

Chapter 3

EARTHWORM COMMUNITIES AS INDICATORS FOR EVALUATING FLOODPLAIN RESTORATION SUCCESS

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ABSTRACT

Floodplains are known to be areas of extraordinary biodiversity with a mosaic of shifting habitats with high interdependency. Such complex ecosystems fulfil a wide range of ecosystem services concerning economic, social and ecological functions. Moreover, functioning as complex ecotones at various spatio-temporal scales, floodplains usually provide a diversity of habitats and microhabitats for many organisms from river channels to uplands. However, these ecosystems have been largely subjected to human pressure through the embanking of rivers. Such damages have led to river restoration projects in order to re-establish a near-natural alluvial dynamics and to recover floodplain naturalness and biodiversity. In Switzerland, several projects have been implemented to maintain or recreate floodplain ecological functions, in particular for flood protection and biodiversity. In such context, this chapter highlights biological and pedological features as indicator tools to evaluate the success of floodplain restoration, focusing on earthworm communities that are assumed to vary in terms of species diversity, abundance and biomass along a gradient of naturalness from the embanked system to the near-natural reference. The first section of the chapter deals with floodplain restoration and potential consequences on soil functions. Then, the second section presents an overview of earthworm communities and activities as ecosystem engineers, their habitats and their

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potential resilience to disturbance and stress. Concerning near-natural floodplains in Switzerland, the third section focuses on earthworm communities and environmental variables that may affect their distribution taking into account two spatial variables: 1) an altitudinal gradient from subalpine to hill levels, and, 2) a gradient perpendicular to the river, stratified by vegetation. The impact of fluvial dynamics is also discussed. The fourth section addresses the comparison of two floodplains that are partly embanked and restored (The Emme and Thur Rivers) and highlights the potential of earthworms as bioindicators of early stages of river restoration. Finally, the last section proposes future prospects to assess the success of ecological restoration, i.e. the self-sustainability of restored floodplains.

Keywords: Floodplains, earthworms, river restoration, alluvial soils

1. FLOODPLAIN RESTORATION

Floodplains are considered as complex ecosystems that provide a wide range of ecosystem services, which could be defined as the beneficial flows arising from natural capital stocks and fulfilling human needs (Dominati et al., 2010). These ecosystem services concern economic, social and ecological functions such as flood protection, recreation areas, biodiversity reservoir and nutrients cycling (Mitra et al., 2005). In a context of global warming, climate change may thus induce deep modifications in the stream flow primarily through variations in precipitation, hydrological conditions and river morphological characteristics which are of the most important issues impacting floodplains (Bertrand et al., 2012; Karamouz et al., 2011). Such modifications have consequences on biogeochemical cycles being concerned especially their central roles in alluvial systems that need investigation to assess likely impacts.

Moreover, within a framework of prevention from flood events, floodplain ecosystems have been deeply modified by dam construction and embanking (Tockner and Stanford, 2002). River infrastructures have however usually negative impacts on freshwater ecosystems as for instance loss of biodiversity as well as river channelling that accelerates water flow. Hence, current floodplain management is now being revised to recreate functional and diverse alluvial ecosystems (Wohl et al., 2005) and removal of in-stream structures is often seen as a viable option for sustainable watershed management (O’Hanley, 2011). River restoration projects are then off-the-moment (Palmer et al., 2005; Palmer and Bernhardt, 2006) notably in Switzerland where the modification of the Federal Law on the Protection of Waters (814.20, Article 38a) on January 1st 2011 has led regional authorities to define, schedule, and carry out restoration strategies for rivers (Palmer and Bernhardt, 2006; Wohl et al., 2005).

Assessing the outcome of river restoration projects is essential for adaptive management, evaluation of project efficiency, optimization of future programs, and gaining public acceptance (Woolsey et al., 2007). Potential indicators or criteria for evaluating river restoration success have been highlighted by several authors who particularly pointed out water quality (especially N and P contents), viability of target species (i.e. nesting possibilities for the Little Ring Plover (*Charadrius dubius*) and increased rates of ecosystems functions (carbon storage, biodiversity) (Jansson et al., 2005; Ruiz-Jaen et al., 2005; Woolsey et al., 2007; Henry et al., 2002). However, few research considered soils, humus forms or pedofauna as potential indicators of restoration success (Cui et al., 2009) albeit soils integrate

information on ecosystem structure and could record past and present events of fluvial dynamics (Gerrard, 1987; Gerrard, 1992; Daniels, 2003; Bullinger-Weber and Gobat, 2006). Thus, pedological ecological functions such as flood regulation or carbon storage may be used as indicators of restoration success (Lorenz, 2003). Despite all these advantages, soils and their inhabitants remain poorly considered and a better knowledge is needed regarding consequences of river restoration on essential functions of soils (notably support for soil biota and organic matter storage).

2. ECOLOGY OF EARTHWORM COMMUNITIES

2.1. Habitats

Earthworms constitute the largest terrestrial faunal biomass and occur worldwide preferring moist habitats of moderate temperature (Lee, 1985; Edwards and Bohlen, 1996) and being the most abundant in forests and grasslands (Coleman and Whitman, 2005). Their spatial distribution is widely heterogeneous depending on environmental factors, i.e. plant cover, and soil properties (texture, organic matter content), and internal population processes, i.e. reproduction rates and dispersal mode (Bullinger-Weber et al., 2012; Jimenez et al., 2011). Earthworms are generally split into three main ecological categories based on their behaviour and feeding ecology (Bouché, 1977): i) epigeic species often prefer substrates enriched with organic matter, and usually live in plant litter onto the soil surface; ii) endogeic species inhabit organo-mineral soil layers and, iii) anecic species take advantages of both the surface litter as a source of food and the mineral soil as a refuge in which they did burrows (Coleman and Whitman, 2005).

2.2. Ecosystem Engineering

Ecosystem engineers change biotic or abiotic materials in their environment thereby creating or modifying habitats and hence controlling availability of resources to other species (Jones et al., 1994, 1997; Lavelle, 1997; Lavelle et al., 1997; Decaëns, 2010). Ecosystem engineers are also well-known to provide ecosystem services (Fonte and Six, 2010).

Earthworms are thus usually classified as allogenic engineers (Lal, 1991; Berke, 2010) belonging to burrowing and excavating organisms (Shipitalo and Le Bayon, 2004; Edwards, 2004), and as chemical engineers through the addition of mucus enriched in carbon, nitrogen and phosphorus during the gut transit (McInerney et al., 2001; Schrader and Zhang, 1997; Le Bayon and Binet, 2006). Furthermore, being major bioturbators in terrestrial ecosystems, earthworms largely contribute to the formation of stable microaggregates within macroaggregates leading to a crumb soil structure that helps the protection of organic carbon (Bossuyt et al., 2005). Until now, most of the studies on earthworm communities have been conducted on mature soils and describe interactions between biota and structure in cultivated soils (Davidson and Grieve, 2006a, 2006b).

Few studies have been carried out in alluvial soils despite the fact that they are unique among terrestrial ecosystems to experiment recurrent primary succession (Bechtold and

Naiman, 2009), and constitute a relevant model to study initial stages of soil formation and in particular the role of earthworms in the topsoil structure formation. The presence of water stable macro-aggregates due to earthworm activities has been showed from pioneer stages of topsoil formation under willow forests (Guenat et al., 1999). Bullinger-Weber et al. (2007) show that epigeic earthworms and enchytraeids are the first engineers producing in a short-term soil structure and then, if texture is favourable, anecic and endogeic earthworms may colonize the different soil layers improving physical and nutrient conditions and creating long-term stable aggregates.

