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Patterns of earthworm communities and species traits in relation to the perturbation gradient of a restored floodplain

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ABSTRACT

Little is known about the diversity and ecology of earthworms in floodplains, as well as their response to natural and anthropic perturbations (*e.g.* floods, river channelisation, floodplain restoration). We characterised the patterns of earthworm communities and species traits in the different habitats of a lowland restored floodplain in Switzerland. In addition to classical species-based metrics, such as species richness and Shannon diversity, species traits were used to calculate the community weighted means (CWMs) of traits and functional dispersion (FDis). We hypothesised that trait-based metrics would reveal clearer patterns than classical approaches. The distribution of earthworm traits varied among habitats in relation to changes in flooding frequency: poorly developed gravel bar soils most exposed to flooding were characterised by high abundance of small epigeic species and low abundance of large anecic species. Differences in anecic and endogeic earthworm community structure matched flood frequency. In agreement with our hypothesis, CWMs were more strongly correlated to environmental variables than species composition, diversity, or functional diversity. Based on these results, the ratio of the relative abundances of epigeic and anecic species, and the differences in species composition within anecic and endogeic ecological types of earthworms were identified as indicators of soil development in floodplains.

1. Introduction

Floodplains are among the most threatened ecosystems worldwide (Malmqvist and Rundle, 2002; Tockner and Stanford, 2002). In the last decades, a paradigm shift has taken place in river management, the dominant view shifting from controlling rivers to restoring their natural states and functions. This has led to major changes in policy, such as the water framework directive (WFD; 2000/60/EC) in the EU. As a result of these policy changes, an increasing number of river restoration projects are being conducted in Switzerland and worldwide (Nakamura et al., 2006; Palmer and Bernhardt, 2006; Palmer et al., 2005; Wohl et al., 2005). These projects generally aim to improve the flood protection and biodiversity reservoir functions of floodplains. However, their impact on the terrestrial ecosystems of floodplains remains poorly understood, especially with respect to the soil fauna. Soil organisms include many potential indicators of river restoration success but this potential has not yet been studied much (Bullinger-Weber et al., 2007; Fournier et al., 2012; Guenat et al., 1999). Among the candidates, earthworms are recognised as good bioindicators of soil conditions in alluvial ecosystems (Bullinger-Weber et al., 2012; Salomé et al., 2011) and could therefore provide useful information for monitoring of restoration projects.

Earthworms are present in most terrestrial ecosystems of the world. Their abundance in soils is principally affected by soil properties (*i.e.* texture, organic matter, pH, depth, and water content), land management (*e.g.* land use, agricultural practices), climate, and other biotic factors (Edwards, 2004; Edwards and Bohlen, 1996). Earthworms modify soils mainly through bioturbation (Meysman et al., 2006) thus participating actively to soil pedogenesis. Their activity affects water infiltration (*e.g.* Shipitalo et al., 2004), nutrient cycling (Butenschoen et al., 2009; Sheehan et al., 2006), organic matter cycling (Koutika et al., 2001), soil structure (Shipitalo and Le Bayon, 2004) and horizon texture (Lavelle, 1997; Lavelle et al., 1997). Their potential as bioindicators of landscape structure, land use and soil pollution has been well studied in many ecosystems

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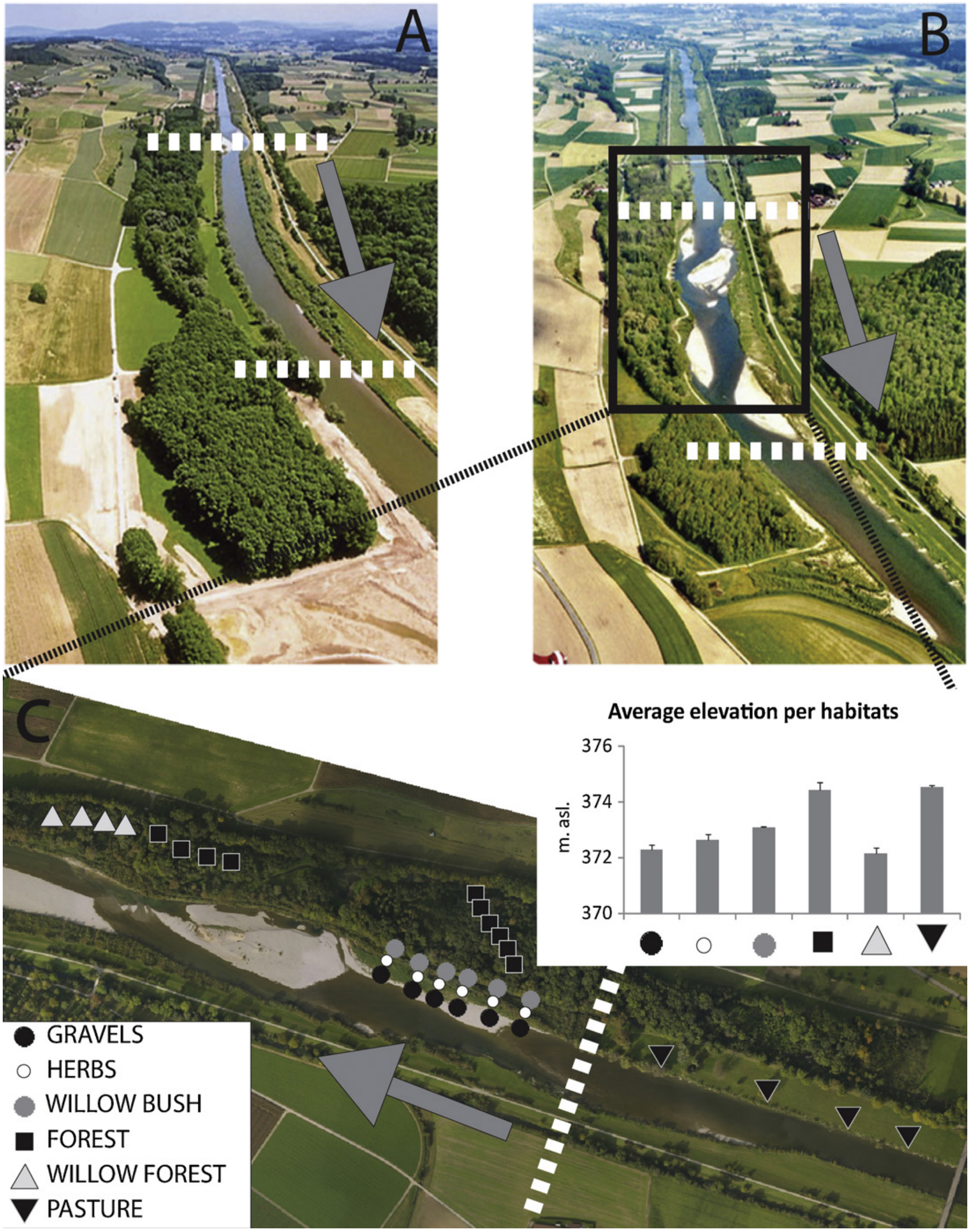

