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PhD Thesis

Above- and below-ground aspects of floodplain restoration: from biodiversity to ecosystem functions

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1 Abstract

Biodiversity sustains ecosytem functioning and services to human societies. However, the diversity of certain taxa including many soil organisms remains poorly known and the processes creating, sustaining, and destroying biodiversity are only partially understood. As a result, restoring diversity in disturbed ecosystem remains a challenging task.

Floodplains cristallize these issues. They host an extraordinary biodiversity that is often poorly charaterized, they are threathen worldwide, and there is little agreement about the ways to restore their biodiversity.

Aiming at improving our understanding of disturbed ecosystems and the many ecological interactions they host, this PhD focuses on three aspects of floodplain ecosystems: floodplain soils, below-ground biodiversity, and the changes in biodiversity among taxonomic groups and along environmental gradients.

With this respect, the results obtained during this PhD fulfill several gaps in the knowledge of riparian ecosystems and provide perspectives for improved management of floodplains and riverine ecosystems. For instance, the spatio-temporal heterogeneity of soil morphology provides structural and functional information on floodplain ecosystems that can be included into restoration project protocols. Moreover, the strong impacts of environmental conditions on community functional characteristics can be developed into bioindication tools. Finally, the results of this PhD revealed the role of diversity as an insurance to community functioning in recently restored ecosystems.

Future challenges include using holistic approaches for the study of the diversity and the functioning of the soil foodwebs, and disentangling the importance of assembly processes in structuring biodiversity patterns in disturbed ecosystems.

2 Résumé

La biodiversité est le moteur du fonctionnement des écosystèmes. Elles est directement responsable des services fournis par les écosystèmes aux sociétés humaines. Cependant, la diversité de certains taxa dont beaucoup d'organismes du sol reste peu connue; et les processus qui créent, maintiennent et détruisent cette biodiversité ne sont que très partiellement compris. De ce fait, il est extrêmement difficile de restaurer la biodiversité dans les écosystèmes perturbés.

Les zones alluviales cristallisent ces problèmes. Elles accueillent une extraordinaire biodiversité qui est souvent mal caractèrisée; elles sont mondialement menacées; et il n'y a que peu de consensus en ce qui concerne les méthodes pour revitaliser leur biodiversité.

Dans le but d'améliorer notre compréhension des écosystèmes dynamiques et de la multitude d'interactions écologiques qu'ils hébergent, cette thèse se concentre sur trois aspects des zones alluviales: les sols alluviaux, la biodiversité hébergée par ces sols et les changements de biodiversité entre les différents groupes taxonomiques étudiés le long des gradients environnementaux.

Les résultats obtenus lors de cette thèse comblent plusieurs lacunes dans la connaissance écosystémique des zones alluviales et fournissent des perspectives pour améliorer la gestion de ces écosystèmes. En effet, l'hétérogénéité spatio-temporelle de la morphologie des sols fournit des informations structurelles et fonctionnelles sur les zones alluviales qui peuvent être inclues dans les protocoles des projets de revitalisation. De plus, les conditions environnementales influencent fortement les caractéristiques fonctionnelles des communautés. Ces caractéristiques peuvent donc être exploitées comme outil de bioindication. Finalement, les résultats du présent travail ont démontré le rôle de la diversité en tant qu'assurance pour le maintient du fonctionnement des communautés dans les écosystèmes récemment revitalisés.

Les prochains défis à relever consistent à adopter une approche holistique des réseaux trophiques du sol, et définir l'importance des processus écologiques dans la structuration de la biodiversité des écosystèmes dynamiques.

3 Introduction

Above- and below-ground aspects of floodplain restoration: from biodiversity to ecosystem functions: Introduction

Bertrand Fournier[1 2]*

Abstract
Biodiversity sustains ecosytem functioning and services to human societies. However, the diversity of certain taxa including many soil organisms remains poorly known and the processes creating, sustaining, and destroying biodiversity are only partially understood. As a result, restoring diversity in disturbed ecosystem remains a challenging task.

Floodplains cristallize these issues. They host an extraordinary biodiversity that is often poorly charaterized, they are threathen worldwide, and there is little agreement about the ways to restore their biodiversity.

Aiming at improving our understanding of dynamic ecosystems and the many interactions they host, this PhD thesis focuses on three aspects of floodplain ecosystems: soils, below-ground biodiversity, and the changes in biodiversity among taxonomic groups and along environmental gradients.

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1. Biodiversity

1.1 What is biodiversity?

Biodiversity refers to the range of variation or differences among life forms within species, communities, ecosystems or biomes. The definition encompasses species, ecosystem, genetic, and molecular diversities. Biodiversity is thus a multi-level concept that can be considered across various spatio-temporal scales. Moreover, biodiversity can be silent [1, 2] or cryptic [3, 4, 5]; and this has deep implications for characterising biodiversity and conserving it [6].

Biodiversity plays a key role in maintaining ecosystem properties and services [7, 8, 9, 10] such as food production [11], climate regulation, nutrient cycling, biogeochemical cycles, protection against environmental catastrophic events (floods).

Biodiversity is not uniformly distributed in space and time. In time, biodiversity is mainly submitted to evolutionnary processes whereas ecological ones are predominant in space. Obviously, evolutionnary and ecological processes overlap. Understanding how they interact and how these interactions impact biodiversity has become a central issue in ecological sciences [12, 13, 14, 15].

Many approaches were used to characterise the spatio-temporal patterns of biodiversity and their interactions. For example, when applied to communities and food webs, biodiversity can be divided into its taxonomic, functional and phylogenetic facets, and spatially partitioned into its alpha, beta and gamma components [16]. Taxonomic diversity (TD) is much more studied than its functional and phylogenetic counterparts. TD was indeed investigated at various spatial levels [17, 18] and in various settings ranging from bacteria in droplets to biomes at the Earth scale [19, 20] revealing patterns and trends.

1.2 Biodiversity patterns and trends

Broad patterns and trends were described such as the ongoing global loss of biodiversity [21]. Stopping this loss and preserving benefits of biodiversity for ecosystems is a major challenge of ecosystem management [22, 23].

In space, a plethora of patterns of biodiversity were described and certain have become core concepts in ecology. Among those, the peak of species richness at low latitudes [20] and the species-area relationship (SAR) are the most famous and well documented ones but are also still strongly debated [24, 25, 26, 27, 28, 29, 30]. Many explainations were evoked for these patterns [31, 32, 33, 34], among which the Species-Energy theory [35] is the most widely accepted one. This theory has led to the formulation of the Metabolic Theory of Ecology (MTE) [36]. However this theory was primarily developed for terrestrial organisms.

Marine habitats, although proportionally less studied, are also characterized by broad patterns of biodiversity with peaks in the Western Pacific and at mid-latitudes for coastal and oceanic species respectively [37].

Nevertheless, gaps exist in the knowledge of biodiversity distribution. Indeed, the distribution of functional and phylogenetic diversity is less studied than that of taxonomic diversity. The distributions of certain taxonomic groups including many soil organisms and their functional importance are poorly characterized (Fig. 1). At the microbial level, a long-standing debate exists about the cosmopolitanism of taxa that started with Bas-Becking tenets *"everything is everywhere, but the environment selects"* [38] and that is still ongoing [39, 40, 41].

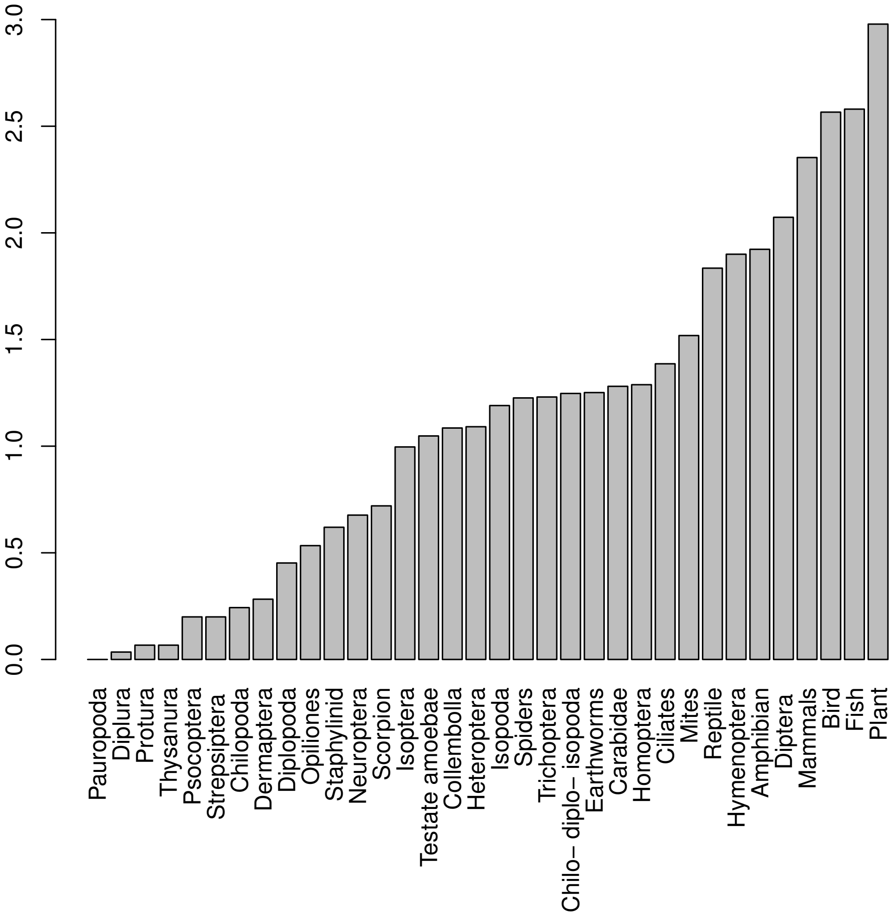

Figure 1. Log number of ecological papers published per year between 2000 and 2011 for various taxa. The Web Of Knowledge (http://portal.isiknowledge.com/) was searched using the name of the taxonomic group and ecology as key words.

Moreover, where broad patterns are widely accepted among ecologists, such agreements tend to vanish when it comes to local scale patterns of biodiversity. Indeed, the interplay of abiotic and biotic factors, assembly processes, historical and spatial factors and the influence of larger scale patterns are responsible for the local distribution of biodiversity. Furthermore, the mechanisms allowing many species to coexist are not fully understood [42], and no integrated theoretical framework allows predicting them in all situations encountered in the field [43]. Moreover, different processes might be responsible for the observed biodiversity patterns depending on the spatial scale considered [44, 45].

As a result, it remains extremely difficult not to say uncertain to restore biodiversity in damaged ecosystems. Given that biodiversity sustains ecosystem functioning and underpins most ecosystem services [8, 9], it is essential to improve our knowledge of the less investigated aspects of biodiversity and the assembly processes that are responsible for species coexistence at all scales, but especially locally.

To disentangle local scale patterns of diversity and their interactions with global ones, ecologists have widely used approaches aiming at identifying species, communities, or ecosystems of key functional importance [46, 47].

1.3 Functional diversity

Understanding the functional importance of biodiversity in ecosystems and its distribution is a critical step toward acquiring a mechanistic understanding of the processes underpinning it. Approaches aiming at characterising the functional importance of taxa in the ecosystem, especially trait-based approaches, have recently re-gained interest because of methodological advances such as developing new metrics [48], partitioning trait values into within and among community or into alpha, beta and gamma components [49, 50], investigating the convergence and divergence of traits using randomization tests to break ecological assembly rules [51], or investigating the impact of disturbances [52].

1.3.1 Trait based approaches

Trait-based approaches allow characterizing the performance of organisms under changing environmental conditions through their biological attributes. Relating traits to environmental variables improves our understanding of biological processes in ecosystems and allows defining general and useful rules of species assembly [53].

Trait-based approaches provide a way to overcome taxonomic limitations. Traits tend to correlate more strongly than traditional species diversity with ecosystem functions such as productivity [9], resilience to disturbances [54], or regulation of biogeochemical fluxes [55], and provide a better understanding of multi-trophic interactions [56, 57].

These approaches led to an improved understanding of the functional facet of biodiversity -functional diversity-.

1.3.2 Functional diversity measures

FD, the amount of variation of functional trait values among species in a community, constitutes a powerful tool for understanding ecosystem functioning [47, 10, 58], defining general principles in community ecology [59, 53], and studying the impact of global changes on communities [58, 60]. FD can be expressed in three major metrics: functional richness (FRic), divergence (FDiv), and evenness (FEve) [61]. Integrative metrics accounting for several components of FD were also developed such as Functional Dispersion (FDis) [62] and Rao's quadratic entropy (FDQ) [63, 64].

FD is linked to assembly processes and changes in FD indices can be used to investigate assembly processes in the field [65, 66, 67, 68].

1.4 Assembly processes

Understanding community assembly processes is among the main challenges of current ecological research. Among the leading theories that were developed with this aim are The Unified Neutral Theory (UNT) [69] and the Metacommunity theory [70, 71]. The UNT succeeded in explaining many patterns and in revealing the importance of ecological drift [72]. However this theory has unrealistic assumptions such as the functional equivalence among species and the absence of environmental differences among localities. To address these limitations, the Metacommunity theory investigates ecological linkages across spatial scales and proposed four main processes ruling community assembly: patch dynamics or competition-colonization trade-offs (PD), species sorting (SS), mass effects or source-sink dynamics (ME), and neutral (N) [70, 71]. PD assumes a trade-off between dispersal and competitive potential where specialist species dispersing poorly are likely to better exploit limiting resources and thus outcompete more generalist species having higher dispersal ability. These species maintain themselves in the system by using vacant sites that are not yet exploited by competitors. In SS, changing environmental conditions sort species according to their degree of adaptations to local conditions. Dispersal needs to be high enough for species to reach suitable habitats but sufficiently low to prevent ME. In ME, dispersal is high. Local assemblies are thus a random mix of well and poorly adapted species, the latter being maintained by dispersal from adjacent areas. Finally, N assumes functional equivalence among organisms and no differences among localities. These four paradigms have received considerable agreement among ecologists.

Empirical approaches to metacommunities highlighted that dispersal and niche (breadth or optimum) are among the main characteristics determining assembly dynamics [73, 74]. They also revealed gaps between theory and practice, the need for integrating different paradigms into a common framework [43], and areas for future development such as considering a broader panel of environmental conditions and organisms. For instance, below-ground organisms, that are poorly known (especially from a functional point of view), were also poorly used to challenge theoretical expectations.

1.5 Above- *VS* below-ground ecology

When characterising the spatio-temporal changes of biodiversity, ecologists have mainly focused on the aboveground compartment of ecosystems, neglecting the importance of the below-ground compartment [77, 78]. Worse, they have often considered the spatial distribution of soil organisms as random noise [79].

However, below-ground biodiversity has many outstanding characteristics. Below-ground biota play a key role in nutrient cycling, pedogenesis, and food-webs. They are much more species-rich than there aboveground counterparts making soil ecosystems one of the last biotic frontiers [80, 81].

No consensus exists to explain these differences. However, the most generally accepted explanations invoke the low mobility and high survival of soil organisms, differences in the number of available habitats between above- and below-ground [82], and differences in the drivers of assembly processes. For instance, competition was shown to be less intense in soils [77] with the notable exception of soil fungal communities [83]. The bell-shaped patterns along disturbance or productivity gradients predicted by the IDH and ISH (Table 1) were generally not observed for soil organisms indicating a low importance of competitive exclusion in shaping biodiversity. This is due to the high heterogeneity of soils [84] and the difficulties of moving in them that decreases the intensity of biotic interactions.

The importance of biotic interactions in structuring the below-ground biota is poorly understood. Biotic assembly rules were shown to have higher importance in structuring communities above- than below-ground [85]. Nevertheless evidences for below-ground competition exist [86].

Below-ground biodiversity can impact its aboveground counterpart since the two components of ecosystems are interlinked [87]. For instance, the composition of plant communities may be strongly influenced by the associations of plants with micro-organisms in the rhizosphere and the regulation of these associations by soil fauna activity [88]. Moreover, the strength of these interactions depends on nutrient availability [89]. In the context of communities' interactions and ecosystem management, it is therefore particularly important to consider all ecosystem compartments.

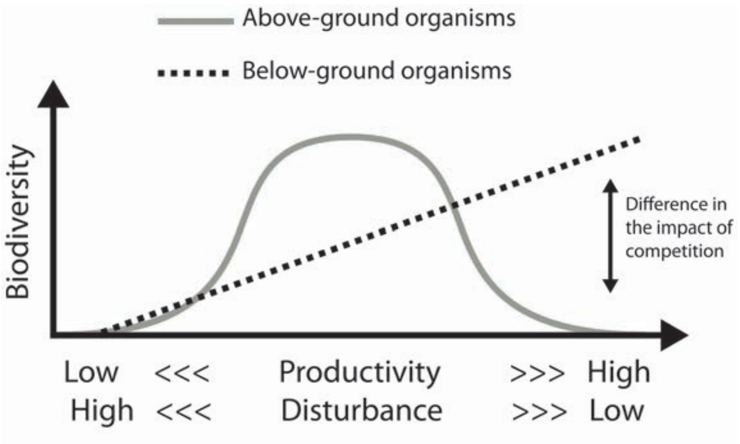

Figure 2. Theoretical patterns of biodiversity along productivity or disturbance gradients for aboveground [75] (but see [76]) and below-ground organisms [77].

2. Floodplains

In the present context of global change, worldwide loss of species and increased human impact on ecosystems, organisms are increasingly submitted to disturbances. For instance, disturbances such as flood and fire have strong impacts on biodiversity [90, 54, 91, 92, 93, 94]. Understanding the impact of these disturbances can provide the key to cope with future challenges for the management of dynamic ecosystems such as fire-prone forests and grassland, or floodplains. The present work aims at understanding the impact of flood disturbances on biodiversity in floodplains.

2.1 Definition

Floodplain are flat or nearly flat lands adjacent to a stream or river that experience occasional or periodic flooding. They vary in space and time, creating four main gradients or patterns: longitudinal to the river [95, 96], lateral [97], vertical and temporal associated with river flow [98]. Moreover, floodplains complexity increases from source to delta [99].
The flooding regime influences all ecosystem conditions. It is mainly responsible for the extraordinary spatial and temporal heterogeneity of floodplains, but several processes (e.g. river flow, soil wetness or dryness, anaerobiosis caused by waterlogging) also play a major role in determining floodplains morphology. These processes occur over different time scales. Indeed, natural floodplains are dynamic ecosystems that can be completely transformed in a few days by a major flood, or more slowly through ecological processes such as pedogenesis and community succession.

2.2 Floodplain ecosystem functions

Floodplains, at the interface between aquatic and terrestrial ecosystems, act as mineral material reservoir furnishing organic matter to aquatic habitats. They regulate floods through slowing down the water and stabilizing banks, providing an important physical protection to human settlements. Their buffer role in preventing river contamination by external pollutant sources such as fertilizers is also well documented [100, 101, 102]. They are important in the groundwater recharging process and enhance water quality by removing organic and inorganic nutrient and toxic material [103, 104].
Floodplains and humans have a long common history and human existence has often been governed by floodplain functioning. Floodplain soils are among the most fertile soils on earth because of the frequent flooding events accompanied by nutrient rich sediments deposition [105, 106]. This high productivity was intensively exploited as economic service for millennia since the dawn of human society in the Middle East and Asia. For example, the abundant plant biomass produced by floodplains is often harvested for cattle foraging in herbaceous habitats such as reeds or exploited as timber wood in forest area. As most temperate floodplains receive fertilizer enriched agricultural runoff, they also play a major role in the available nitrogen balance [107, 108].
Finally, one the most common and appreciated service provided by floodplains is their extraordinary aesthetic value. As such a parameter is very hard to estimate quantitatively in a rigorous way, it is often left aside in the calculations of floodplains economical values. But it constitutes certainly one of the most appreciated aspects of floodplain landscapes.

2.3 Biodiversity and ecological processes

Because of their dynamics, heterogeneity, and position at the interface of aquatic and terrestrial ecosystems, floodplains are among the most complex ecosystems on earth [106], allowing them to host an extraordinary biodiversity [109, 98, 99]. Indeed, it was estimated that half of the Swiss flora (about 1500 species) was present in floodplains, which cover only 0.5% of the land (OFEV). According to Godreau et al., [110], alluvial forests play a great role in maintaining particular species such as the Golden Oriole (*Oriolus oriolus*). In Switzerland, endangered species such as beavers (*Castor fiber*) can find a refuge habitat only in well preserved floodplains. Now extinct species such as the otter (*Lutra lutra*) were also linked to these ecosystems [111].

The frequent flood disturbances and a broad range of hydric conditions leading to drought and waterlogging stresses have dramatic impacts on organisms and are among the main drivers of biodiversity [112, 98]. Disturbance punctually removes part of the biomass while stress more permanently restricts its production [113] and both cause chemical and physical changes to the environment [114]. Moreover, disturbance and stress were shown to influence assembly processes [115, 116].

Through the extraordinary biodiversity they host and their complexity, floodplains offer ecologists ideal stages to study complex ecological interactions, the impact of disturbance and stress on biodiversity, and the assembly processes sustaining this biodiversity. Indeed, attempts to disentangle the interplay of biotic and abitioc factors and their impact on biodiversity in riverine ecosystems have led to the development of many ecological theories, concepts or paradigms (Table 1) that are at the core of ecological sciences.

Despite their functional importance and their scientific value, floodplains are globally threathened by human activities and mis-management of the resources they provide.

2.4 Riparian and riverine ecosystems: Threats and challenges

Globally rivers have suffered from years of destructive engineering and nowadays, most of the earth's major rivers are altered because of centuries of flow control attempts by human construction such as dams. Fertile alluvial floodplains were cleared for agriculture, making alluvial forests a threatened habitat at the European scale. In areas where steepness is a problem for highway and railways construction, floodplains may provide the only practicable route [135], thus causing conflicts between human activities and nature conservation.

Human consideration for floodplains has focused on economical exploitation and protection against flood until the middle of the twentieth century. Larson and Kusler in 1979 [136] described human vision of wetlands in the following terms: *"For most of the recorded history, ..., a good wetland was a drained wetland free of this mixture of dubious social factors."* The most common practices in river management were drainage, dredging, filling, ditching and levee building, resulting in the nowadays well known problems of river space allocation, repeated floods, river bed vertical erosion and broken dynamic of sediments deposition.

As a result of decades of destructive management, floodplains have become one of the most threatened ecosystems worldwide [137, 106, 138, 139]. In the latter part of the 20th century, river management practices have been questioned due to the development of new concepts that changed our understanding of river ecosystems (Table 1). Floodplain management has seen a dramatic paradigm shift from controlling rivers to restoring their ecological quality and related functions and services [106, 138]. The European Commission recognized during the 1990s that there was a need to find a better way of managing the water and near water ecosystems. This gave rise, in 2003, to the Water Framework Directive (WFD), "the most substantial piece of water legislation ever produced by the European Commission" (www.euwfd.com), which is a key driver for achieving "good ecological status" of rivers. Following the same principles, Switzerland, through the BWG ("Bundesamt für Wasser und Geologie") 2001 report, wanted river revitalizations to be an entire part of the flood protection measures.

As a consequence, the number of river restoration projects worldwide has dramatically increased over the past decades [140, 141, 142, 143, 144]. It is not the least of paradoxes that governments are now spending billions of Dollars/Euros of taxpayer's money for attempting to recreate functional and diverse floodplain ecosystems where they previously had spent comparable amounts to master them.

The increasing number of restoration projects calls for an improved understanding of river and near river ecosystem structure and functioning. For this purpose, many studies were conducted in floodplains. However, as for most of ecological research, most of them focused only on the aboveground compartment (but see [145, 146, 147]).

2.5 Assessements of floodplain restoration projects

Assessing the outcome of river restoration projects is vital for adaptive management, evaluation of project efficiency, optimization of future programs, and gaining public acceptance [148]. However restoration projects are often undermined by two facts, 1) in many cases the goals of the restoration project are not clearly defined, and 2) there is a crucial lack of monitoring and quantitative evaluation of restoration projects (NRC 1992). For example, in the Upper Mississippi River Basin, only 34% of projects surveyed incorporated a quantified measure of their success [149]. In Switzerland, only 35% of projects benefit from monitoring mainly based on evolution of flora and fauna (BAFU). When included, such follow-up research typically only represents a small fraction of the total cost of restoration. Post-restoration monitoring provides valuable information on how successful the project was in meeting the objectives, provides a basis for improving ongoing and future projects, and, as a consequence, decreases the cost of future projects by increasing their efficiency [150]. It follows that the two key elements to successful restoration projects are: 1) clear objectives, and 2) adapted monitoring using appropriate indicators.

Although an important literature was produced on the topic [148, 143, 151, 152], assessing the success of floodplain restoration projects has remained an entangled issue mainly because multiple and often antagonistic objectives are considered at the same time. As a result, the choice among the different assessement methods, criteria, and indicators is

Table 1. Non-exhaustive summary of the ecological theories, concepts or paradigms developed in relation to riverine ecosystems

Ecological theories, concepts or paradigms	Short name	References
Intermediate Disturbance Hypothesis	IDH	[75, 117]
Intermediate Stress Hypothesis	ISH	[118, 117]
River Continuum Concept	RCC	[119]
Natural flow regime paradigm	-	[120]
Riverine productivity model	-	[121, 122]
Functional Process Zones	FPZ	[123]
Riverine Ecosystem Synthesis	RES	[123]
Dynamic Equilibrium Model	DEM	[124]
Serial Discontinuity concept	SD	[125]
Habitat templet theory	-	[126, 127, 128, 129, 130, 131, 132]
Flood pulse concept	-	[133]
Interdisciplinary framework	-	[134]

confusing. Moreover, no synthetic indicators that is able to summarize all the information needed to evaluate the success of a restoration project exist. Developping such indicators and improving the existing ones is essential for a sustainable management of floodplain ecosystems.

2.6 Study case: Thur River

This PhD thesis was intimately linked to a specific river restoration project along the The Thur River in north-western Switzerland. Below is a contextual description of the Thur River and the stretch that we used as study site including the changes that occured folowing its restoration.

After a 127 km long course trough the Swiss Plateau, The Thur River flows into the Rhine near the Swiss-German border in canton Zürich at 343 m asl. It runs through five cantons and has its source in the Säntis Mountains at 2503 m asl. The Thur is the largest river in Switzerland without a natural or artificial reservoir. It exhibits fluctuations in discharge and water table similar to unregulated Alpine rivers. The annual average flow is 47 m^3 s^{-1}, but it can go down to 4 m^3 s^{-1} in the driest periods. Nevertheless, during the snow melt period or a big storm, its flow can increase dramatically. For example, on the 13th May 1999 its flow increased from 80 m^3 s^{-1} to 1130 m^3 s^{-1} in 1h45 causing great damages. The name "Thur" itself means hurry ("Dhu" in Indo-European). The Thur is an important river at the country scale. It is a biodiversity resource for Switzerland as it hosts four floodplains of national importance. It is an important drinking water resource for the regions of Frauenfeld (ZH) and Winterthur (ZH). As it flows through an intensive agricultural plain, the Thur has long common history with human society and especially with the farmers living on its sides. The River Thur was a natural braided river. Following the 19th century floods, major works were conducted to canalize the river. The previously meandering route of the Thur was transformed into a linear way down the plain. Two sets of levees were constructed 50 and 150 m apart in order to ensure security. The rise was initially planned for an extensive agricultural exploitation or a floodplain role, but was, in fact, used in an intensive way. The increasing human proximity constituted a strong pressure on the Thur river ecosystem. Because of its new profile, the flow increased and so did erosion forces. River bed erosion started, threatening groundwater quality at the regional scale. But at the same time, alluvial deposition on the rise reduced the flow capacity causing destabilization of the banks. The flood risk increased and inevitably new flood episodes occurred. This led to the second correction of the Thur River (1992), but this time according to hydrological as well as ecological criteria. In 2012, the restoration the Thur River was among the biggest restoration project conducted in Switzerland.

Our study site (Fig. 3) -called Schäuffäuli- is one of the section targeted by the restoration works, and is among the national importance floodplains. It is situated in the "Thurtal" plain near Frauenfeld. At this place, the river marks the border between cantons Zürich and Thurgau. The first restoration of this particular section occurred almost "accidentally" in 1995 following a major flood. The minor bed protection structures were destroyed and an erosion of the major bed started. At this point the focus was on the protection of the river banks. Works were conducted in order to stabilize the banks. A second restoration of the site followed in 2002. The river bed was widened along 1.5 km from 50 to 110 m. The banks were stabilized by artificial plantations of willows (*Salix viminalis*). The reduction of river flow has allowed the creation of gravel banks, and the reconstruction of an "almost natural" perturbations gradient lateral to the river. "Almost" because the erosion process of the minor bed protection structures is still in progress. A zonation in term of vegetation composition was created exhibiting the main steps from the pioneer species colonizing the most dynamical part of the gradient to the competitor species installed in the forest. It also hosts "flagship" species for Swiss biodiversity such as the beaver (*Castor fiber*) or the little ringed plover (*Charadrius dubius*).

Figure 3. Picture of the study site along the Thur River (cantons of Zurich and Arau, Switzerland).

2.7 Aims and Objectives

This PhD thesis aims at improving our understanding of dynamic ecosystems and the many interactions they host. Using an above- and below-ground approach that focuses on key communities (i.e. vegetation, carabid and staphylinid beetles, spiders, diplopoda, isopoda, earthworms, testate amoebae), it aims to bring new insights into the ecology of floodplains. This knowledge will be useful for the management and conservation of floodplains by leading to the development of new methods for project assessment and new bioindicators for monitoring.

This PhD project focuses on three main aspects of the ecology of floodplain ecosystems: 1) floodplain soils, 2) the patterns of diversity of below-ground organisms and their relations with environmental variables, and 3) the relations among different taxonomic groups, their diversity, and ecosystem functions. These aspects are addressed hereafter through a series of four papers published in peer-reviewed journals. The first presents a potential application of the spatio-temporal heterogeneity of riparian soil morphology, the second and third investigate the patterns of soil organism biodiversity (earthworms and testate amoebae) and their relations with environmental variables. Finally, the fourth aims at disentangling the assembly processes responsible for the biodiversity patterns of multiple taxonomic groups.

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4 Spatio-temporal heterogeneity of riparian soils

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Spatio-temporal heterogeneity of riparian soil morphology in a restored floodplain

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Abstract
Floodplains have been intensively altered in industrialized countries, but are now increasingly being restored. It is therefore important to assess the effect of these restoration projects on the aquatic and terrestrial components of ecosystems. However, despite being functionally crucial components of terrestrial ecosystems, soils are generally overlooked in floodplain restoration assessments.

We studied the spatio-temporal heterogeneity of soil morphology in a restored (riverbed widening) river reach along River Thur (Switzerland) using three criteria (soil diversity, dynamism and typicality) and their associated indicators. We hypothesized that these criteria would correctly discriminate the post-restoration changes in soil morphology, and that these changes correspond to patterns of vascular plant diversity.

Soil diversity and dynamism increased five years after the restoration, but some typical soils of braided rivers were still missing. Soil typicality and dynamism were correlated to vegetation changes. These results suggest a limited success of the project in agreement with evaluations carried out at the same site using others, but more resources demanding methods (e.g. soil fauna, fish diversity, ecosystem functioning).

Soil morphology provides structural and functional information on floodplain ecosystems. The spatio-temporal heterogeneity of soil morphology represents a cost-efficient ecological indicator that could easily be integrated into rapid assessment protocols of floodplain and river restoration projects.

Follow-up assessment after several major floods (HQ20) have occurred should allow testing the longer-term validity of our conclusion for the River Thur site. More generally it would be useful to apply the soil morphology indicator approach in different settings to test its broader applicability.

Keywords
Ecological indicator — ecological restoration — floodplains — pedodiversity — pedogenesis — plant diversity — vegetation

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1. Introduction

Floodplains fulfil ecological, economic and social functions such as biodiversity reservoirs, supply of natural resources, and flood regulation [1] and are increasingly appreciated for their aesthetic value and for recreational uses [2]. However, floodplains are also one of the most threatened ecosystems worldwide [1, 3].

In the last decades, the primary goal of floodplain management has shifted from controlling rivers to restoring their biodiversity, ecological quality and related functions and services [1, 3]. As a result, the number of river restoration projects aiming to increase ecosystem goods and services such as flood abatement, biodiversity and drinking water improvement is increasing worldwide [4, 5, 6, 7, 8]. Assessing the outcome of these projects is essential for adaptive management, evaluation of project efficiency, optimization of future programs, and gaining public acceptance [9]. However, restoration projects often lack post-restoration monitoring using standardized evaluation methods (with well-defined criteria and indicators), which would increase their cost-efficiency [10, 11, 12, 13]. This lack of monitoring is mainly due to lack of funding beyond the practical restoration project. Rapid yet informative, cost-effective monitoring tools are extremely sought-after; existing methods consider hydrology, physical and biological structures, and the landscape context [14], but only include general elements with respect to soils.

Soils play a central role in critical ecosystem processes (e.g. decomposition, water filtering), and are among the main drivers of community assembly [15, 16]. For example, soil conditions strongly determine vegetation dynamics [17] and plant productivity and diversity [18]. In turn, the vegetation influences soil properties such as organic matter content [19]. Through their morphology, soils also provide information on ecosystem structure, and record past and present fluvial dynamics [20, 21, 22]. This information may be especially useful when a site has been ditched, drained, and stripped of its vegetation [23]. Soil morphology is influenced by different factors that are related to important processes occurring in floodplain ecosystems such as erosion/sedimentation, flood dynamics, soil biota activity or pedogenesis.