2.3. Resilience to Disturbance and Stress

Across various range of habitats, earthworms display a wide array of morphological, physiological, and behavioural adaptations to environmental conditions. For example, many species are able to enter a temporary dormant state (diapause or quiescent state) or produce resistant cocoons during unfavourable periods (Coleman and Whitman, 2005). Several studies focused on earthworm frost tolerance (Joergensen et al., 2008), their accommodation to heavy metals concentration such as copper (Fisker et al., 2012, 2013), atrazine and cadmium (Wang et al., 2012) and amendments (Lapied et al., 2009). Some others highlight impact of combined effects on earthworms (*Dendrobaena octaedra*) such as synergistic interactions between heavy metals and frost survival, and antagonistic ones between polycyclic aromatic hydrocarbons (PAHs) and frost survival (Bindesbol, 2008). In a floodplain context, Cornelis et al. (2009) observed high copper concentrations both in soil and in *Lumbricus rubellus* tissues while earthworm abundance and biomass were not affected. Thus, effects at the cellular level therefore did not result in a reduced functioning of earthworm communities (Cornelis et al., 2009). Moreover, flood events may greatly influence earthworm communities (see section 3.3 for more details).

3. EARTHWORM COMMUNITIES IN NEAR-NATURAL FLOODPLAINS

3.1. Earthworm Communities' Composition

In near-natural floodplains, succession and community-assembly changes occur more rapidly than in any other ecosystems due to high turnover of habitats and ecosystems (Milner and Tockner, 2010). According to Petts and Amoros (1996), successions of animal and plant communities pledged to alluvial systems are generally arranged along topographic gradients where pedological changes occur over time-scales from months to several hundred years. This variability of pedological stages leads hence to a particularly high soil heterogeneity and habitat diversity compared to other terrestrial ecosystems (Cierjacks et al., 2011). However, research projects on earthworm communities in floodplains are scarce so far (Ivask et al., 2007; Plum and Filser, 2005; Zorn et al., 2005, 2008). Moreover, most of them were conducted at the hill level and focused on flooded meadows in northern Germany (Plum and Filser, 2005), flooded grasslands in river valley in Estonia (Ivask et al., 2007) or short grass and herbaceous vegetation in the Netherlands (Zorn et al., 2005, 2008). All these researchers

recovered from 5 to a maximum of 8 species in their respective study sites. Gathering all results leads to the following diversity: epigeics (*Lumbricus rubellus*, *L. castaneus*, *Eiseniella tetraedra*, *Dendrodrilus rubidus*), endogeics (*Allolobophora chlorotica*, *Octolasion tyrtaeum*, *O. cyaneum*, *Aporrectodea rosea*, *A. caliginosa*) and one anecic species (*L. terrestris*).

Table 1. List of ecological categories and species of earthworms recovered in near-natural floodplains in Switzerland at several altitudinal levels. From Guenat et al. (1999), Bullinger-Weber et al. (2007), Salomé et al. (2011) and Bullinger-Weber et al. (2012)

Epigeic species
<i>Bimastos eiseni</i> (Levinsen, 1884)
<i>Dendrobaena octaedra</i> (Savigny, 1826)
<i>Dendrobaena pygmae cognetti</i> (Michaelsen, 1903)
<i>Dendrobaena pygmae pygmae</i> (Savigny, 1826)
<i>Dendrodrilus rubidus rubidus</i> (Savigny, 1826)
<i>Dendrodrilus subrubicundus</i> (Eisen, 1874)
<i>Eiseniella tetraedra tetraedra</i> (Savigny, 1826)
<i>Eisenia andrei</i> (Bouché, 1972)
<i>Lumbricus castaneus</i> (Savigny, 1826)
<i>Lumbricus meliboeus</i> (Rosa, 1884)
<i>Lumbricus rubellus</i> (Hoffmeister, 1843)
<i>Octodrilus argoviensis</i> (Bretscher, 1899)
Anecic species
<i>Aporrectodea caliginosa nocturna</i> (Evans, 1946)
<i>Aporrectodea giardi giardi</i> (Ribaucourt, 1901)
<i>Aporrectodea longa longa</i> (Ude, 1885)
<i>Aporrectodea longa ripicola</i> (Bouché, 1972)
<i>Aporrectodea longa ripicola viridis</i> (Bouché, 1972)
<i>Lumbricus terrestris</i> (Linnaeus, 1758)
Endogeic species
<i>Allolobophora chlorotica chlorotica</i> (Savigny, 1826)
<i>Aporrectodea caliginosa alternitosa</i> (Bouché 1972)
<i>Aporrectodea caliginosa caliginosa</i> (Savigny, 1826)
<i>Aporrectodea handlirschi handlirschi</i> (Rosa, 1905)
<i>Aporrectodea icterica icterica</i> (Savigny, 1826)
<i>Aporrectodea rosea rosea</i> (Savigny, 1826)
<i>Octolasion cyaneum</i> (Savigny, 1826)
<i>Octolasion tyrtaeum lacteum</i> (Oerley, 1885)
<i>Octolasion tyrtaeum tyrtaeum</i> (Savigny, 1826)

Other studies looked at earthworm communities in floodplains along an altitudinal gradient. Thus, overall in several Swiss near-natural floodplains, Guenat et al. (1999), Bullinger-Weber et al. (2007), Salomé et al. (2011) and Bullinger-Weber et al. (2012) found 27 species and subspecies from subalpine to hill levels (Table 1). This record is the highest compared to studies cited above and corresponds to two-thirds of all inventoried earthworm species and subspecies in Switzerland, confirming that floodplains are among the most diverse terrestrial ecosystems, as already shown for vascular plants, for example (Gallandat et

al., 1993). All earthworm ecological categories are represented and their distribution was observed to be widely heterogeneous within the same floodplain (Bullinger-Weber et al., 2007) as well as in the same vegetation unit (Bullinger-Weber et al., 2012). Moreover, for the first time, the species *Lumbricus moliboeus* was recovered in carbonated soils while usually observed in acidic conditions (Bouché, 1972).

3.2. Environmental Variables Affecting Earthworm Communities

Several environmental variables, independently and/or interacting together, may influence the distribution and the composition of earthworm communities in near-natural floodplains, at different spatio-temporal scales. Hence, according to Emmeling (1995), main factors that may affect the soil macrofauna distribution in floodplains are soil organic matter content, soil moisture and flooding characteristics. Salomé (2011) enhanced these conclusions and highlighted a hierarchy of variables that govern the composition of earthworm communities. Different partitioning variance analyses demonstrated that the interaction between soil parameters and altitude explained the earthworm species diversity, total biomass, total abundance and species abundance, as well as biomass and abundance of earthworm ecological categories (data not shown).

The high temporal and spatial changes of these variables, mostly due to fluvial dynamics, create a broad mosaic of habitats. Consequences of this unpredictable environment are regularly observed on earthworm communities thus reflecting alluvial dynamics (Salomé et al., 2011; Bullinger-Weber et al., 2012). Going further into details, soil types and parameters influence earthworm communities (Guenat et al., 1999), especially depth and texture that drive the distribution of ecological categories. A recent study was conducted on this topic in the Rhine River floodplain (unpublished data; photo 1; Figure 1).



Photo 1. The near-natural site (“Rhäzuns”) is located along the Rhine River (canton of Graubünden, Switzerland) is a site of national importance. The site lies at 600 m a.s.l, annual precipitation ranges between 800 and 1000 mm and mean annual temperature is 7.1°C. The mean annual flow is about $40 \text{ m}^3 \text{ s}^{-1}$, with a minimum and a maximum annual discharge of $23 \text{ m}^3 \text{ s}^{-1}$ and $60 \text{ m}^3 \text{ s}^{-1}$, respectively. The alluvium deposits are mostly composed of calcareous pebbles and sand. The channel pattern corresponds to a braided river.