Fig. 1. Thur River (A) before (June 2001), and (B) after the 2002 restoration (May 2004); (C) aerial view of the study site in 2008 showing the plots, and the average elevation of each habitat. Error bars are standard errors. (Pictures A and B: C. Herrmann, BHAteam, Frauenfeld; picture C: CCES RECORD project.) The dashed white lines delimit the restored area; grey arrows give the direction of the river flow.

(Krivolutsky et al., 1982; Paoletti, 1999; Paoletti et al., 1998; Suthar et al., 2008). However, there are comparatively few data on the ecology of earthworms in floodplains (Kamitani and Kaneko, 2007; Zorn et al., 2005).

In flood prone areas, the water holding capacity as well as the organic matter content of the soil are key factors controlling earthworm abundance (Plum and Filser, 2005). Flooding generally has a negative impact on earthworms (Ausden et al., 2001; Ivask et al., 2007; Plum and Filser, 2005), but this effect is species-specific. For example, flooding reduced the total biomass of *Lumbricus terrestris* and *L. rubellus* whereas it had no or little effect on that of *Allolobophora chlorotica* and *Aporrectodea caliginosa* (Zorn et al., 2005, 2008). In subalpine floodplains, epigeic species are considered as bioindicators of recent flood events because of their relation to topsoil texture and organic matter quality (Bullinger-Weber et al., 2012). River restoration was shown to affect negatively *L. rubellus* biomass through a reduction of suitable habitats and an enhanced exposure to contaminants (Thonon and Klok, 2007). Inundations were reported to increase earthworm abundance and biomass in a human transformed ecosystem used for drinking water production by artificial groundwater recharge (Schütz et al., 2008). These observations, and more generally the central role of earthworms in ecosystem development and functioning (Lavelle et al., 1997), lead us to hypothesise that earthworms could be useful bioindicators for monitoring floodplain restoration.

Research in ecology has shown that the analysis of species traits is a useful and powerful approach for understanding ecosystem functioning (Diaz and Cabido, 2001; Díaz et al., 2007; Loreau et al., 2001). Indeed, species traits are often more closely associated to environmental conditions than the actual species (Grime, 1998; Hooper et al., 2005; Tilman et al., 1997). The dominant idea behind this approach is that environmental conditions filter species through their traits. As a result, a species with a given set of characteristics can only survive in a range of conditions that together constitute its ecological niche. These ground concepts in ecology have led to the development of theories such as the habitat templet theory (Southwood, 1977) and are increasingly studied and challenged by ecologists. The trait approach offers an alternative to species abundance or biomass for bioindication that present interesting advantages. Relating species traits to environmental characteristics allows more intuitive understanding of ecosystem functioning as compared to individual species abundance. The trait approach is not hampered by taxonomic difficulties (at least for morphological traits) and not biased by species biogeography. A bioindicator trait can be used across all biomes where the target taxonomic group is present. Earthworm traits have received little attention in ecological studies except for ecological categories as defined by Bouché (1977). However, given the functional importance of earthworms and their sensitivity to waterlogging, we hypothesised that earthworm traits could be used to develop bioindicator tool for environmental management.

In this context, this paper aims at (1) characterising the patterns of earthworm community structure, species composition and species traits in the different habitats (gravel bars to floodplain forests) of a lowland floodplain in Switzerland, (2) assessing the relationships between these patterns and environmental variables, and (3) discussing the potential use of earthworms as bioindicators of restoration.