Soils are not as quick to change as vegetation and hydrology, making them easier to monitor over short time intervals. In contrast to biological surveys that are dependent on species' developmental stages (e.g. vernal species, or adult stages) or population fluctuations (e.g. seasonal migration, and effects of exceptional climatic event), soil morphology can be assessed in any season and in a single field campaign. However, in order to use soils in monitoring programs it is necessary to understand how they change over time [23]. To date, most research on the impact of river restoration on floodplain soil have focused on processes such as organic matter accumulation and decomposition [24, 25, 26], litter decomposition [27], or denitrification [28, 29]. There is thus a need to integrate soil physical, chemical and biological factors and processes [30] and soil temporal dynamics [27] into the planning and assessment of river restoration projects.

Here we explore the possible use of riparian soil morphology as indicators of floodplain dynamics by studying the spatio-temporal heterogeneity of soil morphology in a restored river reach along River Thur (Switzerland). Our main aim was to assess the post-restoration changes in soil morphology as well as the variations of the main aspects of soil morphology along the river lateral gradient. We considered three criteria (and associated indicators) designed to cover these main aspects: (1) soil diversity, (2) soil dynamism, and (3) soil typicality. We also investigated whether the changes in soil morphology revealed by these three criteria would reflect changes in vascular plant diversity and vegetation type. Strong correlations between vegetation and soil morphology would indicate balanced ecological processes.

2. Material and Methods

2.1 Study site

The Thur River is a perennial river in the north-eastern part of Switzerland. Its catchment (1750 m^2) is limestone dominated but also consists of sandstones and Pleistocene unconsolidated sediments in the lowest sections. It is the longest river in Switzerland (127 km) that flows continuously without any regulation by artificial reservoir or natural lakes. It is a braided river (slope 1.7%) with a nivo-pluvial hydrologic regime characterised by flash floods. In spring and autumn, flood pulses occur as a result of snowmelt or intense precipitations. Discharge may increase dramatically within a few hours and trig both bed load and suspended sediment transport. The mean annual discharge is 47 m^3 s^{-1}, with peak flows up to 1130 m^3 s^{-1} and low flows down to 2.2 m^3 s^{-1}. Originally, the Thur River showed a clear braided morphology in its lower part. In the 1890s, the river was channelized into a 50 m main bed flanked, 150 m further, by a side channel delimited by levees. In 2002, a 1.5 km long section of River Thur near Frauenfeld was restored by completely removing the right side foreland, so that the nearby alluvial forest became part of the active floodplain again.

The Thur River restoration is among the biggest river widening projects in Switzerland to date and includes post-restoration monitoring and evaluations of several stretches [31, 32, 33]. The present study is part of the interdisciplinary RECORD-project (http://www.cces.ethz.ch/projects/nature/Record). We selected a study site along the Thur River near "Schäffäuli" (Supplementary figure 6). The site lies at 365m asl. Annual precipitation is about 1000 mm year^{-1} and the average annual temperature is 7.9 degrees. Restoration of the site was conducted in two steps. Following a major flood in 1995, the bed protection structures were removed. In 2002, the riverbed was widened along a 1.5 km stretch from 50 to 110 m by embankments removal and the new bank stabilized by planting willows (*Salix viminalis*). This work was done with heavy equipment thus strongly impacting floodplain soils in the restoration site. The project aimed to improve flood protection, to maintain drinkable water resources and to enhance the ecological quality of the riverine and riparian habitats.

We distinguished three well-differentiated situations within the study site based on field observations (topography and vegetation), available information on the site restoration, river maps and illustrations from the early 19th century, historical data on Swiss lowland braided rivers [34, 35, 36, 37, 38], and the literature on braided river soils [39, 40, 41]. The first situation corresponds to *open habitats* with poorly developed soils closest to the river. Most restoration works were conducted in this area. Further from the river lays an *riparian forest* growing on deeper soils. This forest was present before restoration and restoration had only a limited impact on this area. Finally, we used an *un-restored section* of the same site located directly upstream from the restored one as a control that was not, or only marginally, impacted by the restoration. We expected the criteria and indicators of soil morphology presented below to show clear differences among these three areas, revealing how the restoration affected the functioning of this riparian zone.

2.2 Data acquisition

Soil surveys were carried out in summer 2007 along five transects corresponding to topographical surveys over time, each starting at the main river bed and ending about 65 m further where no more floodplain soils were encountered. Three transects were selected in the restored area with a sampling point every 1.5 m in the most variable part (up to a distance of about 15 m from the river) and then every 3 m resulting in a total of 73 sampling points. Two transects were selected within the control area with a sampling point every 3 m resulting in 22 sampling points. The precise location, elevation and distance to the river of each sampling point were recorded.

Soils were surveyed by describing the morphology of profiles and horizons from auger borings (1.2 m length). Different

Table 1. Description of eight soil profile groups (1a) and seven topsoil groups (1b) resulting from a cluster analysis based on a simplified set of variables. The number of observations within each group is given in brackets. Soil taxonomy is based on AFES [41] and correspondences to the FAO World reference base for soil resources [39] are given. Depth is the mean depth of a particular group of soil profiles (cm). Texture is based on the US texture triangle [42]. For the soil profiles, texture is described using the total number of loam, sandy loam and sandy horizons within each group of soil profile, and the average number of horizons per soil profile (given below as the range of the most frequent number of horizons per soil profile to represent intra-group heterogeneity). The volumetric percentage of coarse material (blocks, pebbles and gravels) of the coarsest horizon within the soil profile is indicated under coarse material. Proportion of blocks, pebbles and gravels are given for each group in percentage of total volume. Topsoil thickness (1b) is given in cm. Hydromorphic features represent the average depth (in cm) at which hydromorphic features were first observed. The intensity of the hydromorphic features is given using a semi-quantitative scale (absence, weak, moderate, and high). The organic matter (OM) content (null = 0%, low $\leq$ 10%, medium $\leq$ 50%, and high $>$ 50%) and type (no, humified, and coarse residuals) are given.

(a) Table 1a.

Soil profile	Taxonomy		Depth [cm]	Number of Horizons				Coarse material [%]	Hydromorphy	
	AFES, 2008	WRB, 2006		Loam	Sandy loam	Sand	Average per profile		Hydromorphic features	Intensity of hydromorphy
Group 1 (11)	REDOXISOLS fluviques carbonatés	Gleyic Fluvisols Calcaric	111	7	47	0	2-4	0.3	15	Moderate
Group 2 (25)	FLUVIOSOLS typiques carbonatés	Fluvisols Calcaric	95	0	91	2	1-4	1.2	No	No
Group 3 (2)	FLUVIOSOLS typiques redoxiques carbonatés	Fluvisols Calcaric with redoximorphic features	120	1	10	0	3	6.5	50	Weak to moderate
Group 4 (32)	FLUVIOSOLS bruts carbonatés	Regosols Calcaric	0.8	0	1	31	0	87	No	No
Group 5 (22)	FLUVIOSOLS bruts carbonatés	Regosols Calcaric	20	0	42	5	1-2	45	No	No
Group 6 (9)	FLUVIOSOLs typiques redoxiques carbonatés	Fluvisols Calcaric with redoximorphic features	69	0	36	2	3	5.6	25	weak
Group 7 (8)	FLUVIOSOLS typiques redoxiques carbonatés	Fluvisols Calcaric with redoximorphic features	104	0	33	0	2	1.1	50	Weak to moderate
Group 8 (1)	REDUCTISOLS fulviques carbonatés	Gleysols Calcaric	30	0	2	0	1	7	15	High

(b) Table 1b.

Topsoil layer	Thickness [cm]	Organic matter content	Organic matter type	Texture (US triangle)	Blocks [%]	Pebbles [%]	Gravel [%]	Hydromorphic features
Group 1 (27)	8	low-medium	humified	Sandy loam	0	0	0	absent
Group 2 (21)	0	null	no	Sand	0.6	68	29	absent
Group 3 (10)	0	null	no	Sand	0.9	33	55	absent
Group 4 (36)	9	medium-low	coarse residuals	Sandy loam	0	0	5	absent
Group 5 (13)	9.5	medium-low	coarse residuals + humified	Sandy loam	0	0	1	absent
Group 6 (1)	5	medium	humified	Sandy loam	0	0	0	heterogenous iron distribution
Group 7 (2)	15	medium	coarse residuals	Loamy sand	0	0	1	related to roots, spots

variables were used to describe soil profiles and topsoils. Profile characterization was based on: profile depth (cm); number of sandy, loamy, clay, or humic horizons; total number of horizons, volumetric percentage of coarse elements (%); presence, type (reduction or oxidation), and intensity of hydromorphic features; depth of the first horizon with hydromorphic features (cm). Topsoil descriptions were based on: horizon thickness (cm); texture; root density; soil structure type; volumetric proportion of coarse elements and organic matter (%); presence, type (reduction or oxidation) and intensity of hydromorphic features; macroscopic plant remains; biological activity features.

2.3 Soil characteristics and typology

In order to describe changes in soil profiles and topsoils, we constructed site-specific typologies (Table 1). Two typologies (soil profile and topsoil) were generated using the complete linkage algorithm which preserves small clusters of observations [45] and thus prevents groups composed by few points (i.e. rare soil groups) to be included in larger groups. Clusters validity was evaluated using silhouette width - a distance-based method that assesses the quality of each cluster - [46]. Positive values indicate correct classifications and negative un-correct ones. The calculations of the indicators were based on the resulting profile and topsoil groups. To facilitate comparisons among studies, we indicated the correspondence between our typology of soil profiles and two standard soil taxonomy references [41, 39].

2.4 Soil criteria and indicators

For each criterion and indicator derived from the soil typologies we defined the range of possible values, an application

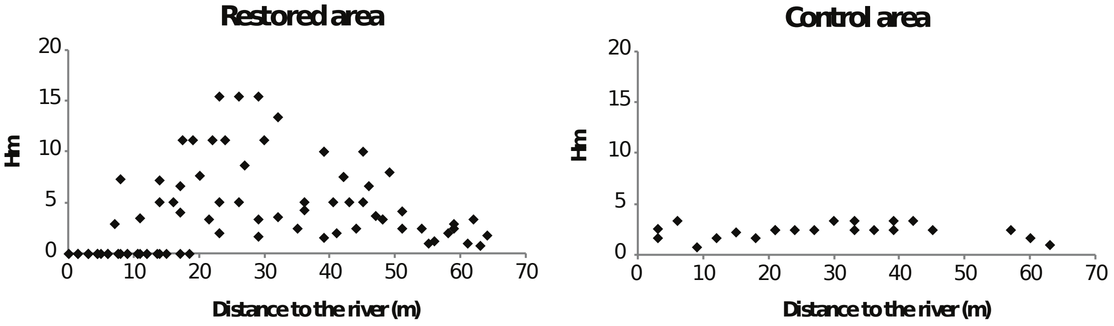

Figure 1. Number of horizons per meter (H_m) versus lateral distance to the river (m) for the restored (1a) and the control areas (1b) of the River Thur site.

Table 2. Criteria and indicators of the soil morphology method for floodplain restoration success assessment.

Criterion	Indicators	Range	Application domain	Reference	Rationale
Diversity	Simpson index	0 → n (*i.e.* no upper limit)	Soil profile Topsoil	[43]	Indicator of soil / topsoil habitat diversity (N2) and evenness (E2)
	Richness	0 → n	Soil profile Topsoil		Indicator of the number of soil/topsoil habitats (N0)
Typicality	Frequency of typical soil profile groups	Expressed in %	Soil profile	[41]	Indicator of soil typical of natural floodplains
	Frequency of typical topsoil groups	Idem	Topsoil	[41]	Indicator of recent changes characteristic of natural floodplains
Dynamism	Total number of horizons per meter (H_m)	0 → n	Soil profile	[44]	Indicator of morphological changes due to fluvial dynamics
	Elevation variation through time (Δ)	-n → n	Topography		Indicator of rate of erosion/sedimentation

domain (soil profiles and/or horizons), and the rationale for its use (Table 2).

2.4.1 Soil diversity

Tools for measuring pedodiversity increasingly attract the attention of soil scientists [47, 48, 49, 50, 51]. Information on richness, diversity and evenness of soil groups may be useful for evaluating restoration projects, especially given the high spatio-temporal heterogeneity of soils that can be observed in floodplains. The spatio-temporal heterogeneity of soil morphology was first estimated by comparing pedodiversity indices, among the forest, the open area closed to the river (restored), and the control managed pasture (non-restored) for soil profile and topsoil groups. We used three measures of alpha diversity according to Hill [43]: richness (N0), Simpson diversity (N2) and evenness (E2=N2/N0). We used soil profile and topsoil groups as surrogate of species for the calculations of these metrics. As a result, N0 accounts for the number of soil profile and topsoil groups, high E2 indicate that all soil profile and topsoil groups are encountered with a similar frequency; and high N2 reveal a large number of soil profile and topsoil groups evenly distributed.

2.4.2 Soil dynamism

Soil dynamism is defined here as the successions through time of sedimentation and/or erosion processes related to the fluvial regime. In natural floodplains, the fluvial dynamic creates through floods and *in situ* pedogenesis between flood events a high spatio-temporal heterogeneity of soil morphologies. Therefore, efficient river restoration should lead to recreating or maintaining such a high heterogeneity of soils.

Practically, we plotted the total number of horizons per meter (H_m) against distance to river to get a 2D picture of the erosion/sedimentation processes along the lateral gradient. The soil dynamism criterion was assessed by comparing the resulting patterns (1) along the river lateral gradient and (2) between the restored (open habitats + floodplain forest) and control areas.

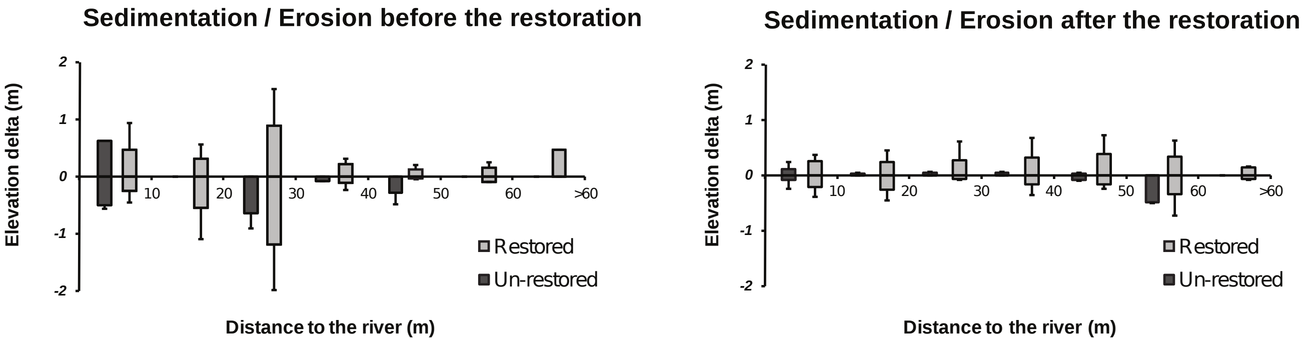

Figure 2. Average positive and negative elevation deltas (m) and their associated standard deviations before (Fig 2a: period ranging from 1996 to 2002) and after the restoration (Fig 2b: period ranging from 2002 to 2007) in the restored and in the reference (un-restored) areas of the River Thur site. Calculations are based on cross sections data for seven classes of distance to the river (10 meters sections). Positive deltas (+) correspond to sedimentation processes and negative deltas (-) to erosion processes.

Table 3. Soil profile and topsoil diversity indices calculated at the Thur site. Soil profile group richness (N0), soil profile group Simpson diversity (N2) and soil profile group evenness (E2) are given for three spatially distinct areas within the River Thur site.

		N0	N2	E2
Profile	Open habitats	7	3.47	0.5
	Forest	2	1.95	0.97
	Control area	4	2.6	0.65
Topsoil	Open habitats	6	3.78	0.63
	Forest	4	2.03	0.51
	Control area	3	2.33	0.78

Elevation deltas (i.e. the surface elevation variation of a given point measured through time) were calculated using cross-section topographical surveys. These surveys were done in the field using theodolite of a precision of about 1 cm. Negative and positive deltas are due respectively to net erosion and deposition processes. Cross sections data covering a period ranging from 1996 to 2002 (before restoration) and from 2002 to 2007 (after restoration) were used to assess elevation variations through time and flood events. Seven classes of distance to the river (10 m sections) were used to characterize the lateral gradient. Average positive and negative elevation deltas before and after the restoration and their associated standard deviations were first calculated for each distance class. Finally, two five-year floods (HQ5) showing similar discharges before and after the restoration were selected based on hydrological surveys of the local authorities (Canton Thurgau) and on the available cross-section data. The elevation values just before and after each of these two floods were used to characterize the erosion/sedimentation patterns for each distance class.

2.4.3 Soil typicality

Typical floodplain soils are mainly characterised by their limited evolution and the impact of water saturation on their morphology and functioning. They all show varying frequency and duration of waterlogging. An efficient restoration should allow the complete range of typical floodplain soils to develop at a site. This potential range of soils depends on the fluvial dynamic and is therefore context-specific. For example, hydromorphic features and clay-rich soils generally increase in frequency in lower river reaches. We compared the frequency of soil groups among the different areas of the site both for the entire profiles and for the topsoil horizons.

2.5 Vegetation survey

Vegetation surveys were conducted seven times between April 2008 and 2009 using the Braun-Blanquet method [52] in 41 plots (4 m radius circles) distributed throughout the restored and reference areas. Among these plots, 26 were selected for their spatial correspondence with the soil survey, 22 in the restored area and 4 in the control. The different sampling sessions were pooled together in order to have a site X species matrix representing an entire year.

We calculated vascular plant species biodiversity for the three areas (open habitats + forest) using the same set of metrics as for pedodiversity. We then assessed whether the changes in soil morphology observed in Figure 1 corresponded to vegetation types, which could be interpreted as an indication that the processes driving soil morphology and vegetation types are similar. All calculations were done with the R framework [53] using package “vegan” [54].

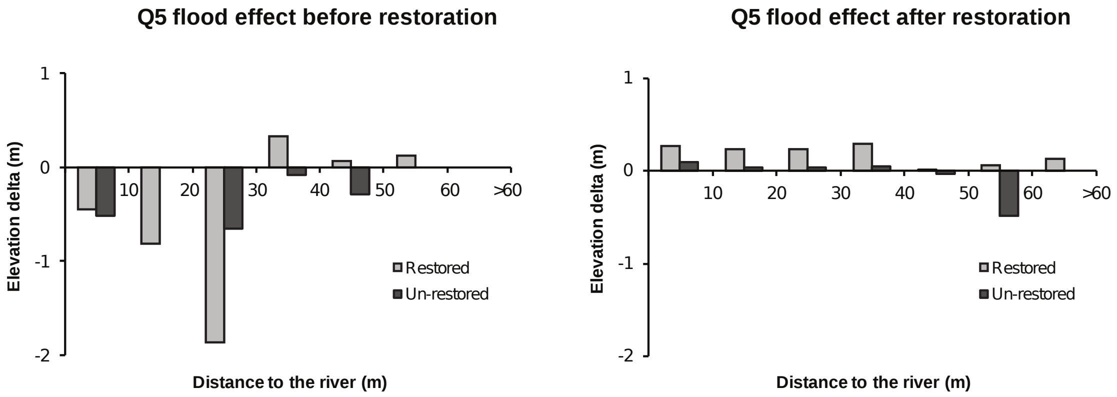

Figure 3. Effects of a single flood with a similar discharge (Q5, five-year flood) on elevation deltas (m) in the restored and in the control area of the River Thur site before (Fig. 3a) and after restoration (Fig. 3b). Calculations are based on cross sections data for seven classes of distance to the river (10 m sections). Positive deltas (+) correspond to sedimentation processes and negative deltas (-) to erosion processes.

Table 4. Relative abundance (%) of soil profile and topsoil groups for the restored (Open habitats and Forest) and control areas of the River Thur site.

(a) Soil profile

	group 1	group 2	group 3	group 4	group 5	group 6	group 7	group 8
Open habitats	1.3	11.8	-	42.1	28.9	10.5	3.9	1.3
Forest	-	58.3	-	-	-	-	41.7	-
Pasture	45.5	40.9	9.1	-	-	4.5	-	-

(b) Topsoil layer

	group 1	group 2	group 3	group 4	group 5	group 6	group 7
Open habitats	7.9	27.6	13.2	39.5	9.2	-	2.6
Forest	58.3	-	-	8.3	25.0	8.3	-
Pasture	63.6	-	-	22.7	13.6	-	-

3. Results

3.1 Soil typology

The cluster analysis revealed eight groups of soil profiles (silhouette width = 0.42) and seven groups of topsoils (average silhouette width = 0.44). Most soil profiles could be classified as Fluvisols and to a lesser extent Stagnosols or Gleysols, according to the WRB classification, or FLUVIOSOL, REDOXISOL or REDUCTISOL according to the AFES classification. The average of each variable within each group are given in Table 1.

3.2 Soil diversity

Soil profile and topsoil diversity and richness were highest in the open habitats of the restored area and lowest in the riparian forest (Table 3). The control area had intermediate values. More soil profile and topsoil groups were present and soil profile variability was higher close to the river. Evenness of groups differed between soil profiles and topsoils. Average evenness of soil profile groups was maximal in the forest and minimal close to the river, while the evenness of topsoil groups was maximal in the un-restored pasture (control) and minimal in the forest.

3.3 Soil dynamism

Soil dynamism as assessed by the variation of the total number of horizons per meter (H_m) along transects differed significantly between the restored and control areas (Kruskal–Wallis Rank Sum Tests, $p = 0.003$ and $p < 0.001$, for H_m values and standard deviation respectively) and between the open and forest habitats in the restored section. The pattern was flat in the control area (Fig. 1). Indeed, the control area was only rarely influenced by fluvial dynamics and as a result, soils were well developed and homogenous all along the lateral gradient. By contrast, in the restored area (Fig. 1), the pattern was highly variable. Five different sectors could be distinguished along the river-upland gradient. Between 0 and 5 m, H_m was null. Erosion processes were dominant and soil development could not occur. Between 5 and 20 m, H_m values increased slightly. Sedimentation could occur with some accumulations of organic matter. Between 20 and 35 m, H_m values showed a high variation. Erosion, sedimentation, and soil development (i.e.

Table 5. Averages of plant species biodiversity metrics for the open and forest habitats of the River Thur site.

	N0	N2	E2
Open habitats	17.88	2.87	0.17
Forest	16.71	4.88	0.3

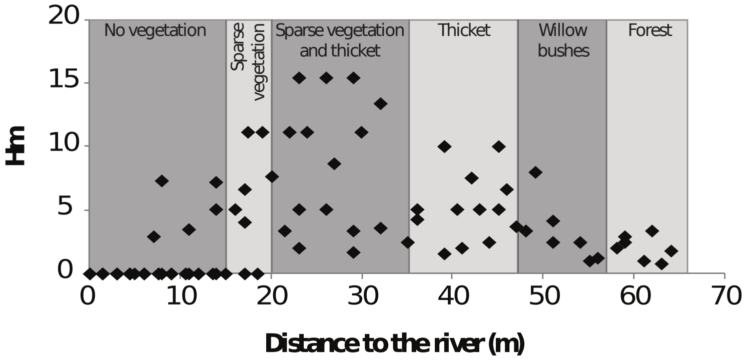

Figure 4. Vegetation successional stages versus soil dynamism (Hm) in the restored area (0-65 m from the river) of the River Thur site.

accumulation of organic matter, soil layer differentiation, in situ pedogenesis) alternated. Between 35 and 50 m, H_m values were more stable. Erosion decreased and soil development increased. Further, H_m values stabilized at about two horizons per meter.

The average sedimentation and erosion rates were higher between 1996 and 2002 than for the period after restoration (Fig. 2). Indeed, the average negative elevation delta before the restoration was -0.54 m and only -0.21 m after. The same trend was found for the average positive delta (before = 0.22 m and after = 0.16 m).

The effect of a similar five-year flood differed significantly before and after the restoration (Fig. 3; Kruskal–Wallis Rank Sum Test p = 0.002), and between the control and restored (i.e. open habitats + forest) areas after the restoration (p = 0.02). Along the river lateral gradient, the patterns were conspicuously different before and after the restoration. Before the restoration, erosion forces concentrated on the first thirty meters from the river. Further away, erosion forces were weaker and sedimentation started to occur. After restoration, the pattern was more regular. Sedimentation processes were dominant, but erosion occurred marginally.

3.4 Soil typicality

Soil group abundances were compared among the open habitats, the alluvial forest and the control for the soil profiles and topsoil layers (Table 4). In the open habitats, restoration led to the creation of thin and coarse soils (profile groups 4 and 5, Table 1) that correspond to the initial stages of soil development under high fluvial dynamism.

The transition between (1) the open and forest areas (profile groups 2 and 3) and (2) the more stable forest and control pasture (profile group 1) was marked by the presence of soil with low coarse material content which are little impacted by erosion and sedimentation processes, and moderately influenced by water table fluctuations. Such soils are not typical of active floodplains along natural braided rivers, but are rather an indication of human activity (i.e. embanking and associated reworking of soil and sediments). A single profile was characterized by the presence of a reduced horizon (profile group 8), indicating quasi-permanent waterlogging, a situation typically encountered along the lateral branches of braided rivers where water discharge is low.

Observed patterns in topsoil groups confirmed those of profile groups (Table 4): Humified organic matter deeply incorporated to the soil was characteristic of the forest and pasture areas (topsoil group 1), whereas organic matter was mainly composed by coarse residues in the open restored area (topsoil groups 4 and 7). Topsoils with coarse material lacking organic matter occurred close to the river (topsoil groups 2 and 3). Topsoils showing hydromorphic features (topsoil group 7) remained marginal since they accounted for 3 % of the investigated topsoils.

3.5 Vegetation

In total, 100 species were identified at the Thur River site. These species were organized into five well-differentiated vegetation successional stages along the lateral gradient: (1) the closest to the river, no vegetation or only isolated plants, (2) patches of pioneer vegetation and, (3) a terrestrial reed dominated by *Phalaris arundinacea*, (4) willow bushes dominated by *Salix viminalis*, (5) a deciduous forest dominated by *Fraxinus excelsior* far from the river. The control (un-restored) area was a managed pasture dominated by *Arrhenatherum elatius*. It was thus not meaningful to include it in the succession and compare it with the other habitats. We rather focused on the succession of plant communities along the river lateral gradient.

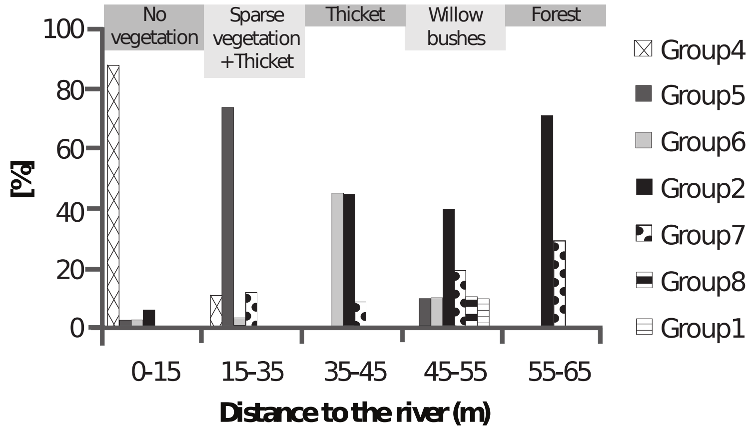

Figure 5. Vegetation successional stages versus frequency of soil profile groups in the restored area of the River Thur site. Soil groups are given according to their zonation along the river lateral gradient. Soil profile group 3 was only observed in the control area.

Plant species diversity (N2) and evenness (E2) were higher in the forest whereas the open habitats and forest had comparable values of species richness (N0). The increase in plant E2 paralleled the one in soil, but this was not the case for N0 and N2. Vegetation stages corresponded to those in soil dynamism (Fig. 4). The notable exception was the *Phalaris* reed vs. willow bushes where differences in vegetation did not match those observed in soil. This is most likely due to the fact that the willow bushes were planted during the restoration and are not part of the natural succession.

Vegetation was expected to respond to the composition of soil profile groups. As expected, changes in the typicality criterion reflected the broad vegetation types within the site (Fig. 5). Pioneer vegetation appeared with the first stages of soil development (soil profile group 5) whereas when soils were too poorly developed (soil profile group 4) no vegetation was present. Vegetation colonization in the most dynamic part of the gradient (soil profile group 4) was associated to organic matter accumulation (topsoil group 4). Data from topsoils, such as organic matter content and origin, are therefore complementary to those from soil profile morphology. Riparian forests (dominated by *Fraxinus excelsior*) mainly occurred on stable, moist soils (soil profile groups 2 and 7). Potential surfaces of suitable hydromorphic soils for the typical vegetation of braided river lateral branches such as textitTypha minima and *Inula helvetica*, for which reintroduction plans exist in Switzerland [55, 56], were only limited in our study area (i.e. only one sampling point for profile group 8).

4. Discussion

The restoration of River Thur globally increased soil diversity, and improved soil dynamism and typicality. It changed the fluvial dynamics leading to changes in soil morphology (e.g. intensity of erosion / sedimentation processes; coarse material and organic matter content) and soil functioning (e.g. loss of hydromorphy). The most striking changes occurred within the first 30 m from the river where post-restoration fluvial dynamics created diverse and dynamic patterns of soils. Habitats located further away from the river were less frequently exposed to floods and therefore less influenced by the restored fluvial dynamic.

Given the known importance of soils in determining vascular plant communities [16]), we hypothesized that investigating the correlations between soil profile and topsoil groups and vascular plant communities would provide information on the ongoing ecological processes of a restored site. These correlations were weak for diversity and richness most likely due to the influence of factors such as soil chemistry, water and nutrient availability, surface, connectivity, biotic interactions and species reservoir. However changes in the evenness of soil profile groups, and in soil dynamism and typicality paralleled those observed for vegetation suggesting that similar ecological processes are driving soils and plant communities. Indeed, the H_m index reflected vegetation successional stages. Such associations were already demonstrated between soil texture and moisture and *Salix nigra* [57]. These results agree with the idea that restoring the physical heterogeneity of a site promotes its biological diversity [58, 59] and gives a positive signal for project evaluation. However, the extent to which weak or strong correlations will improve or hamper restoration projects success remains to be determined.

River restoration by widening had not yet succeeded in creating significant surfaces of hydromorphic soils typical of braided river lateral branches [39, 40, 41] and influencing both fauna and flora [60]. Given that the formation of such soils in natural floodplains can take considerable time, the creation of artificial landscapes where hydromorphic soils could persist may provide more immediate results if restoration objectives require so. Examples of restoration projects that used artificial landscapes to achieve their aims exist. In the framework of the "Project River Recovery" aiming at restoring riverine and wetland habitats in New-Zealand, Caruso [61] concludes that wetland construction and enhancement can maintain and increase usable habitat and native bird populations. Mac Williams et al. [62] show that through the construction of a compound channel, the incision of the main channel was stopped and a significant increase in floodplain vegetation relative to the prior condition was observed. Willows and other types of vegetation have established on the floodplain and within the constructed low-flow channel, and evidence of wildlife utilization of the riparian zone is abundant.

However, hydromorphic soils may also be created naturally following major floods (i.e. HQ20, HQ50 or HQ100) that did not occur between the restoration and the present study (Supplementary Table 6). Indeed, only HQ5 and HQ10 floods resulting in weak sedimentation and/or erosion processes in forest sites occurred during this time period. As a result, it is difficult to conclude whether the restoration succeeded in improving hydromorphic processes.

Nevertheless, five years after restoration, the increased diversity of soil types and the dramatic changes of dynamism suggest a positive impact of restoration, despite the potential for further improvement suggested by the lack of typical hydromorphic soils. Thus, five years after river widening, soil morphology indicators suggest that this restoration project was a partial success in restoring soil habitat and vegetation. Follow-up assessment after several major floods ($\geq$ HQ20) have occurred should allow testing the longer-term validity of our conclusion for the River Thur site.

Previous evaluations of the same Thur River site based on different methods, criteria and indicators, reached similar conclusions. Woolsey et al. [9] found that fish assemblage structure and composition were similar in embanked and restored reaches and concluded that the restoration of River Thur failed to meet the objectives 'near natural abundance and diversity of fauna. Weber et al. [63] showed that hydrophysical habitat diversity had been improved by the widening but that the current geomorphological complexity was still considerably impaired at the restored reach in comparison with historical near-natural shoreline. Rohde et al. [14] used GIS methods based on landscape indexes and vegetation and concluded that the widening improved the degree of vegetation naturalness but in a limited way as compared to other restoration projects. Although the methods used in our study were fundamentally different, the results obtained using soil morphology were in agreement with these other evaluations. Moreover, the indicators we used also allowed investigating complementary aspects of floodplain restoration: the diversity criterion proved to be complementary to vegetation surveys, the dynamism criterion discriminated precisely the zones that were differently impacted by the fluvial dynamic and the typicality criterion allowed characterizing the changes among these zones.

