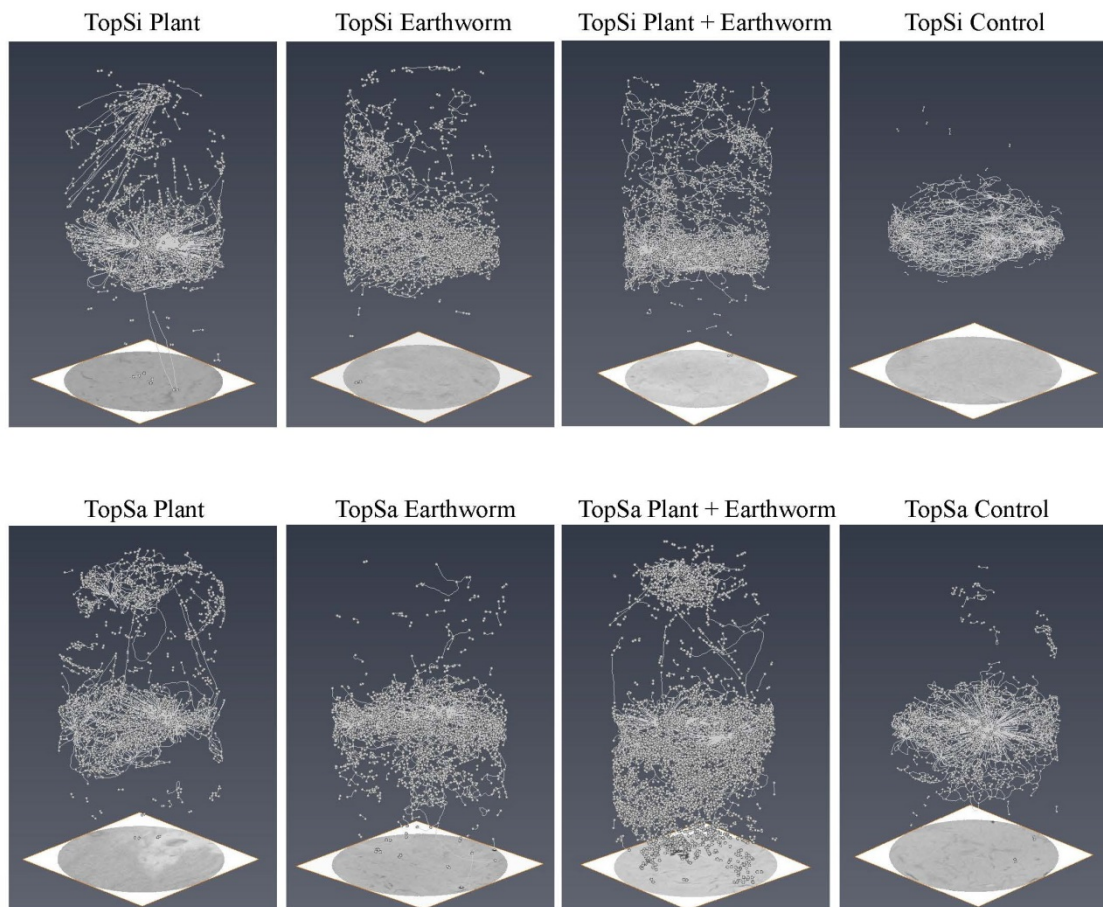


Fig. 2. Visualisation of 3D skeletons for all treatments in both configurations performed in Avizo. Binarised items are illustrated by the grey lines representing root galleries, earthworm burrows, pores and cracks. TopSi stays for the succession silt - buried litter - sand, TopSa for the succession sand - buried litter - silt.

1993). Water-stable macro-aggregates and material from the control treatments were air-dried over an entire week and finely crushed for Rock-Eval pyrolysis.

2.5 Rock-Eval pyrolysis

OM dynamics during its incorporation into soil aggregates and its thermal stability were assessed using a Rock-Eval 6 pyrolyser (Vinci Technologies), which is described in Lafargue et al., (1998) and Behar et al., (2001). About 50

– 60 mg of finely crushed material was stepwise pyrolysed in an inert atmosphere and subsequently combusted using an artificial air supply. Released hydrocarbons were monitored by a flame ionisation detector (FID) and graphed as the “S2 thermogram”, representing the sum of all released hydrocarbons. The analysis of the S2 thermogram provided information on OM bulk chemistry and thermal stability in soils and sediments (Disnar et al., 2003; Hetényi et al., 2005; Sebag et al., 2006). In this study, the area under the S2 curve was subdivided into five areas (A1 to A5) with

predefined temperature ranges : 200–340 °C for A1 (labile biopolymers), 340–400 °C for A2 (resistant biopolymers), 400–460 °C for A3 (immature geopolymers), and A4 and A5, which stands for refractory geopolymers (> 460 °C). These areas were used for the calculation of the R-index and I-index (Sebag et al., 2016). I-index was related to the thermally more labile fraction of OM and measures its degree of preservation as follows:

$$\text{I-index} = \left[\log \right]_{-10} ((A1+A2)/A3) \quad (1)$$

R-index was related to the whole OM content and measured the contribution of thermally more stable fractions as follows:

$$\text{R-index} = (A3+A4+A5)/100 \quad (2)$$

Both indices are independent from CaCO₃ and total organic carbon (TOC) contents. They have recently been calibrated in the I/R diagram by means of more than 1000 soil samples from different soil horizons and indicated a strong correlation in non-disturbed soils, where changes in labile OM fraction drive the bulk thermal stability (Sebag et al., 2016). Thus, the I/R diagram was shown to be pertinent to interpret dynamics of OM during its incorporation into soil aggregates induced by soil engineering organisms (Schomburg et al., 2018a). The R-index representing OM thermal stability has been shown to be an especially powerful indicator for the degree of OM stabilisation in the bulk soil and in soil aggregates (Matteodo et al., 2018; Schomburg et al., 2018a).

2.6 Statistical data processing

All statistical analyses and data visualisations were performed in R (R Core Team, 2013) version 3.5.1. The package "easyanova" was used (Arnhold, 2013) for the split-plot data. The packages "ggplot2" (Wickham, 2009) and "gridExtra" (Auguie, 2016) were used for data visualisation.

2.6.1 One-way analysis of variance (ANOVA)

Data collected at the level of the mesocosm (biomass and weight change) were analysed with a one-way analysis of variance (ANOVA). Normal distribution and variance homogeneity of the data were previously verified using the Shapiro-Wilk test and the Bartlett test. If significant, multiple comparisons at the main factor levels were identified using Tukey's HSD post-hoc test.

2.6.2 Analyses of variance for randomised split-plot designs

The role of the composition of the deposit, its superimposition, and the presence of soil engineers on the structuration patterns, soil structural stability and OM dynamics (see hypothesis in the introduction section) were analysed using three analyses of variance for randomised split-plot designs. Three robust indicators for the structuration patterns (total segment length from X-ray CT), the degree of structuration indicated by water stable macro-aggregates (Six et al., 2000), and the R-index representing OM thermal stability in soil aggregates (Schomburg et al., 2018a) were defined as response variables. Two predictor variables were defined for each analysis: the factor "treatment" with four levels (P, EW, P + EW, NT) and the factor "layer" with five levels (silt.top, silt.bottom, sand.top, sand.bottom, LOM). The factor "layer" thus contained information about both the composition of the deposit and the position within the mesocosm. This information could not be analysed using two different predictor variables due to missing statistical independency. ANOVAs were performed using the sum of squares type III. Criteria for normality and homoscedasticity were checked prior to the analyses using the Shapiro-Wilk test and the Bartlett test. As the total segment length and the R-index failed the criteria for normality, data were logarithmised. Subsequent multiple comparison tests at the main factor levels were performed using Tukey's HSD test. Hypotheses were tested at an $\alpha = 0.05$ significance level, accepting the risk at a p-value < 0.05.

3. Results

3.1 Soil engineers

All earthworms survived and gained on average at least 20 % weight in the TopSi configuration (Table 2). In the TopSa configuration, earthworms tended to loose weight in the EW treatment while they seemed to gain weight in the P + EW treatment. Values for root biomass were similar in all treatments containing plants in both configurations except for P + EW treatment in the TopSi configuration, in which root biomass tended to be reduced. Δ Plant + Root biomass was significantly increased in the P treatment in the TopSa configuration compared to the P and the P + EW treatment in the TopSi configuration.

Table 2: Root biomass and earthworm weight gain (EW weight gain) after the incubation in the two configurations TopSi and TopSa (mean±SE). Negative values correspond to weight loss of earthworms. P stays for Plant, EW for Earthworm, P + EW for Plant + Earthworm and NT for Control. ΔPlant + Root biomass indicates differences in plant + root biomass within eight weeks of incubation. Letters a and b represent results from Tukey's HSD tests for one-way ANOVA at an $\alpha = 0.05$ significance level, accepting the risk at a p-value < 0.001.

Treatment	EW weight gain (%)	Root biomass (g)	ΔPlant + Root biomass (g)
TopSi			
P		2.50 ± 2.10 ^a	6.55 ± 3.50 ^a
EW	32.28 ± 12.90 ^a		
P + EW	24.40 ± 9.32 ^a	0.83 ± 0.46 ^a	4.83 ± 3.91 ^a
NT			
TopSa			
P		1.69 ± 0.77 ^a	16.89 ± 3.63 ^b
EW	-8.96 ± 8.20 ^a		
P + EW	13.81 ± 14.05 ^a	1.61 ± 0.89 ^a	9.13 ± 5.12 ^{a,b}
NT			

3.2 X-ray Computed Tomography (X-ray CT)

Macroporosity, total segment length, and the number of segments were strongly correlated ($r_{\text{pearson}} > 0.94$). Therefore, total segment length was defined as a robust indicator to analyse the structuration patterns (see section 2.6). The contribution of the predictors “treatment” and “layer” to explain the variability of the total segment length was highly significant (p-value < 0.001) (Table 3). Furthermore, interaction terms between “treatment” and “layer” were highly significant (p-value < 0.001) (Table 3), indicating that the effect of “treatment” varied within the five levels of “layer”. Multiple comparisons at the main factor level within “treatment” indicated that the treatments EW and P + EW significantly increased the total segment length. Within the level of “layers”, total segment length was greatest in LOM, followed by silt.top. Total segment length was lowest in the sand.bottom layer (Table 3, 4). Regarding interaction terms, earthworms significantly increased the total segment length in the silt.top and in the LOM layer. Plants tended to increase the total segment length in the top layers only, but interaction terms were not significant (Table 3, 4).

3.3 Aggregate stability

The percentage of water-stable macro-aggregates was significantly affected by both predictors tested. The overall effect of “layer” was highly significant (p-value < 0.001) and the effect of “treatment” was significant (p-value < 0.05). Interaction terms between “treatment” and “layer” were also significant (p-value < 0.05) (Table 3). Multiple comparisons at the main factor level within the four levels of

“treatment” indicated that aggregate stability is generally highest in P + W followed by P and EW (Table 3, 4). Multiple comparisons at the main factor level within the five levels of “layer” highlighted the greatest aggregate stability in the LOM-layer followed by the silt layers regardless of its position, and the top.sand and the bottom.sand layer. Regarding interaction terms, the presence of earthworms significantly improved aggregate stability in the silt.bottom layer, whereas the presence of plants positively contributed to aggregate stability in the sand.top layer (Table 3, 4).

3.4 Rock-Eval pyrolysis

R-index values ranged between 0.55 and 0.67 and I-index values between 0.12 and 0.25. R- and I-indices were strongly correlated in silty sediment ($r_{\text{pearson}} = 0.97$ and 0.72) and less in the LOM layer in both configurations ($r_{\text{pearson}} = 0.67$). No clear correlation was found in the respective sand layers (Fig. 3). OM thermal stability represented by the R-index was significantly affected by “layer” (p-value < 0.001) (Table 3). “Treatment” did not have any significant effect on OM thermal stability. Interactions terms between “treatment” and “layer” were highly significant (p-value < 0.001) (Table 3). Within the five levels of “layer”, R-index values were greatest in the sand layers, followed by the LOM and the silt layers (Table 3, 4). Regarding interaction terms, the effect of EW varied strongly within the five levels of “layer”: EW significantly increased the R-index in the sand.top layer and decreased the R-index in the silt.bottom and the LOM layers (Table 4, Fig. 3). Plants significantly decreased the R-index in the silt.top layer. R-index values for P + EW treatments tended to range between values for P and EW in the sand.top, sand.bottom and the LOM layer (Fig. 3).

4. Discussion

4.1 Behaviour of ecosystem engineers

The treatment, the composition and superimposition of the layers strongly affected the development of the structuration patterns in the mesocosms. Significant interaction terms between these two parameters indicate that the structuration patterns are attributed to the individual behaviour of each specific engineer and are strongly controlled by the physico-chemical properties of the deposits. Both physical and chemical properties of the sediments tended to be limiting factors for rooting. The root network of *P. arundinacea* spread out only in the top layers, although plant

Table 3: Results for the analyses of variance for randomised split-plot designs. Significant overall and interaction effects were specified by a p-value < 0.05. “n.s.” stays for not significant. Letters a, b, c and d represent results from Tukey’s HSD posthoc analysis at an $\alpha = 0.05$ significance level accepting the risk at a p-value < 0.001. “:” represents interaction effects between two predictor variables.

Predictor variables and levels	Response Variables		
	%WSA	Total segment length	R-index
Overall and interaction effects			
Treatment	p < 0.05	p < 0.001	n.s.
Layer	p < 0.001	p < 0.001	p < 0.001
Treatment : Layer	p < 0.05	p < 0.001	p < 0.001
Multiple comparisons of treatments			
Plant	ab	b	a
Earthworm	b	a	a
Plant + Earthworm	a	a	a
Control	c	b	a
Multiple comparisons of layers			
silt.top	ab	b	c
silt.bottom	ab	bc	c
sand.top	b	bc	a
sand.bottom	c	c	a
LOM	a	a	b
Multiple comparisons of treatments within layer levels			
silt.top			
Plant	a	ab	ab
Earthworm	a	a	ab
Plant + Earthworm	a	ab	a
Control	a	b	b
silt.bottom			
Plant	b	a	a
Earthworm	a	a	b
Plant + Earthworm	a	a	a
Control	b	a	a
sand.top			
Plant	a	a	b
Earthworm	bc	a	a
Plant + Earthworm	ab	a	b
Control	c	a	b
sand.bottom			
Plant	a	a	a
Earthworm	a	a	a
Plant + Earthworm	a	a	a
Control	a	a	a
LOM			
Plant	a	b	a
Earthworm	a	a	b
Plant + Earthworm	a	a	a
Control	a	b	a
Multiple comparisons of layers within treatment levels			
Plant (P)			
silt.top	ab	b	b
silt.bottom	b	b	ab
sand.top	a	b	a
sand.bottom	b	b	a
LOM	a	a	a
Earthworm (EW)			
silt.top	ab	b	c
silt.bottom	a	bc	d
sand.top	bc	c	a
sand.bottom	c	c	b
LOM	ab	a	cd

Plant + Earthworm (P + EW)			
silt.top	b	b	b
silt.bottom	a	b	b
sand.top	ab	b	a
sand.bottom	b	b	a
LOM	b	a	b
Control (NT)			
silt.top	a	b	d
silt.bottom	ab	b	c
sand.top	b	b	ab
sand.bottom	b	b	a
LOM	a	a	bc

Table 4: Mean values $\pm$ SE for robust indicators selected for soil structural stability, structuration patterns, and OM dynamics. Values are given for the four levels of “treatment” within the five levels of “layer”. WSA: water stable macro-aggregates P:Plant, EW :Earthworm, P + EW: Plant + Earthworm, NT: Control.