2. Material and methods

2.1. Study site

The study site is a floodplain located along the Thur River, a tributary of the Rhine, in north-eastern Switzerland (8°77′12″E; 47°59′10″N). It is situated at 365 m a.s.l. and has a temperate climate (annual precipitation ca. 1000 mm year^{-1}, average annual temperature 7.9 °C; http://gate.meteoswiss.ch/idaweb). The average annual flow (1904–2005) of the river is 47 m^3 s^{-1} with peaks above 1000 m^3 s^{-1} (http://www.hydrodaten.admin.ch/d/2044.htm). The site was channelised and levies built until 2002 (Fig. 1A) when it was restored through widening of the riverbed from 50 m to 150 m and bank stabilisation by plantation of willows (Fig. 1B). See Hostmann et al. (2005) for more technical details on the study site restoration.

The Thur River site constitutes an ideal lowland river restoration study case to assess in detail the impact of changed inundation regime on the soil fauna. The study site is divided into a restored section and a non-restored section (Fig. 1). Six different habitats were selected based on elevation and distance to the river, soil type, vegetation structure, and impact of restoration (Samaritani et al., 2011). The French soil classification (Baize and Girard, 2009) was preferred over the FAO World Reference Base for Soil Resources (IUSS Working Group WRB, 2006) because the latter does not discriminate different types of Fluvisols (the dominant soil taxon within the study site). Close to the river, three habitats were selected within the dynamic area. Bare gravels with patches of poorly developed soil – FLUVIOSOLS BRUTS – and pioneer vegetation constituted the first habitat (GRAVELS). The second habitat (HERBS) was an area with more developed soils – FLUVIOSOLS JUVENILES – but showing high spatial and temporal heterogeneity (Samaritani et al., 2011) and dominated by tall herbs (*Phalaris arundinacea*). The third habitat (WILLOW BUSH) was characterised by soils of average depth (FLUVIOSOLS TYPIQUES) and patches of planted willow bushes. The last two habitats were forests growing on deep soils (FLUVIOSOLS TYPIQUES), subjected to limited influence of flooding, dominated either by old willows (*Salix alba* – WILLOW FOREST) or composed of mixed deciduous tree species (*Acer pseudoplatanus*, *Fraxinus excelsior* – FOREST). These two forest sites were present before restoration but were increasingly influenced by the fluvial dynamics following the restoration. In addition, a pasture (PASTURE) located directly upstream from the restored site in an area still protected from floods by levees was sampled as a reference of the state of the ecosystem before restoration. This habitat was replaced by GRAVELS, HERBS and WILLOW BUSH in the restored section.

We first analysed the general patterns of earthworm communities in the six habitats. To assess the impact of river restoration, we then compared GRAVELS, HERBS, and WILLOW BUSH to PASTURE. FOREST and WILLOW FOREST were not considered in this comparison because (1) they existed prior to the restoration, (2) they were only marginally influenced by the restoration, and (3) no comparable habitats were available in the reference area (Fig. 1). Given the absence of natural ecosystems comparable to the study site in the region, we selected the PASTURE habitat as reference. The advantage of this approach is that all sites share the same climate, geology, river flow rate, and potential species pool. The selected habitats are exposed to different flood dynamics (ranging from 24 floods per year to one flood every 2 years; www.hydrodaten.admin.ch/d/2044.htm) and different water table levels (high at both extremes and low in the middle of the gradient; lowest in PASTURE), but are otherwise all exposed to the same climatic, geological, and river flow conditions.

2.2. Sampling

Targeting a snapshot of the ongoing ecological processes, earthworms were sampled in September 2008 using the mustard extraction method after a period of two weeks without flood and rain (Lawrence and Bowers, 2002). This method was preferred over electrical or formalin solution extractions because of safety (proximity of the watertable), environmental (pollution of the aquifers), and legal (it is illegal to use formalin in Switzerland) issues. The mustard extraction method preferentially targets anecic species (Chan and Munro, 2001; Lawrence and Bowers, 2002). Indeed, endogeic species may either not be reached by the solution or may escape laterally rather than toward the soil surface. However, the importance of this bias is determined by soil permeability, being strongest for the less permeable soils with high clay content and minimal for well-drained sandy to loamy soils such as the FLUVIOSOLS studied here. Furthermore, should this bias still affect our sites, it may affect the absolute results, but probably not the interpretation of patterns among habitats, which is the main goal of our study.

The sampling design consisted of 36 plots distributed among six habitats. The habitats exposed to more than one flood per year (GRAVELS, HERBS, WILLOW BUSH) were sampled using six replicates, whereas the habitats exposed to less than one flood per year (WILLOW FOREST, PASTURE) were sampled using four replicates (www.hydrodaten.admin.ch/d/2044.htm). Ten replicates were used in the forest (FOREST) to cover a gradient in topography and vegetation within this otherwise relatively homogeneous area.

Each plot consisted of circle of four meters radius disposed regularly in each habitat, avoiding highly heterogeneous areas. Within each plot, two homogeneous areas of one squared meter were delimited and watered with ∼36 l of mustard powder solution [10 g l^{-1}]. On sloping plots, more solution was used in order to compensate for runoff and thus ensure soil saturation. Individuals were sampled within the delimited areas, stored in formaldehyde 4% and brought back to the lab for species level identification (Bouché, 1972; Sims and Gerard, 1999). Juveniles classified as individuals with tanylobic or epilobic prostomium (Bouché, 1972) were not included in the final matrix (sites × species), but were used for overall density and biomass calculations.