In the context of river restoration, indicators should be easily measured, be sensitive to stresses on the system, demonstrate predictable responses to stresses and be integrative [6]. Our results show that soil morphology criterion and indicators fit these requirements. Soils may respond slowly to perturbations such as riverbed widening but in our case, clear changes in soil morphology were already observed five years after restoration even though no major floods had taken place in the time elapsed since restoration. Furthermore, soil indicators provide two different and complementary levels of information (i.e. soil profiles and topsoils). Nevertheless, the time between the restoration and the integration of the changes into soil morphology depends on the fluvial regime. Successive floods (including HQ5, HQ10, or HQ20) have to occur to potentially modify the soil morphology. Erosional and depositional processes should be frequent, ideally corresponding to the "medium-energy non cohesive floodplains" river category of Nanson and Croke [64] with braided, meandering and anastomosing channels. Here, we studied the relatively short-term effects of floodplain restoration. According to Ballantine and Schneider [27] as soil development is a relatively slow process, which only appears to accelerate later in the successional recovery sequence, the role of different soil successional phases in determining long-term trajectories of ecosystem development should be considered in restoration design, research, and monitoring. It would therefore be useful to assess the longer-term trends of soil development at the study site and other comparable restored floodplains to test the broader applicability of the soil morphology approach.

5. Conclusion

Our results show that soil morphology responded fast and clearly to river restoration and that typicality and dynamism correlated to vegetation changes. Analysis of soil morphology has thus the potential to improve the quality and accuracy of rapid assessment protocols [25, 26].

Despite the known importance of soils in terrestrial ecology, soil morphology has been under-used for the assessment of floodplain restoration success. The number of river restoration projects is increasing rapidly but there is still no general agreement on evaluation methods. The analysis of soil morphology offers many advantages (ease of use, quick and cost-effective) that make it a promising approach for the river restoration evaluator's tool kit.

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Appendix to Spatio-temporal heterogeneity of riparian soils

Table 6. Occurrences of floods with a frequency equal or superior to two years ($\geq$ HQ2) between 1994 and 2007. The bolded line separates the flood events that occurred before the restoration from those that occurred after. Forest sites are inundated when river discharge is superior or equal to 630 m^3 s^{-1} and control pasture sites when superior or equal to 415 m^3 s^{-1} [65].

Year	Month	Day	River discharge [m^3 s^{-1}]	HQ
1994	5	25	690	2
1994	7	7	680	2
1995	1	26	660	2
1995	6	1	730	5
1995	8	9	570	2
1995	12	25	630	2
1996	7	9	610	2
1999	5	13	1130	100
2000	8	6	650	2
2000	9	21	710	2
2002	8	12	880	10
2002	9	24	780	5
2004	1	14	768	5
2005	8	23	720	5
2006	3	9	560	2
2006	9	17	717	5
2007	8	9	791	5

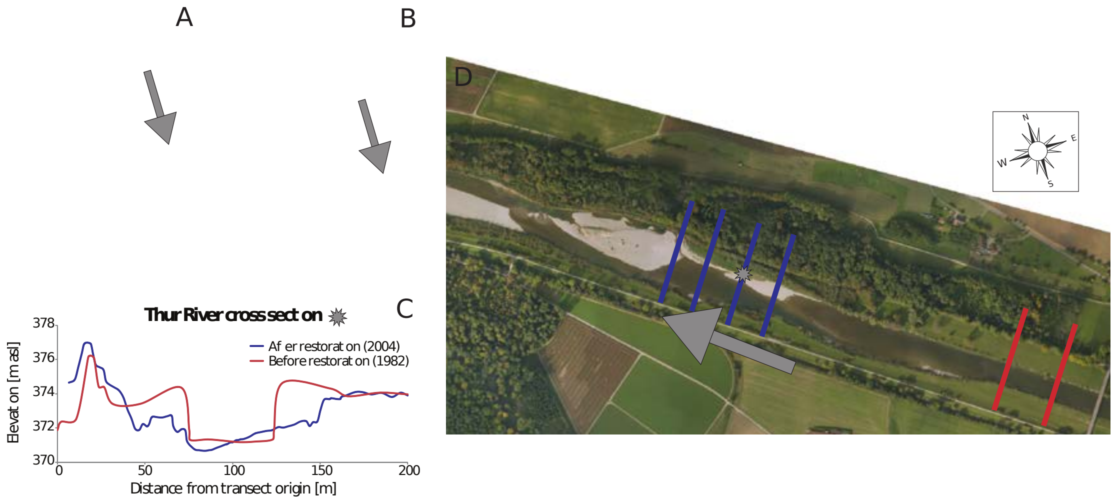

Figure 6. Illustrations of the restoration of the study site. Panels A and B show the state of the site before (June 2001) and after (May 2004) restoration. Panel C provides an example cross section of the study site before and after restoration. Panel D shows an aerial view that locates the different transects surveyed. The gray arrows indicate river flow direction; and the gray star shows the location of the chosen example transect.

5 Earthworms and floodplain restoration

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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.

Keywords
Earthworms – Biodiversity – Flooding – Species traits – Bioindicator – River restoration

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1. Introduction

Floodplains are among the most threatened ecosystems worldwide [1, 2]. 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 [3, 4, 5, 6]. 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 [7, 8, 9]. Among the candidates, earthworms are recognised as good bioindicators of soil conditions in alluvial ecosystems [10, 11] 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 [12, 13]. Earthworms modify soils mainly through bioturbation [14] thus participating actively to soil pedogenesis. Their activity affects water infiltration [15], nutrient cycling [16, 17], organic matter cycling [18], soil structure [19] and horizon texture [20, 21]. Their potential as bioindicators of landscape structure, land use and soil pollution has been well studied in many ecosystems [22, 23, 24, 25]. However, there are comparatively few data on the ecology of earthworms in floodplains [26, 27].
In flood prone areas, the water holding capacity as well as the organic matter content of the soil are key factors controlling earthworm abundance [28]. Flooding generally has a negative impact on earthworms [29, 30, 28], 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* [26, 31]. In subalpine floodplains, epigeic

species are considered as bioindicators of recent flood events because of their relation to topsoil texture and organic matter quality [11]. River restoration was shown to affect negatively *L. rubellus* biomass through a reduction of suitable habitats and an enhanced exposure to contaminants [32]. Inundations were reported to increase earthworm abundance and biomass in a human transformed ecosystem used for drinking water production by artificial groundwater recharge [33]. These observations, and more generally the central role of earthworms in ecosystem development and functioning [21], 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 [34, 35, 36]. Indeed, species traits are often more closely associated to environmental conditions than the actual species [37, 38, 39]. 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 [40] 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 [41]. 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
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 ∼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. [42] 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 [43]. The French soil classification [44] was preferred over the FAO World Reference Base for Soil Resources [45] 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 [43] 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. 1A). 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 [47]. 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 [48, 47]. 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. 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 [49, 50]. Juveniles classified as individuals with tanylobic or epilobic prostomium [50] were not included in the final matrix (sites x 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 [49, 50, 41].

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 [51]. 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 [52]. 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. [53]. The minimum flow rate required to flood each habitat was determined by Samaritani et al. [43] 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 x species), Q (species x traits), and CWM (sites x 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:

$$CWM = \sum_{i=1}^{n} p_i trait_i \tag{1}$$

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:

$$\Delta_x = x_{dynamic\_restored} - x_{restored} \tag{2}$$

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

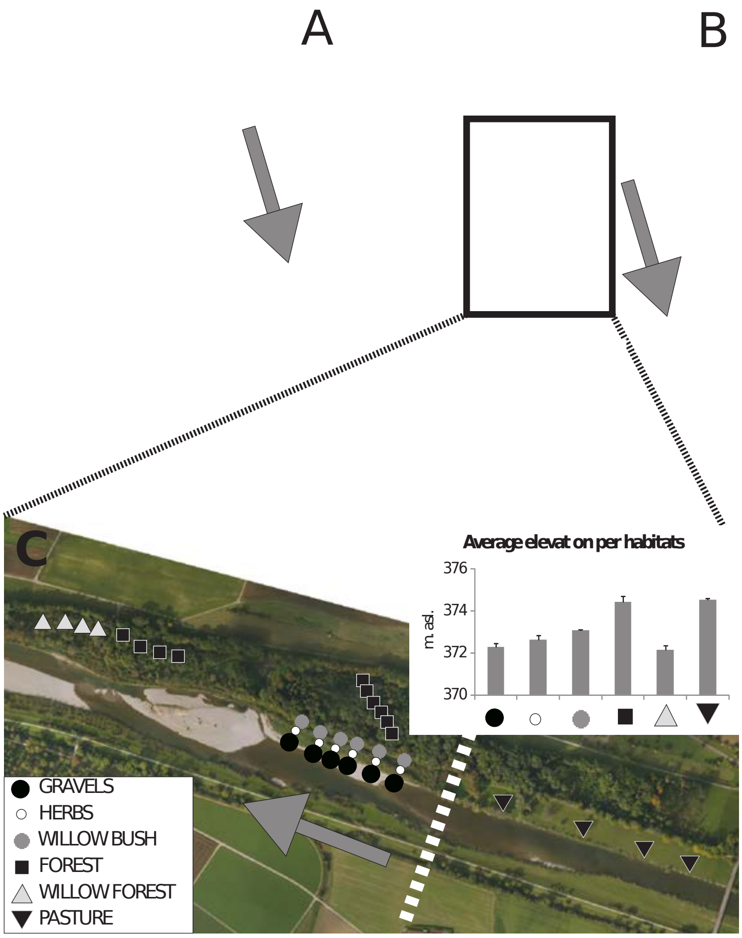

Figure 1. Thur River (A) before (June 2001), and (B) after the 2002 restoration (May 2004); (C) aerial view of the study site in 2008 showing the plots, and the average elevation of each habitat. Error bars are standard errors. (Pictures A and B: C. Herrmann, BHAteam, Frauenfeld; picture C: CCES RECORD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

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 [54]. We used PCA to characterise the distribution patterns of earthworm species and traits and BCA Monte Carlo tests [55] were performed to discriminate the different habitats and areas. Functional dispersion (FDis) was calculated for each plot [56, 57]. 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 [46].

All analyses were performed with the R statistical software [58] using the "vegan" [59], "FD" [60], and "ade4" [61] 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

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	Remarks
Allolobophora chlorotica	48±0.6	312±4.3	19±1	55±2.7	13±0.6	14±0.4	Savigny (1826)
Allolobophora georgii	0±0	0±0	0±0	2±0.1	0±0	0±0	Michaelson (1890)
Aporrectodea caliginosa caliginosa	0±0	18±1.2	7±0.3	38±1.1	13±0.9	1±0.1	Savigny (1826)
Aporrectodea c. nocturna	0±0	3±0.1	9±0.1	48±0.8	12±0.8	13±0.7	Evans (1946)
Aporrectodea c. tuberculata	0±0	3±0.2	4±0.2	14±0.5	22±0.2	24±0.7	Eisen (1874)
Aporrectodea giardi	0±0	0±0	0±0	0±0	1±0.1	1±0.1	Ribaucourt (1900)
Aporrectodea longa	10±0.4	21±0.7	29±0.8	31±0.6	16±0.7	43±1	Ude (1885)
Aporrectodea rosea	0±0	0±0	2±0.1	33±0.7	21±1.1	0±0	Savigny (1826)
Dendrodrilus rubidus	0±0	2±0.1	0±0	0±0	0±0	0±0	Savigny (1826)
Eiseniella tetraedra	14±0.6	18±0.4	0±0	1±0.1	0±0	0±0	Savigny (1826)
Lumbricus castaneus	0±0	3±0.1	2±0.1	2±0.1	7±0.3	1±0.1	Savigny (1826)
Lumbricus meliboeus	0±0	0±0	0±0	0±0	2±0.2	0±0	Rosa (1884)
Lumbricus rubellus	5±0.3	21±0.9	9±0.4	6±0.2	5±0.3	2±0.2	Hoffmeister (1843)
Lumbricus terrestris	0±0	1±0.1	4±0.2	34±0.4	13±0.3	8±0.4	Linnaeus (1756)
Octolasion tyrtaeum tyrtaeum	0±0	1±0.1	1±0.1	5±0.3	1±0.1	0±0	Savigny (1826)
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	Samaritani et al. (2011)
Depth of the water table [m]	1.41	1.65	1.75	1.71	0.93	3.15	

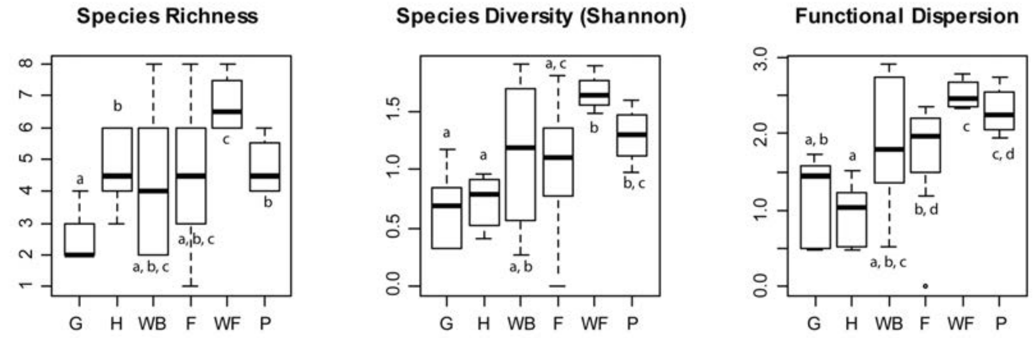

Figure 2. Boxplots of earthworm species richness, diversity, and functional dispersion (alpha values) for all habitats of the Thur River site (G: GRAVELS, H: HERBS, WB: WILLOW BUSH, F: FOREST, WF: WILLOW FOREST, P: PASTURE). Error bars represent standard errors.

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. 2A). 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 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

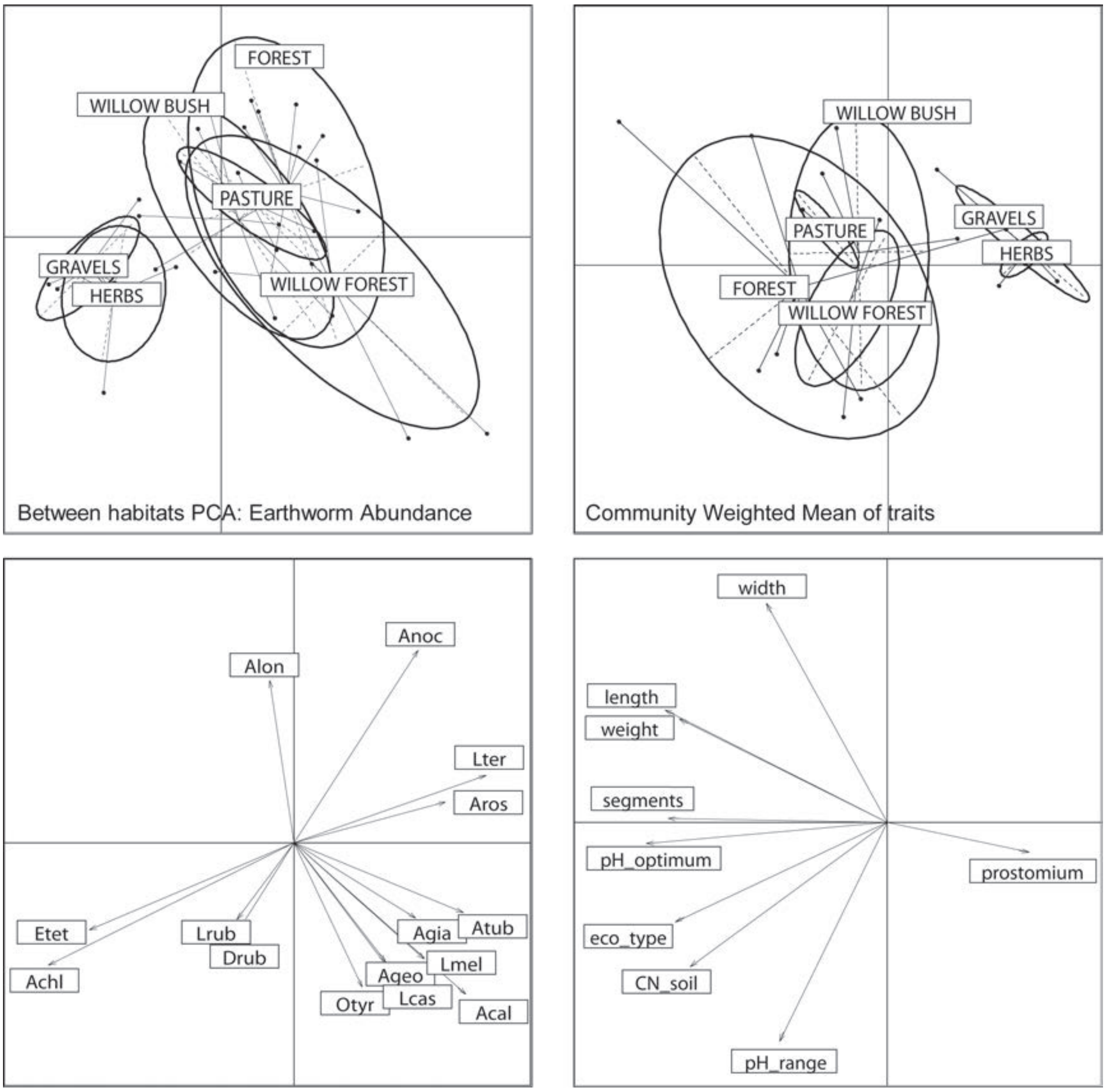

Figure 3. Principal component analyses (PCA) of earthworm abundance and community weighted means of traits data from the Thur River site. Ellipses highlight the different habitats; and arrows the position of species or traits within the ordination space. Species name abbreviations are composed of the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

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, 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).

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 [46].

	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

4. Discussion

At the floodplain scale, the observed values for biomass, abundance, species richness, and diversity were similar to those recorded in comparable settings [28, 29, 26, 10] 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 - pre- dominantly 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 [50, 62, 63] - dominated the communities in GRAVELS and HERBS. *E. tetraedra* is considered as characteristic of river banks [50] 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 [50]. 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 [64] well adapted to flooded soils [65] 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 [31, 66]. 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 [67, 7, 50]. Our study confirmed that *A. c. nocturna* and *L. terrestris* prefer thick soils as already shown by Salomé et al. [10] 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 [50]. 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

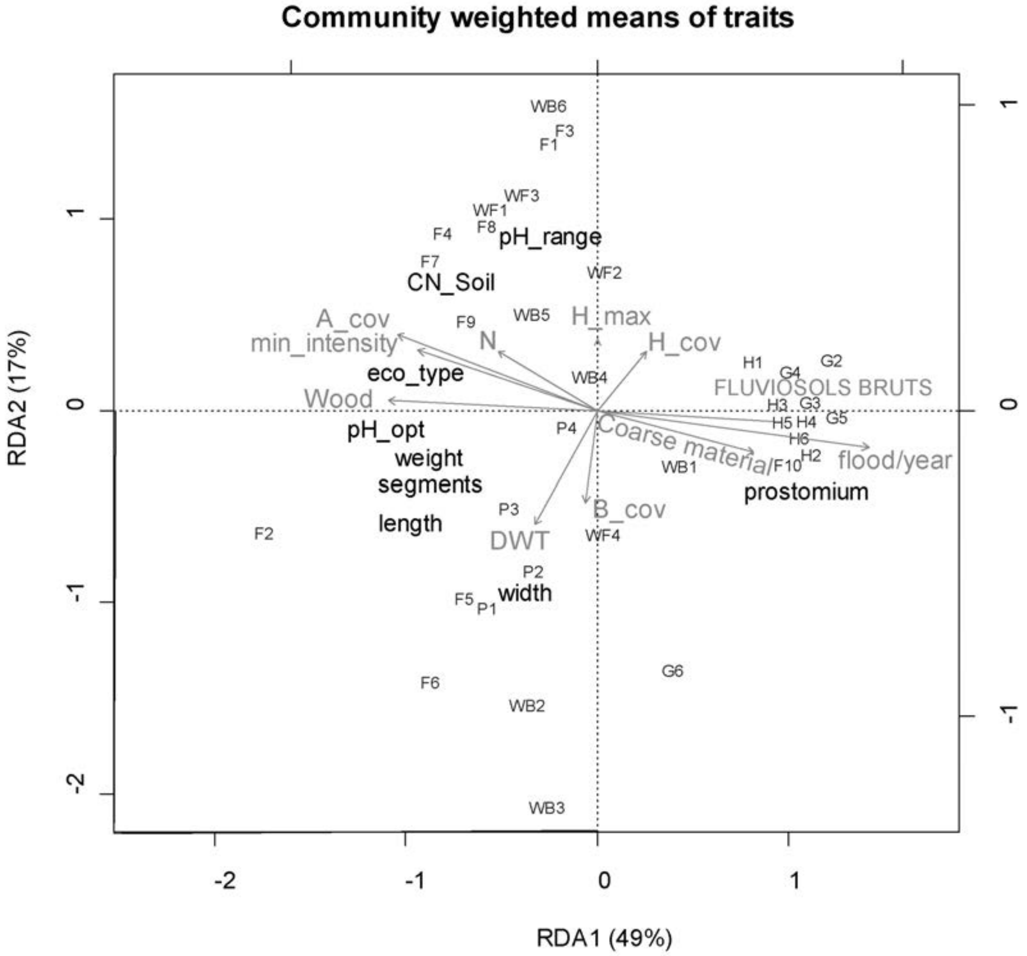

Figure 4. RDA triplot of earthworm community weighted means of traits (black) and environmental variables (grey) from the Thur River site. Explained variance is given in brackets for each axis. Site abbreviations (black, smaller characters) are composed by the first letter(s) of the habitat and the replicate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

tolerant to inundation [31]. 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 [32] 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 [68]. 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 [69]. 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 to Earthworms and floodplain restoration

Table 3. Summary of the environmental variables measured for each habitat from the Thur River site.

	GRAVELS	HERBS	WILLOW BUSH	FOREST	WILLOW FOREST	PASTURE
Tree strata cover [%]	0 ± 0	0 ± 0	0 ± 0	37 ± 1.6	14 ± 3.5	0 ± 0
Bush strata cover [%]	0 ± 0.1	6 ± 1.1	32 ± 1.8	1 ± 0.2	4 ± 0.7	0 ± 0.1
Herbaceous strata cover [%]	47 ± 4	89 ± 1.7	62 ± 3.9	50 ± 0.7	85 ± 0.9	94 ± 0.5
Moss strata cover [%]	0 ± 0	0 ± 0	2 ± 0.2	1 ± 0.1	1 ± 0	2 ± 0.3
Woody debris cover [%]	1 ± 0.1	1 ± 0.1	3 ± 0.3	3 ± 0.2	4 ± 0.5	0 ± 0
Large size gravels (> 5cm) [%]	33 ± 0.8	1 ± 0.3	4 ± 0.2	0 ± 0	0 ± 0	0 ± 0
Medium size gravels (> 2cm) [%]	32 ± 1.7	1 ± 0.3	2 ± 0.2	0 ± 0	0 ± 0	0 ± 0
Small size gravels (< 2cm) [%]	34 ± 1.3	2 ± 0.6	1 ± 0.1	1 ± 0.1	0 ± 0.1	1 ± 0.1
Total carbon [%]	5 ± 0.2	6.8 ± 1.1	6.6 ± 0.2	6.8 ± 0.2	7.2 ± 0.2	5.9 ± 0.3
Total organic carbon [%]	0.8 ± 0.2	2.3 ± 1.1	1.7 ± 0.2	2 ± 0.2	2.5 ± 0.2	1.3 ± 0.2
Total nitrogen [%]	0.1 ± 0	0.1 ± 0.1	0.1 ± 0	0.1 ± 0	0.2 ± 0	0.1 ± 0

Table 4. Summary of trait data for each earthworm species from the Thur River site.

	length	width	weight	segments	pH_opt	pH_range	prostomium	function	CN_Soil
Allolobophora chlorotica	65	5	600	102.5	6.35	3.7	epilobous	epigeic	0
Allolobophora georgii	45	2	215	103	5.5	3	epilobous	epiendogeic	0
Aporrectodea caliginosa caliginosa	70	4	510	147.5	8.5	5.2	epilobous	endogeic	1
Aporrectodea c. nocturna	135	4.5	2300	215	8.5	5.2	epilobous	anecic	1
Aporrectodea c. tuberculata	120	5.25	1180	173	8.5	5.2	epilobous	endogeic	1
Aporrectodea giardi	200	6	2335	193	5.5	3	epilobous	anecic	1
Aporrectodea longa	150	6.75	2500	180	8.05	2.7	epilobous	anecic	0
Aporrectodea rosea	55	2.75	215	142.5	7.35	4.9	epilobous	endogeic	1
Dendrodrilus rubidus	47.5	3.5	165	85.5	5.5	3	epilobous	epigeic	0
Eiseniella tetraedra	45	2.5	117.5	80	5.5	3	epilobous	epigeic	1
Lumbricus castaneus	47.5	2.25	245	86	5.6	4	tanylobous	epigeic	0
Lumbricus meliboeus	72.5	4	750	108.5	5.5	3	tanylobous	anecic	0
Lumbricus rubellus	80	3.5	1340	110	5.95	4.9	tanylobous	epigeic	0
Lumbricus terrestris	190	8	10000	144	8.1	3.8	tanylobous	anecic	1
Octolasion tyrtaeum tyrtaeum	100	4.25	760	117.5	6.2	3.8	epilobous	epiendogeic	1

6 Testate amoeba functional traits in floodplains

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Toward the use of testate amoeba functional traits as indicator of floodplain restoration success

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Abstract
Functional traits (FT) offer a new framework to understand the ecology of organisms and overcome taxonomic difficulties that currently limit the study of minute soil taxa. FT are likely to be selected by environmental filters and hence they may provide more direct information on ecosystem characteristics than the species composition of a community.

We tested the potential of testate amoeba (TA) functional traits as bioindicators of selected ecosystem processes in the context of a restored floodplain in north-western Switzerland. The floodplain was divided into six functional process zones (FPZs) associated to distinct post-restoration successional stages. We selected TA FT and computed three functional indices: functional richness (FRic), divergence (FDiv), evenness (FEve), and dispersion (FDis). We then compared the patterns of functional indices and classical diversity indices such as species richness, diversity and evenness. We assessed whether traits converged or were over-dispersed in the different FPZs using a randomization procedure. Finally, we related environmental variables and functional traits using the “Fourth Corner” statistic. This procedure enabled us to highlight relations that can potentially be used for bioindication. Promising candidates include the relationships between shell biovolume and vegetation structure and between shell compression and plant litter input variables.

Keywords
Testate amoebae — Floodplain — Functional traits — Bioindication

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1. Introduction

A basic assumption of functional ecology is that differences in traits of species imply differences in the functioning of the ecosystem. Relating functional traits (FT) to environmental variables may improve our understanding of biological processes in ecosystems and allow defining a general and useful theory of species assembly [1]. The rationale for this approach is that FT are likely to be selected by environmental conditions and hence analysing them provides more direct information on ecosystem characteristics than the species composition of a community. Functional traits and measures of community functional diversity provide a way to overcome taxonomic limitations that are especially critical for minute soil taxa and tend to correlate more strongly than traditional species diversity with ecosystem functions such as productivity [2], resilience to perturbations [3], or regulation of biogeochemical fluxes [4].

Soil micro-organisms may differ from above-ground communities with respect to their resistance, resilience, dispersal potential, and adaptation strategy [5, 6]. Characterizing the distribution of FT along environmental gradients may help to understand the causes of the different response to perturbation of above- and below-ground organisms. Our focus here is on testate amoebae (TA) FT in the context of floodplain restoration.

After centuries of increasing human impact on rivers (e.g. embankment, flood regulation, etc.), many floodplains are being actively restored. However, restoration projects often do not include monitoring of restoration success and there is currently no consensus on which indicators should be used to assess restoration success [7, 8]. Species data are often used in biomonitoring but because restoration projects are being carried out in different regions, differing in their floras and faunas, specific protocols need to be defined for each biogeographical region. A biomonitoring approach based on functional traits may thus allow overcoming biogeographical limitations.

TA are a polyphyletic group of free-living protozoa that play important roles in soil nutrient cycling [9] and especially the cycles of C, N, and Si in soils [10, 11]. As for many minute to microscopic soil organisms [12] the taxonomy of is poorly resolved [13] and this may undermine their use as bioindicators if species-level identification is required [14]. The solution usually applied in ecological and palaeoecological studies is to lump species in morpho-taxa and species complexes [15]. Here we explore another possible way to overcome this limitation by using species funnctional traits. TA produce shells that differ in their composition, size and shape [16]. These morphological differences are believed to represent adaptations to the soil environment especially the soil moisture regime. As the soil moisture regime is controlled by several factors including soil particle size distribution, organic matter content, vegetation strata structure, litter input, elevation (and hence water table depth and frequency of flood), these different variables may influence TA species traits distribution.

TA are divided into two phylogenetically distinct groups, the Euglyphida (Rhizaria) [17]] and the Arcellinida (Amoebozoa) [18]. Morphological adaptation to the soil (i.e. shell compression and aperture in a ventral position) appeared independently in both groups [19, 20]. Thus TA represent an interesting example of evolutionary convergence and hence an ideal test group for linking phylogeny and functional ecology. The functional importance of TA species traits in ecosystems is poorly understood. Attempts to link TA species traits to environmental gradients are limited to using the ratio of Arcellinida to Euglyphida (or Lobose/Filose amoebae index) [21, 22]]. Arcellinida (Lobose TA) are assumed to be K-strategists while Euglyphida (Filose TA) are considered as r-strategists. Higher L/F ratios are usually recorded in more stable and/or more developed ecosystems or microhabitats.

We explore the potential of TA FT as indicator of ecosystem functions in a recently restored floodplain. First, we selected traits and tested whether they were convergent due to environmental filters or divergent due to competition. We then classified a set of environmental variables according to the ecosystem function they are related to. We then used the existing methods to relate functional traits to environmental variables directly. We hypothesized that the composition and functions of TA communities differ among habitats, and that trait convergence is stronger in the more dynamic zones. We also expected that traits related to the origin or shape of shell material will be the most useful indicators of ecosystem process since they likely reflect adaptations of TA to environmental settings.

2. Material and Methods

2.1 Study area

The study site is a 1.5 km long stretch along River Thur near Frauenfeld, Switzerland (365 m asl; annual precipitation: 1000 mm yearÀ1; average annual temperature: 7.9 C). The site was restored in 2002 through riverbed widening from 50 to 150 m. The major banks were stabilized by plantations of willows (*Salix viminalis*). Further information on this site is given in Woolsey et al. [23]. We selected six habitats based on the functional process zones (FPZ) [24] proposed by Samaritani et al. [25] to represent the different postrestoration successional stages present at the site. These zones represent a gradient of decreasing flood mechanical impact. Closest to the river, FPZ1 ("Tall herbs") was characterized by dense vegetation dominated by Phalaris arundinacea. FPZ2 "Willow bush" was dominated by *S. viminalis* bushes (planted at the time of the restoration). The three forested FPZs were discriminated based on the dominant tree species: FPZ3 (Forest) and FPZ4 (Mixed forest): *Acer pseudoplatanus* and *Fraxinus excelsior*, with higher overall cover in FPZ4. FPZ5 (Willow forest): *Salix alba*. The reference FPZ6 ("Pasture") is located directly upstream from the restored area and represents the prerestoration "control". All soils were described as FLUVIOSOLS [26] with soil depth increasing from the most dynamic to the most stable forest FPZs.

2.2 Sampling methods

Study plots were selected in representative areas of the FPZs: six replicates were used in the more dynamic FPZs (Tall herbs, Willow bush, and Forest), and four in the more stable ones (Mixed forest, Willow forest, and Pasture) representing a total of 30 plots. Each plot consisted in an 8 m diameter circle. Coordinates and elevation of the centre of each plot were measured with a Differential GPS. Environmental variables related to different ecosystem functions (Table 1) were measured in each plot. For Organic (OC) and total carbon (C), and total nitrogen (N) measurements, three cores of 10 cm depth and 6 cm diameter were extracted at each sampling site, homogenized and sieved at 2 mm. Basal respiration (BR) was estimated using Infrared Gas Analyser (Licor 8100). Fresh soil samples were left at room temperature for at least 3 h and then the CO2 emissions from 40 g of fresh soil placed in Licor 8100102 survey chambers were monitored for 9 min. All CO2 emissions measured were highly stable ($R2 > 98\%$). For TA sampling, all litter and soils of the uppermost 5 cm were sampled in a 10 m*2* transect perpendicular to the river within each plot. In order to remove large debris, this material was sieved in the field (mesh = 1 cm). TA were extracted from subsamples of the remaining homogenized material by sieving through 0.5 mm mesh (see [27] for details) and then counted and identified [28, 29] under light microscopy.

2.3 Functional traits

Five functional traits were selected according to their potential significance for ecosystem functions (Table 2):

1. Phylogenetic grouping (binary: Euglyphida = 0, Arcellinida = 1) may imply different functions in the ecosystem and different evolutionary stable strategy to cope with environmental settings [30, 31].
2. The origin of the material used for test construction (binary: Agglutinate = 0, Secreted = 1) may allow an environmental filter to operate, in relation to the availability of the different substrates (e.g. mineral particles of adequate size, fungal hyphae, silica) or the relative cost of building a selfsecreted shell by comparison with an agglutinated one.
3. The position of the aperture reveals a gradient from completely exposed to completely cryptic (semicontinuous coded as continuous: 1 = Axial aperture, 2 = Acrostomic, 3 = Plagiostomic, 4 = Cryptostomic aperture). Increasing protection of the aperture is generally

interpreted as an adaptation to decreasing soil moisture content.

4. Test compression (binary: 0 = noncompressed,1 = compressed) is also interpreted as an adaptation to living in a thin water film and allowing the amoebae to remain active longer when the soil moisture content decreases.