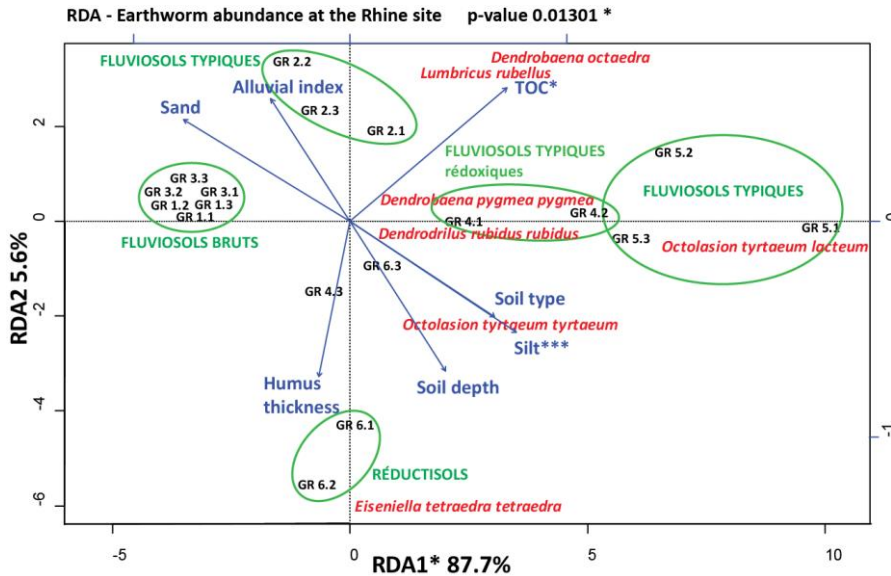


Figure 1. Redundancy analysis on earthworm abundance at the near-natural site “Rhäzuns” along the Rhine River. GR 1 to GR 6 indicated soil profiles with three replicates and their corresponding soil types (in green). Environmental variables are indicated in blue, TOC being the total organic carbon content and the alluvial index reflecting alluvial dynamics (calculated by dividing the total number of layers by the total depth of the profile). Earthworm species are specified in red. Levels of statistical significance are as followed: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Two main types of soils were identified: Fluvisols and Gleysols (IUSS Working Group WRB, 2006) which correspond to FLUVIOSOLS (GR 1- GR 5) and RÉDUCTISOLS (GR 6) according to the Référentiel Pédologique (Baize and Girard, 2009). This latter classification allows discriminating several stages of soil evolution, especially for fluvisols which are then divided in FLUVIOSOLS BRUTS, FLUVIOSOLS JUVÉNILES and FLUVIOSOLS TYPIQUES. Based on the degree of maturation of humiferous topsoil, this subdivision is essential to describe precisely and better understand the functioning of each soil type and to relate it to earthworm communities. This kind of soil succession results from fluvial dynamics that control sedimentation and erosion processes, and in turn the *in situ* pedogenesis duration (Daniels, 2003). In our study case, we thus observed a gradient from bare soils (GR 1, FLUVIOSOLS BRUTS) to developed soils (GR 5, FLUVIOSOLS TYPIQUES). The frequency of flood events and their intensity over the year are essential to explain pedogenesis. At the Rhine site, not the duration of floods but the period of the year at which they occur as well as the water discharge appear to be primordial. Hence, in June when flooding is the highest, floods are rapid and violent thus carrying rough sediment (pebbles, coarse sand), eroding or burying river banks then in turn destroying habitats. All these variables govern the distribution and the composition of earthworm as revealed by alluvial index, soil type and soil texture (Figure 1). Organic matter and especially total organic carbon (TOC) regulates also the presence of epigeic earthworms such as *Dendrobaena octaedra* and *Lumbricus rubellus* (Figure 1). In addition, hydromorphy features led to the identification of FLUVIOSOLS TYPIQUES rédoxiques and RÉDUCTISOLS, which, despite occasional anoxic conditions, seem to be in favour of earthworms as a general trend due to their soil thickness and their fine texture (*Octolasion tyrtaeum tyrtaeum*). In addition, the thickness of

humus favours especially epigeics to live in (*Eiseniella tetraedrea tetraedrea*). Both the fine texture and the humus thickness contribute also to a better water retention that allows earthworms to resist to desiccation, at the opposite from FLUVIOSOLS BRUTS where the moisture and temperature amplitudes are high. Looking at the repartition of earthworms along the gradient of soils and vegetation (Figure 2), the stability of habitats governs widely earthworm communities' distribution which gathered in FLUVIOSOLS TYPIQUES and RÉDUCTISOLS. Despite the fact that no anecic species were observed, epigeic species dominated in terms of species diversity and abundance (*L. rubellus* and *D. octaedra*). The endogeic *Octolasion tyrtaeum lacteum* was recovered everywhere while *Octolasion tyrtaeum tyrtaeum* and some individuals of *Aporrectodea rosea rosea* were collected in deep and fine-textured soils. Other studies confirmed that soil types and parameters influence earthworm communities (Guenat et al., 1999), especially depth and texture that drive the distribution of ecological categories. In this case of deep soils and fine texture, the highest abundance and biomass of earthworms are observed (Guenat et al., 1999). Moreover, a fine soil texture leads to a higher diversity of earthworm categories and species. Thus, epigeics are usually associated with coarse sandy texture in contrast to anecics and endogeics which prefer silty soils from alluvial forests (Guenat et al., 1999; Bullinger-Weber et al., 2007; Salomé et al., 2011).

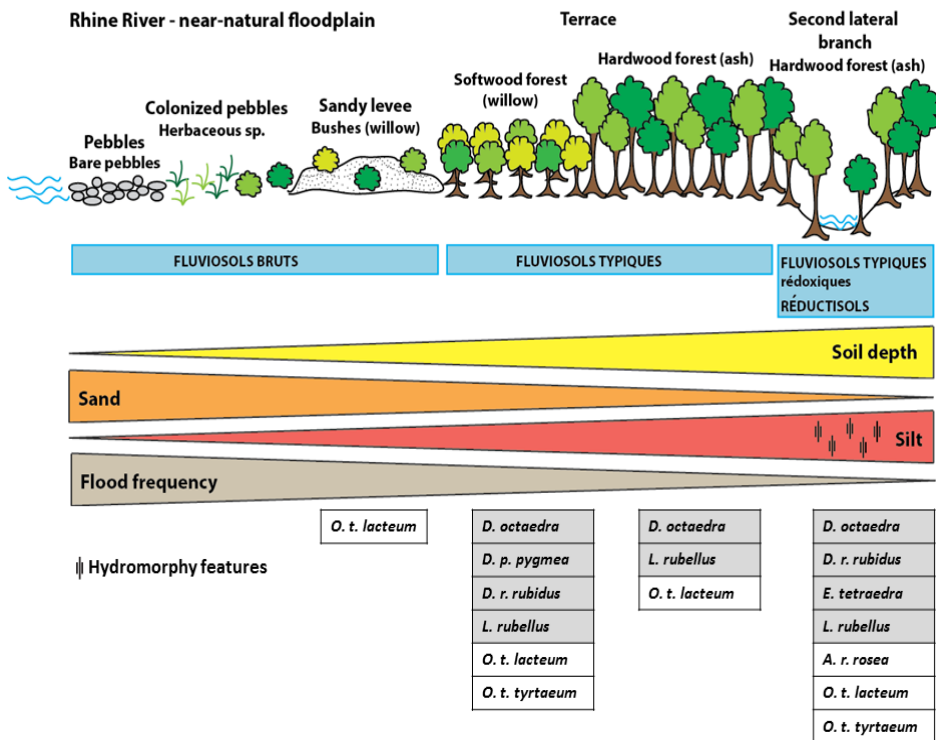


Figure 2. Schematic representation of the near-natural Rhine site. Vegetation succession and topography are represented from the riverbed (left) to the mature forest. All soils are calcareous-rich soils; soil depth, sand and silt contents as well as hydromorphy features and flood frequency are shown. Earthworm species are listed, epigeic and endogeic in grey and white boxes, respectively.