All individuals were measured (see supplementary material) and weighed. Information on other traits such as species length (type of variable: continuous), number of segments (continuous), pH ecological optima and range of tolerance (continuous), prostomium type (binary; tanylobic or epilobic shaped prostomium), ecological type (qualitative ordinal; epigeic, anecic; and endogeic), and preference for given C/N ratios (binary; low = 0 and high = 1) was gathered in the literature (Bouché, 1972, 1977; Sims and Gerard, 1999).

Geographical coordinates and elevation of sample sites were measured at the centre of the plots with a differential GPS. Relative covers of the tree, bush, and herbaceous strata, as well as litter, dead wood, and mosses were expressed as percentage of the total plot area following Braun-Blanquet (1964). Soil variables focused on the structure and chemical composition of the uppermost layer of the soil profile (topsoil). The coarse material size distribution (*i.e.* gravels of various sizes; large > 5 cm, medium > 2 cm, small) of the uppermost 5 cm of soils were visually estimated *in situ* following the key of Baize and Jabiol (1995). For organic (OC), total carbon (C) and total nitrogen (N) measurements, three cores of 10 cm depth and 6 cm diameter were extracted at each sampling site, homogenised and sieved at 2 mm, and measured following the methods of Walthert et al. (2010). The minimum flow rate required to flood each habitat was determined by Samaritani et al. (2011) from inundation maps produced by digital terrain modelling based on river cross section measurements. The average number of floods per year was calculated for each habitat using river flow measurement data covering the period from 2003 to 2008 (www.hydrodaten.admin.ch/d/2044.htm). Water table depth was best estimated as the difference between habitat elevation and river level (Dr. Tobias Vogt, personal communication) (Table 1).

2.3. Numerical analyses

We first structured the data into three matrices: *L* (*sites × species*), *Q* (*species × traits*), and CWM (*sites × traits*). The two earthworm sub-samples for each plot were summed to build the matrix *L*. For matrix *Q*, binary traits were treated as continuous variables, and all other variables were continuous or ordinal. To assess the changes in trait composition at the community level, we calculated the community weighted means (CWMs) of traits using the following formula for each trait:

$$\mathrm{CWM} = \sum^{n} p_i \times \mathrm{trait}_i \tag{1}$$

where p is the relative contribution of species$_i$ to the community and trait$_i$ is the value of the considered trait for species$_i$. CWMs were scaled prior analyses.

To assess the changes of earthworm communities in species composition, species mean density and biomass, species richness and evenness as well as Shannon diversity were calculated for each plot. Deltas were then calculated for the density and biomass of each species, as the difference between the dynamic-restored and reference area as follows:

$$\Delta_{\mathrm{x}} = X_{\mathrm{dynamic\_restored}} - X_{\mathrm{reference}} \tag{2}$$

where X = mean abundance [ind m^{-2}] or mean biomass [g m^{-2}].

Species that increased both in density and biomass were considered as "species that benefit most from the restoration" whereas species that decreased in density and biomass were considered as "most dramatically impacted by the restoration".

We then analysed the internal structure of *L* and CWM matrices using principal component analyses (PCA) and between class analysis (BCA), and their relationships with environmental variables using redundancy analyses (RDA). Earthworm species data were Hellinger transformed before PCA, BCA, and RDA analyses (Legendre and Gallagher, 2001). We used PCA to characterise the distribution patterns of earthworm species and traits and BCA Monte Carlo tests (Dolédec and Chessel, 1987) were performed to discriminate the different habitats and areas. Functional dispersion (FDis) was calculated for each plot (Anderson, 2006; Laliberté and Legendre, 2010). We assessed whether biomass, density, species richness, Shannon diversity, CWM and FDis values differed among habitats and between the two areas using Mann–Whitney tests.

We used redundancy analyses (RDA) to determine the impact of environmental variables on earthworm community composition and functioning. The environmental dataset was scaled and centred and then used as explanatory matrix in the RDA models. The CWM and species per site matrices were alternatively used as response matrices. For each RDA model, we calculated the cumulated proportion of explained variance (EV) by all constrained axes as well as the EV of the two first RDA axes. The significance of RDA models, RDA axes, and variable contributions were then tested using ANOVA permutation tests. The relative goodness of fit of each model was then assessed by calculating the Akaike's Information Criterion (AIC; Sakamoto et al., 1986).

All analyses were performed with the R statistical software (R Development Core Team, 2010) using the "vegan" (Oksanen et al., 2010), "FD" (Laliberté and Shipley, 2010), and "ade4" (Dray and Dufour, 2007) packages.

3. Results

In total, 3707 earthworms were sampled representing an overall biomass of 1126 g. The average biomass was 28 g m^{-2} and 35 g m^{-2} in the restored area and the reference area, respectively, and the average abundances were respectively 93 and 65 individuals per square meter (ind m^{-2}) with maximal values of 394 ind m^{-2} in HERBS and minimal values below 5 ind m^{-2} in GRAVELS. Earthworm biomass was the highest in FOREST with up to 70 g m^{-2} and the lowest close to the river (GRAVELS) with values below 5 g m^{-2}.

A total of 15 species and subspecies were identified (Table 2) of which 10 benefitted from the restoration whereas five and the juveniles with a tanylobic prostomium were negatively impacted. The former accounted for 9.5% of the total biomass and 17.8% of the total density, and the latter 42% and 15.5% respectively. Of the species that benefitted from the restoration, four were epigeic, two were endogeic, and two more were epiendogeic, but none was anecic. Of the five negatively impacted species, four were anecic species and one was endogeic.