5. Biovolume (continuous: mm3) may be constrained or enhanced by given environmental conditions (soil moisture, pore size). It was calculated based on size measurement data (length or diameter, width, and height) using a different formula for each test shape (Table 2):

1. Hemisphere : Biovolume Pi*r 3 * 2 = 3
2. Saucer-shaped : Biovolume Pi = 2*r 2 *h
3. Cylindrical À ovoid : Biovolume Pi = 6 * d2 * h
4. Ovoid : Biovolume Pi=6L *w*h (4)

Where r is the radius, h the height, d the diameter, L the length, and w the width of the shell. For each FPZ and for the entire restored area, we calculated the total number of species, the Shannon index [32], the species evenness, and the density (number of individuals per gram of soil dry weight). Four functional indices were also calculated in order to detect any changes in community functioning: functional richness (FRic), divergence (FDiv), evenness (FEve), and dispersion (FDis) [33, 34]. FRic is the amount of niche space filled by species in the community calculated based on the convex-hull volume method [35]. Low values indicate that some resources available to the community are unused. FDiv measures the spread of abundance along a functional trait axis. High FDiv indicates a high degree of differentiation of the niche and a low competition for resources [36]. FEve accounts for the evenness of abundance distribution in a functional trait space. Low values show that some parts of niche space occupied are under-used [36]. FDis is a measure of multivariate dispersion that estimates the dispersion of species in trait space conceptually similar to Rao's quadratic entropy Q [37]. These indices represent different aspects of functional diversity and provide therefore complementary pieces of information that a single index could not account for. They were computed using the function "dbFD" of the R package "FD" [38]. Mann-Whitney tests were performed to assess differences among FPZs.

To assess whether trait convergence or divergence [39] may be discriminated in the different FPZs, a permutation test was computed. The latter consisted in permuting rows in the species per trait matrix (Q) to randomly attribute trait values to species and preserve species abundance and richness at the same time. FDis was preferred over the other indices [33] as test statistic and computed for each FPZ as well as for the restored area. This was repeated 1000 times allowing us to generate a probability distribution (FDis_sim), which was used to calculate p-values. The three possible outcomes of this test are:

1. 5th percentile of FDis_sim < FDis < 95th percentile of FDis_sim → neither convergence, nor divergence of traits
2. FDis < 5th percentile of FDis_sim → convergence of traits
3. FDis > 95th percentile of FDis_sim → divergence of traits

Along the river perturbation gradient, we thus hypothesize that abiotic constraints will lead to convergence of traits (case 2) in the most dynamic FPZs while strong biotic interactions (competition) will lead to divergence of traits (case 3) in the most stable FPZs. In the intermediate situation neither convergence nor divergence should be observed (case 1).

To assess the relationships between species traits and environmental variables, we used the "Fourth Corner" statistic which measures the link between the species per traits (Q), the sites per species (L), and the sites per environmental variables (R) matrices [40, 41]. To do so, we used the "fourth corner" function of the R package ADE-4 [42]. This function uses different types of correlation coefficients to measure the above-mentioned relationship, and test their significance through a permutation test. Environmental data were standardized prior to the analyses and 1000 repetitions of row permutations in L were computed. This procedure allows preserving the relations between L and Q and corresponds to permutation model two of Dray and Legendre [40]. The R matrix consisted in the quantitative data (% cover of vegetation, ground cover, particle size distribution in the topsoil, physico-chemical soil variables, soil respiration, and plot elevation) and five dummy variables constructed to represent the six different FPZs. P-values were adjusted using Holm's correction to avoid increases of type error I due to multiple testing [43]. All analyses were conducted with the R software for statistical computing [44].

3. Results

3.1 Testate amoeba diversity and functional indices

In total, 25 TA species were identified. Centropyxis and Difflugia were the more common genera. The most common species for both areas was *Plagiopyxis penardi*. Three species were restricted to the reference area, whereas seven occurred only in the restored area (Table 3). The density of *Arcella discoides* was 87% lower, and *Difflugia penardi* density 213% higher in the restored area when compared to Pasture. All other species that occurred in both areas showed smaller relative differences.

Average TA species richness, was lower in the restored FPZs than in the reference site (respectively 5.9 and 9.8, P = 0.01). Similarly, diversity was lower on average in the restored FPZs than in the reference site (respectively 1.6 and 2.1, P = 0.01). There was no significant difference in density between the restored area (1072 ± 121 ind. g soil^{-1}) and the reference area (1039 ± 124 ind. g soil^{-1}). Functional richness, evenness,

Table 1. List of the environmental variables measured at each plot.

Category	Type of data	Code	Variable	Unit	Reference and notes
Litter	Continuous	Hmax	height of the highest herbaceous species	%	species < 5% of the total plot area were excluded
	Continuous	Dead	ground cover of woody debris	%	
	Continuous	Wood	ground cover of plant dead material	%	
C and N cycling	Continuous	OC	topsoil (first 10 cm) organic carbon content	%	Samaritani et al. (2011)
	Continuous	C	topsoil (first 10 cm) total carbon content	%	
	Continuous	N	topsoil (first 10 cm) total nitrogen content	%	
	Continuous	BR	topsoil CO2 emissions (details in text)	ppm mg dry soil^{-1}	
Vegetation structure	Continuous	A_cov	within plot percentage cover of the tree strata	%	
	Continuous	B_cov	within plot percentage cover of the bush strata	%	
	Continuous	H_cov	within plot percentage cover of the herbaceous strata	%	
	Continuous	Mosses	within plot percentage cover of the mosses strata	%	
Flood dynamic	Continuous	Elevation	elevation above sea level	m asl	
Soil morphology	Continuous	Large	> 30 mm	%	Relative abundance of particles of given size in the topsoil (0-5 cm depth)
	Continuous	Medium	10-30 mm	%	
	Continuous	Small	5-10 mm	%	
	Continuous	Sand	1-5 mm	%	
FPZ	Binary		Pasture, Willow forest, Mixed forest, Forest, Willow Bush, Tall herbs	0/1	

diversity, and dispersion were lower in the restored area (0.26, 0.49, 0.72, and 1.01 respectively) than in the reference site (0.41, 0.51, 0.73, and 1.25 respectively), but not significantly ($P > 0.05$).

Clearer differences among FPZs were observed for species richness, species diversity, density and species evenness as compared to functional indices (Figure 1). Pasture stood out by high species richness and diversity and lower species evenness. Species richness and diversity were low in Willow forest. Tall herbs stood out by low density but relatively high species richness, diversity and evenness. There was no significant difference among the three intermediate FPZ (Willow bush, Forest and Mixed forest) for species richness, species diversity, density or species evenness. No difference was found among FPZs for functional divergence. Functional richness was higher in Willow bush and Pasture than in Willow forest (both $P = 0.05$). Functional dispersion was higher in Willow bush than in Forest and Willow forest ($P = 0.05$ and 0.03 respectively). Functional evenness was higher in Tall herbs than in Forest and Mixed Forest ($P = 0.05$ and 0.03 respectively).

3.2 Traits convergence and relationships to environmental variables

The permutation tests suggest that all FPZs correspond to case 2 (convergence of traits, all $P < 0.01$). In the fourth-corner analysis, litter decomposition, vegetation structure, and the type of FPZ all had at least one trait significantly correlated with one of their representative variables. None of the measured traits were significantly related to flood dynamic, soil morphology, and C and N cycling. With the exception of siliceous tests all species traits were correlated to at least one environmental variable (Figure 2).

Our analyses revealed a positive relation between shell biovolume and the relative cover of mosses and a negative correlation with the Willow forest FPZ. We found a negative relation between shell compression and the cover of plant litter (both dead wood and non-woody) and a positive one with the relative cover of herbaceous vegetation. The origin of the test material showed similar relations with the relative cover of herbaceous vegetation and the cover of non-woody plant litter. A negative relation was found between Aperture Position and both Tall herbs and Willow forest. Finally, we obtained a relation between Phylogenetic grouping and the relative cover of non-woody plant litter on the ground.

4. Discussion

4.1 Testate amoeba: community patterns and functional traits distribution

This study revealed contrasted patterns of TA density, diversity and functional traits in the restored and control sites of the River Thur floodplain. Density, species richness and diversity were all low by comparison with more favourable habitats such as upland forest soils [9]. There was no overall difference in density as differences among FPZs of the restored area balanced each other. In agreement with the supposed lower affinity of TA for early succession habitats [45] density was lowest in the most dynamic FPZ. In agreement with the

Table 2. Summary of the trait values for each species. Species codes correspond to the three first letters of the genus and species name and, when necessary, the two first letters of the sub-species name. Phylogenetic grouping: 0 = Euglyphida, 1 = Arcellinida. Origin of the test material: 1 = Agglutinate, 2 = Proteinaceous, 3 = Siliceous. Test shape: 1 = Hemisphere, 2 = Saucer-shaped, 3 = Cylindrical-ovoid, 4 = Ovoid. Position of the aperture: 1 = Axial aperture, 2 = Acrostomic, 3 = Plagiostomic, 4 = Cryptostomic. Test compression: 0 = compressed, 1 = non-compressed. Biovolume is given in μm^3.

	Phylogenetic grouping	Origin of the test material	Test shape	Position of the aperture	Test compression	Biovolume
Arc_dis	1	2	2	1	1	112486
Arc_rot	1	2	2	1	1	28599
Arc_vul	1	2	2	1	1	96211
Ass_mus	0	3	4	2	1	12370
Bul_ind	1	1	4	3	1	932660
Cen_acu	1	1	4	3	1	73304
Cen_acu_ob	1	1	4	3	1	411275
Cen_aer	1	1	4	3	1	35117
Cen_aer_sp	1	1	4	3	1	52360
Cen_cas	1	1	4	3	1	101137
Cen_con	1	1	4	3	1	237583
Cen_eco	1	1	4	3	1	402124
Cen_orb	1	1	4	3	1	527788
Cyc_eur	1	1	2	1	0	42379
Dif_obl	1	1	4	2	0	1154535
Dif_lin	1	1	4	2	0	65424
Dif_mic	1	1	3	2	0	355758
Dif_pen	1	1	4	2	0	36757
Eug_lae	0	3	4	2	1	7257
Hel_pet	1	1	4	2	1	82467
Phr_acr	1	1	1	1	0	23856
Pla_cal	1	1	4	4	1	102102
Pla_pen	1	1	4	4	1	66183
Trigo_min	1	1	2	1	0	112708
Trine_lin	0	3	3	3	0	6185

general positive relationship between habitat diversity and species richness [46], TA total species richness was higher in the restored area than in the reference site and both species richness and Shannon diversity were lower in individual FPZs of the restored area than in the reference area (significantly for three out of five FPZs). Although the restored area covers a wider range of FPZs than the reference site and clear differences among FPZs were identified using classical indices, none of the four functional diversity indices differed between the two areas. This suggests that functional and classical indices provide complementary insights on the structure and functioning of ecosystems.

However, differences among FPZs along the gradient were identified for all functional indices except for Functional Divergence. These are interpreted here in agreement with Mason et al. [36]. Functional Divergence was relatively high for all FPZs indicating a low competition for resources. Functional Richness was generally low, and especially so in Willow forest, indicating that resources were either scarce or poorly exploited. At the site level, in all FPZs, low Functional Richness indicates that TA communities do not reach equilibrium and do not optimally exploit resources. Low Functional Richness indicates the existence environmental pressure, in this case the most likely due to flood dynamic-related factors. As a result, the importance of competition in shaping communities is low. This interpretation is in line with the observation of absence of replacement in TA community assembly in a primary succession [47]. At the level of individual sites, the available niche space is occupied to a greater extent (i.e. the within site distribution of biomass-weighted relative proportion of different TA FT in the available niche space is more uniform) close to the river than in the forest, as indicated by the higher Functional Evenness.

4.2 Functional dispersion: convergence of traits?

We hypothesized that trait convergence would be highest in the most dynamic FPZs and would decrease towards more stable FPZs. In disagreement with our hypothesis, traits were convergent in all FPZs. This shows that environmental filters are selecting TA FT and suggests that these filters were not directly related to flooding, or that alternative, complementary filters were acting in different FPZs (e.g. grazing

Table 3. Average density [individuals g soil^{-1}] of each species of testate amoeba in the restored and reference areas.

	Restored	Reference
Arcella discoides	3	22.6
A. rotundata stenostoma	0	22.6
Arcella vulgaris	0	11.3
Assulina muscorum	45.9	56.5
Bulinularia indica	10.5	45.2
Centropyxis aculeata	18.8	11.3
C. aculeata oblonga	6.8	0
C. aerophila	17.3	56.5
C. a. sphagnicola	112.9	90.3
C. cassis	85.8	56.5
C. constricta	76.8	56.5
C. ecornis	2.3	0
C. orbicularis	10.5	56.5
Cyclopyxis eurystoma	4.5	0
Difflugia oblonga	14.3	0
D. lineare	6	0
D. microstoma	6	0
D. penardi	70.8	22.6
Euglypha laevis	0	11.3
Heleopera petricola	25.6	67.8
Phryganella acropodia	68.7	45.2
Plagiopyxis callida	141.2	112.9
P. penardi	333.2	271
Trigonopyxis minuta	10.5	0
Trinema lineare truncatum	0	22.6

pressure in the pasture, waterlogging in the Willow forest). Flood-related effects on biotic communities are well-known for higher plants [48] and animals [49, 50], but our result tend to show that filters are different for protists than for plants and arthropods. Defining and testing the effects of these filters will improve our understanding of soil microbial ecology and requires further studies ideally combining descriptive approaches such as used here (to confirm the observed pattern for TA and/or other soil organisms) and manipulative experiments (to test the effect of specific factors). The convergence of traits identified here may depend on the set of traits we selected initially. Results may differ for set of traits specifically related to dispersal or reproduction for example. The approach presented here shall therefore be considered as a first step toward the selection of relevant functional traits for TA ecology. The next step was to assess the relationships between FT and environmental variables.

4.3 Relationships between species traits and environmental variables

Trait convergence implies that strong environmental filters are forcing species assembly patterns. The different responses of functional indices along environmental gradients agree with the idea of high functional redundancy in soils [51] and can be explained by the relationships among environmental variables and species traits. These relationships are either direct functional relationships or indirect trait-adaptation to habitat. As aquatic soil organisms, TA live in water films and are particularly abundant in soils with organic humus, high moss cover, and generally sufficiently frequent moist conditions such as peatlands, forests [52]. Soils with a well-developed humus have a higher water holding capacity [53] and generally contain a high density of TA [9]. Such conditions are expected to favour species with uncompressed shells, unprotected aperture, and/or large biovolume. Soil moisture content and dynamics therefore control the density and also community structure of TA.

However TA are believed not to tolerate anoxia. As a result, certain species may regularly die out in waterlogged soil patches and subsequently re-colonize them from adjacent areas. In this case, smaller species will be favoured because they are more likely to be dispersed passively over long distances (owing both to potentially larger population size and small size) [54]. Certain species may encyst and enter a latent phase to cope with anoxia. This strategy may be favoured by larger species with relatively low dispersal ability.

Favourable soil moisture conditions can result from different factors such as high water table, thick litter or moss layers, and shading by trees, etc. Our results show a complex pattern of correlations between individual habitat variables that influence soil moisture and TA species traits. These results add to the well- documented correlation between TA communities

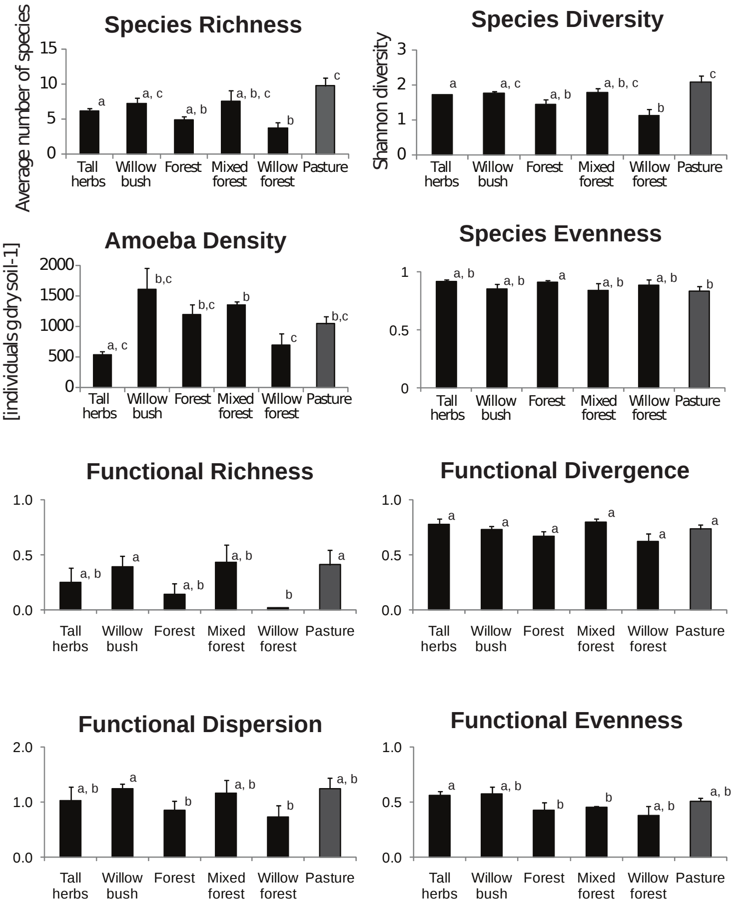


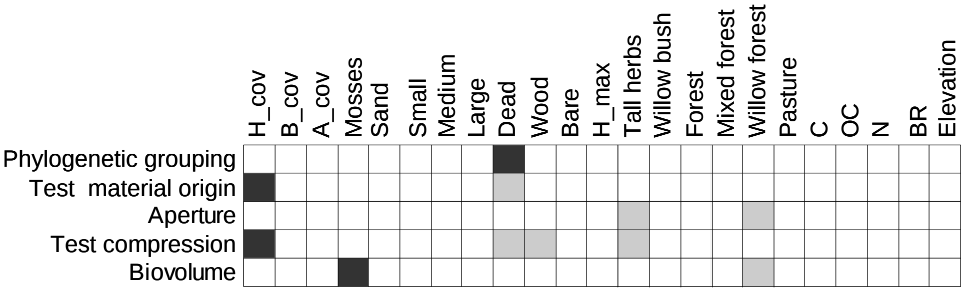
Figure 1. Testate Amoebae average species richness, Shannon diversity, density, and species evenness, and functional richness, evenness, divergences, and dispersion for each functional process zone (FPZ). Standard errors are represented. Black bars indicate FPZs from the restored area, whereas grey bars indicate the reference FPZ (Pasture). Different letters indicate significant differences of the means (ManneWhitney tests).

and soil moisture variables [55].

In this study we did not address the vertical distribution of TA along the soil profile nor the seasonal variations. Given how dynamic floodplain ecosystems are it would be useful to address these questions. The results we obtained are promising, but further comparable descriptive studies are required to provide true replication. In addition, manipulative experiments should be conducted to address specific questions such as long-term and cyclical effect of flood duration, intensity, and frequency on TA communities. Finally the set of traits and the environmental variables considered in this study are in no case exhaustive. The selection of relevant functional traits is a critical point for such approaches [56]. With this respect, traits related to the test (i.e. Biovolume, Shell Compression, Aperture, and Test Material Origin) were strongly associated to litter variables and constitute therefore the best candidates for bioindication. It is premature to propose an index based on these traits but our results show that this can be achieved. The relationship between Phylogenetic Grouping and woody debris is difficult to explain and requires further research to assess its potential value for bioindication. We encourage future studies to develop similar approaches of soil microbial ecology and study additional traits (e.g. related to the cyst forming capacity of TA that may determine their capacity to withstand periods of unfavourable conditions including anoxia).

5. Conclusion

This work confirmed that environmental filters are forcing the assembly patterns of TA communities in a restored floodplain and demonstrated the strong relationships between environmental variables related to soil moisture and TA species traits. In agreement with the idea of functional redundancy among soil organisms, the response of TA to perturbations was clearer for density and diversity than for FT. Selection of FT is however a critical step. We show clear response for shell-related traits but responses of other, e.g. physiological traits such as encystment capacity, should be explored. Finally, the spatial and temporal complexity of floodplain ecosystems represents



	H_cov	B_cov	A_cov	Mosses	Sand	Small	Medium	Large	Dead	Wood	Bare	H_max	Tall herbs	Willow bush	Forest	Mixed forest	Willow forest	Pasture	C	OC	N	BR	Elevation
Phylogenetic grouping									■														
Test material origin	■								▨														
Aperture													▨				▨						
Test compression	■								▨	▨			▨										
Biovolume				■													▨						

Figure 2. Relationships between environmental variables and testate amoeba functional traits. Only significant correlations are indicated ($P < 0.05$). Dark grey indicates positive associations, and light grey negative ones.

an ideal setting to study the factors controlling the distribution of soil micro-organism and their associated functional traits along environmental gradients. The complexity of the system however calls for combined descriptive and experimental studies.

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7 Environmental filtering and competition along disturbance and stress gradients

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Disentangling competition and environmental filtering in a restored floodplain using taxonomic and functional diversity

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Abstract
Environmental filtering and competition are major processes shaping species distribution patterns along disturbance and stress gradients, yet their impact on taxonomic and functional diversity remains unclear.
To fill this gap in knowledge, we investigated the impact of flood disturbance and hydric stress in a restored floodplain on selected indices of taxonomic and functional diversity for seven ecological communities belonging to different trophic levels (vascular plants, spiders, carabid and staphylinid beetles, isopods, diplopods and earthworms). We discriminated the relative importance of competition and environmental filtering in shaping the observed patterns. To do so, we compared patterns of community diversity along stress and disturbance gradients assessed using generalized additive models to theoretical expectations.
Our results revealed stronger impact of disturbance than stress on biodiversity. This difference reflected different ecological processes with environmental filtering dominant along the disturbance gradient and competition along the stress gradient. Differences among communities were mainly explained by different resilience to disturbance and stress. Moreover, community resilience was enhanced by species diversity five years after restoration. However, this process might reverse as communities adapt to the renewed disturbance and stress dynamics.

Keywords
Competitive exclusion — Trophic level — Functional trait — Intermediate disturbance hypothesis — Resilience

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1. Introduction

1.1 Influence of disturbance and stress on communities

Disturbance and stress are among the main factors shaping biodiversity [1, 2]. Impacts of disturbances such as fire, flood, change in management regime, herbivory and predation, and stresses such as temperature, chronic pollution, excess or lack of nutrients and water have been investigated on various taxa including bacteria, insects, plants, fish or birds [3, 4, 5, 6]. From a theoretical perspective, the 'Intermediate Disturbance Hypothesis' – IDH - [7, 8] and the 'Intermediate Stress Hypothesis' – ISH - [7, 9] predict the highest values of diversity at intermediate disturbance or stress. High disturbance or stress impacts communities directly through a process known as environmental filtering (EF) [10]. At low disturbance or stress the less suited species are excluded or maintained at low abundance through competition. The first outcome of competition is competitive exclusion (CE) [11]. CE in turn can potentially lead to community scale niche differentiation, also referred to as limiting similarity (LS) [12].

EF and competition are among the main processes responsible for species distribution patterns along disturbance and stress gradients [13, 14]. However the bell-shaped pattern predicted by the IDH was only verified in a minority of cases [15] suggesting that the influence of EF and competition is more complex that initially believed by Grime and co-workers.

1.2 Disentangling the effect of competition and environmental filtering

How and to what degree stress and disturbance affect biodiversity depends on the impact of competition and environmental filtering [16]. This impact can change according to factors such as habitat complexity [17], the overall size of available habitats [18], relative non-linearity and additive growth [19], assembly processes such as patch dynamics [20], neutral [21], source-sink dynamics (Mouquet et al. 2011), and the interaction between stress (as opposed to productivity) and disturbance [22]. Moreover, mobility, especially when high, allows species to find refuges during disturbances or stress or to faster re-colonize disrupted areas afterwards, thus making the relation between biodiversity and disturbance or stress less visible [23]. Complex biodiversity patterns may emerge from the interactions of all these factors but no theoretical framework exists to predict their extent and intensity. Nevertheless, the relative importance of EF and competition can be disentangled in three distinct cases (Fig. 1).

These cases consist of linear increase (case A), decrease (case B), and unimodal (case C) patterns along decreasing perturbation or stress gradients. When competition is much stronger than EF (Fig. 1A), biodiversity increases linearly with increasing disturbance or stress. For instance, at low disturbance or stress competition rapidly leads to the dominance of few species (CE) potentially with distinct traits (LS). In this case, disturbance or stress will free habitats occupied by these superior competitors. This will delay CE and allow inferior competitors to establish, even at low density, and thus for more species to coexist. To the contrary, when EF is much stronger than competition (Fig. 1B), CE and LS are prevented and biodiversity decreases linearly with increasing disturbance frequency or stress intensity because of the loss of species unable to survive. When the intensity of EF and competition change over the gradient in opposing ways (Fig. 1C), species are eliminated at both ends of the gradient by EF and competition respectively. As a result, biodiversity peaks at intermediate disturbance or stress levels as predicted by the IDH and ISH.

However, the relative importance of EF and competition can be investigated through a variety of biodiversity measures with complementary properties and different responses to environmental gradients [24, 25].

1.3 Taxonomic and functional diversity

Biodiversity has several facets measured by a plethora of indices. Selecting the most appropriate index (or set of indices) is a critical step when characterizing the response of biodiversity to disturbance and stress [26].

When applied to communities and food webs, biodiversity can be divided into its taxonomic and functional facets, and spatially partitioned into its alpha, beta and gamma components [27]. While Taxonomic Diversity (TD) focuses on describing the number of species present and their evenness, Functional Diversity (FD) accounts for the morphological, physiological and behavioral features that enable species to survive in the ecosystem and maximize their fitness. FD is thus based on the functional trait concept [28, 29]. The strength of the correlation between TD and FD depends on community assembly processes. Indeed, the niche space occupied by a community may increase with species richness (random assembly of species) or may be limited by environmental filters (non-random assembly of species from the species pool) [30, 31]. As a result, TD and FD are complementary for studying the impact of disturbance and stress on biodiversity. Indeed divergence between TD and FD patterns informs on environmental filters or other community assembly mechanisms [32].

Measuring species traits is a prerequisite to calculate FD. Functional trait-based approaches allow characterizing the performance of organisms under changing environmental conditions through their morphological, physiological and behavioral attributes. Relating traits to environmental variables improves our understanding of biological processes in ecosystems and allows defining general rules of species assembly [33]. FD measures the amount of variation of functional trait values among species in a community. It accounts for the different functioning of species in their environment. FD is key for assessing community response to environmental filtering, and biotic interactions such as competition [34]. FD can be expressed in three major metrics: functional richness (FRic), divergence (FDiv), and evenness (FEve) [35]. FRic represents the total amount of occupied niche space by a given community. This metric depends on species richness, where high FRic indicates that most of the available resources are used. FDiv, an abundance-weighted metric, measures the spread of abundance along a functional trait axis, where high FDiv indicates a low competition for resources. FEve accounts for the evenness of abundance distribution in a functional trait space, where high FEve shows that resources are evenly exploited by all species [35]. Metrics accounting for several components of FD were also developed. Rao's quadratic entropy (FDQ) [36] estimates the dispersion of species in trait space. In addition, functional redundancy FRed (calculated as the difference between N2 and FDQ) represents the difference between the potential (N2) and observed (FDQ) functional diversity [37], where high FRed indicates that species in the community are functionally similar each other, thus functionally redundant. Moreover, a high functional redundancy enhances the ability of a dynamic system to remain within the same basin of attraction, by adapting its structure to survive severe disturbance or stress, thus preserving its integrity and function. This ability, i.e. ecological resilience [38], is a key factor when studying the impact of disturbance or stress on biodiversity. Resilience enhances community capacity to survive disturbance or temporary stress. Communities might indeed adapt to frequent disturbance or recurrent temporary stress by increasing functional redundancy among species to become more resilient [39]. Such an adaptation would result in opposite trends between TD and functional redundancy along the disturbance or stress gradient.

1.4 Floodplains as model ecosystems

TD and FD are influenced by disturbance and stress. As a result, dynamic ecosystems submitted to disturbance and stress offer good settings to investigate these changes. For instance,

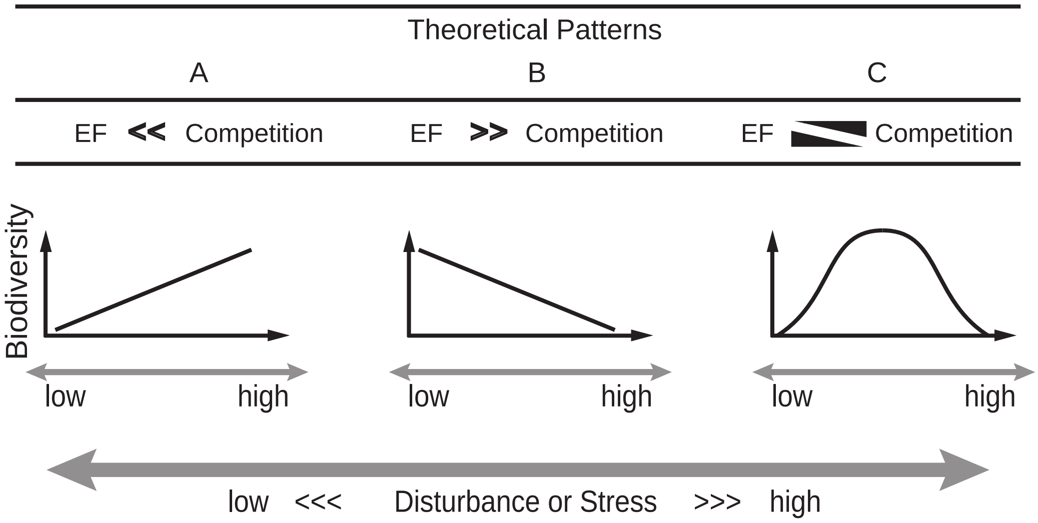

Figure 1. Expected patterns of biodiversity along (linear) disturbance and stress gradients in three situations (A, B, and C) differing in the relative strength of environmental filtering (EV) and competition along the gradients.

floodplains provide sharp environmental gradients mainly related to flood dynamic [40] that strongly structure organism distribution. The impact of flooding has been demonstrated for various kinds of organisms both at the individual and at the community scale [41, 42]. Similarly, hydric conditions influence local biota [43] through changes from dry to water-saturated conditions in short time and space [44]. However, surprisingly few studies have considered FD alongside TD and most focused on a single taxonomic group making comparisons among trophic levels difficult [39, 45, 46]. Moreover, hydric stress and flood perturbations were generally investigated separately. There is thus a lack of integrative understanding of taxonomic and functional aspects of biodiversity patterns along environmental gradients in floodplains.

This study investigates the impact of flood disturbance and hydric stress on selected taxonomic and functional diversity indices for plants, spiders, carabid and staphylinid beetles, isopods, diplopods and earthworms in a restored floodplain NW of Switzerland. We discriminated the relative importance of two major processes responsible for the shape of the disturbance/stress-biodiversity relation, i.e. competition and environmental filtering, by comparing diversity patterns to theoretical expectations (Fig. 1).

We expected flood disturbance and hydric stress to constitute independent gradients with disturbance having a greater influence than stress on biodiversity. This is expected to result in a predominance of EF over competition and thus a majority of linear decreases in biodiversity indices along increasing disturbance or stress.

2. Material and Methods

2.1 Study area

The study was conducted along the Thur River in north-western Switzerland. The Thur River flows from Säntis Mount to the Rhine River without entering any reservoir or lake. Its regime is close to those of alpine rivers. As a general pattern, peak flow occurs in spring after snowmelt and in summer and fall after large storms. As study site, we selected a restored section of the river of 1.5km long. At this place, the river average annual flow was 47 m^3 s^{-1} with maximum and minimum values of 1130 and 2 m^3 s^{-1}, respectively.

2.2 Sampling design

Within the site, we selected 36 plots in six different types of habitats ranging from bare gravels with patchy vegetation to alluvial forests (Appendix figure 4). In the habitats most frequently flooded (bare gravels, herbs, and willow bushes), six plots were sampled, whereas four plots were sampled in the remaining habitats (willow and mixed forests, and pasture). Two plots of the bare gravel habitat were excluded because they were inundated during most of the sampling period. Each plot consisted in a circle of 4 m radius and was sampled using pitfall traps [47], sweep netting [48], and Berlese extractions [49]. Three pitfall traps were placed in each plot and opened for one-week periods nine times from April to October 2008. For sweep netting, 20 sweeps were conducted along three 10 m transects at the direct proximity of the plots using a net of 40cm diameter. This process was repeated nine times for each plot during the same period. All the litter was gathered along the same transects and fauna was extracted during a two-week period using modified Berlese-Tullgren extractors. All individuals were stored in 70% ethanol before species level identification of all mature specimens of spiders, carabid and staphylinid beetles, isopoda, and diplopods. Earthworms were sampled using the mustard extraction method [50, 24]. In addition, vegetation was investigated using phytosociological surveys [51] of the plot surface area. These surveys were conducted nine times during the sampling period. As we concentrated on spatial variability rather than temporal fluctuations, seasonal data were pooled to build one dataset representing the entire sampling period for each taxonomic group.

In parallel, environmental variables describing flood dynamics were used to characterize the disturbance gradient. The minimum river flow required to flood each habitat (Min_Flow) was defined in Samaritani et al. [52] from inundation maps produced by digital terrain modeling. The average number of floods per year (Flood_Year) was calculated for each habitat using river flow measurement data covering a period ranging from 2003 to 2008 (www.hydrodaten.admin.ch/d/2044.htm). Flood periodicity (Periodicity) was calculated as the average number of days between two flood events for the same period. Moreover, variables describing local hydric conditions were used to characterize the hydric stress gradient. Depth of the water table (DWT) was estimated as the average difference between river and plot elevation during the sampling period. The number of days during the sampling period for which DWT was above an arbitrary fixed threshold of 30 cm below soil surface was calculated to account for local dynamics of hydric conditions (Ndays30).