Focusing on humus forms is also an interesting approach regarding the aboveground-belowground ecological relationships. Humus forms hence reflect plant-soil interactions being the place where resonance between these communities takes place, both in functional and evolutionary sense (Ponge, 2013). In the floodplain context, mineral parental material plays a crucial role in the formation and evolution of humus forms. According to Jabiol et al. (2013) classification, most of the studied humus forms belong to the group of Fluvic Parahumus, especially in the vicinity of the river bed where coarse sediments predominate. As for soils, the variability of terraces' topography is correlated to a gradient of humus forms and a large panel of them (from Fluvic Parahumus to Mull, Moder and Amphi forms) could be observed in floodplains. However, research is currently in progress for a better understanding of these aboveground-belowground relationships between vegetation, humus forms soils and macrofauna communities.

3.3. Earthworm Communities and Fluvial Dynamics

As a general rule, earthworms can cope well with submergence short-term floods. However, their resistance differs according to ecological categories and species. Some of them are known to be well adapted to floods and have even been classified as riparian species (Roots, 1956; Sims and Gerard, 1999 in Schütz, 2008). Roots (1956) even reported that some species could survive for 31-50 weeks in submerged soils. Nevertheless, flooding may generally affect negatively earthworm populations by decreasing their numbers immediately after flooding (Zorn et al., 2005). The duration of flooding seems to be the most limiting factor, as species' tolerance is related to high soil moisture and low aeration. The period of flooding is also crucial because effects will not be the same on earthworm communities if it occurs during the reproduction seasons when earthworms move a lot onto the soil surface (Spring and Autumn) or the estivation time when earthworms are deep in the soils (Summer and Winter). When flood occurs, Lumbricidae could use different strategies for flooding survival in wet grassland, *i.e.* horizontal/vertical migration, physiological adaptation, and reproduction strategies (Plum, 2005). Zorn et al. (2005) showed that earthworm numbers and biomasses tend to decrease during flooding and that different earthworm species and ecological categories react differently towards these flooding dynamics. For instance, these authors showed that the anecic *Lumbricus terrestris* was found in high numbers only at the end of a flooding period while the endogeic *Allolobophora chlorotica* was hardly affected by flooding. Moreover, *Aporrectodea caliginosa* showed fluctuating numbers and biomasses during the sampling period that did not correlate with flooding frequency. Finally, the epigeic *Lumbricus rubellus* is a successful colonizer (Eijsackers, 2010) well adapted to flooded soils and that may escape to more favourable habitats when a flood event occurs (Simonsen and Klok, 2010; Zorn et al., 2008). As already mentioned above, not the duration of submersion but mostly the mechanical action of floods (erosion, sedimentation) regulates earthworm communities (abundance, diversity and dispersion) in our studied braided rivers.

4. EARTHWORM COMMUNITIES IN RESTORED FLOODPLAINS

4.1. Earthworm Communities' Composition

Some studies about earthworm communities have been reported in human transformed ecosystem (Thonon and Klok, 2007; Schütz et al., 2008). In Switzerland, Fournier et al. (2012) reported a total of 15 species and subspecies in a restored floodplain of the Thur River, whereas 9 species were found in the non-restored area corresponding to an embanked pasture.



Photo 2. The Emme River (canton of Bern) is one of the oldest river widening projects in Switzerland. The study sites are located between Aeflingen (restored stretch; photo at the top) and Oberburg (embanked stretch; photo at the bottom) in an agricultural floodplain and lies respectively at 560 m a.s.l. and 460 m a.s.l. Annual precipitation is about 1050 mm year⁻¹, as average annual temperature is 9.4 °C. Before river modification by embanking and dam construction, the channel pattern of Emme River was braided. The annual mean flow rate is about 19 m³ s⁻¹ with a minimum and maximum annual discharge of 9 m³ s⁻¹ and 28 m³ s⁻¹, respectively. Alluvial deposits are mostly composed of calcareous pebbles and sand. Aiming at flood protection and water quality improvement, restoration of the site was conducted in two steps. At Aeflingen site, embankments were removed and thus the riverbed was widened (30 m width) in 1991/92 and secondly in 1998/99 on both sides of the river, along a 530 m stretch.

In addition, the average abundances were respectively 93 and 67 individuals per square meter. These authors confirmed the general trend previously observed that *Allolobophora chlorotica*, *Eiseniella tetraedra* and *Lumbricus rubellus* adapted to disturbed environment due to their r-strategy behaviour with fast maturation and high reproduction rates (Bouché, 1972; Bouché, 1977; Gerard, 1967; Satchell, 1967). These species may thus take advantage of the perturbation generated by the restoration process to increase in density and biomass. In thicker soils showing the finest texture, Fournier et al. (2012) found also anecic species such as *Aporrectodea longa*, *A. caliginosa nocturna*, and *L. terrestris*, *A. longa* being the most tolerant species to flooding.

A recent study was conducted comparing earthworm communities in embanked and restored stretch of the Emme floodplain (unpublished data; Photo 2; Table 2).

Table 2. Earthworm abundance (mean \pm standard deviation) per square meter in the Emme River floodplain (embanked and restored stretches)

Ecological category	Earthworm species	N = 21 (ind m ⁻²)	
		Restored	Embanked
Epigeic	<i>Dendrobaena octaedra</i>	14 \pm 27.4	7 \pm 6.0
	<i>Dendrodilus rubidus rubidus</i>	2 \pm 3.5	1 \pm 1.5
	<i>Lumbricus rubellus</i>	1 \pm 1.4	-
	<i>Lumbricus friendi</i>	-	0 \pm 0.8
Endogeic	<i>Octolasion tyrtaeum lacteum</i>	2 \pm 3.7	5 \pm 6.3
	<i>Octolasion tyrtaeum tyrtaeum</i>	0 \pm 0.9	-
	<i>Aporrectodea rosea rosea</i>	1 \pm 3.5	5 \pm 9.2
	<i>Aporrectodea caliginosa caliginosa</i>	1 \pm 1.7	4 \pm 5.0
Anecic	<i>Aporrectodea caliginosa nocturna</i>	4 \pm 7.0	5 \pm 4.8
	<i>Lumbricus terrestris</i>	1 \pm 3.2	14 \pm 10.4

All ecological categories were observed, anecics being more numerous in the embanked site (Table 2) while epigeic species dominated in the restored section of the floodplain. Despite the low number of individuals, 10 species and subspecies were observed, *Lumbricus rubellus* and *Octolasion tyrtaeum tyrtaeum* being only observed in the restored part.

Such comparison of earthworm communities in embanked, restored and near-natural floodplain could be helpful to evaluate river restoration success, and the main unresolved question is to know if earthworm communities could be potential indicators in such a context.

4.2. River Restoration: How Does It Change Earthworm Communities?

The Emme River

As for the near-natural site in the Rhine River floodplain, we looked at the repartition of earthworms along the gradient of soils and vegetation at the Emme site (Figure 3), taking into account soil types and parameters. It appears that the stability of habitats governs widely earthworm communities' distribution which gathered in FLUVIOSOLS TYPIQUES and

FLUVIOSOLS TYPIQUES polyphasés. No earthworm was recorded in FLUVIOSOLS BRUTS but all earthworm categories were observed elsewhere. Compared to the embanked stretch, earthworm species diversity is higher in the restored floodplain (9 species instead of 7). The steep slope behind the willow forest leads to a strong decrease of flood frequency thus maintaining deep and stable soils favourable to earthworm colonization. As in the near-natural site, the endogeic *Octolasion tyrtaeum lacteum* was recovered everywhere while *Aporrectodea rosea rosea* were collected only in deep and fine-textured soils of the embanked floodplain. Moreover, anecic species found suitable conditions for installation in all sites.