Clear differences in community composition, biomass, and density were observed among habitats and especially between the most dynamic habitats and the more stable forest and pasture (Fig. 2). Earthworm abundance was similar across all habitats except for HERBS where the highest average number of individuals per square meters (260 ind m^{-2}) was recorded. The percentage of juveniles within the community was highest in HERBS (75%) and lowest in GRAVELS (56%).

All species were present in the restored area whereas nine were found in the non-restored area (PASTURE). Within the restored area, none of the habitats hosted all the species, the maximal total richness (*i.e.* total number of species and subspecies present in a

Table 1
Summary of the numbers of earthworm individuals caught in the Thur River study site for each species within each habitat. Flood related variables are also given for each habitat.

	GRAVELS	HERBS	WILLOW BUSH	FOREST	WILLOW FOREST	PASTURE
Allolobophora chlorotica	48 ± 0.6	312 ± 4.3	19 ± 1	55 ± 2.7	13 ± 0.6	14 ± 0.4
Allolobophora georgii	0 ± 0	0 ± 0	0 ± 0	2 ± 0.1	0 ± 0	0 ± 0
Aporrectodea caliginosa caliginosa	0 ± 0	18 ± 1.2	7 ± 0.3	38 ± 1.1	13 ± 0.9	1 ± 0.1
Aporrectodea c. nocturna	0 ± 0	3 ± 0.1	9 ± 0.1	48 ± 0.8	12 ± 0.8	13 ± 0.7
Aporrectodea c. tuberculata	0 ± 0	3 ± 0.2	4 ± 0.2	14 ± 0.5	22 ± 0.2	24 ± 0.7
Aporrectodea giardi	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 0.1	1 ± 0.1
Aporrectodea longa	10 ± 0.4	21 ± 0.7	29 ± 0.8	31 ± 0.6	16 ± 0.7	43 ± 1
Aporrectodea rosea	0 ± 0	0 ± 0	2 ± 0.1	33 ± 0.7	21 ± 1.1	0 ± 0
Dendrodrilus rubidus	0 ± 0	2 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Eiseniella tetraedra	14 ± 0.6	18 ± 0.4	0 ± 0	1 ± 0.1	0 ± 0	0 ± 0
Lumbricus castaneus	0 ± 0	3 ± 0.1	2 ± 0.1	2 ± 0.1	7 ± 0.3	1 ± 0.1
Lumbricus meliboeus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	2 ± 0.2	0 ± 0
Lumbricus rubellus	5 ± 0.3	21 ± 0.9	9 ± 0.4	6 ± 0.2	5 ± 0.3	2 ± 0.2
Lumbricus terrestris	0 ± 0	1 ± 0.1	4 ± 0.2	34 ± 0.4	13 ± 0.3	8 ± 0.4
Octolasion tyrtaeum tyrtaeum	0 ± 0	1 ± 0.1	1 ± 0.1	5 ± 0.3	1 ± 0.1	0 ± 0
Juveniles epilobiques	51 ± 4.5	67 ± 1	57 ± 1.7	58 ± 1.4	53 ± 1.5	53 ± 2.6
Juveniles tanylobiques	5 ± 1.6	8 ± 1.4	14 ± 1.2	12 ± 0.9	13 ± 2.5	14 ± 0.6
Number of floods per habitat in 2008	24	17	3	1	1	1
Minimum river flow for inundation [$m^3 s^{-1}$]	175	190	300	630	415	415
Depth of the water table [m]	1.41	1.65	1.75	1.71	0.93	3.15

Table 2
Summary statistics of the redundancy analyses (RDA) of earthworm data from the Thur River site. Explained variances are given in percent. *p*-values result from ANOVA permutation tests. AIC is the Akaike Information Criterion (Sakamoto et al., 1986).

	Total explained variance [%]	Variance explained by the first constrained axis [%]	Variance explained by the second constrained axis [%]	Model *p*-value	First axis *p*-value	Second axis *p*-value	AIC
Species	63.99	19.22	11.23	0.62	0.22	0.9	104.02
CWM	77.72	49.01	15.81	0.04	0.03	0.73	69.34
Species richness	71.79	71.79	NA	0.27	0.27	NA	0.69
Shannon diversity	79.63	79.63	NA	0.08	0.08	NA	−10.69
FDis	78.56	78.56	NA	0.17	0.09	NA	−8.91

habitat) being reached in the forest habitats (FOREST and WILLOW FOREST) with 12 species, and the minimal close to the river (GRAVELS) with four species. The indices accounting for the variance of species and CWMs matrices revealed a trend toward increasing functional and taxonomic diversity with decreasing perturbation (Fig. 3). GRAVELS and HERBS had relatively low values for all indices whereas the contrary occurred in WILLOW FOREST. WILLOW BUSH and FOREST showed a higher variation, although this variation was relatively small for functional dispersion in FOREST.

In both PCAs based on density and on trait data (Fig. 3), the habitats were distributed along the first axis according to their position along the fluvial dynamic gradient. Monte Carlo permutation tests gave strong evidence against the hypothesis that all habitats were similar in the species or trait ordination space (p-value < 0.01 in both cases). The samples were organised in two clusters: the first was composed by the habitats most prone to flooding (*i.e.* GRAVELS and HERBS) and occupying little ordination space, and the second included the habitats influenced to a lesser extent by fluvial dynamism and covering much more ordination space. *A. chlorotica* and *Eiseniella tetraedra*, and to a lesser extent, *Lumbricus rubellus* and *Dendrodrilus rubidus* were associated with GRAVELS and HERBS whereas *L. terrestris*, *A. caliginosa nocturna*, and *A. c. tuberculata* were associated with the most stable conditions. This pattern was identical for abundance data (shown here) as well as biomass data (not shown). In stable habitats, earthworms were large and heavy. Communities contained an important proportion of anecic species and they differed from those of dynamic habitats in their pH optima and C/N ratio preference.