2.3 Diversity indices

We selected three taxonomic (TD) and five functional diversity (FD) metrics. For TD, we retained measures of alpha diversity according to Hill [53]: species richness (N0), Simpson diversity (N2) and evenness (E2=N2/N0). For FD, we selected relevant measures describing the morphological/physiological adaptations of organisms to specific environmental conditions and, whenever possible, dispersal strategies – two key aspects of metacommunity dynamics – [54].These measures are hereafter called traits although some of them accounts for niche optima rather than true functional traits as defined by Violle et al. [29]. A total of 64 traits were retained (ranging from 7 to 14 depending on the group, (Appendix A). We then conducted Principal Component Analysis (PCA) on each scaled trait dataset to balance dimensionality among taxonomic groups and avoid redundancy among traits. Site scores of the first two axes were kept to account for the main strategies developed by each taxonomic group (Appendix E). The selected FD indices (FRic, FEve, FDiv, FDQ, and FRed) were calculated using these site scores. Detailed explanations of the mathematics underpinning each of them are given elsewhere [55, 56, 57, 37].

2.4 Numerical analyses

To obtain two independent synthetic indices for flood disturbance and hydric stress, we adapted the method of Gerisch et al. [39]. We first computed pairwise correlations among all hydrological variables (Appendix figure 5) and applied a PCA to verify that the two sets represent independent gradients related to flood disturbance and hydric stress, respectively. Once checked for independency, site scores of PCA axes 1 and 2 were then scaled from zero to one and used as disturbance index and stress index, respectively.

We then calculated the taxonomic and functional diversity indices and the Pearson correlations among them for all taxonomic groups (Appendix figure 7). The influence of disturbance and stress on these indices was assessed using Generalized Additive Models (GAMs) as they constitute good tools to characterize non-linear patterns. We assumed Poisson distribution for species richness and Gaussian distribution for all other metrics using the “log” and “identity” link functions respectively. The significance of flood disturbance and hydric stress terms was assessed using Wald tests and model fit was estimated using adjusted R2 values and AIC. In total, we fitted 56 GAMs for the seven taxonomic groups and the eight biodiversity indices. All computations were done with the R framework [58] using packages “FD” [59] and “vegan” [60].

3. Results

3.1 Flood disturbance and hydric stress gradients

The analysis of hydrological variables revealed independent disturbance and stress gradients at the Thur River site (Fig. 2; Appendix figure 5). As expected, PCA axis 1 was correlated to flood disturbance indicators and axis 2 to stress indicators (Fig. 2), so that the corresponding synthetic indices were independent from one another. Moreover, the correlations between disturbance and stress indicators were not significant except for one stress indicator, DWT, which was moderately correlated to periodicity as well as to the flood index (Appendix figure 5). The disturbance gradient ranged from rare (0 = 0.2 floods years^{-1}) to frequent (1 = 24 floods years^{-1}) flood events (axis 1 of the PCA biplot; Fig. 2) and corresponded to a toposequence of habitats reflecting a succession in vegetation height and openness, with open herbaceous vegetation on the right of the biplot (high disturbance level) and close forest on the left (low disturbance level). Along the hydric stress gradient (axis 2), intra-habitat heterogeneity was higher and control sites in the non-restored pasture were separated from the others at the bottom of the gradient (potential drought stress). Forest sites situated at low elevation had highest scores on axis 2 of the scatter plot (corresponding to highest probability of waterlogging).

3.2 Biodiversity patterns at the Thur River: influence of disturbance and stress

In total, 99’757 individuals of invertebrates were identified corresponding to 423 species and sub-species (spiders: 87, carabid beetles: 73, staphylinid beetles: 118, isopoda: 8, diplopods: 9, earthworms: 15, vascular plants: 113). The first two PCA axes on individual community trait data accounted for 33.6% (vascular plants) to 76.6% (diplopods) of the variance (Appendix figure 6).

Biodiversity was more influenced by disturbance than by hydric stress (Fig. 3; Table 1). Of the 56 GAMs on taxonomic and functional diversity metrics, 37 revealed a significant influence of disturbance while only 24 models were significant

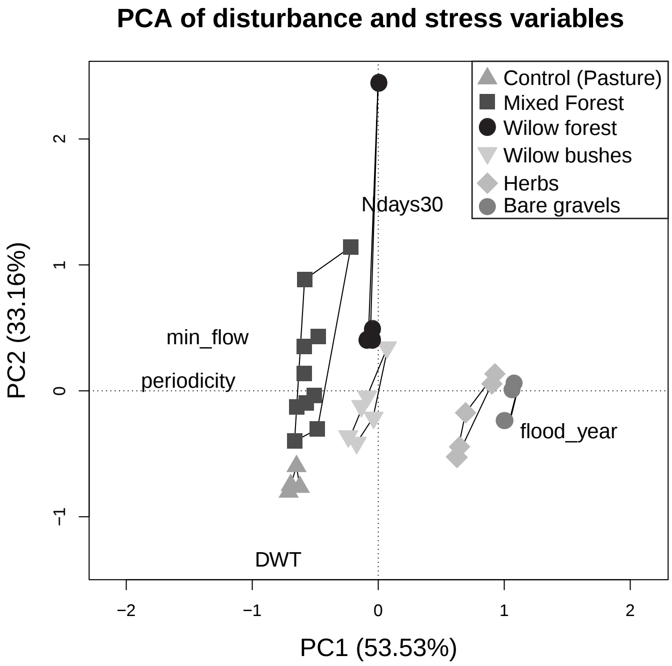

Figure 2. PCA of flood disturbance and hydric stress variables. Site scores of axes 1 and 2 were scaled between 0 and 1 and used as disturbance and stress indices respectively. Flood_Year = the average number of floods per year (from 2003 to 2008); Min_Flow = the minimum river flow required to flood each habitat; Periodicity = the average number of days between two flood (from 2003 to 2008); DWT = depth of the water table; Ndays30 = number of days with DWT at less than 30 cm from soil surface.

for stress. Biodiversity was influenced by stress and disturbance jointly in 21 models, by disturbance alone in 16 cases and by stress alone in 3 cases. Finally, in 16 cases no significant relation among biodiversity and disturbance or stress was found.

3.3 Differences among taxonomic groups

Strong variations of all biodiversity indices were observed among taxonomic groups and along the disturbance and hydric stress gradients (Fig. 3; Table 1). The decomposer communities (i.e. earthworms, diplopods, and isopods) were composed of fewer species (32 in total) as compared to predators (90 species) and plants (121 species), were less diverse (N2 = 3.2, 17.9, and 17.7 respectively), and had lower FRic values (FRic = 1.5, 7.8, and 5.3). E2 followed opposite trends being on average lower for plants (0.24), than for predators (0.36), and decomposers (0.66). FEve was relatively high for predators (0.57) and low for decomposers (0.35) and plants (0.37). FDiv and FRed were low for decomposers (0.46 and 1.21 respectively) as compared to plants (0.72 and 3.44) and predators (0.66 and 4.75). Finally, FDq was lowest for plants (0.64), intermediate for decomposers (0.89) and highest for predators (1.44).

3.4 Relationships among biodiversity indices

Biodiversity indices were significantly correlated in 54% of all cases, but this proportion varied among taxonomic groups (25% in staphylinids to 79% in earthworms, Appendix figure 7 & Appendix table 2). Strong correlations were observed between FRed and N2 for all taxonomic groups although the coefficients tended to decrease for taxa with lower N0 (decomposer). Similarly, strong correlations were obtained between FRic and N0 with higher coefficients on average for decomposer taxa (r = 0.86), than for predatory taxa (r = 0.64) and plants (r = 0.7). E2 stood out being negatively correlated to FDiv (isopods and plants), FRic (isopods, staphylinid beetles and spiders), and N0 (isopods, spiders and earthworms).

3.5 Importance of competition and environmental filtering

The shape of the relation between biodiversity and disturbance or stress differed among taxa and among indices (Fig. 3 and Table 1). Decrease of biodiversity along increasing disturbance frequency (i.e. corresponding to Fig. 1B) was the most frequently observed pattern with 20 out of 56 models showing significant relations. However, this pattern was not observed along the stress gradient. Increase of biodiversity (Fig. 1A) was observed in 3 (disturbance) and 14 (stress) cases, bell-shaped patterns (Fig. 1C) in 7 and 8 cases, and other patterns (bi-, multi-modal, U-shaped) in 6 and 2 cases along decreasing perturbation and stress, respectively.

4. Discussion

Table 1. Summary statistics of GAM analyses for all taxonomic groups and diversity metrics (a and b). a: R2 of significant smooth-terms $p<0.05$; b: AIC values. Bold characters highlight models for which both flood disturbance and hydric stress are significant and regular characters indicate models for which either flood disturbance or hydric stress is significant. c: p-values of individual models. Patterns are coded as follows: increasing: *; decreasing: **; unimodal: ***; different (multi-modal, U-, and Z-shaped): white background (p-values).

(a) R-squared

	N0	N2	E2	FRic	FEve	FDiv	RaoQ	FRed
Plants	0.32	0.39	0.49	ns	ns	0.33	0.17	0.43
Spiders	**0.42**	0.13	ns	ns	ns	0.75	0.70	ns
Carabids	0.46	**0.52**	0.26	ns	**0.33**	ns	**0.62**	**0.53**
Staphylinids	**0.50**	0.33	0.14	0.51	ns	ns	0.16	0.37
Isopods	**0.77**	**0.60**	ns	**0.63**	**0.71**	**0.59**	**0.52**	**0.46**
Diplopods	**0.63**	**0.45**	ns	**0.58**	**0.39**	**0.62**	**0.62**	ns
Earthworms	0.62	0.64	0.50	0.20	0.32	0.53	0.55	ns

(b) AIC

	N0	N2	E2	FRic	FEve	FDiv	RaoQ	FRed
Plants	208.1	134.6	-68.1	ns	ns	-56.6	11.6	127.3
Spiders	**198.7**	171.5	ns	ns	ns	-62.7	**19.9**	ns
Carabids	174.1	**131.9**	-66.3	ns	**-55.4**	ns	**32.5**	**129.3**
Staphylinids	**205.7**	169.7	-36.6	162.2	ns	ns	77.5	166.1
Isopods	**79.7**	**65.5**	ns	**87.4**	**-9.3**	**11.7**	**40.1**	**45.3**
Diplopods	**113.5**	**91.4**	ns	**106.0**	**4.7**	**21.8**	**65.9**	ns
Earthworms	119.9	97.5	-29.7	141.5	6.3	-1.2	62.0	ns

(c) P-values: Flood disturbance

	N0	N2	E2	FRic	FEve	FDiv	RaoQ	FRed
Plants	0.048***	0.002**	<0.001**	ns	ns	0.015*	ns	0.001
Spiders	0.035***	ns	ns	ns	ns	<0.001	0.001	ns
Carabids	ns	0.002***	0.008*	ns	0.034**	ns	<0.001	<0.001***
Staphylinids	0.003**	ns	0.016*	<0.001**	ns	ns	0.009**	ns
Isopods	<0.001**	<0.001**	ns	0.003***	<0.001***	0.001**	0.005**	<0.001**
Diplopods	<0.001**	0.002**	ns	<0.001**	0.005**	<0.001**	<0.001**	ns
Earthworms	0.001	<0.001***	<0.001	0.021**	0.003**	0.001	0.001**	ns

(d) P-values: Hydric stress

	N0	N2	E2	FRic	FEve	FDiv	RaoQ	FRed
Plants	ns	ns	ns	ns	ns	ns	ns	ns
Spiders	0.024	ns	ns	ns	ns	ns	0.033	ns
Carabids	0.013*	0.006*	ns	ns	0.024*	ns	0.025*	0.044*
Staphylinids	0.035*	0.023*	ns	ns	ns	ns	ns	0.018*
Isopods	<0.001*	0.005*	ns	<0.001*	0.003*	0.005*	0.045***	0.025***
Diplopods	<0.001***	0.018***	ns	0.001***	0.033***	<0.001***	<0.001***	ns
Earthworms	0.035*	ns	ns	ns	ns	ns	ns	ns

4.1 Flood disturbance and hydric stress gradients

The influences of disturbance and stress on functional and taxonomic diversities have rarely been assessed simultaneously in field studies. We aimed at filling this gap by disentangling the relative importance of competition and environmental filtering in shaping species distributions of functionally contrasted taxa along disturbance and stress gradients.

We showed that flood disturbances and hydric stress at the Thur River site constituted two independent gradients and that biodiversity patterns strongly diverged within and between these two gradients. The disturbance gradient was linear and perpendicular to the river thus creating a succession in vegetation similar to the one described in Petts and Amoros (1996). By contrast, the stress conditions were spatially distributed within the floodplain and within each habitat (especially clear in the mixed and the willow forests) according to local surface elevation (Appendix A). These gradients strongly influenced biodiversity.

4.2 Impact of disturbance and stress on biodiversity

Flood disturbances and hydric stress were strong drivers of biodiversity at the Thur River as shown by the fact that 75% of the GAMs revealed a significant influence of disturbance and/or stress. Strong impacts of disturbance or stress on biodiversity were already demonstrated individually in floodplains (Gerisch et al. 2012). However studies investigating disturbance and stress simultaneously are much scarcer. Nevertheless, strong impact of both stress and disturbance were observed for alpine (Kammer and Möhl 2002) and riparian plant communities (Brose and Tielborger 2005, Lite et al. 2005) thus confirming the general importance of these gradients in shaping biodiversity.

However, the two gradients were unequal in their influence on biodiversity, both in strength (i.e. number of significant models, strength of correlations) and type of effect. In agreement with our hypothesis, flood disturbance had a greater influence

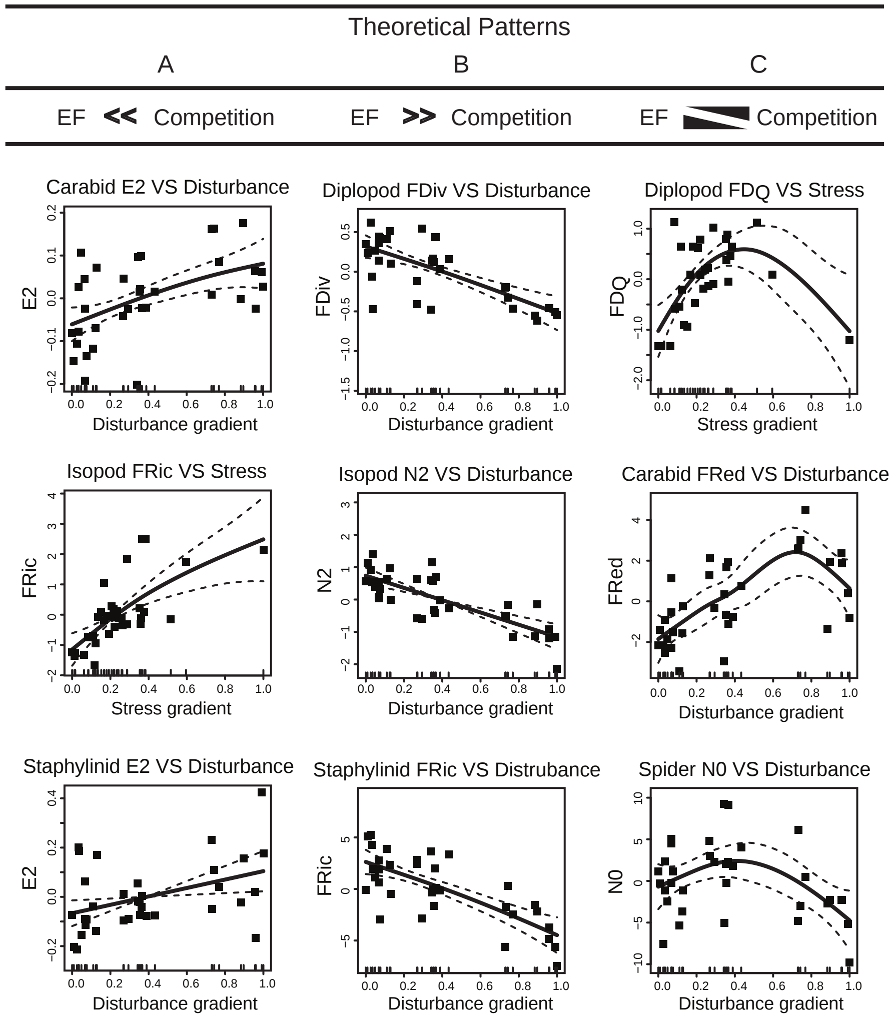

Figure 3. Selected examples of responses of biodiversity indices to flood disturbance or hydric stress. We provide three examples for each of the theoretical patterns depicted in figure 1 A, B, and C. Partial residuals of the disturbance or stress term of fitted GAM, model predictions and 2 standard errors intervals are shown.

on biodiversity than stress (Table 1). Furthermore only in four cases was a significant effect observed for stress alone. This indicates that flood dynamics imposed a stronger filtering on species than hydric stress at our study site. The study site lies on an active aquifer with high water infiltration capacity and the ground water table was shown to closely follow the river water level across the site (Schneider et al. 2011). Waterlogging was thus limited to the lowest elevation areas mostly in the old willow forest while gravel bars could experience drought stress only in relatively short periods in summer. The different impact of disturbance and stress on biodiversity and the contrasted responses of various diversity indices therefore reflected different ecological processes operating along these gradients.

4.3 Relative importance of competition and environmental filtering

Competition and environmental filtering are among the main processes structuring ecological assemblies, yet our understanding of the role and relative importance of these processes remains incomplete (Cornwell and Ackerly 2009). In our study, EF had an overall stronger impact than competition on communities. However, the impacts of EF and competition differed along the two gradients with EF being predominant along the disturbance gradient and competition along the stress gradient in agreement with previous results (Wilson and Keddy 1986, Brose and Tielborger 2005).

As a result, EF and competition were spatially distributed within the site following the disturbance and stress gradients. This agrees with the idea that the habitat provides the templet upon which species traits are sorted (Townsend and Hildrew 1994) leading to the creation of distinct functional process zones (Thorp et al. 2006). However, differences among taxonomic groups and among biodiversity indices could not be explained by these theories.

4.4 What are the key drivers of community response to disturbance and stress?

The impact of disturbance and stress diverged among taxonomic/functional groups. The impact of disturbance was strongest on the diversity of decomposer taxa as compared to predatory arthropods and plants, while the impact of hydric stress was strongest on diplopod and isopod, but unexpectedly low on plant and earthworm biodiversity indices (except for earthworm species richness). These results may be explained by differences in trophic level, mobility, and resilience among communities.

Trophic level and mobility are thought to influence the shape of the response of biodiversity to disturbance or stress. According to Wotton (1998), the responses of plants and decomposer taxa are more likely to be unimodal as predicted by the IDH than those of predatory taxa. Overall our results confirm this trend. However, this was mostly due to the response of diplopod diversity to stress (Fig.3, Table 1). This result may be explained by the nature of the stress gradient at our site that was not linearly increasing but rather ranged from potential drought to waterlogging. Taxa highly sensitive to hydric conditions such as isopods may experience EF at both ends of the gradient thus explaining the observed bell-shaped patterns.

Resilience is an adaptation to cope with disturbance or temporary stress. For instance, low redundant communities were strongly impacted and more redundant ones less strongly impacted by flood disturbance and hydric stress. Resilience as indicated by functional redundancy among species was thus a key driver of community response to disturbance and stress. Moreover, changes in community resilience paralleled changes in community taxonomic diversity.

4.5 Species richness enhanced community resilience to disturbance and stress

The loss of species under high disturbances or stress was not compensated by a higher degree of functional redundancy among species thus impacting community response to both environmental forces. The contrasting patterns between taxonomic and functional diversity with increasing TD and decreasing FD along disturbance gradient observed by Gerisch (2012) were not confirmed by our results. To the contrary, functional redundancy and thus community resilience to disturbance and stress increased with species diversity in agreement with the species insurance hypothesis (Naeem and Li 1997).

Such a result may be explained by the relative short time since restoration that did not allow communities to adapt to the renewed flood dynamic by increasing their resilience. Indeed, the work of Gerisch (2012) was conducted in a protected floodplain with a long flood history. Moreover, in fire-prone ecosystems, species turnover was compensated by high functional redundancy only in ecosystems with a long fire history (Moretti et al. 2009). Comparing patterns of Fred and TD along perturbation gradients may thus represent a way to assess the long-term adaptations of communities to disturbance or stress (Appendix G). If confirmed, this hypothesis will impact our understanding and the management of dynamic ecosystems.

5. Conclusion

Disturbance and stress controls biodiversity through the action of environmental filtering and competition, but the interplay of these ecological forces remained poorly understood.

Our results revealed stronger impact of disturbance than stress on biodiversity. This difference reflected different ecological processes with environmental filtering dominant along the disturbance gradient and competition along the stress gradient. The impact of disturbance and stress diverged among taxonomic groups with trophic level and mobility influencing the shape of the relation and species richness influencing the strength of the impact on communities. Indeed, for all taxonomic groups, more diverse communities were composed by more functionally redundant species and were thus more resilient in agreement with the species insurance hypothesis. However, we hypothesize that communities will further adapt to disturbance and stress by increasing species functional redundancy.

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Appendix to Environmental filtering and competition along disturbance and stress gradients

Table 2. Summary of species trait data for each taxonomic group sampled at the Thur River site.

(a) Carabid beetles

Metrics	Values	Definitions
Habitat	0-1	Habitat specialisation (ratio of the nb of occupied habitat types out of 8)
Moisture	0-4	Moisture conditions requirements (0=steno-xerophilous; 2=mesohygrophilous; 4=steno-hygrophilous)
Elevation	1-4	Number of altitudinal zones occupied out of collineous, montane, sub-alpine, alpine
Overwintering	1-3	Overwintering strategies: 1 = larvae; 2 = both; 3 = adult
Breeding	1-12	Duration in months of the breeding period
Trophism	1-4	Trophic specialistation: number of food regime out of: carnivorous (except insects and molluscs), phytophagous, saprophagous, insect specialists, and mollusc specialists
Mobility	1-6	Size of the species reservoir in CH (Log scale): 1 = 100 catches per 100 days of sampling; 6 = 0.001 to 0.01 catches/100 days
Wings	1-3	1 = no wings; 2 = dimorphic; 3 = winged

Metrics	Values	Definitions
Shading	0-1	Tolerance for changes in shading levels (ratio of the number of shading conditions tolerated out of 5)
Moisture	0-1	Tolerance for changes in moisture levels (idem as shading)
Habitat	0-1	Habitat specialisation (ratio of the nb of occupied habitat types)
Elevation	1-4	Number of altitudinal zones occupied out of collineous, montane, sub-alpine, alpine)
Layer	1-6	Number of occupied layers out of soil, litter, grass, bushes, tree branches, and canopy
Balloonning	0,1	Capacity of ballooning (yes = 1, no = 2)
Mobility	1-3	Mobility strategies: 1 = sedentary; 2 = frequent site changes; 3 = high mobility

(b) Spiders

Metrics	Values	Definitions
Body size	0-n	average body size [mm]
Plasticity	0-n	max body size - min body size
Habitat	0-2	0 = ubiquist, 1 = eurytop, 2 = stenotop
Moisture	0-2	0 = xerophilous; 1 = mesohygrophilous; 2 = hygrophilous
Trophism	0,1	0 = strictly carnivorous; 1 = more diverse food regime
Sp_pool	0-n	0 = large species pool
Elevation	1-4	Number of altitudinal zones occupied out of collineous, montane, sub-alpine, alpine)

(c) Staphylinid beetles

Metrics	Values	Definitions
Male	0-n	average male body size [mm]
Female	0-n	average female body size [mm]
Plasticity	0-n	max body size - min body size
Elevation	1-4	Number of altitudinal zones occupied out of collineous, montane, sub-alpine, alpine
Habitat	0-1	ratio of the number of occupied habitats out of 1020 (Swiss Biodiversity Monitoring)
Sp_pool	0-1	ratio of the number of occupied plots out of 14'306 (Swiss Biodiversity Monitoring)
Moisture	0,1	0 = non hygrophilous; 1 = hygrophilous
Silvicol	0,1	0 = non silvicol; 1 = silvicol

(d) Diplopoda

Metrics	Values	Definitions
Body_size	0-n	average body size [mm]
Plasticity	0-n	max body size - min body size
breeding	0,1	0 = early breading; 1 = fall breeding
Elevation	1-4	Number of altitudinal zones occupied out of collineous, montane, sub-alpine, alpine
Sylvicolous	0,1	0 = non sylvicolous; 1 = silvicolous
Habitat	0,1	0 = non ubiquist; 1 = ubiquist
Humicolous	0,1	0 = non humicolous; 1 = humicolous
Layer	0-3	number of occupied layers out of soil, humus, and above-ground
Moisture	0-3	0 = xerophilous; 1 = mesophilous; 2 = hygrophilous; 3 = stenohygrophilous
M_tolerance	0-2	0 = low tolerance for changes; 1= high; 2 = very high
Mobility	0-1	0 = slow moving; 1 = fast moving

(e) Isopoda

Metrics	Values	Definitions
length	0-n	Body length [mm]
width	0-n	Body width [mm]
weight	0-n	Body weight [g]
segments	0-n	Number of segments
pH_opt	0-14	Preferred pH
pH_range	0-14	Toleration for changes in pH
prostomium	0,1	0 = tanylobous; 1 = epilobous prostomium
function	0-1	0 = endogeic; 0.5 = anecic; 1 = epigeic
CN_Soil	0,1	0 = little or no humus; 1 = high humus content

(f) Earthworms

Metrics	Values	Definitions
Temperature	1-5	1 = alpine and nival; 5 = very warm colline
Light	1-5	1 = full shade; 5 = full light
Moisture	1-5	1 = very dry; 5 = submerged
M_variability	1-3	1 = little variation; 3 = strong variations
Reaction	1-5	1 = extremely acid (pH = 2.5-5.5); 5 alkaline, high pH (6.5-8.5)
Nutrients	1-5	1 = very infertile; 5 = over-rich
Humus	1-5	1 = little or no humus; 5 = high humus content
Aeration	1-5	1 = bad aeration; 5 = good aeration (e.g. sandy, rocky soils)
Root_depth	1-5	1 < 25cm; 5 > 200cm
Dominance	1-5	1 = scattered; 5 = dominant in large areas
Habitat	1-9	Number of habitat types used out of nine
Dispersal	0,1	0 = passive or wind; 1 = active (e.g. zoochory)
Leaf duration	0,1	0 = deciduous; 1 = wintergreen, evergreen
P_change	0,1	0 = stable or decreasing; 1 = increasing populations

(g) Plants

Table -3. Number and percentage of significant and non-significant Pearson correlations among diversity indices

	N total	Significant	Non-significant	Significant [%]
Carabids	28	10	18	0.36
Spiders	28	12	16	0.43
Staphylinids	28	7	21	0.25
Plants	28	14	14	0.50
Diplopods	28	19	9	0.68
Isopods	28	21	7	0.75
Earthworms	28	22	6	0.79
Total	196	105	91	0.54

Figure 4. Aerial view of the Thur River site showing the habitats and sampling plots.

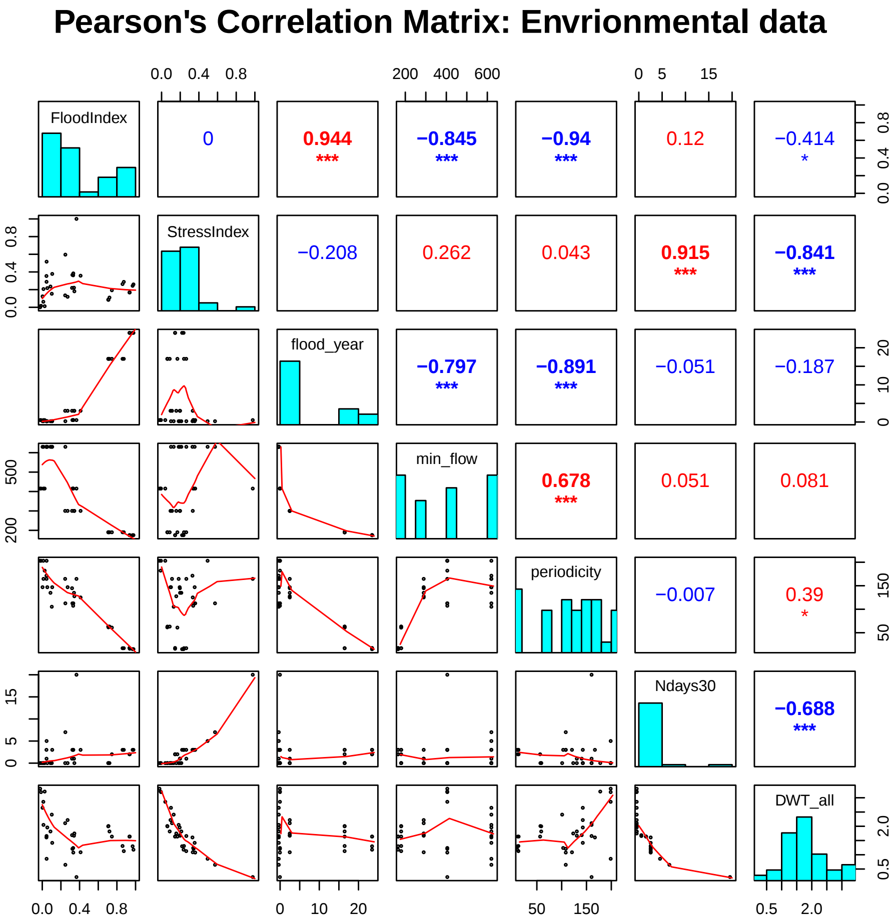


Figure 5. Pairwise Pearson correlations among the disturbance and stress indices and the hydrological variables.