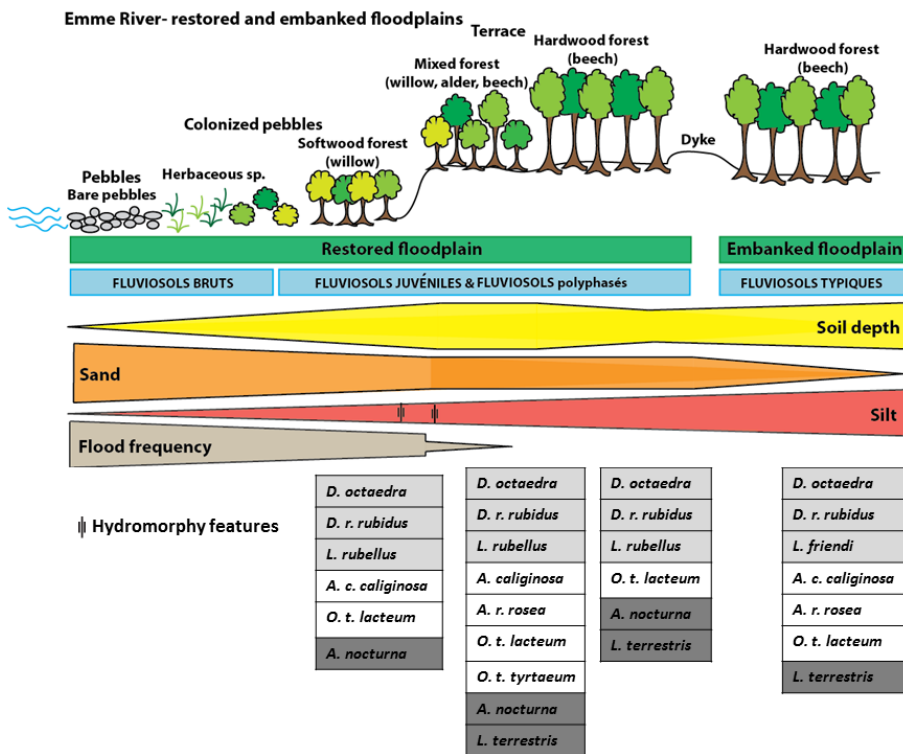


Figure 3. Schematic representation of the Emme site, with the restored and the embanked stretches. Vegetation succession and topography are represented from the riverbed (left) to the mature forest. All soils are calcareous-rich soils; soil depth, sand and silt contents as well as hydromorphy features and flood frequency are shown. Earthworm species are listed, epigeic, endogeic and anecic in grey, white and black boxes, respectively.

The Thur River

Another study was conducted nearby the Thur River (Photo 3; Figure 4). In this case, earthworms were observed all along the gradient of soils, from FLUVIOSOLS BRUTS under herbaceous species to FLUVIOSOLS TYPIQUES and FLUVIOSOLS TYPIQUES rédoxiques.

With reference to the embanked stretch, i.e. pasture, earthworm species diversity is higher in the restored floodplain (11 species instead of 9). The species *Lumbricus rubellus* is present everywhere, as well as *Allolobophora chlorotica chlorotica*, both known to be successful colonizers as mentioned above.

Anecics were recovered in all soils, indicating suitable conditions such as a fine texture and a sufficient soil depth, *Aporrectodea longa ripicola* being a typically riparian species. As in the near-natural Rhine site, the endogeic *Aporrectodea rosea rosea* were collected only in deep and fine-textured soils.



Photo 3. The Thur River (cantons of Thurgau and Zürich) restoration is the biggest river widening project in Switzerland and includes post-restoration monitoring and evaluations of several stretches (Pasquale et al., 2011). The study site “Schäffäuli”, is located near Frauenfeld in an agricultural floodplain and was before its channel rectification considered as a braided river. The average flow is $47 \text{ m}^3 \text{ s}^{-1}$ with a minimum and a maximum annual discharge of $23 \text{ m}^3 \text{ s}^{-1}$ and $76 \text{ m}^3 \text{ s}^{-1}$, respectively. Alluvium deposits are mostly composed of calcareous pebbles. The site lies at 365 m a.s.l. and annual precipitation is about $1000 \text{ mm year}^{-1}$, as average annual temperature is $7.9 \text{ }^\circ\text{C}$. Aiming at flood protection, restoration of the site was conducted in two steps. First, following a major flood in 1995, the riverbank protections were destroyed thus allowing river bank erosion. Secondly, in 2002, the riverbed was widened along a one-side 1.5 km stretch from 50 to 110 m, and the riverbanks were stabilized by plantation of willow bushes. Both reaches (restored, photo at the top, and embanked, photo at the bottom) are adjacent, and the embanked one, located upstream, is used as pasture. Flood events frequently occur in Autumn and in Spring and are of short duration (1 or 2 days).

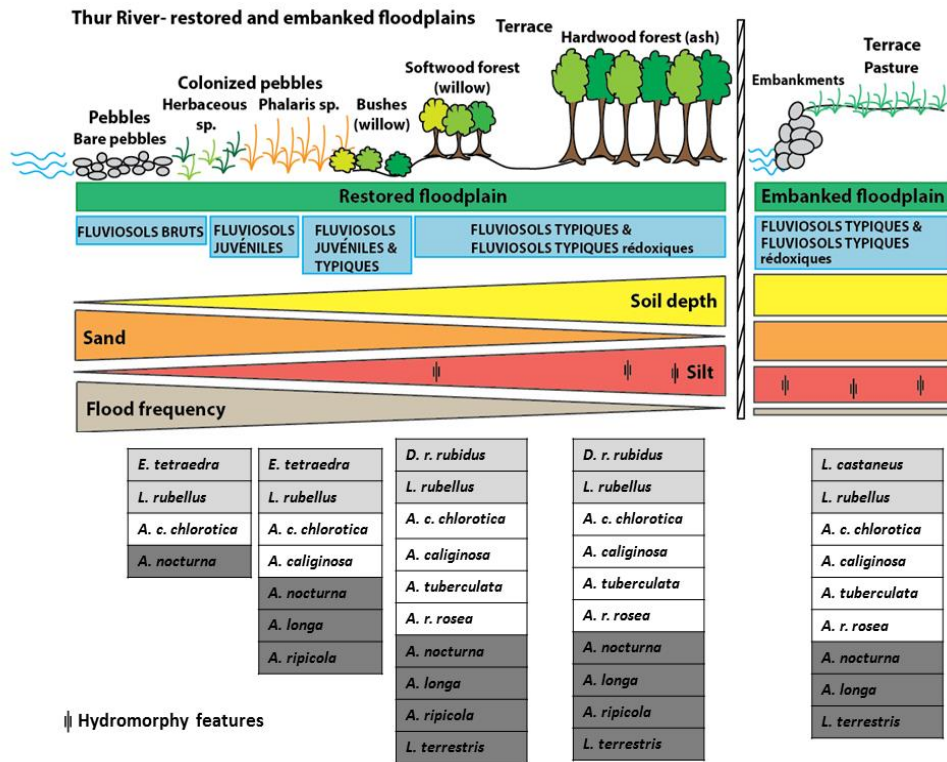


Figure 4. Schematic representation of the Thur site, with the restored and the embanked stretches. Vegetation succession and topography are represented from the riverbed (left) to the mature forest. All soils are calcareous-rich soils; soil depth, sand and silt contents as well as hydromorphy features and flood frequency are shown. Earthworm species are listed, epigeic, endogeic and anecic in grey, white and black boxes, respectively.

The Emme River versus the Rhine River

Regarding the comparison of earthworm communities in a near-natural floodplain (Rhine River), a restored floodplain and its respective embanked section (Emme River), it appears that the abundance of earthworm species is explained by soil parameters in relation with fluvial dynamics (Figure 5).

River restoration re-creates and/or maintains soil habitats that fit more or less to ecological needs of the different species. Indeed, river restoration in the studied braided rivers led to the modification of earthworm communities by enhancing some species and eliminating others. For example, the presence of species such as *Lumbricus rubellus* coincides with the presence of a well-developed structure (i.e. high proportion of water-stable aggregates and high organic matter content; Figure 5).