The RDA model on CWMs was significant ($P = 0.04$) and revealed strong correlation to environmental variables. In this model,

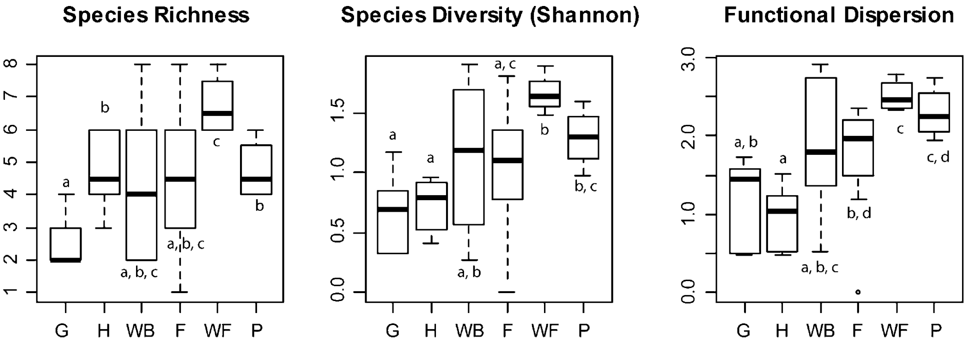

Fig. 2. Boxplots of earthworm species richness, diversity, and functional dispersion (*alpha* values) for all habitats of the Thur River site (G: GRAVELS, H: HERBS, WB: WILLOW BUSH, F: FOREST, WF: WILLOW FOREST, P: PASTURE). Error bars represent standard errors.

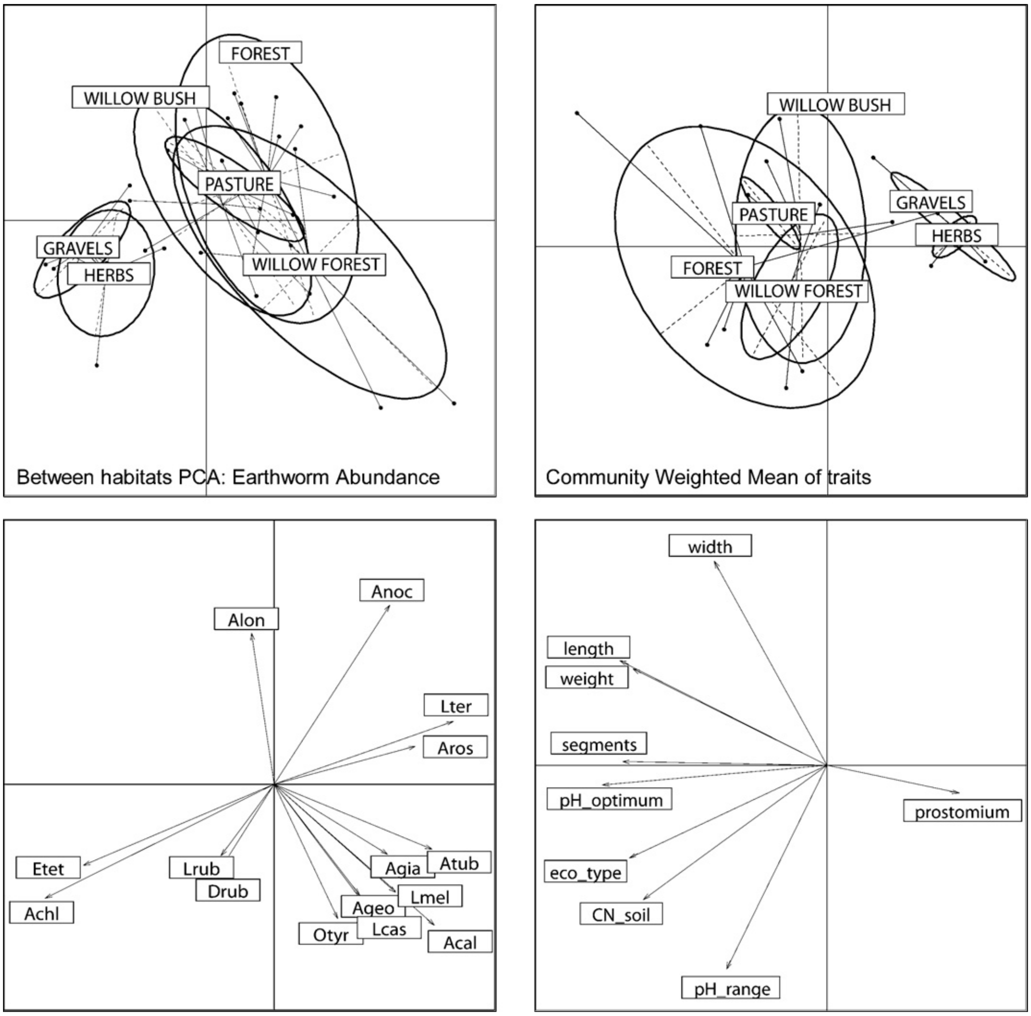

Fig. 3. Principal component analyses (PCA) of earthworm abundance and community weighted means of traits data from the Thur River site. Ellipses highlight the different habitats; and arrows the position of species or traits within the ordination space. Species name abbreviations are composed of the first letter of the genera and the three first letters of the species name.

earthworm communities were distributed along the first axis, which corresponded to the influence of flood regime (Fig. 4) and was significantly correlated with the average number of floods per year and the relative cover of woody debris. By contrast, in RDAs based on species composition, diversity, or functional diversity the correlation was weaker and the models non-significant (Table 2).