Treatment & Layer	WSA (%)	Total Segment Length (mm dm-3)	R-Index	I-Index
silt.top				
P	10.68 $\pm$ 0.84	1979 $\pm$ 1412	0.57 $\pm$ 0.01	0.20 $\pm$ 0.02
EW	9.53 $\pm$ 2.17	5668 $\pm$ 1263	0.58 $\pm$ 0.01	0.18 $\pm$ 0.01
P + EW	9.87 $\pm$ 2.86	3416 $\pm$ 1000	0.59 $\pm$ 0.01	0.18 $\pm$ 0.01
NT	9.17 $\pm$ 0.95	114 $\pm$ 112	0.56 $\pm$ 0.01	0.22 $\pm$ 0.01
silt.bottom				
P	7.55 $\pm$ 2.05	90 $\pm$ 67	0.60 $\pm$ 0.01	0.17 $\pm$ 0.01
EW	12.50 $\pm$ 2.92	2878 $\pm$ 1126	0.56 $\pm$ 0.01	0.22 $\pm$ 0.01
P + EW	14.02 $\pm$ 2.99	2639 $\pm$ 1186	0.59 $\pm$ 0.02	0.19 $\pm$ 0.01
NT	7.99 $\pm$ 1.39	92 $\pm$ 73	0.59 $\pm$ 0.01	0.17 $\pm$ 0.01
sand.top				
P	13.39 $\pm$ 4.58	1017 $\pm$ 223	0.62 $\pm$ 0.01	0.18 $\pm$ 0.02
EW	7.39 $\pm$ 2.03	1013 $\pm$ 140	0.68 $\pm$ 0.05	0.17 $\pm$ 0.03
P + EW	10.72 $\pm$ 3.10	1515 $\pm$ 438	0.63 $\pm$ 0.01	0.20 $\pm$ 0.01
NT	4.67 $\pm$ 3.08	109 $\pm$ 50	0.63 $\pm$ 0.01	0.24 $\pm$ 0.01
sand.bottom				
P	6.07 $\pm$ 4.02	30 $\pm$ 16	0.62 $\pm$ 0.03	0.21 $\pm$ 0.03
EW	4.35 $\pm$ 2.43	193 $\pm$ 53	0.63 $\pm$ 0.03	0.15 $\pm$ 0.02
P + EW	7.65 $\pm$ 1.94	167 $\pm$ 41	0.63 $\pm$ 0.01	0.18 $\pm$ 0.01
NT	4.77 $\pm$ 1.42	24 $\pm$ 18	0.63 $\pm$ 0.01	0.20 $\pm$ 0.01
LOM				
P	13.87 $\pm$ 4.13	29966 $\pm$ 7269	0.61 $\pm$ 0.02	0.18 $\pm$ 0.02
EW	11.72 $\pm$ 2.94	34651 $\pm$ 8008	0.57 $\pm$ 0.01	0.21 $\pm$ 0.02
P + EW	10.83 $\pm$ 1.21	34401 $\pm$ 3806	0.59 $\pm$ 0.02	0.17 $\pm$ 0.02
NT	10.31 $\pm$ 2.23	23140 $\pm$ 4083	0.61 $\pm$ 0.03	0.16 $\pm$ 0.03

roots were able to reach the bottom of the mesocosm within a similar timeframe, as observed in a preliminary experiment. Regardless of the configuration, roots did not enter the underlaying LOM layer. Thus, the LOM layer was either less favourable for rooting or sufficient amounts of nutrients were provided in the deposits or at the top of the LOM layer. In silty sediments, root networks of *P. arundinacea* were less developed compared to sandy sediments, as indicated by the lower root biomass. Thus, plants had to invest more in

the extension of their root system in the sandy sediment to reach an accessible nutrient source, which was provided most likely at the top of the LOM layer. Conversely, the nutrient's stock of the silt tended to be sufficient for *P. arundinacea* requirements. These findings strongly suggest that the structuration progression in alluvial soils initiated by pioneer plants, such as *P. arundinacea*, can differ strongly within a depth profile. Finer textured and nutrient rich top layers and thick buried litter layers might delay the structuration

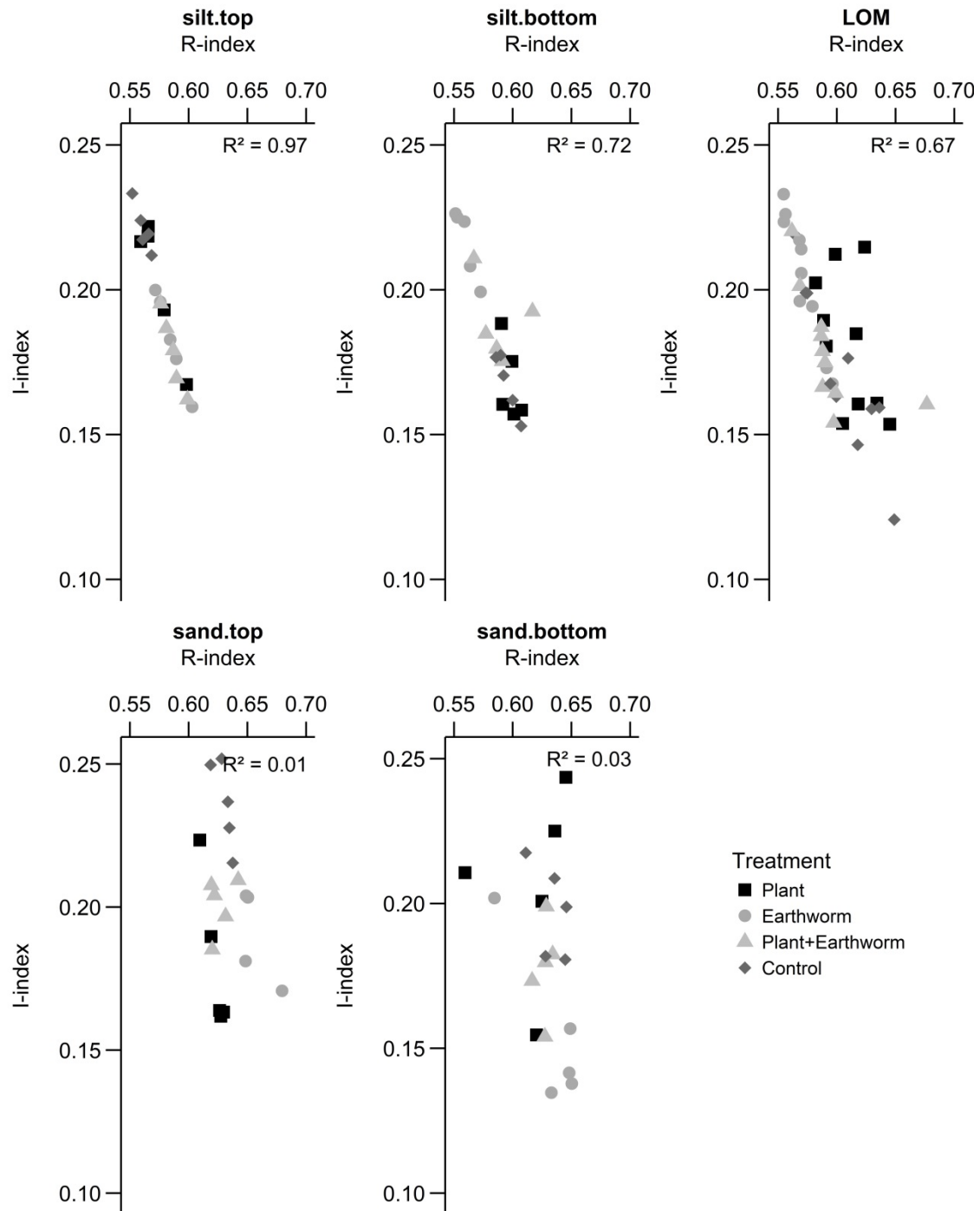


Fig. 3. R-index plotted against I-Index as an indicator for OM thermal stabilisation in aggregates.

progression, whereas the presence of sandy deposits might favour a fast colonisation of the soil by plant roots. This might be true, if water availability in soil is not limiting, which was not investigated in the present study. Earthworms *A. chlorotica* were placed in the LOM layer at the beginning of the incubation experiment, enabling them to choose their "preferred" layer. All individuals were found either in the silt or in the LOM layer, independent of the configuration. This behaviour is most likely

linked to the greater availability of fresh OM and to the finer soil texture (Table 1). *A. chlorotica* tended to avoid the sandy sediment despite sieving at 1 mm. The large quantity of the fine sand fraction must have been unfavourable for earthworms, as shown for many endogeic species (Edwards and Bohlen, 1996). However, *A. chlorotica* attempted to move into the sandy sediment in TopSa configuration, as indicated by the increased total segment lengths in the sand layer

compared to the TopSi configuration. Endogeic earthworms including *A. chlorotica* preferred to move into the topsoil (Lavelle et al., 1997). The weight loss of earthworms thus might be related to the sandy texture of the topsoil in the TopSa configuration, as earthworms attempted to move into it. However, recent studies reported that *A. chlorotica* are also able to survive in disturbed soils with varying environmental parameters (Le Bayon et al., 2013; 2017). Amossé et al. (2015) found comparable values for the number of segments and their total lengths in urban soil material and loamy alluvial material in a similar incubation experiment, which are comparable to values found in the silty sediment of our study. The authors concluded that *A. chlorotica* are among the most efficient earthworm species, creating a macro-porous structure in alluvial soils. As mentioned above, *A. chlorotica* gained weight in the TopSi configuration, regardless of the presence or absence of a plant. In the TopSa configuration, they gained weight only in the presence of a plant. In general, plants and earthworms have a positive mutual effect on their respective fitness, particularly in nutrient poor soil conditions (Laossi et al., 2010; Blouin et al., 2013). Surprisingly, total segment length of the P + EW treatment was otherwise not increased compared to P and EW treatments in both sediments and configurations, although these values are supposed to represent the combined structuring effect of plants and earthworms. Consequently, on one hand, the mutual effect of plants' and earthworms' fitness could have been negative, similar to the findings of Jana et al. (2010) and Milleret et al. (2009a) with *A. chlorotica* and leak roots in mesocosm experiments. The rhizosphere is often subject to local drought due to water uptake by plant roots, which might have resulted in a reduction of the earthworms' structuring activity in the silt layer in the TopSi configuration (Bronik and Lal, 2005). Furthermore, root exudation or production of low quality OM by plant roots could lead to a significant reduction of earthworms' fitness (Eisenhauer et al., 2009). But, on the other hand, mutual beneficial effects might not have been possible to be visualised with X-ray CT, as plants and earthworms could have taken advantage of their respective structures. Plants are known to use earthworm burrows for rooting, as they are enriched in nutrients and provide easier pathways for root network extension. Earthworm structures are furthermore hotspots of nutrients, making them preferentially colonised by plant roots (Spiers et al., 1986; Zaller and Arnone, 1999., Decaëns et al., 2011). However, these mechanisms could not be documented as plant root galleries and earthworm burrows were not distinguishable

using X-ray CT with the resolution used for this study.

4.2 Aggregate stability

The percentage of water-stable macro-aggregates varied significantly among the treatments and within the layers. Aggregate stability is generally thought to be positively correlated to the proportion of silt and clay and negatively correlated to the proportion of sand (Lavelle et al., 1997; Duiker et al., 2003; Kaiser et al., 2012). In our study, the highest aggregate stability was found in the LOM layer. In general, the amount of OM in soil is positively correlated to aggregate stability, as mineral and OM particles form organo-mineral associations and facilitate initial soil aggregation. Furthermore, OM components are efficient bonding agents that agglutinate soil particles (Tisdall and Oades, 1982; Guggenberger et al., 1996; Kong et al., 2005; Jouquet et al., 2008). Fonte and Six (2010) also found a significant increase of soil aggregates produced by earthworms in microcosms with the addition of plant litter. In our study, *A. chlorotica* did not increase aggregate stability in both sediments, except for the silt.bottom layer. Other comparable studies already showed that earthworms were not capable of increasing aggregate stability in short- and middle-term mesocosm experiments (Fonte et al., 2012; Lubbers et al., 2017). Specific earthworm species, such as *A. chlorotica* that was also used in our study, could even decrease aggregate stability compared to control treatments (Milleret et al., 2009b). Nevertheless, *A. chlorotica* was selected for this study for several reasons: *A. chlorotica* has a high survival in mesocosms and it is known to be a highly successful coloniser in floodplain soils, as it is able to tolerate unfavourable soil properties and frequent water table fluctuations (Amossé et al., 2015; Le Bayon et al., 2017; Schomburg et al., 2018b). Loss of aggregate stability induced by *A. chlorotica* was shown to be compensated when combining plants and earthworms in the same treatment (Milleret et al., 2009b). In our study, roots of *P. arundinacea* had a strong positive effect on aggregation, especially in the sand.top layer. Similar results were reported by Fonte et al. (2012) in a short term incubation experiment and by Kohler-Milleret et al. (2013) who measured an increase of aggregate stability by a factor of 1.6 in the presence of a monocotyledonous plant (*Allium porrum*). In our study, a structuration effect was visible in the presence of plants in each sediment, as the root network extension was more independent from the sediment texture than the structuration patterns produced by earthworms. In the

presence of both engineers, aggregate stability was only slightly increased, which was mainly due to the fact that plants and earthworms were almost never present in the same sediment, except for the silt.top layer.

4.3 OM dynamics

4.3.1 Mechanisms of OM incorporation into soil aggregates

In near-natural soils, the strong correlation between R- and I-indices has two main origins: on one hand, mineralisation of OM leads to a decrease in I-index values and simultaneously to an increase of R-index values (Albrecht et al., 2015). On the other hand, strong interactions between OM and mineral matter results in a specific range shift of R-index and I-index values (Sebag et al., 2016), especially in soil aggregates, as already reported by Schomburg et al., (2018a). R-index and I-index values were not correlated in sandy textures, possibly because the low specific surface of fine sand particles reduced OM - mineral matter interactions to a minimum. Additionally, mineralisation of OM can be promoted by the large porosity, which changes the I/R relationship, as predicted by Sebag et al. (2016) for Arenosols. These findings were valid for all treatments, except for the plant treatment in the TopSa configuration. In this specific case, root exudates might interact with the mineral fraction in soil aggregates. In the silt and LOM layer, the correlation between the indices was similar, regardless of the configuration and the treatment. OM and mineral matter interactions in the LOM layer were thus steadily promoted in presence of soil engineers. *P. arundinacea* affected the LOM layer indirectly, as their root network did not sprawl in the LOM layer. Most likely, root exudates were leached into the LOM layer during remoistening of the mesocosms and promoted OM mineralisation in this layer. Earthworms *A. chlorotica* were mostly found in the silt and the LOM layer and likely incorporated material from the silt and the LOM layer into soil aggregates.

4.3.2 OM thermal stability

OM thermal stability in soil aggregates was particularly controlled by the composition and superimposition of the layers. Treatments did not have any significant effect on OM thermal stability. OM is efficiently stabilised into soil aggregates with an increasing amount of the fine sediment fraction (Sollins et al., 1996; Bronik and Lal, 2005). Surprisingly, OM thermal stability was increased in sandy sediments in our study. In general, OM particles

are chemically associated to clay minerals and/or can be occluded by silt particles protecting them from microbial decay. Coarser fine sand grains have a reduced specific surface area resulting in a large porosity, which does not facilitate the increase of OM thermal stability in sandy aggregates. Thus, OM thermal stability in aggregates must be controlled by interaction effects between the treatments and the layers. Plants did not have strong effects on OM thermal stability, as reported by Schomburg et al. (2018a). Plants release root exudates, consisting of easy decomposable OM, which do not increase the thermal stability of OM in soil aggregates. Labile OM generally underlies fast microbial decay, unless OM is physically protected by mineral particles (Sollins et al., 1996). The fine mineral fraction can occlude labile OM, enabling its efficient protection against microbial decay, which can improve the persistence of labile OM in the soil (Schmidt et al., 2011). In the presence of earthworms, OM thermal stability in aggregates was controlled by either inverse mechanisms or controlled by external factors. In general, earthworms incorporate large amounts of bulk OM into soil aggregates (Martin, 1991). Surprisingly, OM thermal stability tended to be already modified after 8 weeks of incubation. Previous studies reported that OM is only protected in aggregates in long-term incubation experiments (Bossuyt et al., 2005; Schomburg et al., 2018a). In general, earthworms promote OM sequestration into soil aggregates, especially in finer soil textures, as the association of mineral and OM is facilitated while particles pass earthworms' digestive tract (Lavelle, 1988; Frouz et al., 2015; Angst et al., 2017). During the gut transit, earthworms excrete easier decomposable OM, such as mucus and saliva, which agglutinate soil particles. Simultaneously, earthworms incorporate more recalcitrant compounds from the bulk soil, such as lignin, into their casts (Lavelle et al., 1997), corresponding to thermally resistant OM (Disnar et al., 2003). Regardless of the configuration, earthworms had an OM stabilisation effect in the silt and the LOM layer and an OM mixing effect in the sand layers. OM thermal stability in aggregates from the sand.top layer is however comparable to the underlying LOM layer. During earthworms' action to structure the sandy sediment, they might have mixed significant amounts of material from the LOM with the sand without modifying their signature. A similar behaviour can be observed regarding the silt.top and the LOM, but in this case, it resulted in an increased aggregate stability in the silty sediment. R-index values for P + EW ranged between values of EW and P and NT in layers in which plants and earthworms were active

(see section 4.1). Similar observations for OM thermal stability were reported by Schomburg et al. (2018a). However, these authors could not estimate whether these values represented an interaction effect of plants and earthworms during OM stabilisation into aggregates, as presented by Zangerlé et al. (2011) for aggregation, or whether it reflected the additive effect of both engineers, individually influencing the OM thermal stability. However, recent studies reported that plants inhabited earthworm casts to take advantage of the enriched amount of nutrients (Spiers et al., 1986; Zaller and Arnone, 1999., Decaëns et al., 2011). Conversely, earthworms prefer feeding on root-derived carbon and easy decayable OM from fine roots and incorporate this carbon into soil aggregates (Gilbert et al., 2014; Sanchez-de-Leon et al., 2014; Yavitt et al., 2015). Furthermore, Schmidt et al. (2011) emphasised that OM stabilisation into soil aggregates is rather an ecosystem property than being linked to one specific soil engineer.

4.4 Limitations of the mesocosm approach

Combining X-ray CT and Rock-Eval pyrolysis was suitable for analysing structuration patterns of soil engineers and OM thermal stability in soil aggregates in an artificially constructed floodplain soil. The experimental design simulating an alluvial soil by superimposing different mineral layers with a buried litter layer, and the detailed analysis of soil structure formation using X-ray CT and Rock-Eval pyrolysis, was an innovative approach. The results reflect the complex challenges involved in the structuration of floodplain soils regarding their highly variable composition and vertical variations at high frequency. Structuration patterns and mechanisms of OM stabilisation were identified for each engineer individually using these two methods. However, several aspects regarding the experimental design need to be addressed in more detail. First, the authors would like to point out that two specific soil engineering organisms were selected for this study, *P. arundinacea* and *A. chlorotica*. These organisms were representative of alluvial ecosystems, but their behaviour and interactions could also be species-specific. Furthermore, results obtained for the P + EW treatment were difficult to interpret. Using Rock-Eval pyrolysis, a mixed signature was found, which either represented interaction or an additive effect of engineer specific indices. Plant root galleries and earthworm burrows could not be differentiated using X-ray CT, at least not with the intermediate resolution provided by the medical scanner. Increasing the resolution of the X-ray CT scanner might be a future possible

approach to make plant and earthworm structures distinguishable. However, high resolution X-ray CT is extremely demanding in terms of costs and time and additionally requires a smaller diameter of the samples. In the present study, downscaling the size of the mesocosm tubes would have led to a loss of information about the structuration patterns. Alternatively, subsampling might have impacted aggregate sampling and collection of ecosystem engineers. Nevertheless, the authors highly encourage the application of a comparable experiment analysing combined effects of plants and earthworms on aggregate formation using high resolution X-ray CT.

5. Conclusions

Structuration patterns of plants and earthworms and mechanisms of OM stabilisation into soil aggregates were identified for a superimposition of different mineral layers and a litter layer, similar to a near-natural floodplain soil, in an *in vitro* experiment. Combining X-ray CT and Rock-Eval pyrolysis in mesocosms simulating alluvial soils was a novelty for the analysis of soil structure formation. Structuration patterns and aggregate stability were strongly controlled by the type of the soil engineer and the composition and superimposition of the layers. Buried litter layers might potentially play a key role in floodplain soils, as they provide OM inputs that promote initial soil aggregate formation, but delay the process of soil structure formation if the overtopping layer supplies a sufficient nutrient stock for soil engineering organisms. Thus, the structural stability can vary significantly within a depth profile of an alluvial soil. OM dynamics in floodplain soils and its thermal stabilisation were controlled by a complex interplay between soil engineers and the composition of the layer and could not be attributed to general effects of one specific soil engineer. Consequently, the chronological sequence, the flood intensity, and the origin of the deposited material are prone to govern the progress and efficiency of soil structure formation and OM stabilisation in floodplain soils. For a more detailed view on the interactions between plants and earthworms, the authors propose a small-scale incubation experiment coupled with an increased resolution of the tomography scanner, which would allow the microporous structures in between the aggregates to be visualised.