Some other species, such as *Lumbricus terrestris*, *L. friendi*, *Aporrectodea caliginosa nocturna*, *A. caliginosa caliginosa* related to silty soils, were present in both restored and embanked floodplains, but absent in the near-natural one. The presence of these species could be considered as relics of the prior embanked floodplain. By contrast, some species such as *Eiseniella tetraedra tetraedra* were recorded only in soils with hydromorphy features (RÉDUCTISOLS) typical of lateral branches of the Rhine River. These soils were not re-created in the Emme restored floodplain, where no lateral branch was formed, even if 20

years have elapsed since the restoration project has started. Finally, no species was found in all the bare soils (FLUVIOSOLS BRUTS) constituted of coarse alluvium deposits and subjected to frequent floods. These soils are characteristic of pioneer stages in near-natural floodplain, and are re-created through the river widening.

Thus, comparisons of restored and non-restored stretches along the Emme River confirmed that, as in near-natural systems such as the Rhine floodplain, pedological characteristics reflecting fluvial dynamics govern the abundance of earthworm species concomitantly to fluvial dynamics as already demonstrated by Fournier et al. (2012). These authors showed that high abundance of small epigeic species and low abundance of large anecic species characterized poorly developed gravel bare soils recently created by the river widening and most exposed to flooding.

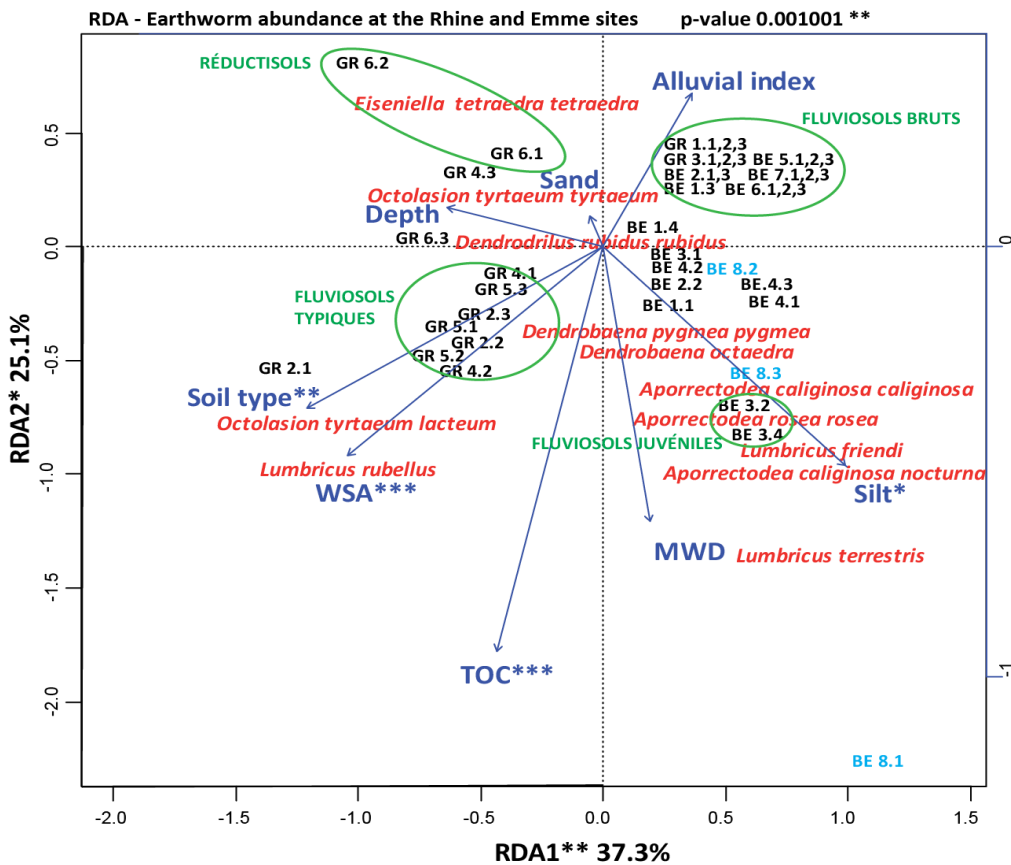


Figure 5. Redundancy Analysis on earthworm abundance at the near-natural site “Rhäzuns” along the Rhine River (GR), and at the Emme site (BE). GR 1 to GR 6, BE 1 to BE 8 indicated soil profiles with three replicates and their corresponding soil types (in green), BE 8.1, BE 8.2 and BE 8.3 in light blue representing the embanked site. Environmental variables are indicated in dark blue, TOC being the total organic carbon content, WSA the percentage of water-stable aggregates, MWD the mean water-stable aggregates diameter, and the alluvial index reflecting alluvial dynamics. Earthworm species are specified in red. Levels of statistical significance are as followed: *P <0.05, **P <0.01, ***P <0.001.

Near-Natural, Restored and Embanked Floodplains: What for Comparison?

As a general trend, we highlighted that our study sites (Emme, Rhine and Thur floodplains) respond similarly to flood disturbance regarding soil types, physico-chemical parameters and earthworm communities whatever they are restored or not. Flood intensity and seasonality, soil depth and stability, soil texture, and soil organic carbon content appear to be the main variables that govern and control earthworm distribution, abundance and species diversity.

River restoration has indeed a positive impact on earthworm communities through the creation or maintenance of diverse habitats. Except for the bare sediments, all these habitats are suitable for some species of earthworms and are then very quickly colonized by earthworms, over only several years after river restoration.

Comparing the Emme and the Thur floodplains, we observed that the stability of habitats obviously manages earthworm communities' distribution. We are also able to affirm that, regarding our results, river restoration enhance earthworm diversity and abundance especially when conducted along a wide and long reach. Thus, the Thur River widening was engaged in 1995 then 2002 while in 1991-92 then 1998-99 for the Emme River. So, it appears that restoration success regarding earthworm communities rehabilitation depends less on the time elapsed since restoration project has started, than on the used engineering technics and the size of the restored reach. A second challenge that needs further research is to assess if the Rhine River is a relevant near-natural reference. Indeed, earthworm diversity was lower in that place than at both the Emme and Thur sites perhaps due to upstream dams and embankments that may cause changes of the natural behaviour of the Rhine River. However, current researches are still in progress about this research of a near-natural floodplain reference.

By contrast to our studies, in some cases, some river rehabilitation may have a considerable negative impact on earthworm population and even may lead to extinction of some species (*Lumbricus rubellus*) in large areas of the restored floodplain. In the case of a lower River Rhine floodplain in Netherlands, the creation of a secondary channel and partial removal of embankment will, i) reduce the part of the floodplain area where the populations can sustain themselves, ii) modify the fluvial dynamics leading to more frequent flooding, especially during late spring and summer and hence a lower viability of the earthworm population, and iii) an increase in pollutants availability, mainly heavy metals, resulting from both more deposition of contaminated sediments and an increased exposure to stored contaminated sediment, may further decrease the area of the floodplain where earthworm population can sustain (Thonon and Klok, 2007).

4.3. Earthworm Communities As Bioindicators of Fluvial Dynamics and River Restoration Success

According to Henry et al. (2002), ecological restoration can be defined as returning an ecosystem to its condition prior to disturbance or to a state as similar as possible to that which prevailed prior disturbance. To assess the restoration success, we have compared the earthworm communities in a near-natural floodplain (considering as the state prior disturbance), a restored floodplain and an embanked floodplain. In the light of above results,

earthworm communities vary depending on the gradient of naturalness from embanked to near-natural sites. Indeed, as the different earthworm ecological categories and species are more or less resistant to flood duration and frequency, earthworm communities can reveal the presence of different pedological habitats resulting from fluvial dynamics (flood frequency and duration, water-table fluctuations, texture of alluvial deposits, woody debris, etc.). Because earthworms are influenced by environment changes, they may therefore be particularly efficient for the purpose of soil bioindication in the context river restoration. Their potential role as bioindicators has already been highlighted by Bullinger-Weber et al. (2012) at the subalpine level. These authors showed that abundance of epigeics can to be used as bioindicator of fluvial dynamics. At the hill level, Fournier et al. (2012) confirmed that changes in flooding frequency have a predominant influence on earthworm community. Thus, the ratio of the relative abundances of epigeic and anecic species, and the differences in species composition within earthworm categories could be used as indicators of soil development and functioning in floodplains. Moreover, the use of ecological traits is one of the key that may improve the potential of earthworms as bioindicators (Fournier et al., 2012). As a complement to this study, we showed that, as earthworm communities rapidly colonize habitats created by river restoration, they can thus be used as bioindicators of early stages of river restoration.