4. Discussion

At the floodplain scale, the observed values for biomass, abundance, species richness, and diversity were similar to those recorded in comparable settings (Ivask et al., 2007; Plum and Filser, 2005; Salomé et al., 2011; Zorn et al., 2005) and testify from well-developed earthworm communities. The PCA and Monte Carlo tests (Fig. 3) clearly showed that the investigated habitats could be separated into two groups.

Earthworm communities of the first group – GRAVELS and HERBS – were dominated by relatively small and epigeic taxa of low biomass, more specifically by species characterised by an epilobic type prostomium, preferring high C/N ratios, more acid conditions, and having relatively low tolerance to pH variations. These adaptations reflect the *in situ* conditions encountered by earthworms in our study. Caution must however be taken talking about relative acid conditions considering that geological substrate consists of carbonates. Moreover, in these habitats, total soil carbon content and litter input (constituted almost exclusively of *P. arundinacea*) were high; soils were thin and poorly developed because of the regular impact of floods (Guenat et al., unpublished results). Indeed, dynamic processes such as sedimentation, aggradation, and – predominantly in our case – erosion did not allow sufficient time for *in situ* pedogenesis to occur. The preference of earthworms for more acidic conditions could be explained by the deposition by the river of exogenous acidic material such as soil layers eroded from upstream banks, vegetation, mineral aggregates of various sizes, and organic matter. At the species level, *A. chlorotica*, *E. tetraedra*, and *L. rubellus* – three epigeic *r*-strategists with fast maturation and high reproduction rates (Bouché, 1972; Gerard, 1967; Satchell, 1967) – dominated the communities in GRAVELS and HERBS. *E. tetraedra* is considered as characteristic of river banks (Bouché, 1972) and indeed this species was among the species that benefitted most from the restoration. *A. chlorotica* is characteristic of perturbed environment (*e.g.* building sites) that are returning to their equilibrium states (Bouché, 1972). This species likely took advantage of the perturbation generated by the restoration process to increase in density and biomass. *L. rubellus* is a successful coloniser (Eijsackers, 2010) well adapted to flooded soils (Roots, 1956) such as those found in the newly created habitats (GRAVELS and HERBS). However, *L. rubellus* was shown to be more sensitive to flooding than *A. chlorotica*; and its response to such perturbations consists mainly of escaping to more favourable habitats (Simonsen

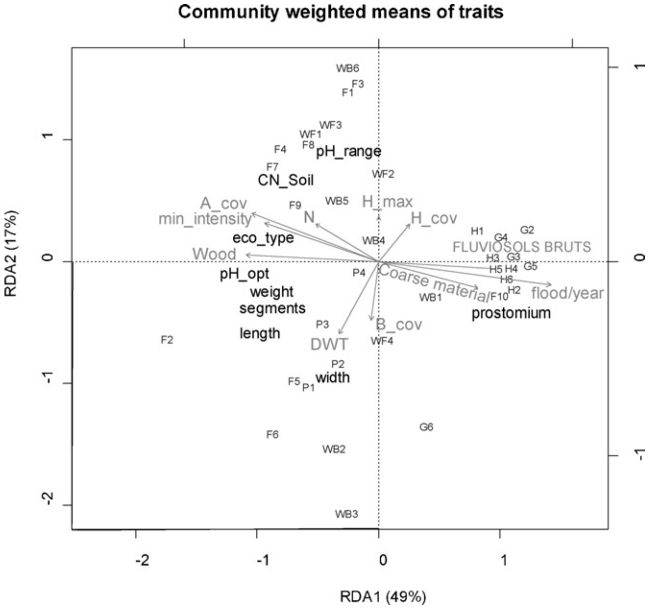

Fig. 4. RDA triplot of earthworm community weighted means of traits (black) and environmental variables (grey) from the Thur River site. Explained variance is given in brackets for each axis. Site abbreviations (black, smaller characters) are composed by the first letter(s) of the habitat and the replicate number (G: GRAVELS, H: HERBS, WB: WILLOW BUSH, F: FOREST, WF: WILLOW FOREST, P: PASTURE).

and Klok, 2010; Zorn et al., 2008). In agreement with this, *L. rubellus* was less abundant and reached lower biomass than *A. chlorotica* and *E. tetraedra* in flood prone sites. We therefore conclude that the optimal strategy for earthworms to colonise habitats submitted to high flood dynamics consists of being epigeic and having fast growth and high reproduction rates and good dispersal ability together with a propensity to tolerate flood. Moreover, the abundance and distribution (including patchiness) of dynamic flood-prone habitats along rivers is likely to play a crucial role in the dispersal of these species.