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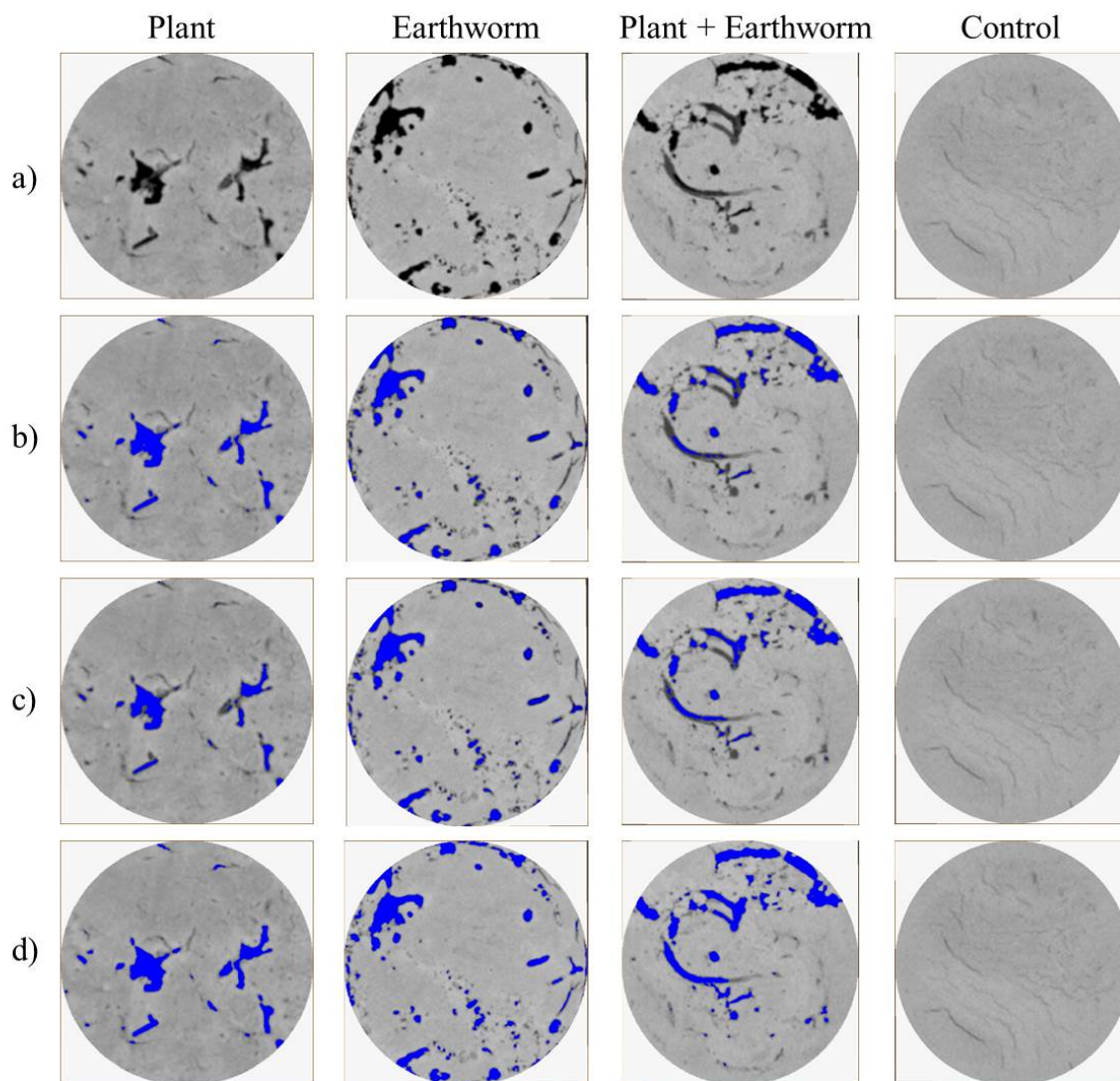
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Appendix 1. Comparison between different binarisation methods for the treatments performed in Avizo. Thresholded voids are coloured in blue. a) shows the raw image, b) the individual threshold value specifically selected for this image, c) the arithmetic mean of all threshold values for each imageset, and d) the automatic thresholding using factorisation.



Main Chapter III): The field plot scale

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Pioneer plant *Phalaris arundinacea* and earthworms promote initial soil structure formation despite strong alluvial dynamics in a semi-controlled field experiment

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Abstract

Soil structure formation is among the most important processes in river floodplains which are strongly influenced by alluvial dynamics. In the context of river restoration projects, a better understanding of soil structure formation in habitats adjacent to the river can help to prevent damages caused by riverbank erosion. Ecosystem engineers such as pioneer herbaceous plants and earthworms likely contribute to soil structure formation even despite the harsh environmental conditions. This study aims at assessing the capacity of the herbaceous perennial and native species *Phalaris arundinacea* and earthworm communities to build up a stable soil structure in alluvial sediments, in particular fresh alluvial deposits, in the short term. Delimited plots were set-up in a restored floodplain adjacent to the Thur River in NE Switzerland and exposed to natural alluvial dynamics for 1.5 years. Four treatments were replicated in a randomized complete block design: (i) plots with *Phalaris arundinacea* as only vegetation, (ii) plots with all vegetation constantly removed, (iii) and (iv) the earthworm community reduced by mustard treatment, otherwise as (i) and (ii), respectively. Soil structure formation was analysed at the end of the experiment using different indicators: aggregate stability, field-saturated hydraulic conductivity and the porosity calculated from X-ray CT reconstructions of freeze cores. *Phalaris arundinacea* was capable of improving the porosity and aggregate stability of both alluvial sediments present at the beginning of the experiment but also of sediments freshly deposited during the observation period. The latter indicates a structuring effect within only one vegetation period. Earthworm abundance was as a whole very low, most likely due to the large proportion of sand. There was a small earthworm effect on soil structure formation, and only in combination with vegetation. Our findings highlight the ability of *Phalaris arundinacea* in

efficiently structuring sandy alluvial sediments in the short term even under strong alluvial dynamics. *Phalaris arundinacea* can therefore play a key role in the early stage of river restoration projects. Thus, facilitating the colonisation by such native pioneer herbaceous plants is a suitable step to improve the success of river restoration projects.

Keywords: Sediment deposition; soil evolution; flooding; river restoration; freeze core; X-ray analysis.

1. Introduction

Interactions between hydrologic and pedologic processes strongly control ecosystem services and the ecological balance in semi-terrestrial systems. In the past, these processes were investigated within their specific research domain and without considering the feedback mechanisms (Ma et al., 2017). For instance, soil development, e.g. the formation of a stable soil structure can be accelerated, inhibited or altered by hydrologic processes (Lin et al., 2005; 2015; Bätz et al., 2015; Schomburg et al., 2018a). Soil structure formation is especially important in young and dynamic ecosystems, such as floodplains (Guenat et al., 1999; Bullinger-Weber et al., 2012; Mardhiah et al., 2014). In the course of alluvial dynamics, unconsolidated shore sediments can be eroded and/or thick and bare sediments can be deposited along the river bank leading to a superposition of the existing soils (Gurnell and Petts, 2006; Gianni et al., 2016; Partington et al., 2017). Soil structure formation in floodplains is necessary with regard to today's river management policies in several countries, including Switzerland (Jncc.defra.gov.uk, 2010). For much of the past 150 years, rivers have been canalised in reaction to the need to protect anthropogenic settlements from floods and to the rising demand for suitable agricultural land, caused by the large growth of the population (Bundesamt für Umwelt BAFU, 2008, 2017). During the last two decades, river management strategies have slowly shifted from prioritising human requirements towards ecological aspects (Malmqvist and Rundle 2002; Tockner and Stanford, 2002). Management goals were defined, among others, for the restoration of floodplains as biodiversity hotspots (Naiman and Decamps, 1997; Malmqvist and Rundle, 2002), and for the creation of inundation areas reducing the flood risk in lowland areas (Bundesamt für Umwelt BAFU, 2015). In the course of these river restoration projects, river channels should be widened and embankments removed. Floodplains adjacent to restored rivers are, in contrast to those next to canalised ones, often subject to severe inundations. Besides river shore erosion and deposition of alluvial sediments, recurring floods can modify the hydraulic properties of alluvial deposits through rearranging particles and clogging macro-pores thereby increasing surface runoff (Bottinelli et al., 2010). On one hand, these processes can lead to strong alterations of the floodplain itself, such as land loss or the introduction of non-native plants, or threaten anthropogenic infrastructure downstream through obstruction of water ways and drainage ditches (Acreman et al., 2003). On the other hand, frequent flooding impedes the development of stable conditions in

floodplain habitats and thus the natural succession of species (Junk and Welcomme, 1990; Bätz et al., 2015; Graf-Rosenfellner et al., 2016). A soil structure, stabilised by a spatial arrangement of macro-pores and aggregates composed of mineral and organic particles (Brussard and Kooistra, 1993; Barrios, 2007), promotes stable conditions in floodplain habitats by reducing soil erosion (Diaz-Zorita et al., 2002; Velasquez et al., 2007; Mardhiah et al., 2014) and facilitating water infiltration (Pérès et al., 1998; Blouin et al., 2013). The entanglement of smaller micro-aggregates of microbial origin into water-stable macro-aggregates is a process particularly involving soil macro-biota (Tisdall and Oades, 1982; Brown et al., 2000; Six et al., 2002; Kong and Six, 2010). In ecosystems of temperate latitudes, plants and earthworms, as soil engineers, strongly contribute to soil structure formation by creating water-stable macro-aggregates (Lavelle et al., 1997; Tanner, 2001; Blouin et al., 2013). Aggregates formed by plants are physically compressed during root network extension and/or cemented by root exudates and associated rhizobacteria (Degens et al., 1994; Angers and Caron, 1998; Czarnes et al., 2000). Earthworms stabilise aggregates by mixing mineral and organic material during burrowing and casting and agglutinate ingested particles with mucus and saliva upon passage through their digestive tract (Blanchart, 1997; Brown et al., 2000; Lavelle & Spain, 2001). Along with aggregate formation, hydraulic properties of the soils can positively affect water infiltration and reduce surface water runoff (Gurnell and Petts, 2006; Blouin et al., 2013). In presence of earthworms, soil erosion rates can be reduced by more than 50 % (Ehlers, 1975; Shuster et al., 2002; Shipitalo et al., 2004; Jouquet et al., 2011). Pioneer plants and earthworms have a great potential of improving soil structural stability in floodplain soils, as they are able to tolerate alluvial dynamics to a certain extent (Plum and Filser, 2005; Gurnell and Petts, 2006; Le Bayon et al., 2013; 2017; Schomburg et al., 2018a; Schomburg et al., submitted). In the course of current river restoration projects, willows (*Salix* spp.) are commonly planted to stabilise the riverbanks, as they grow relatively fast, are well adapted to alluvial dynamics, and are highly efficient in trapping sediments with their roots and thus promoting soil aggregation (Gurnell and Petts, 2002; Crouzy and Perona, 2012; Perona et al., 2012). Willows can help to establish post-pioneer riparian forests in habitats which are resistant to floods occurring every 2-3 years (Corenblit et al., 2009). On the other hand, stronger alluvial dynamics in close proximity to the river retard the engineering effect of willows (Gurnell 2014; Bätz et al.,

2014; 2015) and require a more efficient contribution to soil structure formation. Fast-growing herbaceous pioneer plants, such as *Phalaris arundinacea* and earthworms might be more competitive and promote initial soil structure formation. Such a short-term engineering effect would need to comprise the ability to improve the aggregate stability, the macroporous network and the hydraulic properties of sediments to which they are exposed and of sediments which are deposited during frequent flood events. However, characterising soil structure formation under such conditions in the field is challenging, as the abundance of pioneer soil engineers and the accumulation or loss rates of sediments are highly variable in space and time. Moreover, in-vitro experiments are suitable to determine the efficiency of each individual soil engineer on soil structure formation, but the effects of strong alluvial dynamics cannot be accurately reproduced. A possibility is to install respectively semi-controlled plots in the field and expose them to natural floods. This innovative approach combines the strengths of field and in-vitro experiments, as the treatments can be controlled and develop dynamically under natural alluvial dynamics. However, patterns of soil structure formed by plants and earthworms are difficult to analyse in unconsolidated sandy soil material generally found in close proximity to the river, as the soil structure may collapse when applying conventional soil coring. Liernur et al. (2017) demonstrated freeze coring coupled with X-ray computed tomography (X-ray CT) as a non-destructive method well suited for the analysis of the soil structure in low-cohesive soils. Freezing of the soil matrix largely preserves the soil's structural integrity except for the matrix adjacent to the freezing lance (Humpesch and Niederreiter, 1993; Franchini and Zeyer, 2012; Liernur et al., 2017). Recently, X-ray CT has been used to determine soil structure formation through the analysis of the soil's macroporosity, as well as the length, volume and connectivity of root galleries and earthworm tunnels (e.g. Capowiez et al., 2011; 2015; Amossé et al., 2015; Schomburg et al., submitted). The present study aims at analysing the short-term effects of the pioneer herbaceous plant *P. arundinacea* and earthworms on soil structure formation of alluvial sediments and recent deposits under strong alluvial dynamics, e.g. flooding, erosion and deposition of sediments. To this end, we exposed delimited plots with a well-defined composition of soil engineers to the alluvial dynamics in a restored river floodplain and assessed the short-term soil structure formation by means of innovative methods, e.g. freeze coring and X-ray CT over a period of 1.5 years. We hypothesise that pioneer

vegetation and earthworms contribute to initial soil structure formation in the alluvial sediments and recent deposits by improving their macro-porosity, structural stability and hydraulic properties during this short period.

2. Materials & Methods

2.1 Experimental design

Delimited plots in the field were set up to analyse the individual and combined contribution of pioneer soil engineers to structure recent floodplain sediments under consideration of natural alluvial dynamics. The field experiment was conceptualised as a randomised complete block design (Fig. 1). Four different treatments were set up in plots with two assigned to each of three blocks ($4 \times 2 \times 3 = 24$ plots in total). The arrangement of the plots differed from one block to another (Fig. 1). Four different treatments were designed: 1) with *P. arundinacea*, with earthworms (+V+EW), 2) with *P. arundinacea*, without earthworms (+V-EW), 3) without *P. arundinacea*, with earthworms (-V+EW), and 4) without both soil engineers (-V-EW). At the end of the experiment, sampling and on-site experiments were performed in different depths that were defined specifically for the respective method. This experimental design allowed data analysis at different layouts: i) one and two-factor analyses for data available at the block level (earthworm community, effect analysis of plants and earthworms on sediment accumulation), and ii) analysis of data available for treatments. The treatments themselves had four levels (+V-EW, -V+EW, +V+EW, -V-EW) and the depths with a different number of levels depending on the respective analysis.

2.2 Construction and maintenance of field plots

In February/March 2015, plots were installed in close proximity to the Thur River (3-8 m) at the Schaffäuli site (Fig. 1), located in NE Switzerland close to Niederneunforn (NNF, 8°77'12" E, 47°59'10" N). The Schaffäuli site represents the largest current river restoration project in Switzerland (Schirmer et al., 2014). A 2 km long section of the river was restored in 2002 by removing the embankments. Since then, strong alluvial dynamics have led to several inundations each year of the adjacent floodplain and caused erosion and deposition of unconsolidated alluvial sediments. Inundations are of natural origin, as the Thur River is not regulated by any artificial reservoirs along its course of 130 km. Due to a nivo-pluvial hydrologic regime, floods principally occur in late spring during snow melt and in late summer

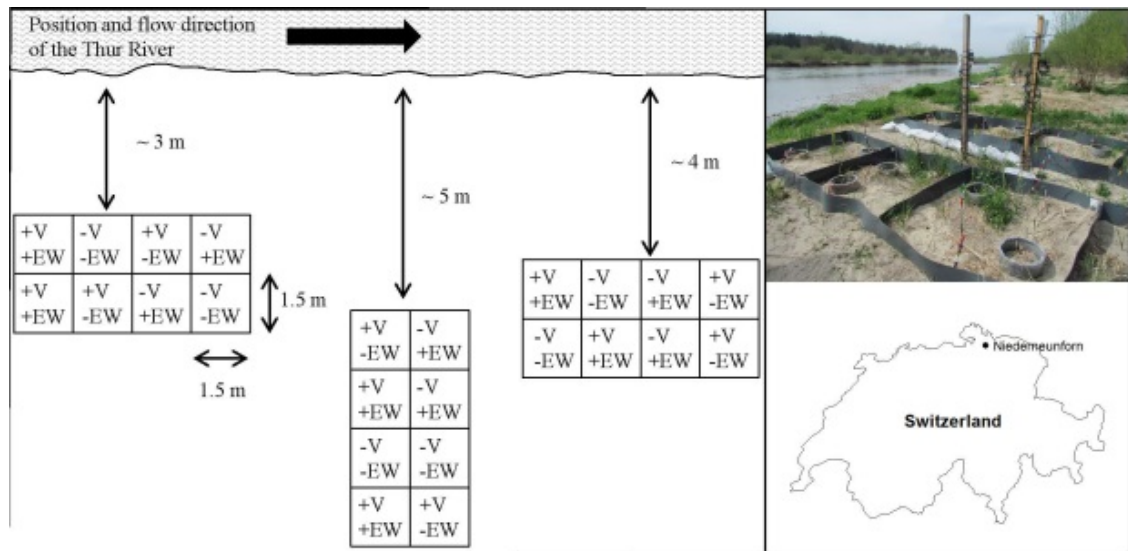


Fig. 1. Schematic spatial arrangement of the field experiment at the Schaffäuli site along the Thur River. Altitude was about 373.5 m a.s.l. V stands for vegetation and EW for earthworms. Example picture of block nr. 2 and the location of the site in Niederneunforn, Switzerland.

after heavy rainfall in the catchment area (Fournier et al., 2013). The plots were installed in a zone which was sparsely colonised by pioneer vegetation. *Phalaris arundinacea* was the predominating herbaceous soil engineering plant, other abundant species were *Urtica dioica* and the non-native species *Impatiens glandulifera*. Soil development was repeatedly reset and the vegetation buried by several major consecutive flood events between 2013 and 2015. Total thickness of accumulated sediments at the installation site was around 80 cm. Each plot measured 1.5×1.5 m, and was delimited by PVC walls extending to a soil depth of 40 to 50 cm at the time of installation. PVC walls minimised root extension or prevented migration of earthworms into or from adjacent plots and the surrounding sediments. Treatments were initially created and maintained through the frequent removal of the alternating soil engineer (removal experiment). For plots without vegetation, the shoots of the entire vegetation were removed biweekly during the vegetation periods in 2015 and 2016, and for plots with vegetation, the shoots of all plants except *P. arundinacea* were removed. Also during the vegetation periods, *P. arundinacea* shoots cut from outside of the experimental plots were applied in equal amounts to all plots without vegetation every two months and after each major flood, in order to provide a nutrient resource for earthworms and to minimise differences in evaporation from plots with and without vegetation. The abundance of earthworms was reduced by using the hot-mustard extraction method, described in Lawrence and Bowers (2002), in May and October 2015. After pre-moisten the soil by

extensive sprinkling with river water, two 24 liter portions of a suspension of 6 % pre-soaked mustard seeds in river water were applied with a watering can. Earthworms appearing at the soil surface during 15 minutes between the two mustard applications and within 30 minutes after the second application were collected and preserved in 70 % ethanol for later identification. Finally, the plots were again extensively rinsed with river water. The latter was also done for all plots without mustard treatment. Once set up, the experiment was exposed to the natural alluvial dynamics. After each flood event, the thickness of the sediment accumulation and the rate of erosion was estimated by measuring the distance between soil surface and the upper rim of the separations walls at 12 locations inside each plot. Sediment loss and gain rates were averaged to one value for each plot. The magnitude of each flood event was determined based on the maximum daily discharge, which was monitored at the Niederneunforn gauging station at a 5 minutes interval in close proximity to the site (Canton Thurgau river gauging station no: F2900, coordinates: $8^{\circ}46'57.78''$ E, $47^{\circ}35'20.76''$ N, altitude: 372 m a.s.l.). Additionally, groundwater levels were monitored at a 30-minutes interval by using a piezometer which was installed in close proximity to the plots. The data logger was out of service in the period between the 08.04.2015 and the 15.05.2015. However, discharge data from the Niederneunforn gauging station did not indicate any obvious groundwater level rise during this period. The experiment ended in October 2016 after 1.5 years of exposure with a final sampling of soil engineers and conducting soil analyses.