CONCLUSION: LIMITS AND PERSPECTIVES

In the framework of this chapter, we focused on study cases in Switzerland, in several braided rivers that carry calcareous-rich alluvial deposits. Regarding restoration impact on earthworm communities, it appears difficult to transpose and extrapolate our results to other fluvial systems. For instance, short-duration floods associated with large and rapid fluctuations of water-table and the coarse sandy texture of soil and sediment, avoid long-term submersion of soils, thus preventing earthworms from asphyxia as observed by Thonon and Klok (2007). In floodplains characterized by long-term anoxic conditions due to semi-permanent water table and loamy texture, earthworm communities may be more severely affected. In our study sites, damages to earthworm communities are mainly due to mechanical impact of floods that have drastic consequences on earthworm habitats through erosion and sediment deposits. Earthworms are infrequent in pioneer stages of soil formation while they may be maintained in areas less affected by flooding events.

The primarily colonisation by earthworms of bare soils that are typical of near-natural floodplains or re-created by river widening remains poorly studied. As highlighted by Eijackers (2010) no study has been found that factually combines primary colonisation by earthworms of bare soils with the impacts of earthworms on soil structure, texture and characteristics. In this context, manipulative mesocosms could be used to better understand involved processes in soil structure formation and in particular the role of earthworm in the early stages of structure formation and stabilisation.

Moreover, in this chapter, we didn't take into account the chemical composition of soil, sediment and water despite it could play an important role on earthworm populations. Pollution by heavy metals or by pesticides tends to increase along the river coarse and often reaches severe values of contaminants in alluvial urban and agricultural lowland floodplains.

In addition, a better knowledge of the ecological needs (such as organic matter supply) and resilience of earthworm communities to disturbances that occur in floodplains (floods, pollution, sedimentation and erosion processes, hydric and thermic stress) could help to use earthworm communities as bioindicators of environmental conditions, of ecosystems functioning and in turn as bio-indicators of river restoration success. In this context, the floodplain characteristics (altitude, hydrological regime, previous landuses and management), the engineering technics applied to restore floodplains (length and width of the widening, partial or total embankment removal) as well as the time elapsed since the restoration should be considered. In addition, according to the aim of the floodplain restoration, the performance of the earthworm as bio-indicators should be compared with other bioindicators more frequently used such as plant communities or macro-invertebrates to assess the restoration success.

Long-term surveys would be also crucial to discriminate the effect of natural successional dynamics from fluctuations, and from human impacts on this ecosystem (Henry et al., 2002). In addition, according to these authors, such surveys also required to assess the success of ecological restoration, i.e. the self-sustainability (i.e. requiring minimal maintenance or management) of restored ecosystems.

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REFERENCES

- Baize, & Girard. (2009). Référentiel pédologique, Quae edition.
- Bechtold, & Naiman. (2009). A quantitative model of soil organic matter accumulation during floodplain primary succession, *Ecosystems*.
- Berke. (2010). Ecosystem engineering in the Marine Realm, *Integrative and Comparative Biology*.
- Bertrand, Goldscheider, Gobat, & Hunkeler. (2012). From multi-scale conceptualization to a classification system for inland groundwater-dependent ecosystems. *Hydrogeology Journal*.
- Bindesbol.. (2008). Interactions between climatic and toxic stress - Studies with the freeze tolerant earthworm *Dendrobaena octaedra*. PhD Thesis, 96 pp.
- Bossuyt, Six, & Hendrix. (2005). Protection of soil carbon by microaggregates within earthworm casts, *Soil Biology and Biochemistry*.
- Bouché. (1972). Lombriciens de France : écologie et systématique. INRA. Paris.
- Bouché. (1977). Stratégies lombriciennes. *Ecological Bulletins*.

- Bullinger-Weber, & Gobat. (2006). Identification of facies models in alluvial soil formation: The case of a Swiss alpine floodplain. *Geomorphology*.
- Bullinger-Weber, Le Bayon, Guenat, & Gobat. (2007). Influence of some physicochemical and biological parameters on soil structure formation in alluvial soils. *European Journal of Soil Biology*.
- Bullinger-Weber, Guenat, Gobat, & Le Bayon. (2012). Impact of flood deposits on earthworm communities in alder forests from a subalpine floodplain (Kandersteg, Switzerland). *European Journal of Soil Biology*.
- Cierjacks, Kleinschmit, Kowarik, Graf, & Lang. (2011). Organic matter distribution in floodplain can be predicted using spatial and vegetation structure data. *River Research and Applications*.
- Coleman, & Whitman. (2005). Linking species richness, biodiversity and ecosystem function in soil systems. *Pedobiologia*.
- Cornelis, Koolhaas, Hamers, van Hoppe, van Rooyert, Korsman, & Reinecke. (2009). Effects of metal pollution on earthworm communities in a contaminated floodplain area: Linking biomarker, community and functional responses. *Environmental Pollution*.
- Cui, Yang, Yang, & Zhang. (2009). Evaluating the ecological performance of wetland restoration in the Yellow River Delta, China. *Ecological Engineering*.
- Daniels. (2003). Floodplain aggradation and pedogenesis in a semiarid environment. *Geomorphology*.
- Davidson, & Grieve. (2006a). Relationships between biodiversity and soil structure and function: Evidence from laboratory and field experiments. *Applied Soil Ecology*.
- Davidson, & Grieve. (2006b). The influence of soil fauna on soil structural attributes under a limed and untreated upland grassland. *Land Degradation and Development*.
- Decaëns. (2010). Macroecological patterns in soil communities. *Global Ecology and Biogeography*.
- Dominati, Patterson, & Mackay. (2010). A framework for classifying and quantifying the natural capital and ecosystem services of soils. *Ecological Economics*. 69(9).
- Edwards. (2004). *Earthworm Ecology*, 2nd ed., CRC Press LLC, St. Lucie Press, Boca Raton.
- Edwards, & Bohlen. (1996). *The Biology and Ecology of Earthworms*. (3rd Ed.). Chapman & Hall, London.
- Eijsackers. (2010). Earthworms as colonisers: Primary colonisation of contaminated land, and sediment and soil waste deposits. *Science of the Total Environment*.
- Emmerling. (1995). Long-term effects of inundation dynamics and agricultural land-use on the distribution of soil macrofauna in fluvisols. *Biology and Fertility of Soils*.
- Fisker, Sorensen, & Holmstrup. (2012). Costs of adaptation and expression of metallothionein in earthworm populations adapted to copper polluted soils. *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology*.
- Fisker, Holmstrup, & Sorensen. (2013). Variation in metallothionein gene expression is associated with adaptation to copper in the earthworm *Dendrobaena octaedra*. *Comp. Biochem. Physiol. C-Toxicol. Pharmacol.*
- Fonte, & Six. (2010). Earthworms and litter management contributions to ecosystem services in a tropical agroforestry system. *Ecological Applications*.
- Fournier, Samaritani, Shrestha, Mitchell, & Le Bayon. (2012). Patterns of earthworm communities and species traits in relation to the perturbation gradient of a restored floodplain. *Applied Soil Ecology*.