Earthworm communities in the second group of habitats (WILLOW FOREST, FOREST, WILLOW BUSH and PASTURE) were dominated by longer and heavier anecic species such as *Aporrectodea longa*, *A. caliginosa nocturna*, and *L. terrestris*, and species with a tanylobic type prostomium (most likely young individuals of *L. terrestris*) that showed greater tolerance for variation in pH values. Previous works showed that anecic species are strongly related to soil depth (Bouché, 1972; Guenat et al., 1999; Phillipson et al., 1976). Our study confirmed that *A. c. nocturna* and *L. terrestris* prefer thick soils as already shown by Salomé et al. (2011) and, by extension, drier conditions; and provide evidence that *A. longa* adopts a similar behaviour. Among the three species, *A. longa* reached the highest abundance in HERBS and GRAVELS thus showing the greatest tolerance to flooding. Moreover, the three species were present in HERBS and GRAVELS, whereas *A. giardi* and *L. meliboeus* were absent, most likely because they are less tolerant to inundation than the three previously mentioned species. However, *A. giardi* and *L. meliboeus* were found in only two sites and in low abundance. Such difference in flooding tolerance can tentatively be explained by changes in behaviour according to age class or environmental factors. For example we observed that juveniles of *L. terrestris* adopt a more active behaviour relatively similar to epigeic earthworms whereas they are less active and behave as anecic species do when mature.

Endogeic earthworms are generally not tolerant to water saturation (Bouché, 1972). In agreement, *A. rosea* preferentially occupied the driest places within habitats rarely flooded (FOREST and WILLOW FOREST). However, among the exceptions is *A. c. caliginosa*, a relatively small species tolerant to inundation (Zorn et al., 2008). This species was the only endogeic earthworm present in relatively large number in HERBS where the influence of floods is pre-dominant. It was also characteristic of WILLOW FOREST where the influence of floods was relatively low, but where water table was high. The influence of water table most likely prevented species that tolerate water saturation to a lesser extent (*e.g.* anecic species) to develop in large numbers in this habitat.

The observed distribution patterns of individual species across the six studied habitats agree well with their known biological and ecological characteristics. The differences between the dynamic and stable habitats are in line with the decrease of biomass expected by Thonon and Klok (2007) in response to river restoration and illustrate the potential of earthworms as bioindicators.

As a result, different tolerance for flooding within anecic and endogeic species may help discriminating soils less prone to flooding and with no to low hydromorphy, and, by extension, indicating the initial development of alluvial terraces (either by erosion of the river bed leading to a general lowering of the water table, or by deposition of material). It remains to be determined how fast communities adapt to changing conditions, during shifts to either wetter or drier conditions and increasing or decreasing exposure to floods.

Our study confirmed that flood dynamics have a predominant influence on earthworm communities. Most of the patterns observed can indeed be explained by changes in the frequency of flooding along the gradient. Moreover, the linear increase of all indices with decreasing perturbation agreed with hypotheses of increasing belowground diversity with decreasing perturbations (Wardle, 2002). However, high variation in WILLOW BUSH and FOREST complicated the interpretation of the patterns.

Beside this main effect, our results highlighted the impact of litter quality on earthworm traits. Woody debris can enhance water residence time or trap fallen leaves and seeds thus increasing the food resource for earthworm. Moreover they can constitute hot spots of biological interaction among species (*e.g.* predation) because of the large number of small species (*e.g.* arthropods, mammals, and birds) that preferentially live in woody debris. In forest ecosystems, the relation between litter quality (*i.e.* relative cover of woody debris) and earthworm communities suggest possible positive feedbacks leading to spatial differentiation of ecological conditions through time (*e.g.* Ponge et al., 1999). The significant effect of woody debris on earthworm traits suggests that such processes are likely to occur also at the Thur River and contribute toward maintaining forest communities.

The Thur site, despite its small size, provides a good experimental setting to understand the changes that occurred following restoration at a fine scale. Although generalisation of the present results may be difficult, the agreement with findings of other studies confirmed the pertinence of this approach. Moreover the present study is the first, to our knowledge, that deals with earthworm species traits in floodplains. The results showed that this approach is indeed relevant and confirms the potential of earthworms as bioindicators. Moreover, ecological traits revealed more pertinent than anatomical ones, with the exception of earthworm body length. In addition, our results suggest that the ratio of the relative abundances of epigeic and anecic species, and the differences in species composition within anecic and endogeic ecological categories could be used as indicators of soil development and functioning in floodplains. The next steps would require the improvement of the spatio-temporal variability covered by the data, for example, through comparisons with other (natural) floodplains, together with modelling and manipulative mesocosm or field experiments to calibrate bioindication tools usable for management in general.

5. Conclusion

Restoration created habitats (GRAVELS and HERBS) that imposed strong constraints on earthworms mainly related to flood perturbations. This process was the main driver of changes within earthworm communities at the floodplain scale. Epigeic species that are able to live in thin soil (*r*-selected or able to cope with flooding/inundation) rapidly colonised this area (*i.e.* within 5 years) possibly by hydrochory along the river whereas anecic species that dig vertical galleries prone to inundation were rare or absent. The change in species composition of endogeic communities can be interpreted as a shift toward more flood-tolerant species.

As a result, in the context of floodplains, high abundance of epigeic species at the community scale can be considered as indicative of pioneer conditions and early soil developmental stages, while dominance of anecic species indicates low influence of floods and good soil development. Moreover differences in species composition of the anecic and endogeic communities can help in further discriminating local conditions. In the context of river restoration, these results provide environmental management authorities with a potential new tool for monitoring and assessing soil development.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2012.03.015.

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