Vegetation was cut and dried at 65°C for 48 hours. In addition, plant litter was collected quantitatively from each plot (naturally produced litter on plots with vegetation, and the one remaining from the last addition on plots without vegetation). The abundance of earthworms was assessed for all plots using the same application as described above. The method was applied to three standard-size subplots (0.5 × 0.5 m) per plot, using standard amounts of 6 % mustard suspension in river water, i.e. 2 portions of 5 liters per subplot. Earthworms were weighed individually, identified at species level following the identification key of Blakemore (2008) and assigned to its ecological category (Bouché, 1972). Unidentifiable juveniles were just grouped and weighed.

2.3 Hydraulic properties

The infiltration capacity of the soil was measured using a Guelph Permeameter, model 2800K1, Soilmoisture Equipment Corporation. Two measurements were performed per plot, one in 10 cm and in 30 cm depth. The aim was to perform one measurement in a sediment which was deposited during the experimental period and another one in a sediment deposited before the experiment was set up. Cylindrical holes of 3 cm radius were prepared for each measurement in the respective depths using an auger, and water-saturated before starting the infiltration test. The double-head method was applied for each hole, i.e. one measurement was conducted with a first head height of 5 cm (H1) and a second head height of 10 cm (H2). The scale was read at the inner reservoir of the device. Fall rate was noted in intervals of 30 seconds until a steady state fall rate was reached after four identical consecutive measurements. The field saturated hydraulic conductivity (Kfs) was calculated from the infiltration tests according to the equations 1-5 (Appendix A) (Reynolds et al., 2002). In case that the results of the double head method showed invalid values for Kfs, calculations were performed according to the single head method separately for both head heights using equation 6 (Appendix A) and the results were averaged (Reynolds et al., 2002).

2.4 Soil monolith excavation

One soil monolith from each plot was excavated using the freeze core method described in Humpesch and Niederreiter (1993). For this purpose, a tubular metal lance of 50 cm in length and 4 cm in diameter, in which a spiral pipe was installed and which was hollow in the

center, was used. The metal lance was carefully hammered into each plot at a randomly selected location. 30 liters of liquid nitrogen were continuously injected over 45 minutes into the spiral cooling down the metal lance. During this period, the surrounding soil matrix froze around the lance via thermal conductivity. Immediately afterwards, the core was mechanically excavated using a hydraulically controlled crane fixed by a tripod (Fig. 2a). The metal lance was subsequently melted from the core with a heating stick which was inserted into the hollow. Freeze cores were stored in styrofoam boxes at -20 °C for further treatments.

2.5 X-ray CT analysis

Freeze cores were prepared for X-ray computed tomography (X-ray CT) by storing them in cylindrical PVC tubes of 35.5 cm in diameter and 65 cm in height and 0.8 cm in thickness which were closed at both ends (Liernur et al., 2017). The remaining space between the freeze core and the PVC tube was filled with styrofoam chips in order to prevent movements of the core during the scanning process. A LightSpeed VCT (GE Medical Systems) medical scanner was used for the scanning. The scanner rotates around the PVC tube and emits X-ray beams on a 1.2 mm focal spot reaching a peak energy of 120 KeV and a tube current of 500 mA. Data were acquired by a 64 channel detector and an axial pitch of 0.625 mm. Recent X-ray CT analyses of freeze cores and soil mesocosms were already performed using the same settings (Turberg et al., 2014; Amossé et al., 2015; Liernur et al., 2017; Schomburg et al., submitted). Image projection of the sequence was defined on a grid of 512 × 512 pixels and adapted to the transaxial field of view. This led to a voxel size of in average 0.55 × 0.55 × 0.3 voxels per image. Treatment of the raw images was performed using the programs imageJ (Schneider et al., 2012) and Avizo version 9.3.0 (FEI, 2016) (Fig. 2b). Cylindrical substacks of image sequences were produced in ImageJ based on the predefined depth of soil samples (see chapter 2.6). In a second step, substacks of the recent alluvial deposits were created according to the thickness measured after their deposition. Image sequences of each substack were afterwards implemented in Avizo. The void representing the macro-pores formed by cracks and macro-biological activity was separated from the mineral and organic matrix applying a binarisation. Binarisation was performed using the default Otsu-algorithm (Otsu, 1979) which was already applied to determine the void of soil matrices in recent studies (Iassanov et al., 2009; Liernur et al., 2017) (Fig. 2c). The macro-porosity of the

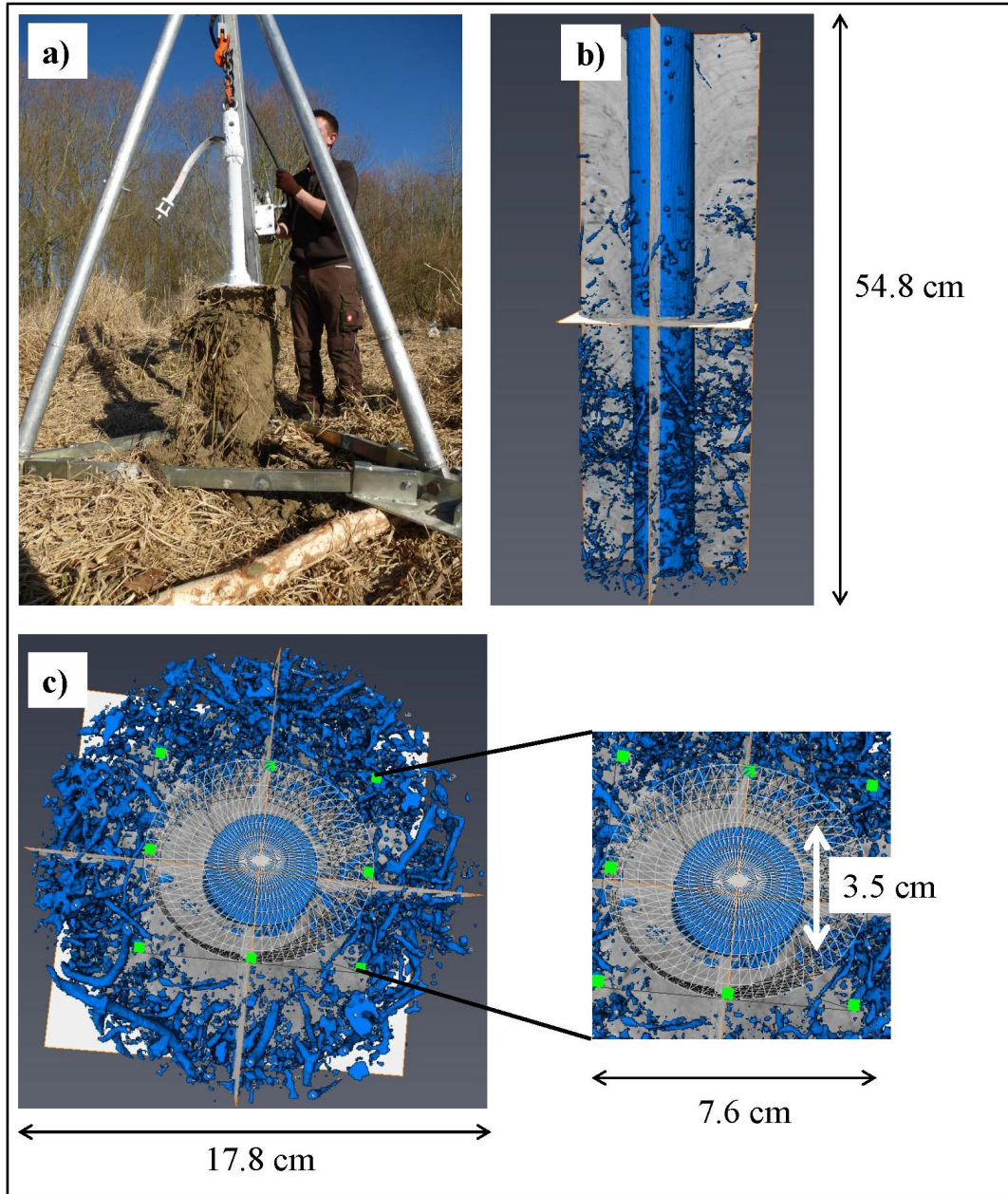


Fig. 2. Freeze core excavation in the field a), and image analysis of X-ray CT scans. b) shows the binarisation of a substack volume according to the Otsu algorithm for automatic thresholding. Identified voids which were separated from the mineral matrix are shown in blue. c) shows the cylindrical buffer zone around the metal lance which was defined visually. Matrix and voids located inside the cylindrical mesh were not considered for porosity analysis.

matrix was analysed via the void/matrix ratio of each slide using the material statistics function. Afterwards, a skeleton of the binarised data was produced by the auto-skeleton function allowing the total number and length of the segments and the number of nodes to be calculated. An estimation of the pore connectivity was calculated as the ratio between the number of segments and the number of nodes. However, pushing the metal lance into the soil significantly affects the structural integrity of the freeze cores (Strasser et al., 2015; Liernur et al., 2017). Therefore, a buffer

zone around the metal lance needed to be defined, in order to consider only the undisturbed matrix for the analyses. The image-set of each core was visually checked for anisotropic lines, indicating a compaction or displacement of the matrix along the metal lance. The area containing anisotropic lines was excluded from the analysis by defining a cylindrical buffer area around the metal lance (Fig. 2d). This buffer area was defined individually for each substack of an image sequence, ranging from 1.8 to 3.2 cm distance from the metal lance.

2.6 Additional soil sampling

Using an auger, soil samples were collected from three randomly chosen locations within each plot at the following depths: 0–7.5 cm, 7.5–22.5 cm, 22.5–37.5 cm and 37.5–52.5 cm. The depth 0 was defined as the top surface at the start of the experiment. Sediments deposited during the observation period were not sampled. For each plot, the samples taken at the same depth were pooled for later analysis. Texture of the composite soil samples was determined using the pipette method (Gee and Bauder, 1986). Soil aggregates were collected in the same four predefined depths. Since freezing and thawing of a soil matrix can break down soil aggregates and reorientate soil particles, soil samples were not directly taken from the freeze cores (Singer et al., 1992; Dalal and Bridge, 1996). Aggregate stability was analysed by determining the proportion of water-stable macro-aggregates which is a classic and robust indicator for estimating soil structural stability (Six et al., 2000). Macro-aggregates between 250 and 2000 μm size were considered and carefully plunged into demineralised water for 5 minutes (Kemper and Rosenau, 1986) using an automatic sieve-diving apparatus described in Murer et al. (1993).

2.7 Statistical data processing

Data were processed using different implementations of analyses of variance (ANOVA) and adapted to the layout of the experiment. Earthworm data were analysed using a one-way ANOVA. Effect analyses of vegetation and earthworms on the thickness of sediment accumulations during the 1.5 years exposure period were performed using a two-way ANOVA for 2×2 factorial designs. The variability of the field-saturated hydraulic conductivity, total segment length, porosity and pore connectivity within the treatments and the depths of the plots were analysed using ANOVAs for randomised complete block designs. The variability of the field-saturated hydraulic conductivity, total segment length, porosity and pore connectivity were defined as response variables. The treatments and the depths were set as predictor variables. The predictor “treatment” had four levels (+V -EW, -V +EW, +V +EW, -V -EW) and the predictor “depth” had four levels for the analysis of precedent sediments (0 - 7.5 cm, 7.5 - 22.5 cm, 22.5 - 37.5 cm, 37.5 - 52.5 cm) and three levels for the analysis of recent alluvial sediments deposited during the observation period (sediment deposit summer 2016, sediment deposit 21.11.2015, initial sediment). Since the experimental design was not orthogonal,

ANOVAs were calculated using the sum of squares type III. Prior to the analyses, requirements for normality and homoscedasticity were checked by means of the Shapiro-Wilk test and the Bartlett test. As the total segment length failed the criteria for normality, data were logarithmised prior to the ANOVA. Post-hoc analyses at the main factor levels were performed using Tukey’s HSD test. Hypotheses were tested at an $\alpha = 0.05$ significance level, accepting the risk at a p-value < 0.05. Statistical analyses and data visualisations were conducted in R version 3.5.1 (R Core Team, 2013) using the packages “easyanova” (Arnhold, 2013) for ANOVAs, as well as “ggplot2” (Wickham, 2009) and “gridExtra” (Auguie, 2016) for graphs.

3. Results

3.1 Alluvial dynamics

During the 1.5 years exposure period, four flood events occurred leading to a considerable deposition of alluvial sediments (Table 1): largest sediment depositions resulted from the flood occurring on 21.11.2015. Three consecutive events in summer 2016 led to smaller sediment accumulations, despite higher discharge rates. Only during the event in november 2015, significantly larger amounts of sediment were deposited in plots containing vegetation (Table 1). In addition, groundwater levels reached the soil surface during three days (30.03.2015, 01.06.2015 and 31.01.2016) without either the plots were inundated by surface water nor sediments were deposited (Fig. 3).

3.2 Vegetation and earthworms

Mean vegetation biomass of *P. arundinacea* in +V-EW plots was 3184 g. In the presence of earthworms, the vegetation biomass (mean value of 2951 g) was moderately reduced, but the effect was however not significant (Fig. 4a). Mean litter biomass was similar for +V+EW and +V-EW (mean values around 350 g) (Fig. 4b). Thus, the removal of earthworms did not have any significant effect on the litter biomass. Almost 75 % of the earthworms found in the treatments were juveniles. More than 80 % of the juveniles could not be assigned to their ecological category, especially for anecic and epigeic species for which juveniles were almost indistinguishable. Total abundance and biomass of earthworms were 2.5 times higher in the +V +EW treatment than in the treatments without vegetation (Table 2). Results were similar for the total number of juveniles, but not for adults. Proportions for ecological groups did not vary

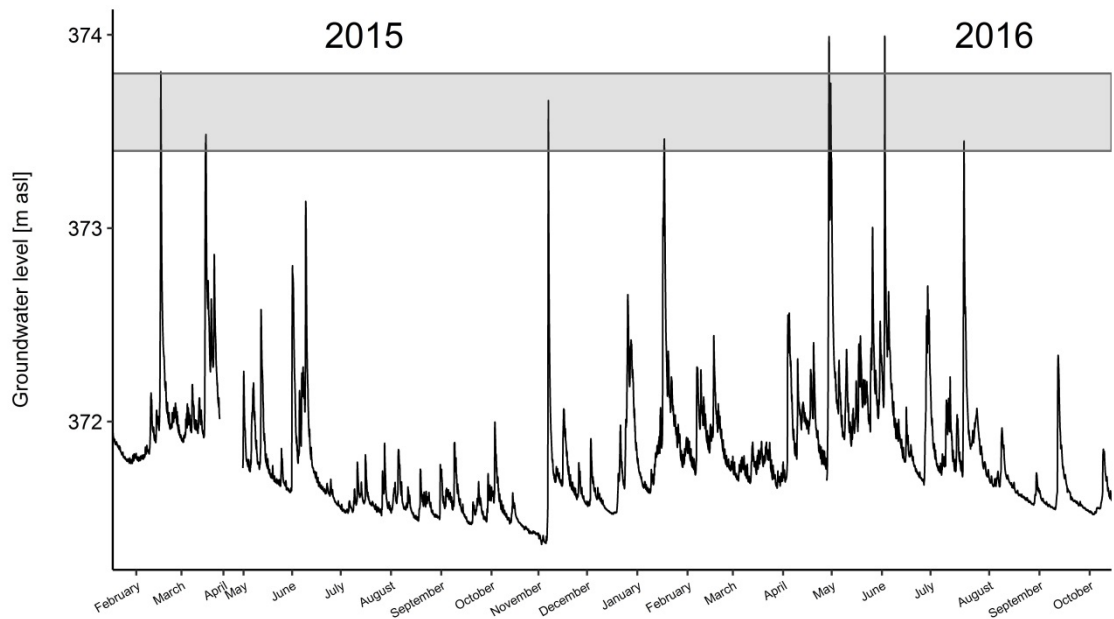


Fig. 3. Groundwater level at the site monitored by a piezometer in the period between February 2015 and October 2016 in close proximity to the plots. The grey rectangle comprises the altitude of the plots above sea level.