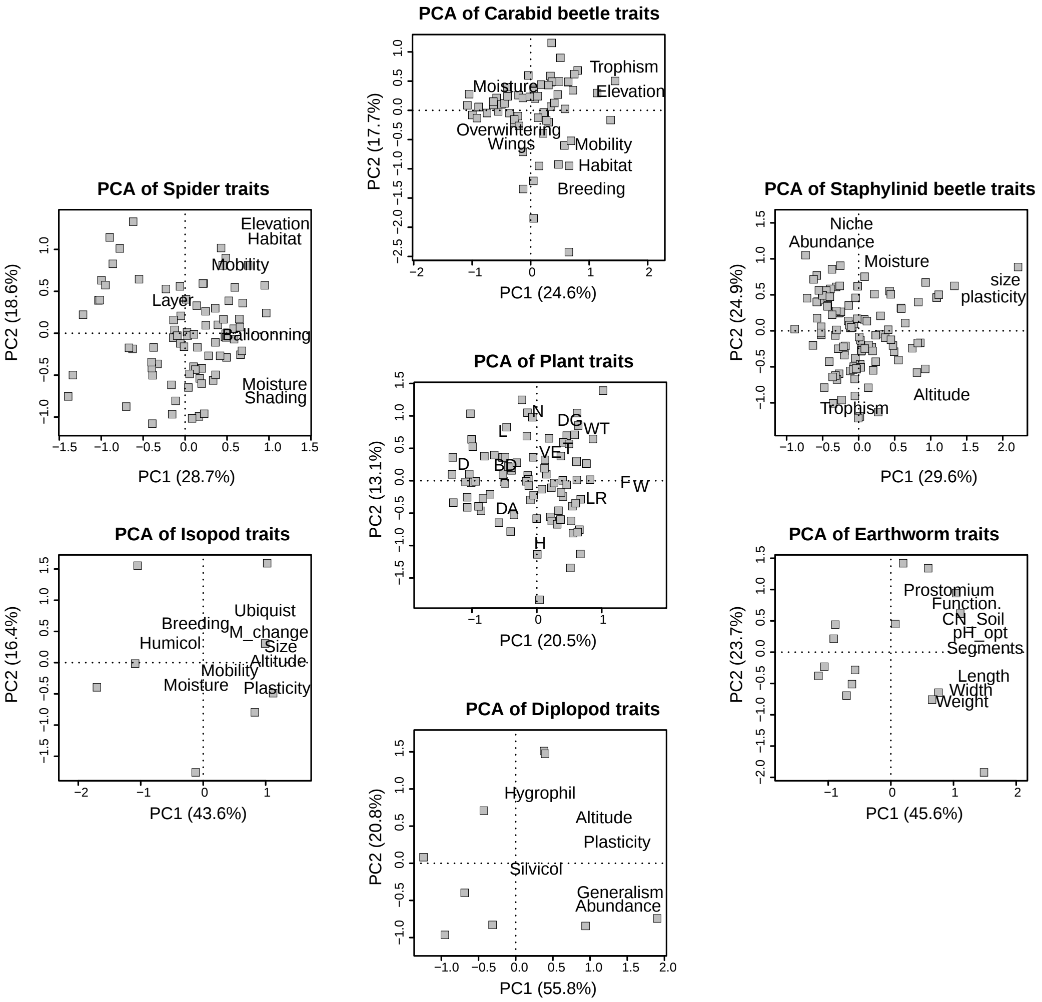
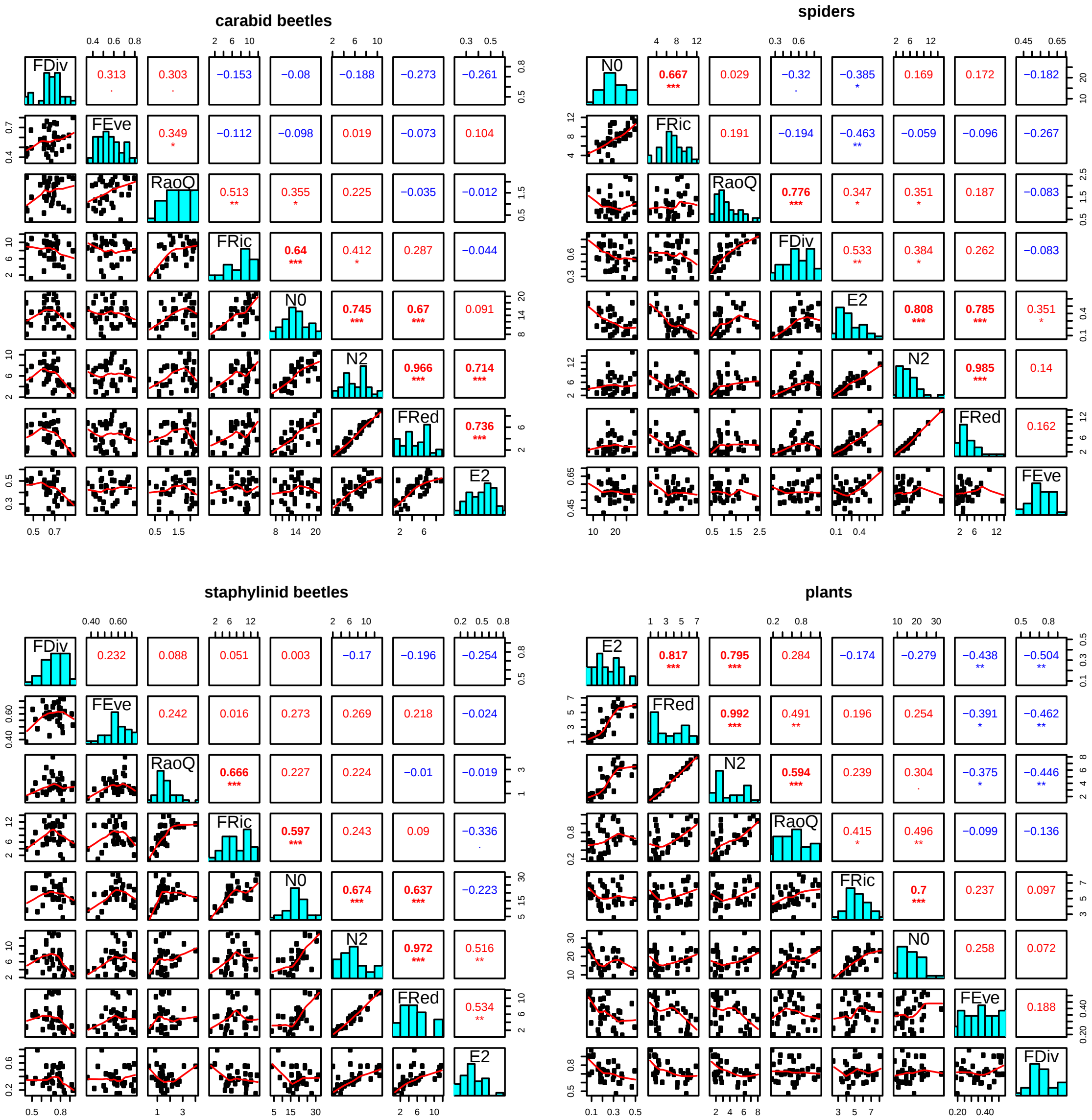
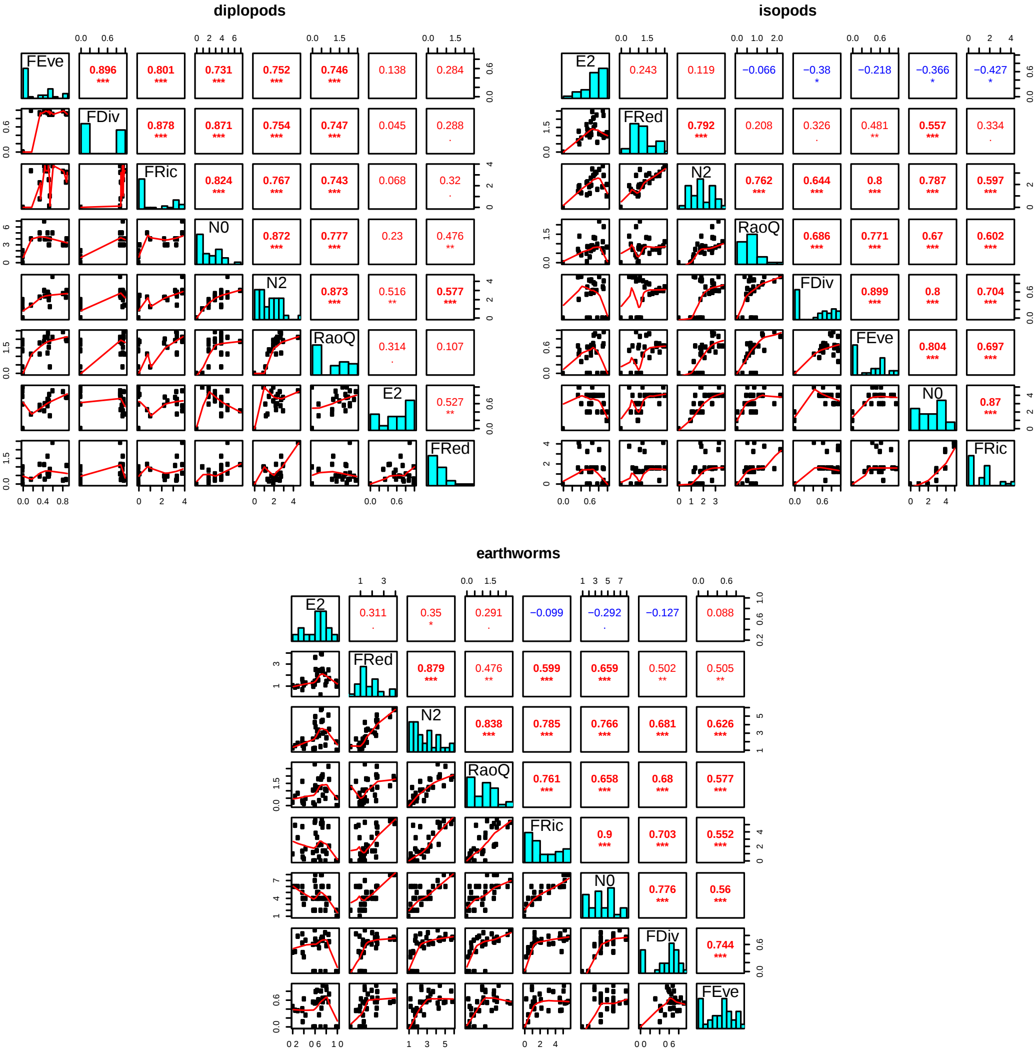


Figure 6. PCA of trait data for each taxonomic group. Species short names (first three letters of genus and species name) are indicated in light gray and traits in black. The percentage of variance in species trait data explained by each axis is given in brackets. The first two PCA axes accounted for 33.6% (plants), 42.3% (carabids), 47.3% (spiders), 54.5% (staphylinids), 60.0% (isopods), 69.3% (earthworms), 76.6% (diplopods) of the variance in trait data.



(a)

Figure 7. Pearson correlations among taxonomic and functional diversity indices for all taxonomic groups.



(b)

Figure 7. Pearson correlations among taxonomic and functional diversity indices for all taxonomic groups.

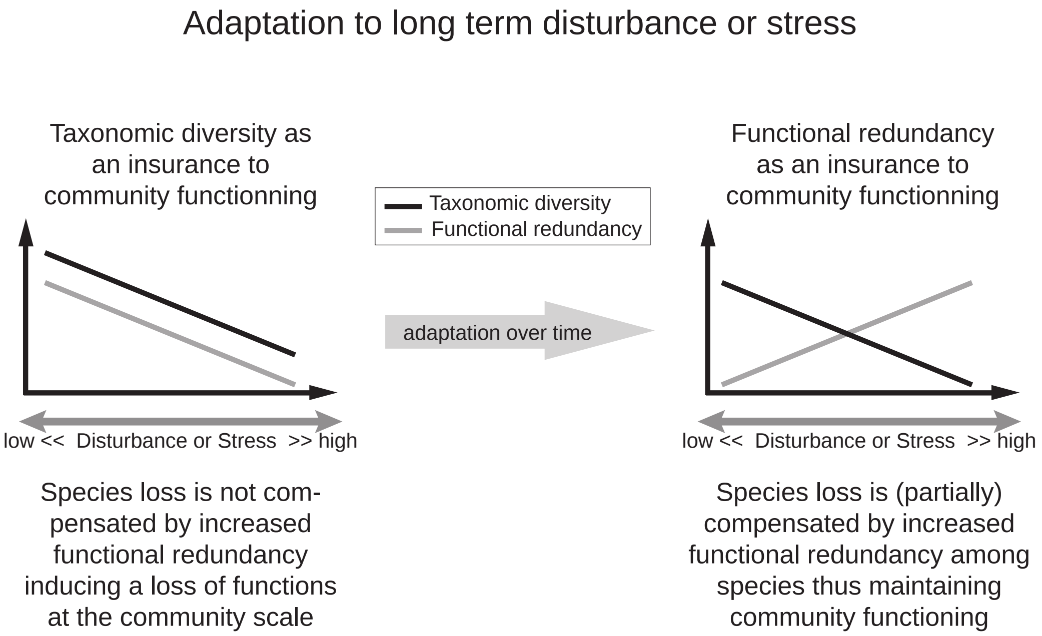


Figure 8. Schematic representation of how communities adapt to disturbance or stress by increasing their resilience over time. When a new disturbance or stress dynamic starts (for instance after floodplain restoration works), communities might not be adapted to disturbance or stress. In this case, species diversity and functional redundancy are strongly correlated as stated by the species insurance hypothesis. Environmental filters thus eliminate species and this impacts both species diversity and functional redundancy among species. As a result, strong environmental filtering induces a loss of functions at the community scale. To the contrary, communities become more resilient over time by increasing species functional redundancy. This is the result of the filtering of un-adapted species. In this situation, the increased functional redundancy (partially) prevents the loss of functions at the community scale.

8 Discussion & Conclusion

Above- and below-ground aspects of floodplain restoration: from biodiversity to ecosystem functions: Discussion & Conclusion

Bertrand Fournier[1 2]*

Abstract
This PhD thesis project focused on three major although neglected aspects of the ecology of floodplain ecosystems: floodplain soils, below-ground biodiversity, and the changes in biodiversity among taxonomic groups and along environmental gradients. With this respect, the results obtained during this PhD fulfill a gap in the knowledge of riparian ecosystems and provide perspectives for improved management of floodplains and riverine ecosystems. Future challenges include using holistic approaches for the study of the diversity and the functioning of the soil foodwebs, and disentangling the importance of assembly processes in structuring biodiversity patterns in disturbed ecosystems.

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1. Background

Biodiversity sustains ecosystem functioning and plays a key role in maintaining their properties and the services they provide to human populations [1, 2, 3, 4, 5]. However human activities threaten this biodiversity worldwide [6] with particularly strong impact on floodplains [7, 8].

Billions of Euros/Dollars/CHF tax payer's money is currently spent to restore floodplain biodiversity [9], yet no ecological theory exists that could provide guidelines to restoration projects. Moreover, no *a priori* knowledge of the biodiversity of certain taxa among which many soil organisms exists.

The Thur River is a good illustration of these issues. Indeed, little information about the local biodiversity was available before the restoration. The restoration was designed following general guidelines for restoring riverine ecosystems [10, 11] but without clear concerns about riparian soils and their associated biodiversity and ecological assembly processes. Such a situation is typical of densely human populated areas such as the Swiss plateau or Japan [12]. Moreover, The Thur River is a good example of braided river [13]. As a result, the conclusions of the presnt PhD extand beyond the limit of the study site.

2. Achievements and Advances

The present PhD thesis was conducted at the frontier of applied and theoretical ecology. Starting with the will to fulfill lacks in floodplain ecosystem understanding and management, it ended up highlighting general gaps between ecological theory and practice in ecosystem submitted to disturbances and/or stress.

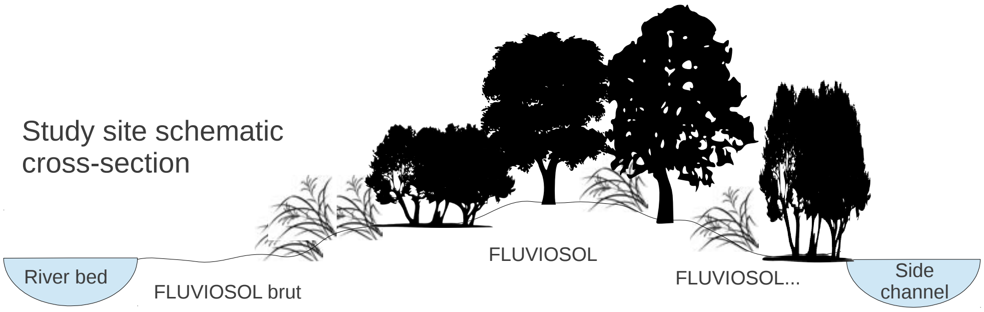
It was articulated around three main axes: floodplain soils, the patterns of diversity of below-ground organisms and their relations with environmental variables, and the relations among the different taxonomic groups, their diversity, and ecosystem functions. It highlighted the importance of soil morphology in floodplain ecosystems and its potential role in restoration project assessements. Using trait-based approaches to understand the dynamics of below-ground communities, it highlighted strong impacts of environmental conditions on community functional characteristics that can be developed into bioindication tools. Finally, using a multi taxononomic group approach, it related disturbance and/or stress to biodiversity, disentangled the relative importance of competition and environmental filtering in shaping this relation, and highlighted the difficulties of revealing the mechanisms responsible for the observed patterns and thus gaps between theory and practice.

These key findings highlight the complexity of ecological interactions occurring over the relatively small spatial scale of the study site. They showed the central importance of riparian soils and their associated biodiversity for the management of floodplain ecosystems. They are summarized in Figure 1 and explained in more details hereafter.

2.1 Soils

Floodplains soils are generally less studied than their forest or agricultural counterparts, yet they are considered among the most fertile soils on earth [14, 8]. They are extremely heterogenous and this heterogeneity is intimately related to flood dynamic. They host a higher and often functionally more important biodiversity than aboveground [15, 16]. However, soil ecosystems have remained widely overlooked in river restoration projects.

This PhD thesis showed that soil morphology provides struc-



General trends	+++	Impact of flood disturbances	---
	>>>	High hydric stress	<<<
	---	Taxonomic diversity	+++
	---	Functional diversity	+++
	+++	Environmental filtering	---
	<<<	Competition	>>>
Soil trends	+++	Soil dynamism	---
	---	Soil diversity	+++
	---	Soil typicality	---
Testate amoeba trends	---	Biovolume	+++
	---	Shell compression	+++
Earthworm trends	---	Body size	+++
	Epigeic	Ecological types	Endogeic/Anecic

Figure 1. Schematic cross-section of the study site that illustrates the main trends observed during the present PhD.

tural and functional information on floodplain ecosystems and allows predicting broad changes in plant diversity. The proposed indicators of the spatio-temporal heterogeneity of soil morphology should thus be integrated into the tool kits of floodplains and river restoration project managers.

2.2 Below-ground organisms

If soil morphology was poorly considered in river restoration porjects, what to say about soil organisms? As example, the ecology of earthworm communities in floodplain was indeed poorly known (but see [17, 18]) and that of testate amoebae was completely unknown to our knowledge before the present work. Similarly, the taxonomy of these groups remains a work in progress [19, 20]. This strongly contrasts with the acknowledged key functional importance of these organisms and soil fauna in general [21, 22, 23, 24, 25, 26].

Testate amoebae (TA) are top-predators of the soil microbial foodweb [27] that have key importance in nutrient cycling [28, 29]. Paper 3 pioneered the use of trait-based approaches for the study of these taxa. It confirmed that environmental filters related to flood dynamic force the assembly patterns of TA communities and demonstrated the strong relationships between environmental variables related to soil moisture and TA biovolume and compression suggesting no differences between the processes ruling macro- and microbial biodiversity.

Earthworms are ecosystem engineers of key importance for soils and riparian foodwebs in general [30, 31, 32, 33]. They were strongly influenced by flood disturbance (papers 2 and 4) but they were suprisingly only marginally influenced by the watertable (paper 4). Indeed, the changes in earthworm taxonomic and functional diversity correlated to the flood disturbance gradient. And, changes in the relative abundances of ecological types of earthworms were identified as indicators of soil development in floodplains. Given their central role in riparian ecosytems and their potential as bioindicators, earthworms should be integrated into floodplain restoration and management projects.

These results provide perspectives for improved management of floodplains and riverine ecosystems, fulfil several gaps in the knowledge of riparian ecosystems and more generally confirm the strong impact of flooding on below-ground organisms. However they leave unresolved the important question of the drivers of the observed diversity patterns.

2.3 Biodiversity patterns

Comparing biodiversity patterns between trophic groups and among above- and below-ground organisms can help defining the drivers of this biodiversity and lead to the formulation of general ecological rules.

However, biodiversity patterns did not show clear differences between above- and below-ground organisms or among trophic groups. These results provide no clear support to the idea that competition or, more generally, bioitic interactions are weaker among below-ground organisms [15, 34], suggesting a continuum between the above- and below-ground compartments of ecosystems.

The strong differences among taxonomic groups and the absence of clear trend among above- and below-ground organisms and among trophic groups rather suggest that properties specific to each taxa had a strong influence on the disturbance-diversity relationship. As proposed in paper 4, species competitive ability and adaptations to environmental filtering, and community resilience (that was strongly dependent on species richness) can be responsible for the observed differences. These results confirm the pertinence of trait-based approaches. More generally, the relative importance of competition and environmental filtering in shaping the biodiversity-disturbance relationship can be disentangled from field data using a simple framework. This framework allows defining the balance between two major ecological forces, but do not provide information about the processes responsible for this outcome. Indeed, assembly processes were shown to impact the diversity-disturbance or diversity-stress relationship [35, 36, 37]. However, this impact was widely overlooked thus creating gaps between ecological theory and practice. Indeed, among the many hypotheses that were proposed to explain the shapes of the diversity-disturbance or diversity-stress relationships [38, 39, 40, 41, 42], none were rooted in ecological theory [43]. Attempts were made in this direction, but considered almost exclusively the competition-colonization trade-off [44, 45]. It follows that the impact of assembly processes on the diversity-disturbance or diversity-stress relationship was widely overlooked thus creating gaps between ecological theory and practice.

3. Filling the gaps in biodiversity knowledge

The above-mentioned findings were based on a highly valuable database that allowed answering questions related to specific taxa or more general ones about multi-trophic interactions. Indeed, information on 448 species of plants, macroinvertebrates, testate amoebae, their associated traits describing niche width, niche breadth, and dispersal, and environmental factors was gathered. This work led to the (re-)discovery of five arthropod species for the Swiss fauna:

- *Atheta deformis* (Staphylinidae, Kraatz, 1856)
- *Atheta scotica* (Staphylinidae, Elliman, 1909)
- *Oxypoda arborea* (Staphylinidae, Zerche, 1994)
- *Collinsia distincta* (Aranea, Simon, 1884)
- *Xysticus viduus* (Aranea, Kulczynski, 1898)

These (re-)discoveries cannot be explained by specific characteristics of the study site that is located in an intensive agricultural area highly impacted by human activites and hosting a relatively poor diversity, but rather to the lack of investigations of certain taxonomic groups such as for instance spiders an staphylinid beetles. This comes together with a lack of taxonomic expertise of these groups. Indeed, the number of taxonomist declines and taxonomic publications are not *well-quoted* in ISI rankings thus fastening the decline [46] and this phenomenon is even stronger for soil organisms. This trend confirms and further emphasizes the need for filling in the gaps in biodiversity knowledge.

4. Follow-up and Perspectives

The present work offers many perspectives for the understanding of dynamic ecosystems among which two are, in our opinion, of the utmost interest.

First, the present work focused on several key communities with well-contrasted ecologies. This constitutes a time-efficient approach of biodiversity that makes the investigation of the functional properties of taxa with a species level resolution possible. However it overlooked many potentially interesting taxa and interactions. Future challenges include using holistic approaches for the study of the diversity and the functioning of the soil foodweb. The emergence of new sequencing techniques [47, 48] allows investigating the diversity of riverine soil microbial metacommunities as a whole, a task that was impossible so far. Although submitted to certain limitations [49], these techniques offer promising avenue for investigating the diversity and functional importance of soil organisms [50]. Moreover, these techniques are well-accepted by high-ranked journals. This has the potential to renew the interest for the taxonomy and the ecology of soil organisms.

Then, bridging the gaps between theory and practice requires that predictions be sufficiently discriminant to identify changes in assembly processes. In this case they could be applied to real cases. Previous work with this aim revealed that combinations of well-selected diversity indices allowed discriminating among assembly processes [51]. In the case of ecosystems prone to stress, measures of functional diversity proved especially powerful [52].

Building on the results of this PhD thesis, a follow-up was already initiated. Indeed, metabarcoding data of eukaryotic diversity obtained through next generation sequencing (Illumina) of soil samples of the same locations (SNSF project of Emanuela Samaritani) were gathered and complete the previously described database (data analyses in progress). Exploiting the information it contains will constitute a promising follow-up of the present work. Similarly, the impact of assembly processes will be further investigated in a post-doc project that couples theoretical and applied approaches to identify FD indices having the power to discriminate among assembly processes in ecosystems undergoing disturbance and stress (SNSF Nr-P2NEP3_148841).

5. Toward an integrated framework to understand dynamic ecosystems

The present PhD thesis and its follow-up alongside others ongoing advances pave the way toward an integrated framework to understand dynamic ecosystems. Doing so require an integrated theoretical framework to predict biodiversity patterns, and thus the unification of the metacommunity theory [53, 54] and the many theories describing the impact of disturbance and stress on biodiversity [35, 38, 39, 40, 41, 42], but also high quality field data and exprimental work that supports the theoretical predictions. Such a framework will facilitate the use of metacommunity thinking in conservation and restoration ecology potentially leading to improved management practices of dynamic ecosystems.

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Appendix A Heterogeneity of soil carbon in floodplains

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Hydrology and Earth System Sciences

Heterogeneity of soil carbon pools and fluxes in a channelized and a restored floodplain section (Thur River, Switzerland)

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Abstract. Due to their spatial complexity and dynamic nature, floodplains provide a wide range of ecosystem functions. However, because of flow regulation, many riverine floodplains have lost their characteristic heterogeneity. Restoration of floodplain habitats and the rehabilitation of key ecosystem functions, many of them linked to organic carbon (C) dynamics in riparian soils, has therefore become a major goal of environmental policy. The fundamental understanding of the factors that drive the processes involved in C cycling in heterogeneous and dynamic systems such as floodplains is however only fragmentary.

We quantified soil organic C pools (microbial C and water extractable organic C) and fluxes (soil respiration and net methane production) in functional process zones of adjacent channelized and widened sections of the Thur River, NE Switzerland, on a seasonal basis. The objective was to assess how spatial heterogeneity and temporal variability of these pools and fluxes relate to physicochemical soil properties on one hand, and to soil environmental conditions and flood disturbance on the other hand.

Overall, factors related to seasonality and flooding (temperature, water content, organic matter input) affected soil C dynamics more than soil properties did. Coarse-textured soils on gravel bars in the restored section were characterized by low base-levels of organic C pools due to low TOC contents. However, frequent disturbance by flood pulses led to high heterogeneity with temporarily and locally increased C pools and soil respiration. By contrast, in stable riparian forests, the finer texture of the soils and corresponding higher TOC contents and water retention capacity led to high base-levels of C pools. Spatial heterogeneity was low, but major floods and seasonal differences in temperature had additional impacts on both pools and fluxes. Soil properties and base levels of C pools in the dam foreland of the channelized section were similar to the gravel bars of the restored section. By contrast, spatial heterogeneity, seasonal effects and flood disturbance were similar to the forests, except for indications of high CH_4 production that are explained by long travel times of infiltrating water favoring reducing conditions. Overall, the restored section exhibited both a larger range and a higher heterogeneity of organic C pools and fluxes as well as a higher plant biodiversity than the channelized section. This suggests that restoration has indeed led to an increase in functional diversity.

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1 Introduction

Embracing spatial heterogeneity is a major challenge in ecosystem ecology. The composition, spatial configuration and temporal dynamics of habitat patches determine biodiversity and ecosystem processes. Ecosystems therefore need to be considered as dynamically interacting mosaics rather than homogeneous entities (Ward et al., 1999; Pinay et al., 2002). Floodplains are an ideal model to study spatial and temporal heterogeneity.

Floodplains are defined as low-relief areas that extend from the edge of permanent water bodies to the edge of uplands and are subject to flooding. In their natural state, the interaction between flood dynamics and geomorphic processes create a shifting mosaic of habitat patches (Naiman and Décamps, 1997; Stanford et al., 2005). These hydrogeomorphically distinct patches differ in age, inundation regime, and soil properties, thereby expressing a different productivity, system metabolism, organic matter dynamic, and biotic community composition. These patches can be referred to as "Functional Process Zones" (FPZs) as described by Thorp et al. (2008), although, in the context of the present study we apply the FPZ concept at a smaller scale to hydrogeomorphic patches within a single reach. Furthermore, we extend "functional" to ecological processes rather than to restrict the term to physical functioning of geomorphic and hydrologic forces. In dynamic floodplains, the various FPZs are arranged along distinct succession gradients (Naiman and Décamps, 1997), from recently deposited sand or gravel to mature alluvial forests.

Due to their spatial complexity and dynamic nature, floodplains provide a wide range of ecosystem functions and related services. Because flow alteration is one of the most serious threats to ecological integrity of river-floodplain systems (Tockner et al., 2008), the widespread regulation of the flow regime of large rivers, in particular in Europe and North America has led to the loss of characteristic environmental heterogeneity, biodiversity and associated ecosystem services in many floodplains (Tockner and Stanford, 2002). In the last decades, restoration of floodplain habitats and the consequent rehabilitation of key ecosystem functions has become a major goal of environmental policy, and concurrently scientific approaches to evaluate its success have been put forward (Henry et al., 2002; Palmer et al., 2005; Woolsey et al., 2007). Motivated to a large extent by flood protection, restoration is achieved, e.g., by widening the main river channel through the removal of embankments and by the setback of flood levees (Rohde et al., 2005; van Stokkom et al., 2005).

Ecosystem services such as provision of plant and animal resources, removal and/or degradation of pollutants, nutrient retention, and carbon (C) storage are tightly linked to organic C dynamics in riparian soils (Hill and Cardaci, 2004; Wilson et al., 2011). Although the need for a fundamental understanding of the factors that drive the processes involved in C cycling in heterogeneous and dynamic systems such as floodplains is recognized, knowledge is still fragmentary (Pacific et al., 2008; Zehetner et al., 2009). There have been an increasing number of publications in recent years on abundance and community structure of microorganisms in riparian soils (e.g., Rinklebe and Langer, 2006; Unger et al., 2009), but still little information is available on bioavailable and mobile soil organic carbon (Bishop et al., 1994; Hill and Cardaci, 2004). The heterogeneity of soil-atmosphere exchange of CO_2 and methane has been addressed previously (e.g. Pulliam 1993; Gulledge and Schimel, 2000; Pacific et al. 2008). However, combined studies addressing both "active" carbon pools and gas exchange as proxies of different aspects of soil functionality have been rare.

In this study we quantify C dynamics in adjacent channelized and widened sections of the Thur River, NE Switzerland. This is the main test site of the interdisciplinary project RECORD (http://www.cces.ethz.ch/projects/nature/Record; Linde et al., 2011; Pasquale et al., 2011; Schneider et al., 2011). The site is composed of three different types of FPZs: (i) frequently flooded, dynamic patches in the restored section, (ii) mature, stable alluvial forests that are flooded once or twice a year in the restored section, and (iii) geomorphologically homogeneous pasture in the channelized section. The objective was to assess spatial heterogeneity (among and within FPZs) and temporal variability of selected soil organic C pools (microbial C and water extractable organic C) and fluxes (soil respiration and methane fluxes) and how they relate to physicochemical soil properties on one hand, and to soil environmental conditions and flood disturbance on the other hand. In particular, we wanted to test the hypotheses that (i) frequent disturbance by flood pulses in the dynamic FPZs affects the C pools and fluxes temporarily and locally and (ii) such effects are an essential precondition to achieve a broad spectrum of conditions and processes supporting a large variety of organisms and, thus biodiversity. Our motivation was to better understand C dynamics in the different types of floodplain FPZs, and, as a consequence, how differences in floodplain structure, in particular between regulated and restored river sections, may affect related ecosystem services such as carbon storage and habitat provision.

2 Test site

The Thur River (catchment area: 1750 km^2) originates in the limestone formation of the Mount Säntis region (2500 m a.s.l.), crosses the Swiss Plateau, and enters the Rhine River at 345 m a.s.l. The river exhibits a flashy flow regime due to the absence of reservoirs and natural lakes. Maximum, mean, and minimum flow rates are 1130, 47, and 2 $m^3 s^{-1}$, respectively (recording period 1904–2005: http://www.hydrodaten.admin.ch/d/2044.htm). Flood events occur mainly during the snowmelt period in spring, and heavy

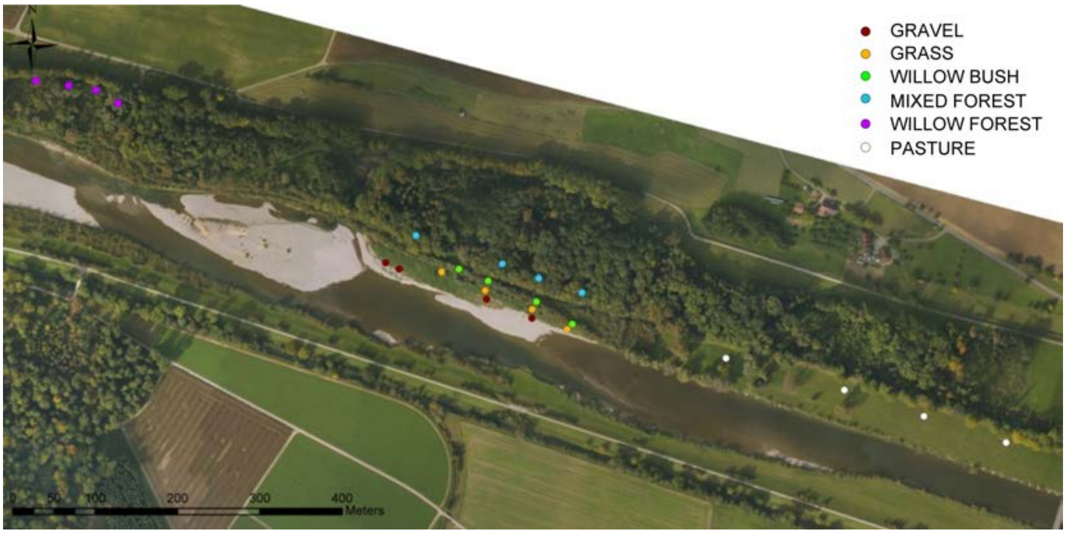

Fig. 1. Aerial view of the Thur River test site near Niederneunforn (North-Eastern Switzerland) showing the different plots for each of the six functional process zones.

rainfall events in summer and autumn. The formerly braided river was channelized in the 1890s to protect the river valley against flooding. In the 1970s, a plan to concurrently improve the flood protection and ameliorate the ecological state of the river corridor was elaborated. Since 1993, several 1–3 km long river sections were widened to allow the formation of alternating gravel bars and to increase hydrological connectivity between the main channel and its riparian zone. One of these sections is the test site. Basic data on the chemical quality of the Thur River and the adjacent alluvial aquifers can be found in Hoehn and Scholtis (2011).

The test site is located in the river corridor at Niederneunforn (Canton Thurgau, 8°77′12″ E; 47°59′10″ N), where a 2 km long section was restored in 2002. The main channel was widened from 50 m to 110 m by removing the foreland in front of the levees. In addition, the levees were lowered in some places to reconnect the old alluvial forest with the river during high floods. The newly exposed banks were partly reinforced by tree trunks, and additionally by planting a strip of willow saplings. In the widened river channel, discharge fluctuations and sedimentation have led to the evolution of a dynamic succession of gravel bars. At the test side, this morphodynamic has been monitored using innovative methodology (Pasquale et al., 2011), and the subsurface structure of the gravel bars was characterized with the help of geophysical methods (Linde et al., 2011; Schneider et al., 2011). The mean annual precipitation at the test site is 908 mm and the average monthly temperature ranges from 0.9 °C in January to 19.0 °C in July (study period; http://gate.meteoswiss.ch/idaweb).