- Gallandat, Gobat, & Roulier. (1993). Cartographie des zones alluviales d'importance nationale, Cahier de l'environnement, OFEV, Berne.
- Gerard. (1967). Factors affecting earthworms in pastures. *Journal of animal ecology*.
- Gerrard. (1987). Alluvial soils, Hutchinson Ross, New York.
- Gerrard. (1992). Soil geomorphology : an integration of pedology and geomorphology. Chapman & Hall, London.
- Guenat, Bureau, Weber, & Toutain. (1999). Initial stages of soil formation in a riparian zone: Importance of biological agents and lithogenic inheritance in the development of the soil structure. *European Journal of Soil Biology*.
- Henry, Amoros, & Roset. (2002). Restoration ecology of riverine wetlands: A 5-year post-operation survey on the Rhône River, France, *Ecological Engineering*.
- IUSS Working Group WRB. (2006). World reference base for soil resources. FAO, Rome.
- Ivask, Truu, Kuu, Truu, & Leito. (2007). Earthworm communities of flooded grasslands in Matsalu, Estonia. *European Journal of Soil Biology*.
- Jabiol, Zanella, Ponge, Sartori, Englisch, van Delft, de Waal, & Le Bayon. (2013). A proposal for including humus forms in the *World Reference Base for Soil Resources*. (WRB-FAO). Geoderma.
- Jansson, Backx, Boulton, Dixon, Dudgeon, Hughes, Nakamura, Stanley, & Tockner. (2005). Stating mechanisms and refining criteria for ecologically successful river restoration: a comment on Palmer et al. (2005). *Journal of Applied Ecology*.
- Jimenez, Decaëns, Amezquita, Rao, Thomas, & Lavelle. (2011). Short-range spatial variability of soil physico-chemical variables related to earthworm clustering in a neotropical gallery forest, *Soil Biology and Biochemistry*.
- Joergensen, Overgaard, Holmstrup, & Westh. (2008). Cryoprotectants are metabolic fuels during long term frost exposure in the earthworm *Dendrobaena octaedra*. *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology*.
- Jones, Lawton, & Shachak. (1994). Organisms as ecosystem engineers. *Oikos*.
- Jones, Lawton, & Shachak. (1997). Ecosystem engineering by organisms: Why semantics matters. *Trends in Ecology and Evolution*.
- Karamouz, Noori, Moridi, & Ahmadi. (2011). Evaluation of floodplain variability considering impacts of climate change. *Hydrological Processes*.
- Lal. (1991). Soil conservation and biodiversity. Biodiversity of microorganisms and invertebrates: its role in sustainable agriculture. Proceedings of the First Workshop on the Ecological Foundations of Sustainable Agriculture (WEFSA 1), London.
- Lapied, Nahmani, & Rousseau. (2009). Influence of texture and amendments on soil properties and earthworm communities. *Applied Soil Ecology*.
- Lavelle. (1997). Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. *Advances in Ecological Research*.
- Lavelle, Bignell, Lepage, Wolters, Roger, Ineson, Heal, & Dhillion. (1997). Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology*.
- Le Bayon, & Binet. (2006). Earthworms change the distribution and availability of phosphorous in organic substrates. *Soil Biology and Biochemistry*.
- Lee. (1985). Earthworms: Their ecology and relationships with soil and land use. Academic Press. Australia.

- Lorenz. (2003). Bioindicators for ecosystem management, with special reference to freshwater systems. in *Bioindicators and Biomonitors : Principles, concepts and applications*. Markert, Breure, Zechmeister, Elsevier.
- McInerney, Little, & Bolger. (2001). Effect of earthworm cast formation on the stabilization of organic matter in fine soil fractions. *European Journal of Soil Biology*.
- Milner, & Tockner. (2010). River science - What has it contributed to general ecological theory?. *River Research and Applications*.
- Mitra, Wassmann, & Vlek. (2005). An appraisal of global wetland area and its organic carbon stock. *Current Science*.
- O'Hanley. (2011). Open rivers: Barrier removal planning and the restoration of free-flowing rivers. *Journal of Environmental Management*.
- Palmer, & Bernhardt. (2006). Hydroecology and river restoration: Ripe for research and synthesis. *Water Resources Research*.
- Palmer, Bernhardt, Allan, Lake, Alexander, Brooks, Carr, Clayton, Dah, Shah, Galat, Loss, Goodwin, Hart, Hassett, Jenkinson, Kondolf, Lave, Meyer, O'Donnell, Pagano, & Sudduth (2005). Standards for ecologically successful river restoration. *Journal of Applied Ecology*.
- Pasquale, Perona, Schneider, Shrestha, Wombacher, & Burlando. (2011). Modern comprehensive approach to monitor the morphodynamic evolution of a restored river corridor. *Hydrology and Earth System Sciences*.
- Petts, & Amoros. (1996). *Fluvial Hydrosystems*. Chapman & Hall. London.
- Plum. (2005). Terrestrial invertebrates in flooded grassland: A literature review. *Wetlands*.
- Plum, & Filser. (2005). Floods and drought: Response of earthworms and potworms. (Oligochaeta : Lumbricidae, Enchytraeidae) to hydrological extremes in wet grassland. *Pedobiologia*.
- Ponge. (2013). Plant-soil feedbacks mediated by humus forms: A review. *Soil Biology and Biochemistry*.
- Roots. (1956). The water relations of earthworms. Resistance to desiccation and immersion, and behaviour when submerged and when allowed a choice of environment. *Journal of Experimental Biology*.
- Ruiz-Jaen, & Aide. (2005). Restoration success: How is it being measured? *Restoration Ecology*.
- Salomé. (2011). La structure des sols en zones alluviales : importance des communautés lombriciennes et du matériel parental dans les premières étapes de la pédogénèse. *Doctorat es Sciences thesis*. Neuchâtel.
- Salomé, Guenat, Bullinger Weber, Gobat, & Le Bayon. (2011). Earthworm communities in alluvial forests: Influence of altitude, vegetation stages and soil parameters. *Pedobiologia*.
- Satchell. (1967). Lumbricidae, *Soil biology* (A. Burges and F. Raw, eds). Academic Press, London.
- Schrader, & Zhang. (1997). Earthworm casting: stabilization or destabilization of soil structure ? *Soil Biology and Biochemistry*.
- Schütz, Nagel, Dill, & Scheu. (2008). Structure and functioning of earthworm communities in woodland flooding systems used for drinking water production. *Applied Soil Ecology*.
- Shipitalo, & Le Bayon. (2004). Quantifying the effects of earthworms on soil aggregation and porosity. *Earthworm Ecology*. Edwards, CRC Press, Boca Raton.

- Simonsen, & Klok. (2010). Genetic and ecological impacts of heavy metal and flooding stress on the earthworm *Lumbricus rubellus* in floodplains of the Rhine river. *Soil Biology and Biochemistry*.
- Sims, & Gerard. (1999). Earthworms: Note for the identification of British species. *Field Studies Council, Shrewsbury*.
- Thonon, & Klok. (2007). Impact of a changed inundation regime caused by climate change and floodplain rehabilitation on population viability of earthworms in a lower River Rhine floodplain. *The Science of the Total Environment*.
- Tockner, & Stanford. (2002). Riverine flood plains: present state and future trends. *Environmental Conservation*.
- Wang, Zhu, Meng, Wang, Xie, & Zhang. (2012). The combined stress effects of atrazine and cadmium on the earthworm *Eisenia fetida*. *Environmental Toxicology and Chemistry*.
- Wohl, Angermeier, Bledsoe, Kondolf, MacDonnell, Merritt, Palmer, Poff, & Tarboton. (2005). *River restoration Water Resources Research*.
- Woolsey, Capelli, Gonser, Hoehn, Hostmann, Junker, Paetzold, Roulier, Schweizer, Tiegs, Tockner, Weber, & Peter. (2007). A strategy to assess river restoration success. *Freshwater Biology*.
- Zorn, Van Gestel, & Eijsackers. (2005). Species-specific earthworm population responses in relation to flooding dynamics in a Dutch floodplain soil. *Pedobiologia*.
- Zorn, Van Gestel, Morrien, Wagenaar, & Eijsackers. (2008). Flooding responses of three earthworm species, *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *Lumbricus rubellus*, in a laboratory-controlled environment. *Soil Biology and Biochemistry*.