Table 1: Accumulation of sediment deposits at four sedimentation events ($\pm$ SE) in cm for each treatment. V stands for vegetation, EW for earthworms. Omnibus effects represent results of the Two-way ANOVA comparison test at an $\alpha = 0.05$ significance level accepting the risk at a p-value < 0.05 . n.s. denominates non-significant effects. V:EW represents interaction effects between the vegetation and earthworms.

Date of deposit	max. discharge [m ³ s ⁻¹]	Thickness of the sediment deposit according to treatments [cm] $\pm$ SE				Omnibus effects		
		+V -EW	-V +EW	+V +EW	-V -EW	V	EW	V:EW
21.11.2015	554	8.6 $\pm$ 1.7	6.1 $\pm$ 1.3	10.2 $\pm$ 2.1	4.8 $\pm$ 1.4	P < 0.05	n.s.	n.s.
13.05.2016	633	6.1 $\pm$ 0.9	3.2 $\pm$ 0.5	6.1 $\pm$ 1.5	4.9 $\pm$ 1.4	n.s.	n.s.	n.s.
17.06.2016	715	4.1 $\pm$ 0.7	3.3 $\pm$ 0.8	4.1 $\pm$ 0.7	3.5 $\pm$ 1.1	n.s.	n.s.	n.s.
05.08.2016	516	0.9 $\pm$ 0.3	1.6 $\pm$ 0.3	0.9 $\pm$ 0.3	0.9 $\pm$ 0.3	n.s.	n.s.	n.s.

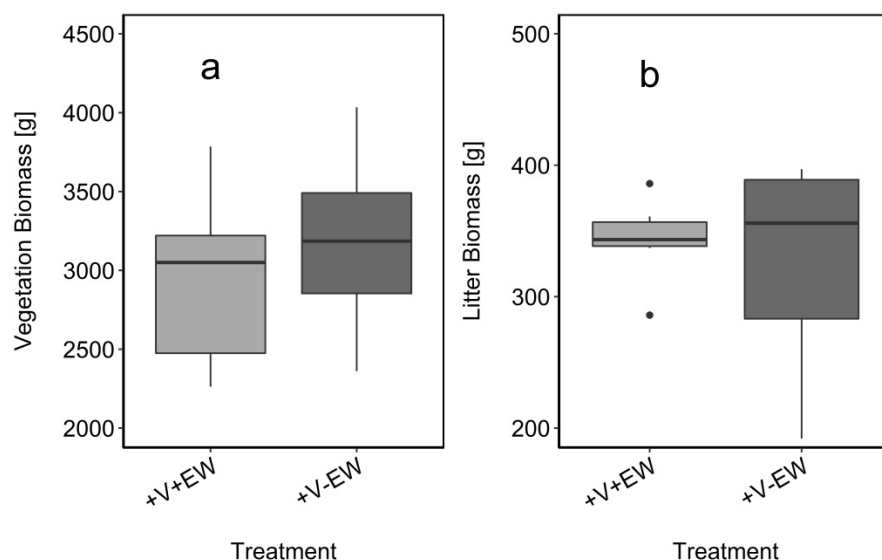


Fig. 4. Vegetation biomass (a) and litter biomass (b) determined after the exposure period of 1.5 years. V stands for vegetation and EW for earthworms.

Table 2: Abundance and biomass of earthworms $\pm$ SE collected in October 2016. V stands for vegetation and EW for earthworms. Letters a and b represent results from Tukey's HSD tests for one-way ANOVA at an $\alpha = 0.05$ significance level accepting the risk at a p-value < 0.05 .

Ecological category	+V-EW	-V+EW	+V+EW	-V-EW
earthworm abundance $\pm$SE (individuals plot-1)				
juveniles				
epigeic	0.00 $\pm$ 0.00a	0.00 $\pm$ 0.00a	0.00 $\pm$ 0.00a	0.00 $\pm$ 0.00a
endogeic	0.00 $\pm$ 0.00a	0.83 $\pm$ 0.50a	2.17 $\pm$ 1.28a	0.00 $\pm$ 0.00a
anecic	0.50 $\pm$ 0.31a,b	0.17 $\pm$ 0.15a,b	1.17 $\pm$ 0.50a	0.00 $\pm$ 0.00b
unidentified	6.50 $\pm$ 1.56a	4.67 $\pm$ 2.18a	14.33 $\pm$ 4.48a	5.50 $\pm$ 1.97a
total	7.00 $\pm$ 1.63a,b	5.67 $\pm$ 2.05b	17.66 $\pm$ 4.79a	5.50 $\pm$ 1.97b
adults				
epigeic	0.00 $\pm$ 0.00a	1.00 $\pm$ 0.91a	0.17 $\pm$ 0.15a	0.00 $\pm$ 0.00a
endogeic	0.67 $\pm$ 0.38a,b	0.17 $\pm$ 0.15a	1.67 $\pm$ 0.56b	0.33 $\pm$ 0.30a,b
anecic	0.67 $\pm$ 0.38a	0.17 $\pm$ 0.15a	1.00 $\pm$ 0.33a	0.50 $\pm$ 0.31a
unidentified	1.00 $\pm$ 0.74a	0.00 $\pm$ 0.00a	0.67 $\pm$ 0.30a	1.00 $\pm$ 0.47a
total	2.33 $\pm$ 1.02a	1.33 $\pm$ 0.90a	3.50 $\pm$ 0.70a	1.83 $\pm$ 0.83a
juveniles + adults				
epigeic	0.00 $\pm$ 0.00a	1.00 $\pm$ 0.91a	0.17 $\pm$ 0.15a	0.00 $\pm$ 0.00a
endogeic	0.67 $\pm$ 0.38a	1.00 $\pm$ 0.58a	3.83 $\pm$ 1.72a	0.33 $\pm$ 0.30a
anecic	1.17 $\pm$ 0.68a	0.33 $\pm$ 0.19a	2.17 $\pm$ 0.76a	0.50 $\pm$ 0.31a
unidentified	7.50 $\pm$ 2.04a	4.67 $\pm$ 2.18a	15.00 $\pm$ 4.68a	6.50 $\pm$ 2.21a
total	9.33 $\pm$ 2.55a,b	7.00 $\pm$ 2.76b	21.17 $\pm$ 5.39a	7.33 $\pm$ 2.69b
earthworm biomass $\pm$SE (g plot-1)				
juveniles				
total	2.25 $\pm$ 0.64a,b	2.02 $\pm$ 0.68a,b	4.12 $\pm$ 1.08a	0.82 $\pm$ 0.22b
adults				
total	2.70 $\pm$ 1.10a,b	0.71 $\pm$ 0.50a	3.97 $\pm$ 0.79b	1.27 $\pm$ 0.55a,b
juveniles + adults				
total	4.96 $\pm$ 1.54a,b	2.73 $\pm$ 0.93a	8.09 $\pm$ 1.47b	2.09 $\pm$ 0.75a

significantly between the treatments, except for juvenile-anecics and adult-endogeics (Table 2).

3.3 Hydraulic properties of the soil

Values for field saturated hydraulic conductivity were between 8.45×10^{-4} and 2.49×10^{-6} cm s⁻¹ and indicated a large variability within the main factor levels of "treatment" and "depth" (Fig. 5). There were no significant single effects of "treatment" and "depth" to explain the variability of the field saturated hydraulic conductivity. Interaction effects were not significant either.

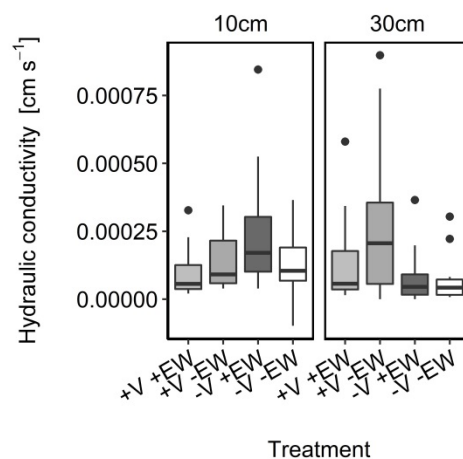


Fig. 5. Boxplots showing the variability of the hydraulic conductivity (Kfs) according to treatments and depths. V denominates vegetation and EW earthworms.

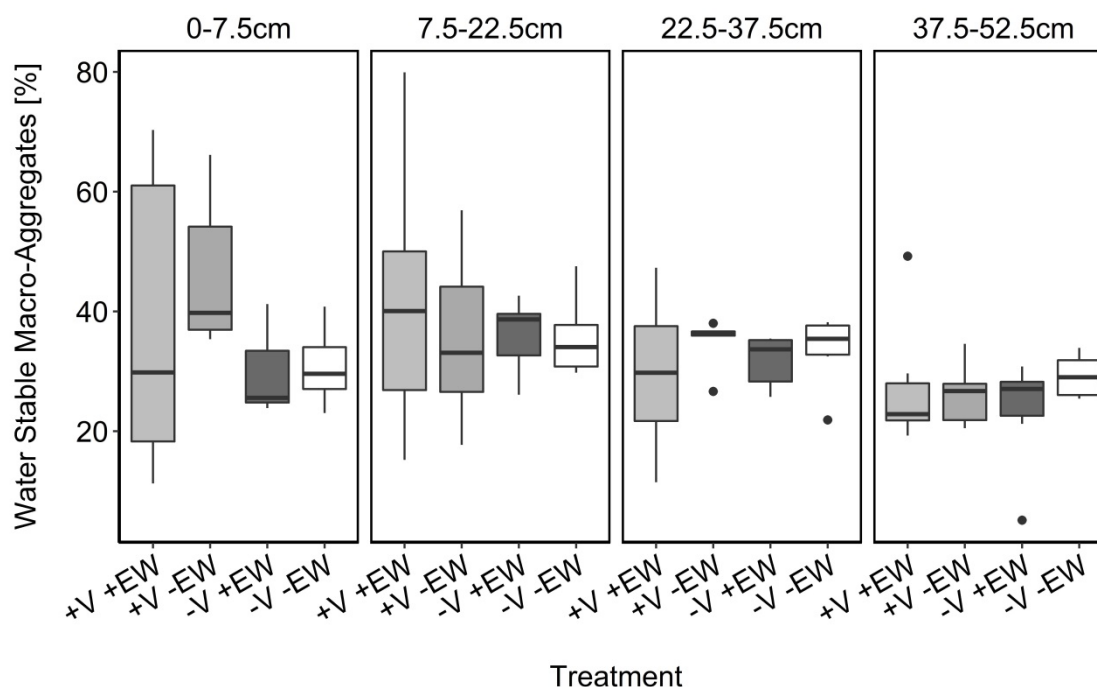


Fig. 6. Boxplots showing the aggregate stability according to the treatments and the depths. V stands for vegetation and EW for earthworms.

3.4 Soil texture and aggregate stability

Soil texture class was similar among the plots and was identified as loamy sand (IUSS Working Group WRB, 2006). Mean proportions were 78.96 ± 5.95 % for sand, 14.67 ± 4.96 % for silt and 6.37 ± 1.40 % for clay. Soil texture did not show any significant correlation to the values for aggregate stability in this study (p -value < 0.6 , $r_{\text{pearson}} = 0.045$). Thus, soil texture could be neglected as a predictor variable in the effect analysis. Nevertheless, soil texture indicated a depth gradient with an increasing proportion of the sand fraction and a decreasing proportion of the clay fraction in the topsoil (not shown). The contribution of “depth” to explain the variability of aggregate stability was highly significant ($p < 0.001$) (Table 3). On the other hand, there was no significant “treatment” effect. The effect of the interaction between “treatment” and “depth” was not significant either, but the p – value (p -value = 0.07) was close to the threshold level of acceptance. Therefore, multiple comparisons at the main factor levels were nevertheless performed. Within the levels of “depth”, aggregate stability was lowest in 37.5 – 52.5 cm, increasing gradually to the soil surface. Regarding interaction terms, aggregate stability was significantly higher in the +V -EW treatment in the uppermost layer compared to the undermost layer. Values for the layers between 7.5 and 37.5 cm ranged in between (Fig. 6; Table 3). Considering the +V +EW

treatment, aggregate stability was greatest in the second uppermost layer and lowest in the undermost. Treatments without vegetation did not show any significant modification of the aggregate stability within the depth profile.

3.5 X-ray CT

3.5.1 Soil layer analysis

Soil macroporosity and total segment length of macropores were significantly affected by “depth” (p -values < 0.05). Both variables were largest in the second uppermost layer and lowest in the undermost layer. Furthermore, total segment lengths in the two uppermost layers were similar as were those in the 3rd and 4th layer, and porosity was maximum in the second uppermost layer (Fig. 7). By contrast, the treatments did not explain the variability of the two response variables at all. However, interaction terms between “treatment” and “depth” were significant (p -values < 0.05) (Table 3). In the +V +EW treatment, total segment length was highest in the second uppermost layer followed by the uppermost one (Fig. 7). In the +V -EW treatment, total segment length decreased along the depth gradient, whereas porosity was significantly increased in the uppermost and the 3rd layer. For treatments without vegetation neither total segment length nor porosity varied with soil depth (Table 3). In contrast to total segment length and porosity, “treatment” significantly

Table 3: Results for the analyses of variance for randomised split-plot designs. Significant overall and interaction effects were specified by a p-value < 0.05. “n.s.” stands for not significant. WSA stands for water stable aggregates, Seglen for segment length, V for vegetation and EW for earthworms. Letters a, b, c and d represent results from Tukey’s HSD posthoc analysis at an $\alpha = 0.05$ significance level accepting the risk at a p-value < 0.05. “:” represents interaction effects between two predictor variables.

Predictor variables and levels	Response Variables			
	%WSA	Seglen	Porosity	Pore connectivity
Overall and interaction effects				
Treatment	n.s.	n.s.	n.s.	p < 0.05
Depth	p < 0.001	p < 0.05	p < 0.05	p < 0.001
Treatment : Depth	n.s.	p < 0.05	p < 0.05	p < 0.05
Multiple comparisons of “treatments”				
+V -EW	a	a	a	a
-V +EW	a	a	a	b
+V +EW	a	a	a	ab
-V -EW	a	a	a	b
Multiple comparisons of “depth”				
0.0 – 7.5 cm	a	a	ab	a
7.5 – 22.5 cm	a	a	a	a
22.5 – 37.5 cm	ab	b	bc	b
37.5 – 52.5 cm	b	b	c	c
Multiple comparisons of “treatments” within “depth” levels				
0.0 – 7.5 cm				
+V -EW	a	a	a	a
-V +EW	b	b	b	b
+V +EW	ab	a	a	a
-V -EW	b	b	b	b
7.5 – 22.5 cm				
+V -EW	a	ab	a	a
-V +EW	a	b	b	bc
+V +EW	a	a	ab	ab
-V -EW	a	b	b	c
22.5 – 37.5 cm				
+V -EW	a	a	a	a
-V +EW	a	a	a	a
+V +EW	a	a	a	a
-V -EW	a	a	a	a
37.5 – 52.5 cm				
+V -EW	a	a	a	a
-V +EW	a	a	a	a
+V +EW	a	a	a	a
-V -EW	a	a	a	a
Multiple comparisons of “depth” within “treatment” levels				
+V -EW				
0.0 – 7.5 cm	a	a	a	a
7.5 – 22.5 cm	ab	ab	b	a
22.5 – 37.5 cm	ab	b	a	b
37.5 – 52.5 cm	b	c	b	b
-V +EW				
0.0 – 7.5 cm	a	a	a	a
7.5 – 22.5 cm	a	a	a	a
22.5 – 37.5 cm	a	a	a	ab
37.5 – 52.5 cm	a	a	a	b
+V +EW				
0.0 – 7.5 cm	ab	ab	a	a
7.5 – 22.5 cm	a	a	a	a
22.5 – 37.5 cm	ab	b	a	b
37.5 – 52.5 cm	b	b	a	b

-V -EW				
0.0 – 7.5 cm	a	a	a	a
7.5 – 22.5 cm	a	a	a	a
22.5 – 37.5 cm	a	a	a	a
37.5 – 52.5 cm	a	a	a	a

Table 4: Results for the analyses of variance for randomised split-plot designs for recent alluvial deposits. Significant overall and interaction effects were specified by a p-value < 0.05. “n.s.” stands for not significant. WSA stands for water stable aggregates, Seglen for segment length, V for vegetation and EW for earthworms. Letters a and b represent results from Tukey’s HSD posthoc analysis at an $\alpha = 0.05$ significance level accepting the risk at a p-value < 0.05. “.” represents interaction effects between two predictor variables.

Predictor variables and levels	Response Variables		
	Seglen	Porosity	Pore connectivity
Overall and interaction effects			
Treatment	p < 0.05	p < 0.05	p < 0.001
Depth	p < 0.001	p < 0.001	n.s.
Treatment : Depth	p < 0.05	p < 0.05	n.s.
Multiple comparisons of “treatments”			
+V -EW	a	a	a
-V +EW	b	b	b
+V +EW	a	a	a
-V -EW	b	b	b
Multiple comparisons of “depth”			
Sediment deposit summer 2016	b	b	a
Sediment deposit 21.11.2015	a	a	a
Initial Sediment	ab	ab	a
Multiple comparisons of “treatments” within “depth” levels			
Sediment deposit summer 2016			
+V -EW	a	a	a
-V +EW	a	a	b
+V +EW	a	a	a
-V -EW	a	a	b
Sediment deposit 21.11.2015			
+V -EW	a	a	a
-V +EW	b	b	b
+V +EW	a	a	a
-V -EW	b	b	b
Initial Sediment			
+V -EW	ab	a	a
-V +EW	b	b	b
+V +EW	a	a	a
-V -EW	b	b	b
Multiple comparisons of “depth” within “treatment” levels			
+V -EW			
Sediment deposit summer 2016	b	b	a
Sediment deposit 21.11.2015	a	a	a
Initial Sediment	b	a	a
-V +EW			
Sediment deposit summer 2016	a	a	a
Sediment deposit 21.11.2015	a	a	a
Initial Sediment	a	a	a
+V +EW			
Sediment deposit summer 2016	b	b	a
Sediment deposit 21.11.2015	a	a	a
Initial Sediment	a	ab	a

-V -EW

Sediment deposit summer 2016	a	a	a
Sediment deposit 21.11.2015	a	a	a
Initial Sediment	a	a	a

affected pore connectivity (p-value < 0.05), in addition to a highly significant “depth” effect (p-value < 0.001). Furthermore, interaction terms between “treatment” and “depth” were significant (Table 3). The presence of vegetation significantly improved the pore connectivity within the four levels of “treatment”. Pore connectivity significantly decreased within the depth profile within the four levels of “depth”. Pore connectivity in the two uppermost layers was higher than below in plots with vegetation and in those of the -V +EW treatment (Table 3).