Six FPZs were identified based on vegetation, distance to the river and topography (Fig. 1): five in the restored section and one in an adjacent channelized section upstream. As a result of their topographic position, these FPZs are flooded at different river discharge levels and are exposed to different flooding frequencies and durations (Table 1, Fig. 2). Starting from the riverbed, the first FPZ (GRAVEL) is a mosaic of bare gravel and patchy vegetation covering on average 33 % of the ground. It is frequently inundated and has very little fine soil. The second FPZ (GRASS) is gravel covered by up to 1 m of fine sediments that were trapped mainly by the dominant grass *Phalaris arundinacea*. This plant tolerates both wet and dry conditions characteristic of soils in pulse-flooded riparian systems (Foster and Wetzel, 2005). The third FPZ (WILLOW BUSH) comprises the banks composed of older sediments with shrubby vegetation dominated by planted *Salix viminalis*. Other willow species were also present, and the relatively dense understory was dominated by *Rubus* sp. and various grass species. This strip varies in width from 5 to 10 m, and the study plots were selected in the middle of the bank slope. The last two FPZs, MIXED FOREST and WILLOW FOREST, are forest communities characteristic of floodplains with a deep and shallow average groundwater level, respectively (Schmider et al., 2003). MIXED FOREST is dominated by *Acer pseudoplatanus* and *Fraxinus excelsior* trees and the understory was dominated by *Allium ursinum* and *Ranunculus ficaria* in spring and *Carex pendula* and *Rubus* spp. later in the year. The North side of this FPZ is bordered by a side channel that drains the neighbouring agricultural hill slope. The WILLOW FOREST FPZ at the downstream end of the restored section is dominated by mature *Salix alba* trees. The understory was dominated by *R. ficaria* in spring, and by very dense and monospecific patches of *Urtica dioica* later in the year. The northern border of this part of the forest is formed by an old side channel that has partly silted up, but still drains

Table 1. Hydro-geological characteristics of the six functional process zones of the test site in the Thur River floodplain, Switzerland.

		GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
Maximum elevation within the plots[1]	m a.s.l.	373.0	373.4	373.6	374.9	372.5	374.7
Minimum elevation within the plots[1]	m a.s.l.	371.8	372.5	372.5	373.6	371.6	374.2
Minimum river discharge for flooding lowest lying plot[2]	$m^3 s^{-1}$	75	125	150	650	400	400
Minimum river discharge for flooding highest lying plot[2]	$m^3 s^{-1}$	180	250	270	> 800	400	400
Flooding frequency[3]	times $year^{-1}$	> 10	> 10	4–6	1–2	1–2[4]	1–2
Flooding duration per event[3]	days	< 1 to 14	< 1 to 14	≤ 1	< 1	< 1[4]	< 1

[1] As measured in May 2010.

[2] Estimated from inundation maps produced by digital terrain modeling based on river cross section measurements.

[3] Approximated using the river discharge data for the years 2007 to 2009 and the minimum river discharge for flooding half of the plots within an FPZ.

[4] In WILLOW FOREST more and longer inundation events can occur due to ponding of precipitation or delayed drainage.

the hill slope and collects back flow water from River Thur. The PASTURE FPZ lies in the channelized section and is used by farmers for grazing and grass fodder production. The plant community was typical of managed grasslands and dominated by grass species (mainly *Elymus repens*, *Dactylis glomerata*, and *Arrhenatherum elatius*) and forbs such as *Taraxacum officinale* and *Trifolium repens*.

In this study, we have considered the first three FPZs in the restored section as "dynamic" FPZs, and the two forest FPZs as "stable" FPZs. In each FPZ, four plots of eight-meter diameter were selected. The upstream half-circle was used for vegetation mapping and gas sampling while the downstream half-circle was used for destructive soil sampling.

3 Methods

3.1 Vegetation

In each plot, all vascular plant species were recorded, and cover was estimated using Braun-Blanquet codes (Braun-Blanquet, 1964). Observations were repeated six times during the 2008 growing season and species richness was calculated from the combined data set.

3.2 Soil sampling

Topsoil sampling was carried out in April and October 2008, and in January, April and August 2009. The first sampling served to obtain basic background information on physico-chemical soil properties, while the other four samplings were used for detailed measurements of C pools and fluxes. In each plot, three cores (6.5 cm diameter × 10 cm depth) were pooled. In GRAVEL plots, soil was collected from pits. One half of the field moist soil was sieved (2 mm) and stored at 4 °C while the other half was dried (40 °C, 48 h) and then sieved at 2 mm. In May 2008, two 1m long soil cores were taken with a drill corer from two plots of each FPZ except GRAVEL where coarse gravel prevented the use of the equipment. Each core was split into 20 cm long segments, and the samples were dried and sieved as described before.

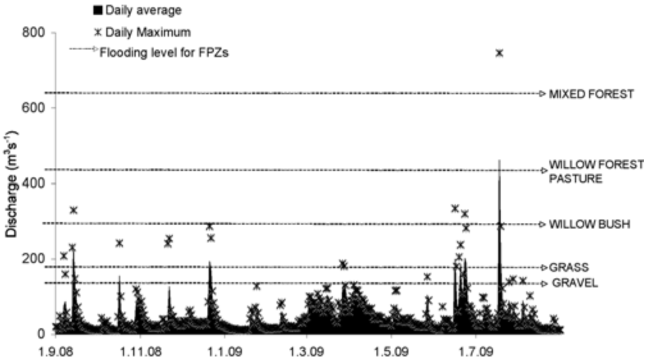

Fig. 2. Daily average and maximum discharge of the Thur River at the test site. Minimum discharge required for inundation is different for each functional process zone (FPZ) and the flooding level shown here is the average elevation of the four plots for each FPZ.

3.3 Basic soil properties

Soil texture of dried samples was measured using the pipette method (Gee and Bauder, 1986) after removing organic matter with hydrogen peroxide and dispersing with sodium hexametaphosphate. Grain size classes were defined as clay ($< 2\,\mu m$), silt (2–63 µm) and sand (63 µm–2 mm). Soil pH was measured in a 1:2 slurry of dried soil in 0.01 M calcium chloride after 30 min equilibration. Total N and organic and inorganic C contents of finely ground, dried soils were determined as described by Walthert et al. (2010). For Olsen P as a proxy of available P, dried soil was extracted for 30 min at 25 °C with 0.5 M sodium hydrogen carbonate at pH 8.5 with a soil to extractant ratio of 1:20. The extracts were filtered through Schleicher and Schuell 0790½ and the extracted phosphate measured colorimetrically using the molybdenum blue method (Kuo, 1996).

3.4 Soil environmental conditions

Soil temperature (T) at 5 cm depth was measured in the centre of each plot during the entire observation period (30 min resolution; TidBit v2 temperature loggers, onset, Bourne, MA, USA). The temperatures recorded at the time of the soil samplings were used in this study. Gravimetric Water Content (WC) was determined as weight loss upon drying 20 g of fresh soil at 105 °C for 24 h. The elevation of the plots was measured in May 2010 by triangulation. The minimum river discharge required for flooding a plot was estimated from inundation maps for different river discharge levels as produced by a 2-D hydrodynamic model (details see Pasquale et al., 2011). The estimate of days after last inundation (LI) was based on the minimum discharge value for a given plot and the date at which discharge fell below this threshold.

3.5 Carbon pools

Water extractable organic carbon (WEOC) was extracted from dried soils with 10 mM calcium chloride at a soil:extractant ratio of 1:2 for 10 min on an end-over-end shaker (Embacher et al., 2007). The soil slurries were then centrifuged for 10 min at 1335 g and filtered through a 0.45 µm membrane filter. The filtered extracts were measured for non-purgeable organic C (NPOC) using a TOC analyzer (Formacs HT, Skalar Analytical, Breda, The Netherlands). Water extractable organic matter of soils, measured as WEOC, is an operationally defined proxy of dissolved organic matter in the soil solution, playing important roles as substrate of microorganisms and as transport agent (Embacher et al., 2007). Although WEOC also represents part of the microbial biomass when extracted from dried soils as in the present study (Embacher et al., 2007), we consider this pool mainly as proxy of available substrate.

Microbial biomass C (MC) was determined by the chloroform fumigation extraction method (Beck et al., 1997). Fresh soil samples corresponding to 10 g dry mass were placed in a desiccator containing chloroform. The desiccator was evacuated and left in the dark for 24 h. These fumigated soil samples and another set of fresh soil samples were extracted for one hour with 0.5 M potassium sulphate at a 1:5 soil to extractant ratio. The extracts were filtered (0.45-µm) and frozen. The NPOC in these samples was measured using a TOC analyzer (TOC-V CPH/CPN, Shimadzu, Kyoto, Japan). Microbial C was calculated as

$$\mathrm{MC} = \frac{(\mathrm{C}_{\mathrm{fumigated}} - \mathrm{C}_{\mathrm{unfumigated}})}{k_{\mathrm{EC}}} \tag{1}$$

where $\mathrm{C}_{\mathrm{fumigated}}$ and $\mathrm{C}_{\mathrm{unfumigated}}$ are the NPOC contents of chloroform-fumigated and unfumigated samples, and $k_{\mathrm{EC}} = 0.45$ corrects for extraction efficiency (Beck et al., 1997).

3.6 Carbon fluxes

For soil respiration (SR) and methane flux (MF) measurements, PVC rings with 30 cm diameter and 30 cm height (20 cm below and 10 cm above surface) were installed in each plot. Immediately before sampling, vegetation within the rings was clipped and the chamber closed with an airtight lid. Headspace air samples were collected after 5, 25 and 45 min, injected into pre-evacuated exetainers, and analyzed for CH_4 and CO_2 using a gas chromatograph with a flame ionization detector (Agilent 6890, Santa Clara, USA). Soil-atmosphere CH_4 and CO_2 exchange were calculated by linear regression of concentration against sampling time. Temperature dependence of SR was modeled for each FPZ using an exponential equation (Buchmann, 2000)

$$y = a \cdot e^{(b \cdot T)} \tag{2}$$

where a and b are regression coefficients, and T is the temperature at the time of gas sampling. Q_{10} values were calculated as

$$Q_{10} = e^{(10 \cdot b)} \tag{3}$$

Soil respiration normalised to a reference temperature of 10 °C (SR_T10) was calculated according to Doering et al. (2011) as

$$\mathrm{SR\_T10} = \mathrm{SR} \cdot e^{(b(10-T))} \tag{4}$$

Soil respiration is an indicator of the actual biological activity at the sampling site including both microbial and root respiration. Positive methane flux indicates net methane production while negative flux indicates net methane consumption in the soil.

3.7 Statistical analyses

Differences in the soil physicochemical properties among the sites were tested using one-way analysis of variance (ANOVA, SPSS 17, SPSS Inc.). Interactive effects of time and FPZ were tested by one-way repeated measures ANOVA. Post hoc tests were carried out using Tukey HSD if homogeneity of variance could be assumed or else using Games Howell (Field, 2005). Principal component analysis (PCA) was carried out for soil physicochemical properties measured in the soil profile samples. Redundancy analyses (RDA) were carried out for C pools and fluxes as multivariate response to soil properties and environmental conditions. The RDA triplot was projected using scaling method 2 (Kindt and Coe, 2005). The program R (R Development Core Team, 2010) with package vegan (Oksanen et al., 2010) was used for PCA and RDA.

Table 2. Mean ± standard deviation of vegetation characteristics and physicochemical soil properties in the six functional process zones ($n = 4$) of the test site in the Thur River floodplain, Switzerland. Soil properties are for the top 10 cm of soil. Values with different superscript letters in the same row are significantly different ($P < 0.05$; Tukey post-hoc test).

	Units	GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
Species richness		55.0 ± 13.6^{bc}	41.5 ± 11.2^{c}	79.8 ± 8.8^{a}	50.8 ± 4.5^{bc}	41.5 ± 3.1^{c}	67.7 ± 3.5^{ab}
pH		7.6 ± 0.1^{a}	7.4 ± 0.1^{a}	7.5 ± 0.0^{a}	7.5 ± 0.0^{a}	7.4 ± 0.0^{a}	7.5 ± 0.0^{a}
Sand	$\mathrm{g\,kg^{-1}}$	806 ± 52^{a}	660 ± 17^{abc}	442 ± 90^{bc}	378 ± 57^{c}	245 ± 40^{c}	651 ± 69^{ab}
Clay	$\mathrm{g\,kg^{-1}}$	53 ± 13^{d}	83 ± 36^{bcd}	117 ± 18^{abc}	148 ± 18^{ab}	177 ± 24^{a}	78 ± 16^{cd}
Inorganic C	$\mathrm{g\,CaCO_3\,kg^{-1}}$	355 ± 25^{b}	385 ± 18^{ab}	408 ± 5^{a}	390 ± 6^{a}	390 ± 3^{a}	382 ± 7^{ab}
Organic C	$\mathrm{g\,kg^{-1}}$	10.1 ± 3.7^{c}	16.3 ± 5.8^{bc}	17.1 ± 3.2^{abc}	21.4 ± 3.6^{ab}	24.8 ± 1.5^{a}	12.9 ± 2.9^{bc}
Total N	$\mathrm{g\,kg^{-1}}$	0.7 ± 0.2^{c}	1.0 ± 0.4^{bc}	1.1 ± 0.3^{bc}	1.6 ± 0.3^{ab}	1.8 ± 0.1^{a}	0.9 ± 0.2^{c}
C:N	$\mathrm{g\,g^{-1}}$	15.2 ± 0.5^{ab}	16.2 ± 1.6^{a}	15.2 ± 0.7^{ab}	13.4 ± 0.6^{b}	14.0 ± 0.2^{b}	14.0 ± 0.4^{b}
Available P	$\mathrm{mg\,kg^{-1}}$	24.6 ± 11.1^{ab}	35.9 ± 10.1^{a}	16.7 ± 5.5^{b}	14.2 ± 4.5^{b}	22.3 ± 7.6^{ab}	8.3 ± 4.5^{b}

4 Results

4.1 Vegetation

Mean plant species richness was lowest in GRASS and WILLOW FOREST, and highest in WILLOW BUSH (Table 2). Spatial variability was higher in GRAVEL and GRASS than in the other FPZs (Table 3). A principal component analysis of plant species composition and cover revealed that the vegetation in PASTURE and in both forested FPZs was rather similar, while it exhibited completely different characteristics in the three dynamic FPZs (data not shown).

4.2 Basic soil properties

All soils were rich in carbonates and, accordingly, had a pH of about 7.5 (Table 2). In the restored section, soils became more finely textured along a gradient from GRAVEL to WILLOW FOREST. Total organic carbon (TOC) and total nitrogen (TN) contents increased along the same gradient, while the C/N was around 15 in all FPZs. Available P was significantly higher in GRASS than in WILLOW BUSH and MIXED FOREST. Soil properties of PASTURE were similar to GRASS except for a significantly lower available P content. Spatial variability of texture and TOC content were highest in GRAVEL and GRASS, and lowest in the two forest FPZs (Table 3).

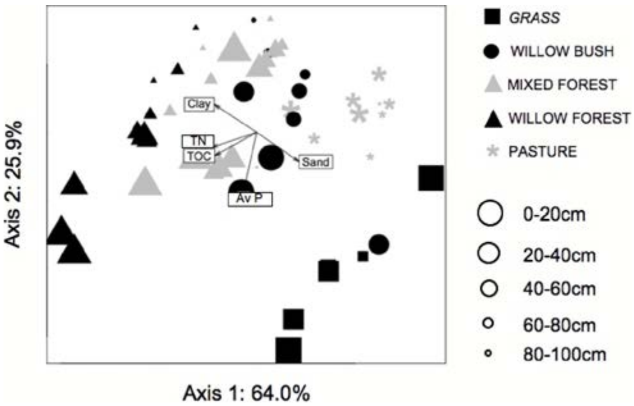

Fig. 3. Five functional process zones at the test site in the Thur River floodplain, Switzerland, with two replicates each represented on the two first axes of a PCA performed on soil physicochemical properties (total organic carbon TOC, total nitrogen TN, available phosphorus Av P, sand and clay content) measured in the soil profiles. The decreasing size of the symbols represents increasing soil depth.

Soil texture did not vary much with depth in any of the FPZs (data not shown). TOC and TN contents were also homogenously distributed within the soil profiles except for WILLOW FOREST. There, TOC and TN decreased with depth to $15\,\mathrm{g\,C\,kg^{-1}}$ and $1.1\,\mathrm{g\,N\,kg^{-1}}$ respectively. Available P decreased gradually with depth to $7\,\mathrm{mg\,kg^{-1}}$ in WILLOW FOREST, and to about $5\,\mathrm{mg\,kg^{-1}}$ in MIXED FOREST and WILLOW BUSH. In GRASS available P did not vary with depth and in PASTURE it first decreased to less than $5\,\mathrm{mg\,kg^{-1}}$ at 20–40 cm depth and then increased to $12\,\mathrm{mg\,kg^{-1}}$ at 80–100 cm depth. The PCA (Fig. 3) showed soil texture as the main factor separating the different FPZs, and demonstrated a generally larger lateral than vertical variation of the soil properties. It also showed that PASTURE soils were relatively homogeneous and overall most similar to the soil in WILLOW BUSH.

According to the world reference base for soil resources (IUSS Working Group WRB, 2006) the soils in GRASS, WILLOW BUSH, MIXED FOREST, and PASTURE can be classified as haplic Fluvisols (calcaric, humic) and those in WILLOW FOREST as haplic or gleyic Fluvisols (calcaric, humic, siltic).

Table 3. Coefficients of variation (CV) for species richness and soil properties (clay content Clay, total organic carbon TOC) within different functional process zones (FPZs) of the test site in the Thur River floodplain, Switzerland ($n = 4$); mean CV for soil environmental conditions (temperature T, gravimetric water content WC), carbon pools (water extractable organic carbon WEOC, microbial carbon MC) and soil respiration (SR as measured, SR_T10 normalised to reference T of 10 °C) within different FPZs ($n = 4$) at the different sampling times ($n = 4$).

	GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
Species richness	0.25	0.27	0.11	0.09	0.07	0.05
Clay	0.23	0.43	0.16	0.12	0.14	0.20
TOC	0.37	0.35	0.19	0.17	0.06	0.22
WC	0.36	0.20	0.11	0.09	0.08	0.08
T	0.005	0.004	0.002	0.001	0.002	0.001
WEOC	0.33	0.38	0.19	0.17	0.22	0.18
MC	0.41	0.42	0.31	0.24	0.31	0.16
SR	0.50	0.42	0.49	0.17	0.30	0.37
SR_T10	0.49	0.47	0.49	0.17	0.33	0.38

4.3 Soil environmental conditions

Temperature measured in GRAVEL was significantly different from all other FPZs at all seasons (Table 4). At each sampling date, either the lowest or highest temperatures were measured there, including the extremes (−0.7 °C, and 20.2 °C). Overall, there was no significant difference in T among the FPZs, but in August all non-forested FPZs exhibited distinctly higher temperatures than the forested FPZs. WILLOW FOREST and GRAVEL represented the wettest and driest conditions, respectively. The spatial variability of soil moisture was highest in GRAVEL and GRASS (Table 3). Particularly high WCs were measured in August sampling, which was carried out two weeks after a major flood (see LI in Table 4), and in January when the soils were covered by snow and partially frozen.

4.4 Carbon pools

On average, the WEOC contents increased from GRAVEL to WILLOW FOREST, and PASTURE exhibited low WEOC contents (Table 4). WEOC was significantly higher ($P < 0.05$) in August, and lower in April, compared to other samplings. Spatial variability of WEOC was largest in GRAVEL and GRASS (Table 3), with particularly high variability in GRASS in April and August.

Microbial C was higher in WILLOW FOREST than in other FPZs (Table 4). In October, MC contents were significantly lower than at the other samplings ($P < 0.05$) and highly variable. With the exception of PASTURE, spatial variability of MC was large (Table 3).

4.5 Carbon fluxes

Soil respiration (SR and SR_T10) was lowest in GRAVEL and highest in GRASS and WILLOW BUSH at most of the samplings, but differences were statistically not significant (Table 4). Within-patch variability of SR was generally high in all dynamic FPZs (Table 3) with hot spots in GRASS in April and August and in WILLOW BUSH in October and August. While SR values were lowest in January and highest in August, SR_T10 values varied only little with time. The Q_{10} value was highest for GRAVEL, while it was similar for all other FPZs (Table 5).

All FPZs took up methane except for August. Then uptake was observed only for WILLOW BUSH and MIXED FOREST, while the other FPZs emitted methane into the atmosphere. At all samplings, plots in GRAVEL showed very low uptake or even low emissions, while MIXED FOREST exhibited the highest uptake rates of all FPZs.

4.6 Carbon pools and fluxes as multivariate proxy of soil C dynamics

Carbon dynamics are presented as multivariate response comprising C pools (WEOC, MC) and fluxes (SR MF), explained by soil properties and environmental conditions (LI, T, WC, TOC, clay). Data were clearly distributed according to sampling date (Fig. 4). The model explained 38.0 % (adjusted R^2) of the variance of the response dataset and the two first canonical axes were significant ($P = 0.001$, 1000 permutations). Overall, WC and T explained the main gradient of C pools and fluxes along axis 1, which separates samples of August from all others. Soil respiration was positively correlated with T and negatively correlated with the number of days since the last inundation. WEOC correlated mainly with WC, whereas MC was strongly linked with clay and TOC content.

Table 4. Mean ± standard deviation of soil environmental conditions (days since last inundation LI, temperature T, gravimetric water content WC), carbon pools (water extractable organic carbon WEOC and microbial carbon MC), and fluxes (soil respiration SR as measured, SR_T10 normalised to reference T of 10 °C, and methane flux MF) in the six FPZs ($n = 4$) of the test site in the Thur River floodplain, Switzerland. Samplings were repeated four times from autumn 2008 to summer 2009. Also shown are results of repeated measures ANOVA over all samplings; different lower case letters in the same row indicate significant differences ($P < 0.05$; Tukey or Games-Howell post-hoc test).

			GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
October 2008	LI	days	21	21	21	49	49	49
	T	°C	16.0 ± 1.9	14.5 ± 2.9	13.7 ± 0.4	13.4 ± 0.3	13.0 ± 0.6	13.5 ± 0.2
	WC	g kg^{-1}	171 ± 48	268 ± 37	220 ± 34	251 ± 19	302 ± 17	210 ± 11
	WEOC	mg kg^{-1}	127 ± 37	141 ±24	82 ± 15	160 ± 27	164 ± 37	80 ± 18
	MC	mg kg^{-1}	132 ± 92	168 ± 131	158 ± 119	132 ± 100	227 ± 161	73 ± 12
	SR	mmol m^{-2} day^{-1}	43 ± 22	327 ± 39	322 ± 117	194 ± 22	214 ± 47	228 ± 86
	SR_T10	mmol m^{-2} day^{-1}	17 ± 3	224 ± 24	203 ± 74	144 ± 16	150 ± 26	144 ± 55
	MF	µmol m^{-2} day^{-1}	−2 ± 1	−15 ± 3	−25 ± 9	−58 ± 11	−22 ± 9	−6 ± 6
January 2009	LI	days	14	14	14	140	140	140
	T	°C	−0.1 ± 0.4	0.5 ± 0.3	0.3 ± 0.4	0.0 ± 0.2	0.2 ± 0.3	0.5 ± 0.1
	WC	g kg^{-1}	325 ± 57	296 ± 50	255 ± 33	257 ± 26	347 ± 35	252 ± 29
	WEOC	mg kg^{-1}	85 ± 29	143 ± 22	123 ± 19	155 ± 38	147 ± 50	116 ± 11
	MC	mg kg^{-1}	208 ± 99	178 ± 71	297 ± 56	231 ± 42	471 ± 58	331 ± 49
	SR	mmol m^{-2} day^{-1}	8 ± 5	50 ± 28	58 ± 37	41 ± 9	55 ± 36	37 ± 14
	SR_T10	mmol m^{-2} day^{-1}	52 ± 34	172 ± 98	251 ± 169	128 ± 30	170 ± 111	120 ± 44
	MF	µmol m^{-2} day^{-1}	−1 ± 3	−6 ± 7	−18 ± 13	−35 ± 19	−17 ± 9	−6 ± 5
April 2009	LI	days	5	21	112	240	240	240
	T	°C	15.2 ± 2.8	11.4 ± 0.7	11.0 ± 0.7	10.3 ± 0.5	11.7 ± 0.5	10.7 ± 0.8
	WC	g kg^{-1}	169 ± 99	204 ± 43	248 ± 7	219 ± 26	276 ± 23	152 ± 13
	WEOC	mg kg^{-1}	84 ± 28	96 ± 67	117 ± 20	98 ± 16	139 ± 15	94 ± 28
	MC	mg kg^{-1}	148 ± 30	135 ± 49	210 ± 28	223 ± 29	445 ± 72	208 ± 15
	SR	mmol m^{-2} day^{-1}	91 ± 40	304 ± 143	134 ± 47	130 ± 10	178 ± 25	139 ± 43
	SR_T10	mmol m^{-2} day^{-1}	72 ± 46	303 ± 179	147 ± 49	135 ± 8	144 ± 42	118 ± 46
	MF	µmol m^{-2} day^{-1}	7 ± 23	−9 ± 2	−15 ± 5	−55 ± 5	−21 ± 5	−18 ± 3
August 2009	LI	days	2	7	14	14	14	14
	T	°C	19.3 ± 1	18.4 ± 0.8	16.6 ± 0.2	16.3 ± 0.1	16.6 ± 0.6	18.8 ± 0.2
	WC	g kg^{-1}	181 ± 70	388 ± 117	348 ± 41	365 ± 30	493 ± 44	276 ± 15
	WEOC	mg kg^{-1}	155 ± 60	324 ± 168	418 ± 103	480 ± 44	608 ± 131	297 ± 34
	MC	mg kg^{-1}	334 ± 90	351 ± 48	306 ± 46	361 ± 36	263 ± 66	190 ± 47
	SR	mmol m^{-2} day^{-1}	283 ± 127	432 ± 237	654 ± 390	260 ± 67	315 ± 48	345 ± 145
	SR_T10	mmol m^{-2} day^{-1}	50 ± 18	152 ± 90	246 ± 148	124 ± 31	147 ± 29	115 ± 46
	MF	µmol m^{-2} day^{-1}	8 ± 8	17 ± 43	−23 ± 10	−27 ± 9	52 ± 79	151 ± 236
ANOVA results	T		a	b	b	b	b	b
	WC		c	ab	bc	b	a	bc
	WEOC		c	bc	bc	ab	a	bc
	MC		b	b	b	b	a	b
	SR		b	a	a	ab	a	ab
	SR_T10		a	a	a	a	a	a
	MF		b	b	b	a	b	b

Table 5. Modeled relationship between soil respiration (y, mmol CO_2 m^{-2} day^{-1}) and soil temperature (T, °C) in different FPZs of the test site in the Thur River floodplain, Switzerland.

FPZ	$y = a\,e^{(bT)}$	SE_a	SE_b	Q_{10}	n	F	R^2	P
GRAVEL	$y = 6.85\ e^{(0.179T)}$	0.02	2.1	6.0	13	54.7	0.83	<0.0001
GRASS	$y = 51.09\ e^{(0.128T)}$	0.02	15.1	3.6	16	28.6	0.67	<0.0001
WILLOW BUSH	$y = 43.02\ e^{(0.148T)}$	0.02	9.86	4.4	16	55.8	0.80	<0.0001
MIXED FOREST	$y = 40.84\ e^{(0.117T)}$	0.01	3.53	3.2	16	235.7	0.94	<0.0001
WILLOW FOREST	$y = 44.83\ e^{(0.116T)}$	0.02	8.46	3.2	16	56.1	0.80	<0.0001
PASTURE	$y = 33.96\ e^{(0.124T)}$	0.01	6.18	3.4	16	77.9	0.85	<0.0001

a and b: regression coefficients.
SE_a and SE_b standard errors of a and b.
Q_{10}: relative increase in soil respiration upon a T increase of 10 °C.
n: number of individual measurements. F, R, P: F-value, coefficient of determination, and level of significance of the regression, respectively.

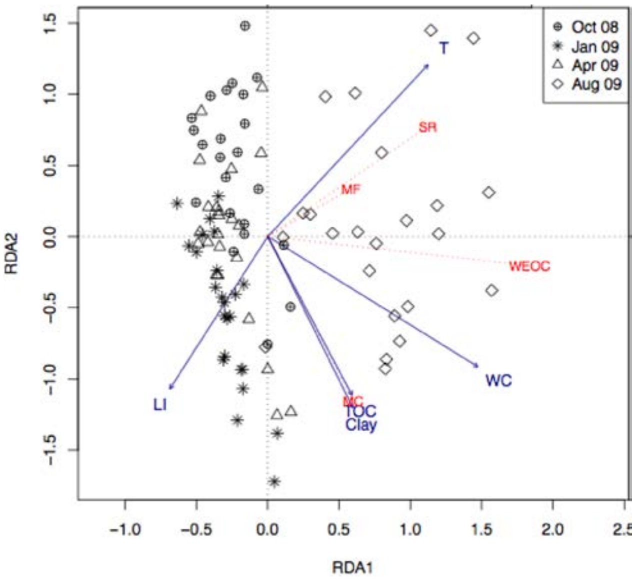

Fig. 4. RDA triplot for carbon pools and fluxes in the six functional process zones at the test site in the Thur River floodplain, Switzerland (water extractable organic carbon WEOC, microbial carbon MC, soil respiration SR, methane flux MF) as multivariate response variables (red font), constrained by soil properties and environmental conditions (days since last inundation LI, soil temperature T, gravimetric water content WC, clay content Clay and total organic carbon TOC) as explanatory variables (blue font). Four soil sampling dates are represented with different symbols. Axis 1 explains 35.4 % and axis 2 11.3 % of the variance. Data were projected using scaling method 2.

5 Discussion

Our data allow us (i) to relate differences between soil C dynamics in different functional process zones (FPZs) of the Thur River floodplain to differences in physicochemical soil properties on one hand and to effects of flood disturbance as driving force of a geomorphically dynamic system on the other hand, and (ii) to evaluate the relative magnitude of temporal variability as well as among and within-FPZ spatial heterogeneity of C dynamics. Based on this, conclusions about the effects of river restoration on C dynamics can be drawn.

5.1 Soil properties, environmental conditions and degree of disturbance in different FPZs

With their high carbonate content the soils at our test site are representative of young, weakly developed alluvial soils (Guenat et al. 1999). The mostly homogeneous distribution of soil properties with depth and the strong correlation between TOC and TN contents and soil texture indicates soil formation by fluvial sedimentation of homogeneous source material (Cabezas and Comin, 2010). Further homogenization can be attributed to bioturbation by earthworms. This was especially clear in the forested FPZs where earthworm biomass was highest (Fournier et al., unpublished data), most likely because of the lower frequency of inundation and fluvial dynamics (Guenat et al. 1999). On the other hand, the depth gradient of TOC and TN in WILLOW FOREST, representing an advanced stable FPZ, indicates in situ pedogenesis. Soil texture, the main factor differentiating the FPZs according to the PCA (Fig. 3), reflects the average sedimentation conditions with texture becoming finer with decreasing stream energy (Nanson and Croke, 1992). The TOC contents are within the range found in floodplain sediments of other large rivers in Europe (Graf et al., 2007; Pies et al., 2007). The low C/N ratios and high available P contents (Morel et al., 1992) indicate high nutrient availability in all FPZs, which is characteristic of many river floodplains (Tockner and Stanford, 2002). The particularly high P availability in GRASS can be explained by high sedimentation rates (Steiger and Gurnell, 2003). Low C/N values also indicate favourable conditions for organic matter degradation, which is confirmed by the observation of fast mineralisation of leaf litter in most FPZs and by the humus morphology (carbonate-rich Mull; data not shown).

The high variability and extreme values of T measured in GRAVEL are consistent with the general finding of bare gravel bars as extreme environments. The absence of stable vegetation cover to buffer temperature variations accompanied by high thermal conductivity due to low water contents explain this harshness (Tonolla et al., 2010). The differences in WC among FPZs can be explained mainly by a combined effect of precipitation, inundation frequency and water retention capacity of the soils. In particular, the maximum WC in WILLOW FOREST can be attributed largely to the finely textured soil that retains water efficiently. The additional effects of shading and water uptake by the plants on WC via evapotranspiration are not obvious from the data.

Considering the days after the last inundation (LI), the samplings carried out over the course of this study represent conditions that are typical for this site (Table 1, Fig. 2), i.e. inundation of the low-lying dynamic FPZs on a regular basis, and flooding of the entire floodplain once or twice a year. The high spatial heterogeneity of physicochemical soil properties, environmental conditions, and plant species richness in GRAVEL and GRASS (Table 3) reflects the patchy and dynamic geomorphology due to the frequent disturbance by flooding, while the low variability in the forested FPZs can be related to stable conditions leading to homogenization of properties, conditions and communities. The low variability in PASTURE can in addition be explained by its particularly homogeneous geomorphology strongly reducing erosion and sediment deposition. In agreement with the hypothesis of maximum biodiversity at intermediate levels of disturbance or connectivity (Ward et al., 1999), the pattern of plant species richness in the restored section FPZs reflects the degree of disturbance. This hypothesis predicts highest species richness in habitats characterised by intermediate inundation frequency (i.e. WILLOW BUSH), and lower diversity under high or low degrees of disturbance (i.e., GRASS and the two forested FPZs, respectively) where ruderal or competitive species dominate, respectively (in particular *Phalaris arundinacea* as flood tolerant species in GRASS, Foster and Wetzel, 2005). Considering the low inundation frequency, the relatively high species richness observed in PASTURE can be explained mainly by the regular harvesting, which reduces the effect of competition.

5.2 Carbon pools and fluxes as related to soil properties, environmental conditions and disturbance in different FPZs

The strong correlation between MC and TOC suggests C-limitation of microbes, which is especially common in nutrient rich soils (Wardle, 1992). The pattern of WEOC suggests an influence of both TOC and WC. The correlation with TOC indicates similar solubility of soil organic matter across FPZs. The influence of WC is mainly a flooding effect as demonstrated by the highest WEOC contents in August after the major flood. On one hand, this pattern suggests temporarily increased soluble C pools due to input of non-structured fine soil and fresh litter along with the decreased aeration in the waterlogged soils. During soil saturation, dissolved organic matter production is expected to increase (Kalbitz et al., 2000). On the other hand, flooding has also been shown to increase the rates of enzymatic soil organic matter degradation (Wilson et al., 2011). The flood-related increase in available C is also reflected by increased MC, except in WILLOW FOREST where the almost completely saturated soil suggests longer unfavourable conditions for microbial growth (Rinklebe and Langer, 2006; Unger et al., 2009).