3.5.2 Analysis of new alluvial sediments

Sediments deposited during the exposure period were analysed for two events: 1) the flood on 21.11.2015 and 2) the sum of three floods in summer 2016 (Fig. 7). Sediment deposition rates of the latter were summed-up, as each individual event did not result in a sufficient sediment accumulation for X-ray CT image analyses. The pre-existing sediment ranging to the soil surface at the beginning of the experiment was summarised as “initial sediment” for the respective plots. Results from the analyses of variance for randomised complete block designs were almost identical for the total segment length and the porosity of the analysed sediments. For both parameters, the factor “treatment” was significant (p-value < 0.05) and the factor “depth” was highly significant (p-value < 0.001) (Table 4). Both total segment length and porosity of the sediments were significantly higher in plots with than without vegetation. The deposits of 21.11.2015 exhibited both the highest porosity and total segment length, whereas these variables were lowest in the most recent deposit. Also, interaction terms between “treatment” and “depth” were significant (p-value < 0.05). The presence of vegetation significantly increased the total segment length and the porosity in the deposit from the 21.11.2015 and in the initial sediment (Table 4). The contribution of “treatment” to explain the variability of the pore connectivity was highly significant (p-value < 0.001), whereas “depth” and interaction terms did not show any significant contribution (Table 4). However, since the p-value for interaction terms was close to the level of acceptance, multiple comparison tests at the main factor level were nevertheless performed. In summary, pore connectivity was

the highest in plots with vegetation, whatever the sediment deposition.

4. Discussion

The contribution of *P. arundinacea* and earthworms to soil structure formation in plots installed in a highly dynamic floodplain habitat was successfully analysed by coupling freeze coring and X-ray CT. The results clearly demonstrated the effect of the two engineers in the plots, even though the structural integrity of the freeze cores was not completely warranted (Strasser et al., 2015; Liernur et al., 2017) and the applied resolution of the medical scanner did not allow to distinguish between plant root galleries and earthworm tunnels (Schomburg et al., submitted).

4.1 Short-term engineering effect of pioneer vegetation

P. arundinacea as a pioneer herbaceous plant efficiently structured the two uppermost layers of the initial sediment by improving the pore network, the pore connectivity and the stability of the soil aggregates within 1.5 years. Additionally, these plants were also capable of improving these parameters in the new sediment deposit originating from 21.11.2015. Thus, *P. arundinacea* required only one year, corresponding to one single vegetation period, to improve the soil structure in a recent alluvial deposit. In our study, this efficiency of *P. arundinacea* despite strong impairment of alluvial dynamics was highlighted for the first time. Chantigny et al. (1997) already showed that *P. arundinacea* can significantly contribute to aggregation in agricultural soils in less than three years. In recent micro- and mesocosm experiments, *P. arundinacea* and other pioneer herbaceous plants were able to significantly improve aggregate stability and macro-porous networks of soils and sediments within a short time period of several weeks (Milleret et al., 2009; Fonte et al., 2012; Kohler-Milleret et al., 2013; Schomburg et al., submitted.). However, the physical conditions, e.g. the temperatures and soil moisture contents during the latter experiments were stable and herbaceous plants were not challenged by any water stress or buried by a sediment layer. Both stress factors can cause severe damages to plant seedlings and

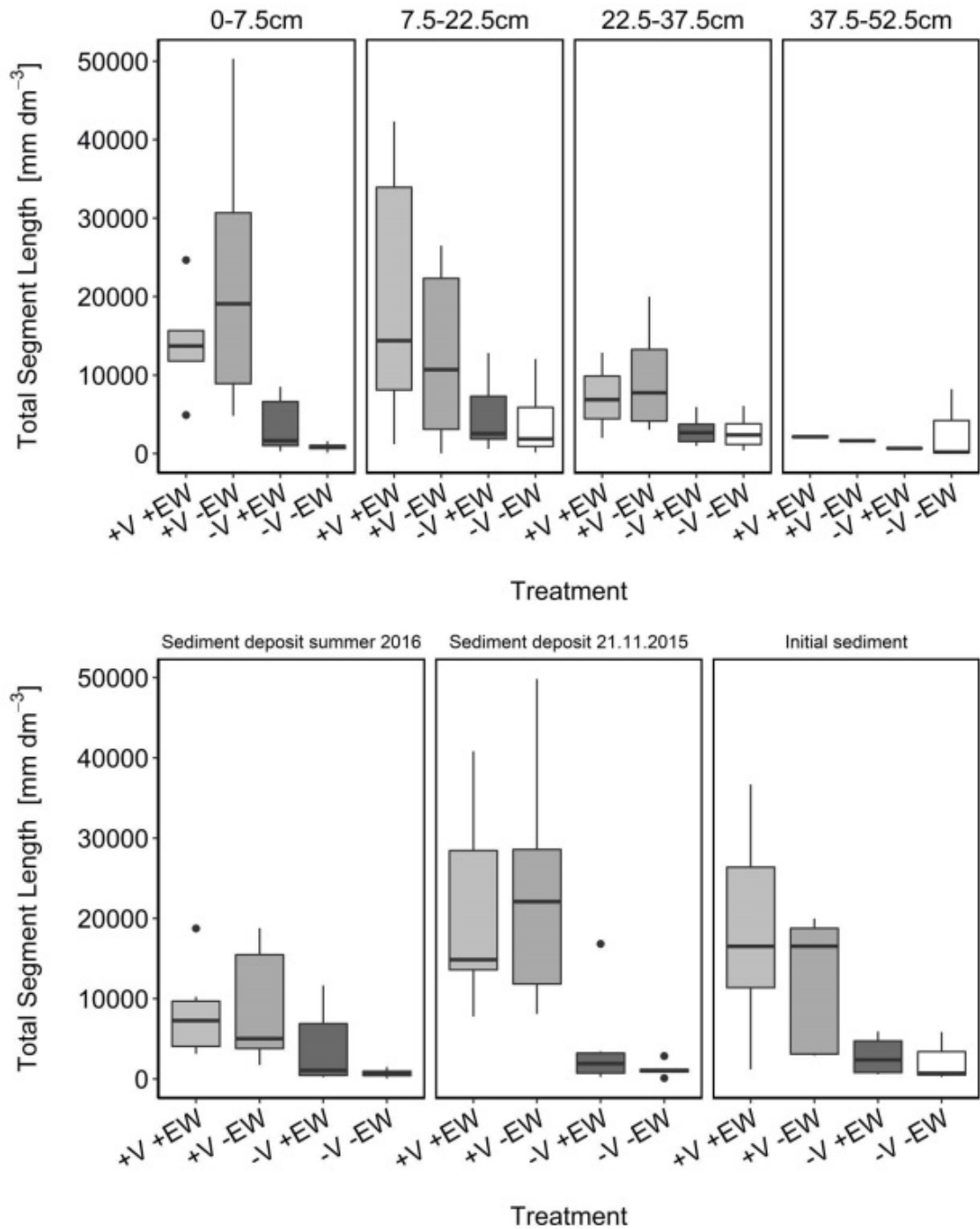


Fig. 7: Boxplots showing the total segment length according to the treatments and the depths. V stands for vegetation and EW for earthworms.

slow down the progress of soil structure formation in close proximity to rivers (Bätz et al., 2015). Therefore, it is even more astonishing that the progress in soil structure formation became clearly visible after one year only. In contrast, the most recent deposits from summer 2016 and the two undermost layers of the initial sediments were not significantly structured by *P. arundinacea*. Most likely, half a year was not sufficient to structure a fresh

alluvial deposit.

4.2 Short-term engineering effect of earthworms

In contrast to the pioneer vegetation, earthworms contributed to soil structure formation only to a small extent within 1.5 years. In presence of earthworms, pore connectivity was positively affected in the two

uppermost layers and the aggregate stability showed a slight increase in the second uppermost layer. This zone corresponded to the drilosphere, i. e. the zone preferentially resided by endogeic and anecic earthworms (Lavelle et al., 1997). In general, earthworms are known to be highly efficient soil engineers that significantly contribute to soil structure formation (Brown et al., 2000; Six et al., 2002; Blouin et al., 2013). However, environmental conditions at the Thur River were most likely less favourable for earthworms, resulting in a low total abundance and thus to their engineering capacity. Total abundance was up to 10 times lower compared to other floodplain habitats in Switzerland which were sampled with the same method (Bullinger-Weber et al., 2007; 2012; Salomé et al., 2011; Fournier et al., 2012). On one hand, the textural composition of the sediments was most likely problematic for earthworms. Large proportions of coarse sand (around 80 % in this case) lead to skin and intestinal damages of earthworms during burrowing activity, most likely explaining the low presence of endogeics and anecics (Edwards and Bohlen, 1996; Curry and Schmidt, 2007). Results of a recent study indicate that the endogeic species *A. chlorotica* preferentially chose the finer textured alluvial sediment, when sediments of different textural composition are superimposed (Schomburg et al., submitted). On the other hand, numerous studies report that the abundance of earthworms is crucially reduced in presence of strong alluvial dynamics (Ausden et al., 2001; Plum and Filser et al., 2005; Ivask et al., 2007). Nevertheless, earthworms have developed physiological and morphological adaptations to survive water-saturated conditions for a certain time (Plum and Filser, 2005; Zorn et al., 2008) or produce water-resistant cocoons (Roots, 1956; Plum and Filser, 2005). Cocoons can be transported during floods and might be an explanation for the large number of juveniles in the plots and the presence of earthworms found in -EW plots in which earthworms were reduced at the beginning of the experiment and migration was prevented. Most likely, larger communities of earthworms could not be developed as a consequence of the high proportion of sand.

4.3 Interactions between pioneer vegetation and earthworms

The abundance of earthworms was increased by factor 2.5 in presence of vegetation. Conversely, vegetation biomass was not affected by the presence of earthworms. Earthworms could benefit from the shadowing effect of the vegetation which generally

moderates the soil temperatures and retards the desiccation of the soil in dry periods. Habitats in close proximity to rivers, which are mostly sparsely covered by vegetation, are often subject to severe summer droughts (Naiman et al., 2000; Nilsson and Berggren, 2000; Bätz et al., 2014). On the other hand, plants provide OM inputs through above-ground litter biomass and through root exudates belowground which can be beneficial for earthworms (Yavitt et al., 2015). These inputs are especially important coarse textured soils or under nutrient poor soil conditions (Laossi et al., 2010; Blouin et al., 2013). On the functional scale, the contribution of earthworms to soil structure formation in the vegetation treatments is difficult to assess, as the single effects of vegetation massively exceeded the effects of earthworms. Nevertheless, aggregate stability and total segment length were higher in the second uppermost layer in the +V +EW treatments than the maxima in the uppermost layer of the +V - EW treatments. Since the second uppermost layer corresponded well to the drilosphere, the increased values can be most likely attributed to concomitant effects of vegetation and earthworms to soil structure formation. However, interaction effects between the two engineers could not be confirmed by X-ray CT, as plant root tunnels and earthworm galleries were not distinguishable using an intermediate resolution of the scanner (Schomburg et al., submitted). Nevertheless, findings of recent meso- and microcosm studies strongly suggest that several plant and earthworm species contribute concomitantly to soil structure formation (Zangerlé et al., 2011; Fonte et al., 2012; Kohler-Milleret et al., 2013), also presumed for *P. arundinacea* and the earthworm *A. chlorotica* (Schomburg et al., 2018b; Schomburg et al., submitted) which was abundant in our plots. Most likely *P. arundinacea* and earthworms, such as *A. chlorotica* and *A. caliginosa* positively affect each other with respect to their effect on soil structure formation (Milleret et al., 2009; Schomburg et al., 2018b). Several plants use earthworm tunnels for root network extension and preferentially colonise their nutrient enriched casts and burrow walls (Spiers et al., 1986; Zaller and Arnone, 1999., Decaëns et al., 2011). Earthworms take advantage of easy decomposable OM released by plant roots as an energy source or feed directly on small dead plant roots (Gilbert et al., 2014; Sanchez-de-Leon et al., 2014; Yavitt et al., 2015). Values for field saturated hydraulic conductivity were comparable to those from other studies measured in sandy soils (Rodgers and Mulqueen, 2004; Lewis, 2016; Rezaei et al., 2016). None of the treatments modified the field-saturated hydraulic conductivity of the soil

despite extension of the macro-porous network, especially in plots containing vegetation. Note, however, that hydraulic conductivity is a parameter which can vary over orders of magnitude across short distances and field-measurements of this parameter are uncertain. In general, hydraulic properties can be significantly improved in presence of plants and earthworms, leading to an increased water infiltration rate (Gurnell and Petts, 2006; Jouquet et al., 2011; Guéi et al., 2012; Blouin et al., 2013). This can result in a decrease of soil erosion by more than 50 %, as surface water runoff is strongly reduced (Shuster et al., 2002; Shipitalo et al., 2004; Blouin et al., 2013). Most likely, hydraulic properties were altered by alluvial dynamics in the plots. Flood events can restructure the pore system and clog macropores through the deposition of fine sediment particles (Bottinelli et al., 2010; Gianni et al., 2016). Furthermore, the sediment composition in dynamic floodplain habitats strongly varies in space and time. Most likely, this heterogeneity could not be accurately reproduced by Guelph Permeameter measurements.

4.4 Future challenges for management strategies of near natural and restored floodplains

Since the last two decades, river management strategies in Switzerland have started to focus more intensively on ecological aspects and ecosystem services provided by rivers and floodplains. These policy changes were the reason for an increasing number of river and floodplain restoration projects initiated all over Switzerland. To mitigate strong on- and off-site damages caused by frequent erosion and deposition of sediments, willow trees were planted to stabilise the river shore. Willow trees were shown to be highly efficient as soil engineers after a few years under moderately strong alluvial dynamics (Gurnell and Petts, 2002; Crouzy and Perona, 2012; Perona et al., 2012). Our results indicate that herbaceous vegetation, especially *P. arundinacea*, is a highly efficient soil engineer in areas which are more strongly threatened by alluvial dynamics. Furthermore, *P. arundinacea* contributed immediately to soil structure formation and significantly increased the macro-porous system and the structural stability of aggregates after only one year. *P. arundinacea* tolerated strong alluvial dynamics by resisting flood periods and deposition of recent alluvial sediments. However, the frequency and magnitude of flood events at the Thur River in 2015 and 2016 were lower compared to the years before. In the recent past, a larger amount of intermediate and

strong flood caused stronger erosion and the deposition large sediment layers in the Thur River floodplain (Schirmer et al., 2014; Schomburg et al., 2018a). One single event can bury seedlings of herbaceous plants and interrupt the progress of soil structure formation. Furthermore, fluctuating groundwater levels can also strongly affect the vegetation leading to conditions in the rhizosphere alternating between water saturation and drought. In 2015 and 2016 which were marked by hot and dry summer periods, the plots were only saturated three times by rising groundwater levels without surface water entering the floodplain. Nevertheless, Schomburg et al. (2018a) clearly demonstrated that fluctuating groundwater levels strongly control the development of plant communities and thus their capability to contribute significantly to soil structure formation. On one hand, the herbaceous vegetation community is strongly affected by alluvial dynamics. On the other hand, it can rapidly recover in case of a destruction, by means of viable seeds that are transported and deposited at the river shore during flood events (Gurnell, 2007; Corenblit et al., 2009). However, not only seeds of native herbaceous plants are deposited, but also non-native species. Non-native species can coexist or become invasive by replacing native species at the river shore. Some of the invasive species can even have negative effects on the soil structure in floodplain habitats. The Himalayan *Impatiens glandulifera*, which was also found at the Thur River, has a destabilising effect on alluvial sediments. They develop a shallow root system at the soil surface and build up a closed canopy that blocks the sunlight and impedes the growth of other plants (Chapman and Grey, 2012). As they are intolerant to cold water, they die in late autumn and expose the bare and unprotected soil to floods in the winter season (Skálová et al., 2011). A recent study showed that soil erosion was strongly promoted in a floodplain habitat settled by *Impatiens glandulifera* (Greenwood and Kuhn, 2014). All processes found in our study are based on the results of one specific pioneer plant species and native earthworms monitored in controlled plots at one specific site in Switzerland. However, the general mechanisms of soil structure formation induced by plants and earthworms do not differ from one habitat to another (Brown et al., 2000). We strongly suggest that our results are transferable to similar near-natural or restored floodplains influenced by strong alluvial dynamics in the temperate zone. Soil structure formation in close proximity to the river can be a self-regulating process that can be interrupted after a strong flood event, but resumed through viable seeds.

5. Conclusions

This study investigated the effect of the herbaceous pioneer plant species *P. arundinacea* and earthworms on soil structure formation under consideration of strong alluvial dynamics in a restored floodplain section in the short-term. The coupling of freeze coring and X-ray CT provided clear results about the recent development of a soil structure in controlled field plots. The article highlights the novelty that *P. arundinacea* can significantly improve soil structure of recent alluvial sediments within only one year. Earthworms alone did not improve the soil structure within the exposure period, most likely due to the unfavourable textural composition of the deposits. They however promoted the effect of soil structure formation in presence of vegetation. Reciprocally, vegetation increased the total abundance of earthworms. Thus, our results strongly suggest that herbaceous plants, such as *P. arundinacea*, can play a key role for the initial soil structure formation in near-natural and restored floodplains in the short-term. Pioneer herbaceous plants and earthworms thus should to be considered to improve the success of river restoration projects. As pioneer herbaceous plants disperse naturally, no further action is warranted except for removal of invasive species that have a destabilisation effect on alluvial deposits and promote soil erosion. Furthermore, the authors recommend to release earthworm communities that help to structure alluvial sediments.

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Appendix A: formula for the calculation of the field saturated hydraulic conductivity from the infiltration test performed using the Guelph Permeameter

$$K_{fs} = G_2 Q_2 - G_1 Q_1 \quad (1)$$

$$G_1 = \frac{H_2 C_1}{\pi(2H_1 H_2 (H_2 - H_1) + a^2 (H_1 C_2 - H_2 C_1))} \quad (2)$$

$$G_2 = \frac{H_1 C_2}{\pi(2H_1 H_2 (H_2 - H_1) + a^2 (H_1 C_2 - H_2 C_1))} \quad (3)$$

$$Q_1 = Y R_1 \quad (4)$$

$$Q_2 = Y R_2 \quad (5)$$

Y representing the inner reservoir constant of 2.16, R_1 and R_2 the steady state fall rates of water in the reservoir at head height H_1 and H_2 , respectively, and a the radius of the well. Equations for shape factors C_1 and C_2 depend on the soil texture-structure category which were adapted according to Elrick et al., (1989) and Zang et al., (1998). Decisions for the shape factor equations were made based on the soil texture analyses of the sediments.

$$K_{fs} = \frac{C_1 Q_1}{2\pi H_1^2 + \pi a^2 C_1 + 2\pi \left(\frac{H_1}{\alpha^*}\right)} \quad (6)$$

Here α^* represents the macroscopic capillarity length parameter that also depends on the soil texture-structure category. Values are provided by Elrick et al., (1989).

General discussion

The role of plants and earthworms in soil structure formation in floodplains

Plants and earthworms were expected to hold a great potential to promote initial soil structure formation in alluvial soils and to efficiently stabilise OM in macro-aggregates. The results of the three stage experiment indicated that each soil engineer was able to make an important contribution to soil structure formation in different textured sediments and/or to the stabilisation of OM in macro-aggregates. However, the dimension and the persistence of the created structures strongly depended on the type of engineer, physicochemical soil parameters, the landscape hydrology and the soil development over time. Plants and earthworms were to varying degrees positively or negatively affected by each parameter individually indicating a specific engineering effect being highly variable in space and time (Fig. 3).

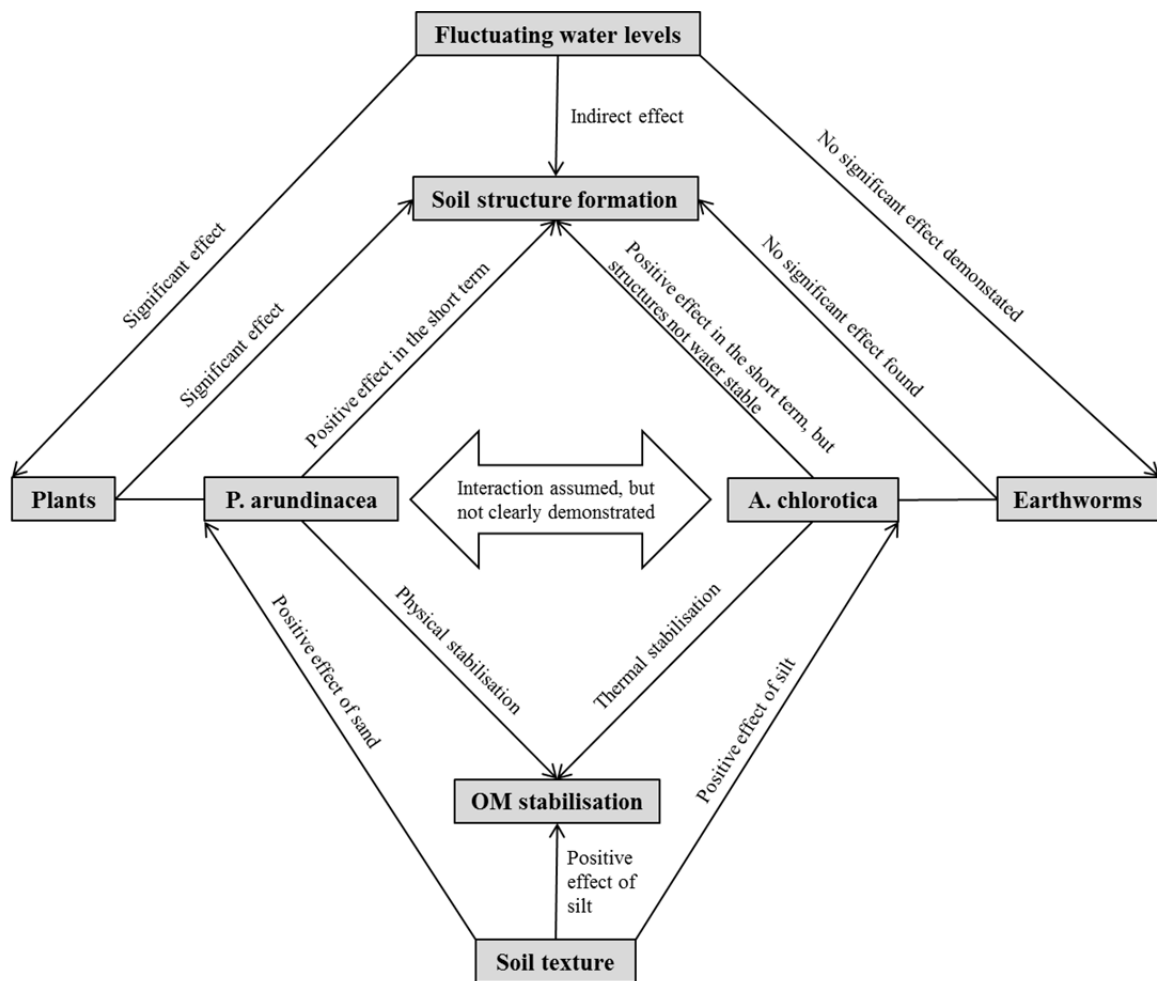


Fig. 3: Schematic overview of effects, pathways and mechanisms of soil structure formation and OM stabilisation in alluvial soils including hydrologic parameters, soil physicochemical properties and soil engineering organisms, demonstrated in the main chapters I - III.

The results generally indicated that plants, regardless of their species, shape or community (pioneer herbaceous plants, willow bushes or plants associated to alluvial forest habitats), significantly increased the structural stability of the topsoils in different floodplain habitats. Pioneer herbaceous plants were furthermore capable to develop a stable soil structure in sandy alluvial sediments even in the short-term and despite extensive alluvial dynamics. Nevertheless, the abundance and the morphology of roots were influenced by surface water – groundwater dynamics (Fig. 3). Most likely, these factors were decisive for the development of different floodplain habitats settled by a specific vegetation community being adapted to the conditions in the respective habitat. Soils in habitats which were frequently waterlogged were colonised by a pioneer vegetation community. Soils in habitats being rarely affected by complete or nearly complete water saturation were settled by shrubs and an herbaceous vegetation community associated to alluvial forest species. Each community of shrubs and herbaceous plants was therefore well adapted to its physical environment and made an important contribution to soil structure formation in their specific habitat. Decreasing influences of alluvial dynamics with increasing distances to the river usually leads to a continuous succession of vegetation communities along a topographical gradient (Gurnell and Petts, 2002; Bullinger-Weber et al., 2012; Le Bayon et al., 2013). A comparable development is visible at the Thur River to a certain extent (Fournier et al., 2013), but the distinctive micro-relief formed a mosaic of habitats, each specifically influenced by surface water – groundwater dynamics and settled by both pioneer herbaceous plants and shrubs and those associated to alluvial forest communities. Therefore, the traditional approach of analysing soil structure formation as a function of vegetation and habitat development along a topographical gradient needed to be discarded at the “Schaffäuli” site.

The capacity of macro-aggregate formation induced by the herbaceous plant *P. arundinacea* specifically depended on the soil texture (main chapter II) (Fig. 3). The species-specific characteristics of *P. arundinacea* might have been a possible explanation why the structural stability of macro-aggregates was only increased in the sandy alluvial sediment. Since *P. arundinacea* is physiologically and morphologically adapted to sandy sediments deposited in close proximity to rivers, their effect on the stability of macro-aggregates in the silty sediment was lower. Conversely, incubating an herbaceous plant species associated to alluvial forests, such as *Equisetum hyemale* or *Aegopodium podagraria* might had shown opposite results, e.g. a significant increase of the stability of

macro-aggregates in the silty sediment. Against expectations, *P. arundinacea* was able to improve the stability of macro-aggregates and the porosity in sandy soils significantly after only eight weeks of incubation. Similar studies already demonstrated that herbaceous plants are capable to build up stable macro-aggregates in short-term incubation experiments (Milleret et al., 2009a, b, Fonte et al., 2012; Kohler-Milleret et al., 2013), but not in a sandy matrix in which aggregate formation is generally more complicated (Bronik and Lal, 2005). Even under strong alluvial dynamics, *P. arundinacea* significantly contributed to soil structure formation within only one year. Both experiments highlighted the extraordinary efficiency of *P. arundinacea* to build up a stable soil structure under distinctive environmental conditions and less favourable soil properties. Thus, pioneer herbaceous plants such as *P. arundinacea* are supposed to be highly efficient soil engineers in floodplains in the short term.

In the field experiment, earthworm communities did not respond to physicochemical soil parameters, fluctuations of the water levels and did not actively affect the structural stability of the topsoil (main chapter I) (Fig. 3). These results were surprising, as earthworms generally show strong negative reactions to waterlogging in the soil (Ausden et al., 2001; Plum and Filser et al., 2005; Ivask et al., 2007) and to certain soil physicochemical parameters, such as large proportions of sand (Shipitalo and Protz, 1988; Curry and Schmidt, 2007), low pH values and low OM contents (Edwards and Bohlen, 1996; Edwards, 2004; Eijsackers, 2010). However, as reported in previous studies, earthworms still have a great potential to contribute to soil structure formation in alluvial soils (Thonon and Klok, 2007; Le Bayon et al., 2013; 2017). They developed efficient strategies to tolerate or avoid waterlogging in soils for a short time by escaping the habitat, staying in diapause or producing water-resistant cocoons (Plum and Filser, 2005; Zorn et al., 2008). Thus, the results from the field experiment indicated two possibilities of interpretation: 1) There is, in fact, no effect of earthworms at the Thur River. The landscape hydrology and the physicochemical soil parameters might be equally unfavourable in all sampled plots likewise reducing the abundance of earthworms and suspending their contribution to increase the structural stability of the topsoils. 2) The models applied to analyse the field data did not accurately reproduce multiple interaction effects between earthworms and the environmental parameters, most likely due to temporal and spatial deferments. In controlled *in vitro* experiments, earthworms increased the porosity and produced macro-aggregates regardless of the soil texture, but these macro-

aggregates were not water stable. These results correspond to findings of similar short-term incubation experiments, demonstrating that the stability of macro-aggregates formed by earthworms were not increased in the short-term (Bossuyt et al., 2005; Jana et al., 2010; Fonte et al., 2012; Lubbers et al., 2017). Similarly, macro-aggregates in fresh sediment deposits sampled from the earthworm treatment in the semi-controlled field experiment were not water stable. Macro-aggregates produced by earthworms, such as burrows and casts, were demonstrated to be highly unstable in the fresh state and can be easily dissolved by water (Shipitalo and Protz, 1988; Barrois et al., 1993; Bottinelli et al., 2010; Decaëns et al., 2011). With aging, physical processes such as alternating desiccation and remoistening combined with biological processes such as OM exudation by bacteria and fungal hyphae lead to a significant stabilisation of burrows and casts (Marinissen and Dexter, 1990; Lavelle and Martin, 1992; Zhang and Schrader, 1993; Schrader and Zhang, 1997). In recent alluvial sediments deposited before 2015, a slight increase of the aggregate stability was found in the drilosphere which could be attributed to earthworm activity. Mardhiah et al. (2014) monitored the development of aggregate formation in a young floodplain soil colonised by earthworms within a chronosequence of 40 years and found a significant increase of the aggregate stability delayed by five years. All these results indicate that the effect of earthworms on soil structure formation in alluvial soils deemed to be effective only after several years. This temporal shift was also most likely the main reason, why the models applied in the field study could not accurately reproduce the effect of earthworms. Moreover, the contribution of earthworms to soil structure formation was relatively low compared to the contribution of plants, especially in close proximity to the river, as indicated by the low macro-porosity in the earthworm treatment in the semi-controlled field plots. This disequilibrium might be an additional reason why it is difficult to detect the effect of earthworms at the field scale.

The role of plants and earthworms in the stabilisation of OM in macro-aggregates

The stabilisation of OM through its incorporation into macro-aggregates is an important mechanism initiated by soil structure formation, as it promotes the sequestration of OM in the soil. The dimension and mechanisms of OM protection are thereby of major importance, as the residence time of OM in the soil can be extended independent of the molecular composition through its efficient protection against microbial decay (Schmidt et al., 2011). OM stabilisation on the process scale could be successfully analysed in

mesocosms in which the soil matrix was homogenised and the amount and bulk chemistry of OM inputs were controlled. OM inputs and transformations by *P. arundinacea* and *A. chlorotica* were extremely low relative to the initial content and bulk chemistry of OM in the matrix. In the field, OM of different decomposition states is incorporated into the soil matrix. In alluvial soils, OM contents and bulk chemistry are particularly variable in space and time, as the carbon pools are composed of autochthonous OM sources produced by the vegetation and allochthonous OM sources introduced to the soil during floods. The allochthonous source can be highly variable depending on the degree of decomposition and humification of OM (Zehetner et al., 2009; Cierjacks et al., 2011; Sutfin et al., 2016; Mayer et al., 2019). Therefore, OM signatures in macro-aggregates sampled in the field were distinguishable by the habitat type (unpublished data), but could not be assigned to one specific engineer or to the mechanisms of OM stabilisation. Even in the semi-controlled field plots in close proximity to the river, which were superposed by the same layers during flood events, the heterogeneity of OM deposited along with the sediments overprinted the signatures of plants and earthworms (unpublished data). Thus, OM signatures in macro-aggregates could only be successfully analysed in mesocosms.

P. arundinacea did not have any effect on OM thermal stabilisation in macro-aggregates (main chapter IIb). Similar to other plants, *P. arundinacea* released root exudates consisting of easy decomposable OM which agglutinates soil particles to stable macro-aggregates. As the light fraction of OM can be efficiently protected inside soil aggregates, *P. arundinacea* can contribute to the physical stabilisation of OM in macro-aggregates. In contrast, *A. chlorotica* contributed to the thermal stabilisation of OM, but the dimension of the effect highly depended on the textural composition of the matrix. *A. chlorotica* had a mixing effect of mineral and OM in the sand and a stabilisation effect of OM in the silt. Similar results were reported by Angst et al. (2017) for a silty soil matrix. In contrast to a sandy matrix, the chemical association of mineral and organic matter is promoted in the silt when the material passes the digestive tract of earthworms (Lavelle 1988; Bossuyt et al., 2005; Frouz et al., 2015). Most likely, physical, chemical and biogeochemical processes are actively involved in the stabilisation of OM in macro-aggregates. The biogeochemical process starts temporally delayed and is accompanied by the hardening of the macro-aggregates, as fresh earthworm structures are hotspots of microbial activity transforming OM into thermally more stable compounds (Brown et al., 2000). Similar to the physical stabilisation of macro-aggregates, OM thermal stability most likely increases over time.

Recent experiments indicated that microbial respiration in macro-aggregates rapidly decreases with time resulting in the relative enrichment of thermally more stable OM which improves the long-term carbon sequestration in macro-aggregates (Zhang et al., 2013; Frouz et al., 2015; Angst et al., 2017). Macro-aggregates formed by *A. chlorotica* in silty alluvial deposits thus can contribute to the carbon sink function in alluvial soils with time.

Interaction effects between plants and earthworms

One of the research questions was whether plants and earthworms contribute concomitantly or independently to soil structure formation in floodplains. However, both field and mesocosm experiments suggested interactions between the engineering organisms, but the outcomes could not provide a clear response to this question (Fig. 3). In general, 80 % of the studies investigating interaction effects between plants and earthworms reported beneficial effects with regard to their respective fitness and to functional aspects (Eisenhauer et al., 2009). Several studies also demonstrated that the aggregate stability was increased in presence of both soil engineering organisms in mesocosms (Fonte et al., 2012; Kohler-Milleret et al., 2013). Generally, plants and earthworms can take advantage of their respective structures. Roots tend to use earthworm tunnels to efficiently enlarge their root network and colonise fresh earthworm casts which are enriched in nutrients (Spiers et al., 1986; Zaller and Arnone, 1999; Decaëns et al., 2011). On the other hand, earthworms feed on plant residues and easy decomposable OM provided by root exudates (Gilbert et al., 2014; Sanchez-de-Leon et al., 2014; Yavitt et al., 2015). However, the quality of OM inputs provided by some plant species can be low causing negative effects on earthworms (Eisenhauer et al., 2009). To date, there is hardly anything known about the quality of root exudates released by *P. arundinacea*. Moreover, certain limitations of the experimental designs and the methods did not allow analysing interaction effects between plants and earthworms. In the data from the field experiment (main chapter I), interaction effects could not be analysed in the same structural equation model, due to the limited number of observations (Grace and Bollen, 2006, 2008). However, as the effect of plants massively exceeded the effect of earthworms as shown in the semi-controlled plots (main chapter III), interpretations of these results might have to be done carefully. Moreover, mesocosm experiments did not provide any clear answer although the conditions were controlled. Using Rock-Eval pyrolysis, OM signatures could

clearly discriminate macro-aggregates according to their origin (main chapter IIa). In treatments containing both engineers, a mixed signature was found in the macro-aggregates, either representing the mean of the individual signatures of macro-aggregates formed by plants and earthworms independently or the additive effect of both engineers on the same macro-aggregate indicating interaction. Furthermore, root galleries and earthworm tunnels could not be clearly distinguished using X-ray CT with the intermediate resolution of the medical scanner. Furthermore, the resolution did not allow the visualisation of whether plants and earthworms took advantage of their respective structures in the samples. Nevertheless, results of previous studies and some of the results of the main chapters II and III indicated that interaction takes place during soil structure formation and OM stabilisation in macro-aggregates. The porosity in treatments containing both organisms was only slightly increased compared to treatments containing only one engineer in mesocosms and in the semi-controlled field plots. Since it was unlikely that one engineer outcompeted the other one almost completely, this result indicated that plants and earthworms used their respective structures in the soils and sediments. Furthermore, the stability of macro-aggregates at least tended to be highest in the silty sediment in the mesocosms and in the layer corresponding to the drilosphere and rhizosphere in the semi-controlled field plots in presence of both engineers. Moreover, OM signatures in macro-aggregates sampled from the treatments containing both engineers were more similar to the signatures of earthworms indicating an OM stabilisation effect in presence of both engineers. Thus, these results rather indicate interaction between plants and earthworms during soil structure formation and OM stabilisation in macro-aggregates.

Application of methods

Soil structure measurements

Soil structure formation is a process that cannot be measured directly, as its characterisation is based on different approaches and includes an undetermined number of mechanisms running at different spatial and temporal scales (Miedema, 1997; Diaz-Zorita et al., 2002; Rabot et al., 2018). Soil structure represents the interface of different spheres in which interactions between physical, chemical and biological processes contribute to its development and stabilisation (Tisdall and Oades, 1982; Bronik and Lal, 2005; Rabot et al., 2018). Currently, the dimension of soil structure is determined using either traditional pedologic indicators (Miedema, 1997) or modern imaging techniques (Vervoort and Cattle,

2003). To date, there are no existing guidelines or defined standard procedures, by what methods soil structure needs to be exactly measured (Rabot et al., 2018). For the experiments presented in the main chapters, both pedologic and modern indicators were applied depending on the experimental design and their applicability. In the field study (main chapter I), the stability of macro-aggregates which is the most pertinent pedologic indicator (Six et al., 2000) was used to determine the structural stability of the topsoil. Additional indicators would have been worthwhile, but the model fit of the SEM did not allow additional parameters to be added. Additional parameters would have required a transformation of the response variable into a composite which would have demanded a large additional number of observations in the field. For the analyses performed in the main chapters IIb) and III), traditional pedologic indicators, e.g. the stability of macro-aggregates and the field-saturated hydraulic conductivity was coupled with a X-ray CT allowing the calculation of modern indicators, e.g. the total length of the segments, the macro-porosity and the connectivity of the macro-pores. The results of the different approaches indicated that using different methods was worthwhile, as the traditional and modern indicators were correlated only to a certain extent. For instance, the macro-porosity in presence of earthworms in the silty treatment in the mesocosm experiment (main chapter IIb) was strongly increased, but the stability of macro-aggregates did not show any significant improvement. Moreover, the field-saturated hydraulic conductivity was not modified in presence of *P. arundinacea*, but the macro-porosity and the stability of macro-aggregates of sandy alluvial sediments was significantly improved (main chapter III). It is therefore highly suggested to combine different traditional and modern indicators to accurately evaluate the development of a stable structure in soils.

However, suggesting imaging techniques as a standard method for the analysis of soil structure would be inappropriate, as these techniques require expensive equipment and software. Furthermore, sampling techniques need to guarantee the preservation of the structural integrity of samples which can be highly demanding in costs and time when relying on cobra samples or freeze coring. Nevertheless, a soil structure index similar to the soil quality index (e.g. Bünemann et al., 2018) would be highly useful to evaluate the evolution of the soil structure on a general scale and provide the possibility to compare the quality of the soil structure within similar ecosystems. Traditional pedologic indicators, such as the stability of macro-aggregates, soil texture, OM content, bulk density and calculated porosity, are robust indicators which are appropriate to be considered for a soil

structure index. Similar to the soil quality index, a soil structure index could be applied dynamically and adapted to the respective research question (Hussain et al., 1999; Cécillon et al., 2009; Ponge et al., 2013). Rabot et al. (2018) proposed to create a database for soil structure measurements categorised according to soil types allowing users to add new measurements and to compare the data with their own measurements. Including data from X-ray CT would help to increase the impact of the observations in a database, but considering them in a soil structure index would not be mandatory.

Considering the landscape hydrology to determine the soil architecture

The landscape hydrology needs to be considered for the analysis of soil structure formation in ecosystems that are strongly influenced by fluctuating water levels (Lin et al., 2015; Ma et al., 2017). Feedback mechanisms between pedologic and hydrologic processes have already been demonstrated to be of particular importance in different semi-terrestrial ecosystems, such as raised bogs and mangrove swamps (Lin et al., 2005; 2015; Bouma 2012, 2016; Ma et al., 2017). The results of the main chapters I and III indicated that the development of a stable soil structure at the Thur River floodplain is to a large extent controlled by surface-water groundwater interactions and by the erosion and deposition of alluvial sediments caused by flooding. Analysing soil structure formation as a function of the landscape hydrology was much more appropriate than as a function of decreasing alluvial dynamics along a toposequence. Since the soils were much more frequently (at least partially) waterlogged by rising groundwater levels than inundated by surface water inflow, the influence of hydrologic processes on soil engineers and the topsoil structure stability would have been dramatically underestimated. As the Thur River floodplain was, representative for others, characterised by a distinctive micro-relief, surface water – groundwater dynamics have a variable influence on the soil independent of the distance to the river. Thus, soil structure formation in floodplains needs to be analysed rather for entire landscape units under consideration of the landscape hydrology than specifically for habitats. For this purpose, Ma et al. (2017) defined the term “soil architecture” considering different landscape units and the landscape hydrology. The field study (main chapter I) focused on the development of the soil architecture as a function of the landscape hydrology analysed through numerical surface water - groundwater flow modelling. However, analysing the landscape hydrology does not automatically require complex numerical modelling. Modelling was performed to estimate the mean annual influence of

inundation by surface water and fluctuating groundwater levels in the recent past. Moreover, the model allowed soil moisture contents to be extracted which were of particular importance for the study. In general, installing a network of piezometers or soil moisture sensors in the field during an observation period is sufficient to analyse the influence of hydrologic processes at the landscape scale. However, numerical flow modelling is more appropriate to analyse hydrologic processes at high spatial and temporal resolution. Moreover, modelling is preferable in highly sensitive or protected areas in order to minimise the environmental impact at the sampling site.

Rock-Eval pyrolysis

Rock-Eval pyrolysis has recently found broad applications in biogeochemical issues, such as for the determination of carbon pools in soils (Saenger et al., 2013; Sebag et al., 2016; Matteodo et al., 2018) or for the transformation of OM in composts (Albrecht et al., 2015). In the main chapters IIa and IIb, Rock-Eval pyrolysis was successfully tested and applied to identify OM signatures in macro-aggregates produced by *P. arundinacea* and *A. chlorotica* and to analyse the mechanisms of OM stabilisation during macro-aggregate formation. In the results, information about the quantity, bulk chemistry and thermal stability of incorporated OM was provided. Gathering this information, macro-aggregates could be successfully assigned to the engineer that contributed to its formation. Discriminating macro-aggregates according to the origin has already been successfully performed by several authors using NIRS (Velasquez et al., 2007; Zhang et al., 2009; Zangerlé et al., 2011). However, as already mentioned before, the application of NIRS is restricted to several physicochemical soil conditions (Cozzolino and Moron, 2004; Chodak, 2008; Bottinelli et al., 2013). Rock-Eval pyrolysis was shown to be more robust, and delivered pertinent results also for samples depleted in OM and enriched in CaCO₃ (Disnar et al., 2003; Carrie et al., 2012). However, under favourable soil conditions, NIRS might be a more useful method to discriminate macro-aggregates according to their origin. OM signatures of a plant and of earthworms are reflected in a specific range of wavelengths corresponding to functional groups of OM (Hedde et al., 2005; Velasquez et al., 2007; Zangerlé et al., 2011). As the peaks of plants and earthworms occur at different wavelengths, macro-aggregates can be clearly assigned to their engineer. Macro-aggregates containing signatures in both ranges of wavelengths strongly indicate to be created by both plants and earthworms. Zangerlé et al. (2011) thus came to the conclusion

that plants and earthworms contribute concomitantly to aggregate formation in the soil. Rock-Eval pyrolysis allows aggregates to be distinguished according to its origin as well, here by using the hydrogen index and the relation between the I-index and the R-index. Using this approach, no clear information about the interactions between *P. arundinacea* and *A. chlorotica* was provided. Furthermore, Rock-Eval pyrolysis could not be successfully applied to macro-aggregates sampled in the field, as the quantity and bulk chemistry of initial OM in different alluvial sediments was too variable in space and time (Tockner and Stanford, 2002; Cabezas and Comin, 2010). Using NIRS, OM extracted from aggregates collected in the field were marked by similar signatures as aggregates produced in the lab when relying on similar soil textures. Comparing aggregates from the field and the lab allowed assigning aggregates from the field to the specific engineer (Zangerlé et al., 2016).

However, in contrast to NIRS, Rock-Eval pyrolysis was able to determine the thermal stability of OM in macro-aggregates (main chapters IIa and IIb). Using the R-index and I-index diagrams, mechanisms of OM stabilisation could be described for *P. arundinacea* and *A. chlorotica* in alluvial deposits of different texture. Better understanding these mechanisms is of crucial importance to improve the knowledge about OM dynamics and the mechanisms of carbon sequestration in the soil (Schmidt et al., 2011). Rock-Eval pyrolysis can make a decisive contribution to this purpose. Nevertheless, the pertinence of Rock-Eval pyrolysis still needs to be evaluated more in detail, as OM signatures in macro-aggregates from different soil engineers might vary, as indicated by Fischer et al. (unpublished) for different earthworm species. Furthermore, the authors demonstrated that the size of the aggregates as well as different pre-treatments, such as plunging the aggregates into water can influence the OM signatures found in macro-aggregates. Thus, standard methods for aggregate sampling and pre-treatments of the samples need to be defined in order to increase the validity of samples analysed with Rock-Eval pyrolysis.

General applicability of the data within different scales

The contribution of plants and earthworms to soil structure formation was analysed in a three stage experiment starting with observations in the field, followed by analyses in mesocosms and semi-controlled field plots exposed to natural alluvial dynamics. In the field, plant and earthworm communities were considered, while each one specific species

had to be selected for mesocosm experiments and one specific pioneer herbaceous plant for the semi-controlled field plots. The respective species needed to be representative for the floodplain, efficient colonisers and resistant to physical conditions and distinctive soil physicochemical properties. The fast-growing herbaceous plant species *P. arundinacea* was selected due to its wide abundance in habitats in close proximity to the river. *A. chlorotica* was selected as a representative earthworm species, as it is an efficient coloniser in alluvial soils being able to tolerate a broad range of soil characteristics and environmental conditions (Le Bayon et al., 2013; Amossé et al., 2015). However, *A. chlorotica* was shown to be rather a compacting species contributing to a lesser extent to the formation of stable macro-aggregates (Blanchart et al., 1997; Milleret et al., 2009a, b). Other endogeic earthworm species such as *Aporrectodea caliginosa* or *Aporrectodea rosea* would have been more appropriate to analyse soil structure formation as they highly contribute to the formation of macro-aggregates (Bossuyt et al., 2005; Yavitt et al., 2015; Lubbers et al., 2017). However compared to *A. chlorotica*, both species are highly sensitive to waterlogging in soil and to coarse textured soils (Ivask et al., 2007; Zorn et al., 2005, 2008; Eijssackers, 2010; Amossé et al., 2015). As the sandy soils were frequently affected by high soil moisture contents, *A. chlorotica* was nevertheless selected for mesocosm analyses. Despite selecting two specific soil engineering organisms for the controlled analyses, the results describing the mechanisms of macro-aggregate formation and OM stabilisation can be to a certain extent considered representative for mechanisms running in floodplain systems. *P. arundinacea* was the predominant species in close proximity to the Thur River being also abundant on the riverbanks of several other floodplains, at least in Switzerland (Joye et al., 2006; Greenwood and Kuhn, 2014). Most likely, the results of macro-aggregate formation and OM stabilisation can also be projected to other pioneer herbaceous grass species, but not to shrubs and trees as the chemical composition and the quality of root exudates can differ among plants (Nardi et al., 2005; Shukla et al., 2011; Li et al., 2013). Results obtained for *A. chlorotica* might be more species-specific and can be at most representative for other endogeic earthworms. Fischer et al. (unpublished) demonstrated that the mechanisms of OM stabilisation vary among species and ecological categories. Nevertheless, the structuration behaviour of *A. chlorotica* described in mesocosms can be most likely projected to the field scale.

Soil structure and river restoration – future challenges under climate change

Increasing the structural stability of soils is extremely important in young and dynamic floodplain ecosystems and can play a key role in river and floodplain restoration projects. Both plants and earthworms have shown their great potential to contribute to soil structure formation, either immediately despite strong alluvial dynamics or in the long term. Facilitating the colonisation of alluvial deposits with pioneer herbaceous plants and releasing earthworm communities might be efficient strategies to improve the success of current river restoration projects. However, global change might alter the landscape hydrology in floodplain ecosystems creating more challenging conditions for soil engineering organisms in the future. In floodplain ecosystems of temperate regions, warming climate is suspected to modify the intensity, frequency and the timing of flood events (IPCC, 2012). Based on observations at 4262 hydrometric stations in 38 countries across Europe, discharge characteristics of rivers have dramatically changed within the last 50 years (1960 – 2010) (Blöschl et al., 2017). In recent years, spring floods were shown to occur earlier due to earlier snow melt, summers were marked by an extended period of low water discharge and flash floods were prone to occur more frequently and intensively in late summer after heavy thunderstorms in the catchment areas (Blöschl et al., 2017). This trend imposes special challenges on soil engineering organisms in the future, particularly on the resistance to stronger physical forces, extended periods of waterlogging in soils as well as more intense heat and drought periods in summer (Thonon and Klok, 2007). Post-monitoring in current restored river and floodplain sections clearly indicate that river restoration mainly has positive effects on the biodiversity and ecosystem services (Fournier et al., 2012; Bullinger-Weber et al., 2014). However, modified discharge characteristics in the future might decrease the abundance of soil engineers either directly or indirectly through the reduction of suitable habitats. The latter might be a general problem for earthworms, as the hydrologic reconnection between river and floodplain was shown to decrease the abundance of earthworms in a restored floodplain section anyway (Thonon and Klok, 2007; Fournier et al., 2015). Modified discharge characteristics might even accelerate the reduction of earthworms in restored floodplains. Increased impacts of alluvial dynamics are also supposed to affect plants. Particularly pioneer herbaceous plants might be threatened by stronger physical forces causing damages on the leaves, or buried by thick sediment layers. Stronger alluvial dynamics might be indirectly less impacting on the colonisation potential of pioneer herbaceous plant communities, as alluvial sediment deposits usually contain large amounts of viable seeds allowing riverbanks to be rapidly

colonised by plants (Tabacchi et al., 2005; Gurnell, et al., 2006; Hayashi et al., 2011; Corenblit et al., 2014; Gurnell, 2014). Since *P. arundinacea* was shown to efficiently stabilise recent alluvial sediments within only one year, the progress of soil structure formation by pioneer herbaceous plants might not be suspended with increasing alluvial dynamics. However, alluvial sediments also contain large amounts of seeds from non-native plants being able to colonise riverbanks as well (Paillex et al., 2009). Some of these might compete with native species and are thus not automatically supposed to increase the habitat biodiversity (Fournier et al., 2015). Moreover, some invasive herbaceous plants such as the Himalayan *Impatiens glandulifera* which was also found at the “Schaffäuli” site can have a destabilising effect on the soil and impair the development of a stable soil structure (Greenwood and Kuhn, 2014). Recent findings indicated that the seed dispersal of *I. glandulifera* can be positively affected by floods as the seeds are highly resistant to water saturation (Čuda et al., 2017). In case that *I. glandulifera* outcompetes *P. arundinacea* at the Schaffäuli site, soil structure formation is suspended most likely resulting in strong river shore erosion. To maintain the process of soil structure formation and to improve the success of river restoration, herbaceous plant communities in restored river corridors need to be controlled. Invasive species such as *I. glandulifera* need to be removed throughout in order to ensure the success of the river restoration project.

General conclusions

The three stage experimental design allowed the contribution of plants and earthworms to soil structure formation in floodplain soils to be analysed at three different scales. Multiple interactions including the landscape hydrology and soil physicochemical parameters were considered in the field, the mechanisms of macro-aggregate formation and OM stabilisation in mesocosms, and the time and efficiency of soil engineering organisms under extensive alluvial dynamics by means of semi-controlled field plots. Plants and earthworms were demonstrated to be highly successful soil engineers in floodplain soils, whereby plants in the short term and earthworms in the long term. Plants were strongly affected by fluctuating water levels in the field, but nevertheless improved the structural stability of the topsoils. In particular, the pioneer herbaceous plant *P. arundinacea* was able to create a stable soil structure of especially sandy alluvial sediments and to build up stable macro-aggregates in the short term despite extensive alluvial dynamics. Earthworm abundance did not indicate any correlation to the topsoil structure stability, soil physicochemical parameters and the landscape hydrology. However, *A. chlorotica* improved the macro-porosity of especially silty sediments in the short term, but their structures were not water stable. Since *A. chlorotica* was demonstrated to improve the thermal stability of OM in macro-aggregates and earthworm structures generally become water-stable with aging, *A. chlorotica* might successfully contribute to the long term sequestration of OM in soil macro-aggregates in silty alluvial soils. The results of the three stage experiment could not clearly confirm, but strongly indicate that plants and earthworms, at least *P. arundinacea* and *A. chlorotica*, contribute concomitantly to the formation of stable macro-aggregates and to the thermal stabilisation of OM. The methodologies used for soil structure analyses were highly useful, but accurate implementations and precise applications still need to be defined. Rock-Eval pyrolysis was a promising tool to discriminate soil aggregates formed by plants and earthworms and to identify the mechanisms of OM thermal stabilisation in macro-aggregates, but the procedures of sample preparation prior to the analysis still need to be standardised. Assuming an increased soil development along a topographical gradient with decreasing flood frequency does not accurately reproduce the influence of hydrologic processes on soil structure formation in floodplains. The landscape hydrology, particularly the surface water – groundwater dynamics need to be considered when analysing soil structure formation in floodplains at different landscape units. Currently, soil structure is measured using a broad variety of pedologic indicators and modern imaging techniques.

Measurement procedures of soil structure need to be standardised, potentially by means of a soil structure index or in a database in order to make observations on soil structure comparable. Despite future changes of alluvial dynamics which can be challenging for plants and earthworms, *P. arundinacea* and earthworm communities can help to improve the success of river restoration projects. To maintain their functioning, colonisation of the species needs to be favoured and the spread of invasive species controlled.

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