The measured range of SR, which includes root and microbial respiration, was similar to results from other floodplains (Pulliam, 1993; Gulledge and Schimel, 2000; Pacific et al., 2008; Doering et al., 2011). The strong correlation of SR with T has been commonly observed (Lloyd and Taylor, 1994; Buchmann, 2000) and explains the differences between the samplings to a large extent. The temperature dependence in terms of Q_{10} values in most FPZs is similar to riparian and uphill forests (Buchmann, 2000; Doering et al., 2011), while the Q_{10} value of GRAVEL is much higher than in similar systems (Doering et al., 2011). According to Pacific et al. (2008) soil CO_2 efflux is determined both by CO_2 production and diffusive transport in the entire soil, and soil moisture levels observed in our study would support high respiration in all FPZs most of the time. Considering this, the often highest CO_2 efflux in GRASS and WILLOW BUSH can be explained on one hand by the coarse soil texture allowing optimal gas diffusion, on the other hand by the frequent and large input of available organic C during flooding (Doering et al., 2011). In addition, the sediment translocations during high floods may increase the content of available organic C also at greater depths. Together with the high spatial variability in sedimentation, this can explain the hot spots of SR observed in these two FPZs. The low SR in GRAVEL is likely due to the low fine soil content.

Consumption of atmospheric methane is largely determined by CH_4 diffusion in the soil (Dörr et al., 1993), and CH_4 produced in water saturated soil layers can be consumed in upper aerated soil layers (Boon and Lee, 1997). Net CH_4 production can therefore be considered as an indicator of the balance between overall soil aeration and underlying CH_4 production. The observed decrease of net CH_4 production along the elevation gradient from GRAVEL to MIXED FOREST is in line with the aeration increasing with the average thickness of unsaturated soil, and confirms earlier studies showing a strong influence of landscape position on CH_4 consumption (Burke et al., 1999; Gulledge and Schimel, 2000). This interpretation is supported by an increase in earthworm diversity (Fournier et al., unpublished data). In WILLOW FOREST, net CH_4 production was higher than expected at that elevation, which suggests a relatively weak aeration, confirmed by hydromorphic features in upper soil layers (data not shown) and/or high CH_4 production. These observations are both congruent with the maximum WC and finest soil texture found in this FPZ (Dörr et al., 1993). The high net CH_4 production in the relatively high laying PASTURE, characterized by a sandy soil texture, suggests generally high CH_4 production in the water-saturated layers of this FPZ. This can be explained by the relatively long travel time of infiltrating water in the channelized section of the river (Vogt et al., 2010), favouring reducing conditions in deeper soil layers.

In summary, microbial and available C pools are determined mainly by physicochemical soil properties with some additional effects of flooding via WC. By contrast, C fluxes are strongly influenced by flood disturbance, and either T (SR) or geomorphology (net CH_4 production).

5.3 Temporal variability and within-FPZ heterogeneity of soil C pools and fluxes

Carbon pools and fluxes as multivariate proxy of soil C dynamics differed more among sampling dates than among FPZs. This indicates that overall factors related to seasonality and flooding (T, WC, and organic matter input) influence soil C dynamics more than differences in soil physicochemical properties in the test site.

The high spatial heterogeneity of all C pools and fluxes within GRAVEL and GRASS can be related to the variability in both soil properties and environmental conditions caused by frequent flooding disturbance. The high variability of MC in all FPZs of the restored section cannot be explained exclusively by the large-scale variability between replicate plots but might in addition be due to small-scale variability at the soil aggregate level as well as to additional heterogeneity brought by the rooting pattern and related exudation of plants. Similarly, it can be speculated that hot spots of CO_2 and CH_4 emissions in otherwise homogeneous FPZs (WILLOW BUSH, PASTURE) are due to small-scale heterogeneities in substrate availability and water saturation in the subsoil (Ramakrishnan et al., 2000; Sey et al., 2008).

6 Conclusions

This study of organic C dynamics in the Thur River floodplain revealed that in the dynamic FPZs of the restored section characterised by low TOC contents and coarse-textured soils, frequent disturbance by flood pulses temporarily and locally increased SR and the otherwise low base-levels of organic C pools. By contrast, in the stable forested FPZs, the finer texture of the soils was responsible for higher TOC contents and water retention capacity both leading to high base-levels of C pools. Spatial heterogeneity was smaller than the effects of major floods and seasonal T differences on C pools and fluxes. The PASTURE FPZ stood out by (i) low C pools due to coarse-textured soils low in TOC, as in the dynamic FPZs, (ii) spatial heterogeneity, seasonal effects and flood disturbance, similar to the forest FPZs, and (iii) high CH_4 production that can be explained by slow travel times favouring reducing conditions.

Irrespective of the FPZ, the input of non-structured allochthonous soil material and possibly the destruction of local aggregates during flood pulses appear to be the driver for a temporary and, in dynamic FPZs, local increase of microbial activity. The related variability in available carbon or soil respiration cannot be explained by the spatial and temporal heterogeneity of bulk soil properties or the variability of environmental conditions. Our results thus confirm our first hypothesis that spatial and temporal C variability are affected mainly by flood disturbance. However, they also show that the temporal effects are not restricted to dynamic FPZs. The strong increase in plant biodiversity brought about by the recurrent rejuvenation of the habitats seems to support our second hypothesis, that frequent disturbance – defined as temporary and strong changes in environmental conditions and substrate availability- creates a large functional diversity. Our results therefore support recent findings that short-term inundations are important drivers of microbial habitat structure and function in floodplains (Wilson et al., 2011). Further comprehensive studies in similar as well as contrasted sites are required for generalisation of the results. In particular, since soil organic matter turnover differs between acidic and carbonate-containing soils (Walse et al., 1998), studies in sites with carbonate-free fluvial source material would be of great interest.

Based on our results, we recommend that river restoration, in order to achieve maximum recovery of ecosystem functions, should aim at creating near-natural floodplains comprising both dynamic gravel bars and stable alluvial systems. On one hand, this ensures the provision of a large diversity of habitats. On the other hand, the complex interplay of organic matter input and hot spots of both mineralisation and incomplete degradation strongly affects the potential of floodplains to store carbon, an ecosystem service of great current interest (Cierjacks et al., 2010). River widening combined with hydrological reconnection with former floodplains (from the time before channelization) as in the example presented here, is likely to be a successful recipe to achieve this goal, at least for a river characterised by pulse flooding. The Thur River example also shows that doing so on a rather small scale is sufficient to achieve a high heterogeneity of carbon pools and habitats. In cases where, in contrast to the Thur, the river is dammed upstream, this may have to be combined with controlled outflow mimicking the natural discharge regime including a few larger floods.

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Appendix B Species list

Table 1: List of species identified at the Thur River site.

Species	**Taxonomic group**
Abax parallelepipedus	Carabid beetles
Abax parallelus	Carabid beetles
Agonum micans	Carabid beetles
Agonum muelleri	Carabid beetles
Agonum viduum	Carabid beetles
Amara aenea	Carabid beetles
Amara fulva	Carabid beetles
Amara lunicollis	Carabid beetles
Amara montivaga	Carabid beetles
Amara ovata	Carabid beetles
Amara schimperi	Carabid beetles
Amara similata	Carabid beetles
Anchomenus dorsalis	Carabid beetles
Anisodactylus binotatus	Carabid beetles
Asaphidion austriacum	Carabid beetles
Asaphidion flavipes	Carabid beetles
Badister bullatus	Carabid beetles
Badister lacertosus	Carabid beetles
Bembidion biguttatum	Carabid beetles
Bembidion decoratum	Carabid beetles
Bembidion decorum	Carabid beetles
Bembidion dentellum	Carabid beetles
Bembidion femoratum	Carabid beetles
Bembidion lampros	Carabid beetles
Bembidion prasinum	Carabid beetles
Bembidion properans	Carabid beetles
Bembidion ruficorne	Carabid beetles
Bembidion testaceum	Carabid beetles
Bembidion tetracolum	Carabid beetles
Bembidion varicolor	Carabid beetles
Blemus discus	Carabid beetles
Calathus fuscipes	Carabid beetles
Carabus auratus	Carabid beetles
Carabus coriaceus	Carabid beetles
Carabus granulatus	Carabid beetles
Carabus nemoralis	Carabid beetles
Chlaenius nigricornis	Carabid beetles
Clivina collaris	Carabid beetles
Clivina fossor	Carabid beetles

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Species	**Taxonomic group**
Cychrus caraboides	Carabid beetles
Diachromus germanus	Carabid beetles
Elaphrus aureus	Carabid beetles
Haraplus dimidiatus	Carabid beetles
Harpalus affinis	Carabid beetles
Harpalus griseus	Carabid beetles
Harpalus latus	Carabid beetles
Harpalus luteicornis	Carabid beetles
Harpalus rufipes	Carabid beetles
Limodromus assimilis	Carabid beetles
Loricera pilicornis	Carabid beetles
Nebria brevicollis	Carabid beetles
Nebria picicornis	Carabid beetles
Oodes helopioides	Carabid beetles
Panagaeus cruxmajor	Carabid beetles
Paranchus albipes	Carabid beetles
Paraphonus maculicornis	Carabid beetles
Paratachys bistriatus	Carabid beetles
Patrobus atrorufus	Carabid beetles
Poecilus cupreus	Carabid beetles
Poecilus versicolor	Carabid beetles
Pterostichus anthracinus	Carabid beetles
Pterostichus cristatus	Carabid beetles
Pterostichus madidus	Carabid beetles
Pterostichus melanarius	Carabid beetles
Pterostichus niger	Carabid beetles
Pterostichus strenuus	Carabid beetles
Pterostichus vernalis	Carabid beetles
Stomis pumicatus	Carabid beetles
Synuchus vivalis	Carabid beetles
Tachyura quadrisignata	Carabid beetles
Thalassophilus longicornis	Carabid beetles
Trechoblemus micros	Carabid beetles
Trechus quadristriatus	Carabid beetles
Brachydesmus superus	Diplopods
Craspedosoma rawlinsii	Diplopods
Cylindroiulus caeruleocinctus	Diplopods
Julus scandinavius	Diplopods
Melogona voigti	Diplopods
Nemasoma varicorne	Diplopods

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Species	**Taxonomic group**
Ophyiulus pilosus	Diplopods
Propolydesmus testaceus	Diplopods
Tachypodoiulus niger	Diplopods
Allolobophora chlorotica	Earthworms
Allolobophora georgii	Earthworms
Aporrectodea caliginosa nocturna	Earthworms
Aporrectodea caliginosa tuberculata	Earthworms
Aporrectodea caliginosa caliginosa	Earthworms
Aporrectodea giardi	Earthworms
Aporrectodea longa	Earthworms
Aporrectodea rosea	Earthworms
Dendrodrilus rubidus	Earthworms
Eiseniella tetraedra	Earthworms
Lumbricus castaneus	Earthworms
Lumbricus meliboeus	Earthworms
Lumbricus rubellus	Earthworms
Lumbricus terrestris	Earthworms
Octolasion tyrtaeum tyrtaeum	Earthworms
Armadillidium opacum	Isopods
Haplophthalmus mengii	Isopods
Hyloniscus riparius	Isopods
Ligidium hypnorum	Isopods
Oniscus asellus	Isopods
Philoscia muscorum	Isopods
Trachelipus rathkei	Isopods
Trichoniscus pusillus aggr.	Isopods
Acer pseudoplatanus	Plants
Achillea millefolium	Plants
Aegopodium podagraria	Plants
Agrostis stolonifera	Plants
Alchemilla vulgaris aggr.	Plants
Alliaria petiolata	Plants
Allium ursinum	Plants
Alopecurus pratensis	Plants
Amaranthus retroflexus aggr.	Plants
Anagallis arvensis	Plants
Anemone nemorosa	Plants
Angelica sylvestris	Plants
Anthriscus sylvestris	Plants
Arrhenatherum elatius	Plants

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Species	**Taxonomic group**
Arum maculatum	Plants
Barbarea vulgaris	Plants
Bellis perennis	Plants
Brachypodium sylvaticum	Plants
Bromus sterilis	Plants
Caltha palustris	Plants
Calystegia sepium	Plants
Cardamine amara	Plants
Cardamine flexuosa	Plants
Carex brizoides	Plants
Carex pendula	Plants
Carex remota	Plants
Carum carvi	Plants
Circaea lutetiana	Plants
Clematis vitalba	Plants
Cornus sanguinea	Plants
Crataegus laevigata	Plants
Crepis biennis	Plants
Cynosurus cristatus	Plants
Dactylis glomerata	Plants
Deschampsia cespitosa	Plants
Echinochloa crus-galli	Plants
Elymus repens	Plants
Epilobium hirsutum	Plants
Equisetum hyemale	Plants
Equisetum telmateia	Plants
Euonymus europaeus	Plants
Festuca arundinacea	Plants
Festuca pratensis	Plants
Filipendula ulmaria	Plants
Frangula alnus	Plants
Fraxinus excelsior	Plants
Galium album	Plants
Galium aparine	Plants
Galium odoratum	Plants
Geum urbanum	Plants
Glechoma hederacea	Plants
Heracleum sphondylium	Plants
Holcus lanatus	Plants
Humulus lupulus	Plants

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Species	**Taxonomic group**
Hypericum tetrapterum	Plants
Impatiens glandulifera	Plants
Lamium galeobdolon	Plants
Lamium purpureum	Plants
Lathyrus sylvestris	Plants
Leucanthemum vulgare aggr.	Plants
Lolium multiflorum	Plants
Lotus corniculatus	Plants
Lycopersicon esculentum	Plants
Lythrum salicaria	Plants
Nasturtium officinale	Plants
Panicum capillare	Plants
Petasites hybridus	Plants
Phalaris arundinacea	Plants
Phleum pratense	Plants
Phragmites australis	Plants
Plantago lanceolata	Plants
Plantago major	Plants
Pleurospermum austriacum	Plants
Poa annua	Plants
Poa trivialis	Plants
Polygonum aviculare	Plants
Polygonum persicaria	Plants
Populus nigra	Plants
Potentilla anserina	Plants
Potentilla reptans	Plants
Prunella vulgaris	Plants
Prunus padus	Plants
Quercus robur	Plants
Ranunculus acris	Plants
Ranunculus ficaria	Plants
Rorippa sylvestris	Plants
Rubus fruticosus aggr.	Plants
Rumex obtusifolius	Plants
Salix alba	Plants
Salix purpurea	Plants
Salix viminalis	Plants
Sanguisorba officinalis	Plants
Saponaria officinalis	Plants
Scrophularia nodosa	Plants

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Species	**Taxonomic group**
Scrophularia umbrosa	Plants
Senecio vulgaris	Plants
Solanum dulcamara	Plants
Solidago canadensis	Plants
Sonchus asper	Plants
Stellaria media	Plants
Taraxacum officinale s. l.	Plants
Taraxacum palustre s. l.	Plants
Trifolium campestre	Plants
Trifolium pratense	Plants
Trifolium repens	Plants
Triticum aestivum	Plants
Tussilago farfara	Plants
Urtica dioica	Plants
Veronica arvensis	Plants
Veronica beccabunga	Plants
Veronica filiformis	Plants
Veronica montana	Plants
Veronica serpyllifolia	Plants
Vicia cracca	Plants
Alopecosa cuneata	Spiders
Alopecosa pulverulenta	Spiders
Araeoncus humilis	Spiders
Arctosa leopardus	Spiders
Arctosa maculata	Spiders
Bathyphantes gracilis	Spiders
Batyphantes nigrinus	Spiders
Centromerus albidus	Spiders
Centromerus dilutus	Spiders
Centromerus sylvaticus	Spiders
Ceratinella brevis	Spiders
Cicurina cicur	Spiders
Clubiona germanica	Spiders
Clubiona lutescens	Spiders
Collinsia distincta	Spiders
Dicymbium nigrum	Spiders
Diplocephalus cristatus	Spiders
Diplocephalus latifrons	Spiders
Diplostyla concolor	Spiders
Dismodicus bifrons	Spiders

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Species	**Taxonomic group**
Drassyllus pusillus	Spiders
Erigone atra	Spiders
Erigone dentipalpis	Spiders
Gnathonarium dentatum	Spiders
Gongylidium rufipes	Spiders
Hahnia nava	Spiders
Hahnia pusilla	Spiders
Haplodrassus signifer	Spiders
Hylyphantes graminicola	Spiders
Hypomma cornutum	Spiders
Lepthoroptrum robustum	Spiders
Lessertinella kulczynskii	Spiders
Liocranoeca striata	Spiders
Maso sundevalli	Spiders
Mermessus trilobatus	Spiders
Metellina mengei	Spiders
Metellina segmentata	Spiders
Micaria pulicaria	Spiders
Micrargus subaequalis	Spiders
Microneta viaria	Spiders
Monocephalus fuscipes	Spiders
Oedothorax agrestis	Spiders
Oedothorax apicatus	Spiders
Oedothorax fuscus	Spiders
Oedothorax retusus	Spiders
Ozyptila praticola	Spiders
Pachygnatha clercki	Spiders
Pachygnatha degeeri	Spiders
Pachygnatha listeri	Spiders
Palliduphantes pallidus	Spiders
Pardosa agrestis	Spiders
Pardosa amentata	Spiders
Pardosa hortensis	Spiders
Pardosa palustris	Spiders
Pardosa pullata	Spiders
Pardosa saltans	Spiders
Pelecopsis parallela	Spiders
Phrurolithus festivus	Spiders
Pirata hygrophilus	Spiders
Pirata knorri	Spiders

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Species	**Taxonomic group**
Porrhomma campbelli	Spiders
Porrhomma microphthalmum	Spiders
Robertus lividus	Spiders
Robertus neglectus	Spiders
Singa hamata	Spiders
Tenuiphantes flavipes	Spiders
Tenuiphantes tenuis	Spiders
Tetragnatha montana	Spiders
Theridiosoma gemmosum	Spiders
Trochosa ruricola	Spiders
Trochosa terricola	Spiders
Troxochrus scabriculus	Spiders
Walckenaeria alticeps	Spiders
Walckenaeria atrotibialis	Spiders
Walckenaeria nudipalpis	Spiders
Walckenaeria obtusa	Spiders
Walckenaeria vigilax	Spiders
Xysticus viduus	Spiders
Zelotes latreillei	Spiders
Zodarion italicum	Spiders
Acrotona parvula	Staphylinid beetles
Aleochara brevipennis	Staphylinid beetles
Aleochara curtula	Staphylinid beetles
Aleochara haematoptera	Staphylinid beetles
Aleochara ruficornis	Staphylinid beetles
Aloconota gregaria	Staphylinid beetles
Aloconota insecta	Staphylinid beetles
Aloconota sulcifrons	Staphylinid beetles
Amischa analis	Staphylinid beetles
Amischa forcipata	Staphylinid beetles
Amischa nigrofusca	Staphylinid beetles
Anotylus hamatus	Staphylinid beetles
Anotylus insecatus	Staphylinid beetles
Anotylus rugosus	Staphylinid beetles
Anotylus sculpturatus	Staphylinid beetles
Anotylus sculpturatus/mutator	Staphylinid beetles
Anotylus tetracarinatus	Staphylinid beetles
Atheta aegra	Staphylinid beetles
Atheta amplicollis	Staphylinid beetles
Atheta deformis	Staphylinid beetles

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Species	**Taxonomic group**
Atheta elongatula	Staphylinid beetles
Atheta fungi	Staphylinid beetles
Atheta palustris	Staphylinid beetles
Atheta scotica	Staphylinid beetles
Atheta triangulum	Staphylinid beetles
Bisnius fimetarius	Staphylinid beetles
Bledius cribricollis	Staphylinid beetles
Bledius erraticus	Staphylinid beetles
Bledius longulus	Staphylinid beetles
Callicerus obscurus	Staphylinid beetles
Carpelimus bilineatus	Staphylinid beetles
Carpelimus corticinus	Staphylinid beetles
Carpelimus elongatulus	Staphylinid beetles
Coprophilus striatulus	Staphylinid beetles
Deleaster dichrous	Staphylinid beetles
Dinaraea angustula	Staphylinid beetles
Drusilla canaliculata	Staphylinid beetles
Eusphalerum luteum	Staphylinid beetles
Falagrioma thoracica	Staphylinid beetles
Gabrius appendiculatus	Staphylinid beetles
Gabrius breviventer	Staphylinid beetles
Gabrius nigritulus	Staphylinid beetles
Gnypeta ripicola	Staphylinid beetles
Gyrohypnus angustatus	Staphylinid beetles
Ischnosoma splendidum	Staphylinid beetles
Lathrobium castaneipenne	Staphylinid beetles
Lathrobium fulvipenne	Staphylinid beetles
Lathrobium laevipenne	Staphylinid beetles
Lathrobium pallidipenne	Staphylinid beetles
Lesteva longoelytrata	Staphylinid beetles
Liogluta longiuscula	Staphylinid beetles
Lobrathium multipunctum	Staphylinid beetles
Megarthrus depressus	Staphylinid beetles
Meotica filiformis	Staphylinid beetles
Mycetoporus longulus	Staphylinid beetles
Neobisnius villosulus	Staphylinid beetles
Ochthephilus flexuosus	Staphylinid beetles
Ochthephilus omalinus	Staphylinid beetles
Ocypus brunnipes	Staphylinid beetles
Ocypus olens	Staphylinid beetles

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Species	**Taxonomic group**
Omalium caesum	Staphylinid beetles
Omalium rivulare	Staphylinid beetles
Oxypoda acuminata	Staphylinid beetles
Oxypoda arborea	Staphylinid beetles
Oxypoda brevicornis	Staphylinid beetles
Oxypoda carbonaria	Staphylinid beetles
Oxypoda opaca	Staphylinid beetles
Paederus fuscipes	Staphylinid beetles
Paederus littoralis	Staphylinid beetles
Pella cognata	Staphylinid beetles
Pella limbata	Staphylinid beetles
Philonthus carbonarius	Staphylinid beetles
Philonthus cognatus	Staphylinid beetles
Philonthus coruscus	Staphylinid beetles
Philonthus decorus	Staphylinid beetles
Philonthus laminatus	Staphylinid beetles
Philonthus mannerheimi	Staphylinid beetles
Philonthus rotundicollis	Staphylinid beetles
Philonthus succicola	Staphylinid beetles
Philonthus tenuicornis	Staphylinid beetles
Phyllodrepa melanocephala	Staphylinid beetles
Platystethus arenarius	Staphylinid beetles
Platystethus nitens	Staphylinid beetles
Proteinus brachypterus	Staphylinid beetles
Proteinus ovalis	Staphylinid beetles
Pycnota paradoxa	Staphylinid beetles
Quedius cinctus	Staphylinid beetles
Quedius curtipennis	Staphylinid beetles
Quedius fuliginosus	Staphylinid beetles
Quedius fuliginosus/curtipennis	Staphylinid beetles
Quedius levicollis	Staphylinid beetles
Quedius molochinus	Staphylinid beetles
Quedius semiobscurus	Staphylinid beetles
Rabigus pullus	Staphylinid beetles
Rabigus tenuis	Staphylinid beetles
Rugilus rufipes	Staphylinid beetles
Scopaeus laevigatus	Staphylinid beetles
Staphylinus dimidiaticornis	Staphylinid beetles
Stenus biguttatus	Staphylinid beetles
Stenus bimaculatus	Staphylinid beetles

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Species	**Taxonomic group**
Stenus boops	Staphylinid beetles
Stenus circularis	Staphylinid beetles
Stenus ochropus	Staphylinid beetles
Tachinus corticinus	Staphylinid beetles
Tachinus rufipes	Staphylinid beetles
Tachyporus abdominalis	Staphylinid beetles
Tachyporus formosus	Staphylinid beetles
Tachyporus hypnorum	Staphylinid beetles
Tachyporus nitidulus	Staphylinid beetles
Tachyporus obtusus	Staphylinid beetles
Tachyusa constricta	Staphylinid beetles
Tetralaucopora longitarsis	Staphylinid beetles
Tetralaucopora rubicunda	Staphylinid beetles
Thinodromus arcuatus	Staphylinid beetles
Thinodromus dilatatus	Staphylinid beetles
Xantholinus elegans	Staphylinid beetles
Xantholinus laevigatus	Staphylinid beetles
Xantholinus linearis	Staphylinid beetles
Xantholinus longiventris	Staphylinid beetles
Xantholinus tricolor	Staphylinid beetles
Arcella discoides	Testate Amoebae
Arcella rotundata stenostoma	Testate Amoebae
Arcella vulgaris	Testate Amoebae
Assulina muscorum	Testate Amoebae
Bulinularia indica	Testate Amoebae
Centropyxis aculeata	Testate Amoebae
Centropyxis aculeata oblonga	Testate Amoebae
Centropyxis aerophila	Testate Amoebae
Centropyxis aerophila sphagnicola	Testate Amoebae
Centropyxis cassis	Testate Amoebae
Centropyxis constricta	Testate Amoebae
Centropyxis ecornis	Testate Amoebae
Centropyxis orbicularis	Testate Amoebae
Cyclopyxis eurystoma	Testate Amoebae
Difflugia lineare	Testate Amoebae
Difflugia microstoma	Testate Amoebae
Difflugia oblonga	Testate Amoebae
Difflugia penardi	Testate Amoebae
Euglypha laevis	Testate Amoebae
Heleopera petricola	Testate Amoebae

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Species	**Taxonomic group**
Phryganella acropodia	Testate Amoebae
Plagiopyxis callida	Testate Amoebae
Plagiopyxis penardi	Testate Amoebae
Trigonopyxis minuta	Testate Amoebae
Trinema lineare truncatum	Testate Amoebae

Appendix C Study site illustrations

Figure 1: Downstream view of the study site.

Figure 2: Upstream view of the study iste.

Figure 3: Gravels colonized by pioneer plant species (GRAVELS) and thicket dominated by *Phalaris arundinacea* (HERBS) in spring.

Figure 4: Thicket dominated by *Phalaris arundinacea* (HERBS) and willow bushes mainly composed of *Salix viminalis* (WILLOW) in spring.

Figure 5: Mixed deciduous forest mianly dominated by *Fraxinus excelsior* (FOREST) in spring.

Figure 6: Willow forest mianly dominated by *Salix alba* (WILLOW FOREST) in spring.

Figure 7: Control site accounting for the pre-restoration flood dynamic (PASTURE).

Figure 8: Succession of habitat (GRAVELS, HERBS, WILLOW).

Figure 9: Arthropod sampling (sweep net)

Figure 10: Clues of beaver presence.

Appendix D Curriculum vitae

Bertrand Fournier | Bertrand Fournier – Curriculum Vitae

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✉ bertrand.fournier@unine.ch
http://www2.unine.ch/biolsol/page-6106.html

I am a dynamic scientist mainly interested in ecosystems functioning and biodiversity. I use descriptive, experimental and theoretical approaches to tackle this complex subject.

Education

University of Neuchâtel **Switzerland**
PhD in Ecology, *08.2009–08.2013*
Above- and below-ground aspects of floodplain restoration: from biodiversity to ecosystem functions

University of Lausanne **Switzerland**
M.Sc. in Biology, *02.2007–02.2009*
Relationships among aboveground and below-ground communities and ecosystem functioning along the perturbation gradient of a restored floodplain

University of Lausanne **Switzerland**
B.Sc. in Biology, *10.2005–02.2007*

Professional situation

University of Neuchâtel **Switzerland**
PhD assistant, *08.2009–08.2013*
organisation and teaching of practicals in statistics, botany, invertebrates, soil fauna, and humus forms, University of Neuchâtel; supervision of MSc students

Swiss Federal Research Institutes WSL & EPFL **Switzerland**
Scientific Collaborator, *02.2009-07.2009*
Research on CCES Research Project RECORD: River restoration

University of Lausanne **Switzerland**
Student assistant, *01-2008–02.2009*
Botany praticals: teaching and organisation

Ecole de ski arc-en-ciel **Nendaz, Switzerland**
Ski and snowboard teacher, *1999-2008*

Academic achievements & Awards

- Participation to major research projects in CH (RECORD, PERMANENT.PLOT.CH)
- Discovery of 5 new species for the Swiss arthropod fauna
- 2010 LATSIS Ecohydrology Symposium Poster Award
- 2008 Interakademische Kommission Alpenforschung (ICAS) encouragement award for a work on plant traits repartition along altitudinal gradients

Teaching expertise

- Basic Statistics, numerical ecology, multivariate analyses
- Basic and advanced use of R as a research tool
- Plant taxonomy, ecology, and field methods
- Invertebrate & soil fauna taxonomy, ecology, and sampling methods
- Humus form

Computer skills

Basic: Java, HTML, C++, Illustrator, Inkskape

Intermediate: Latex, Linux shell scripting, GIS, Office

Advanced: R

Community involvements & Administrative activities

- Delegate of the intermediate corpus at the committee of the Master in Biogeosciences (UNINE and UNIL)
- Member of the nomination committee of the Assistant professor position in Medical Entomology (UNINE)
- Member of the nomination committee of UNINE scientific collaborator in statistics (UNINE)

Projects & Grants

- SwissBOL application: Earthworm biodiversity in Switzerland. Applicants: Drs Le Bayon R.C. and Lara E. (UniNE). Co-applicants: Dr Gonseth Y. (CSCF), Dr Arnaud Maeder (MHNC), Drs Guenat C., Bullinger-Weber G. (EPFL), Cuendet G, Fournier B. (UniNE); Granted amount = 1'500CHF
- SwissBOL application: Barcoding of Swiss Gastropods. Applicants: Bertrand Fournier & Edward A.D. Mitchell; Granted amount = 5'000CHF
- Early Postdoc.Mobility: Swiss National Science Foundation carrier grant for Fournier Bertrand; Granted amount = 85'000CHF

Oral communications & Posters

Marcisz K, Mitchell EAD, Fournier B, Gilbert D, Siegenthaler A, Buttler A, Slobodeanu R, Lamentowicz M. (27 February – 2 March 2013). Testing the response of peatland testate amoebae to in-situ water table changes. 32nd Meeting of the German Society for Protistology. Warth-Weiningen, Switzerland (Poster).

Mitchell EAD, Szelecz I, Klang C, Seppey C, Fournier B, Mulot M, Amendt J, Heurich M, Lara E. (27 February – 2 March 2013). Response of soil testate amoebae to the presence of a decomposing pig cadaver – a study using morphological and molecular approaches. 32nd Meeting of the German Society for Protistology. Warth-Weiningen, Switzerland (Oral communication).

Seppey C, Fournier B, Mulot M, Mitchell EAD, Szelecz I, Lara E. (27 February – 2 March 2013). Changes in soil Euglyphida communities under pigs cadavers assessed by high throughput sequencing : a new indicator of the post mortem interval (PMI)? 32nd Meeting of the German Society for Protistology. Warth-Weiningen, Switzerland (Poster).

Szelecz I, Klang C, Fournier B, Amendt J, Heurich M, Mitchell EAD. (27 February – 2 March 2013). Testate amoebae in soil – their potential as an indicator of time since death 32nd Meeting of the German Society for Protistology. Warth-Weiningen, Switzerland (Oral communication).

Coffey E.E.D., Fournier B. & Mitchell E.A.D. (2012). Amoebae or finches? Walking in the footsteps of Darwin, but looking under our feet! 97th annual meeting of the Ecologcial Society of America, Portland, USA (oral communication).

Marcisz K., Mitchell E.A.D., Siegenthaler A., Buttler A., Gilbert D., Fournier B., Slobodeanu R. & Lamentowicz M. (2012). The response of peatland testate amoebae communities (Protists) to in-situ water table changes. The 6th International Symposium on Testate Amoebae (ISTA6). Xiamen, China.

Fournier B., Samaritani E., Le Bayon R.C., Bullinger-Weber G., Frey B., Moretti M., Gillet F., Guenat C. & Mitchell E.A.D. (2011). Impact of restoration on floodplain biodiversity: decoupling taxonomic and functionnal responses. River corridor restoration conference 2011 (RCRC11), Ascona, Switzerland (poster).

Lara E., Heger T.J., Roussel-Delif L., Fournier B. & Mitchell E.A.D. (2011). Euglyphid diversity: business as usual or terra incognita? 65th annual Phycological Society of America meeting with the International Society of Protistologists, Seattle, USA (oral communication).

Mitchell E.A.D., Fournier B., Samaritani E., Shrestha J., Le Bayon R.C., Bullinger-Weber G, Luster J, Frey B, Moretti M, Gillet F & Guenat C (2011). Effects of river restoration on soil diversity and terrestrial communities. (2010). LATSIS symposium 2010, EPF Zurich (poster).

Shrestha J., Samaritani E., Fournier B., Frossard E., Gillet F., Guenat C., Niklaus P.A., Tockner K., Mitchell E.A.D. & Luster, J. (2011). Soil carbon pools and fluxes in the Thur river floodplain. Swiss Soil Science Society meeting (poster).

Bullinger-Weber G., Fournier B., Pfund S.,Le Bayon R.-C. & Guenat C., (2010). Assessing a new method based on soil morphology to evaluate floodplain restoration success. Swiss Society of Pedology Annual Confer-ence 2010, Fribourg, Switzerland (poster).

Fournier B., Guenat C. & Mitchell E.A.D. (2010) Can terrestrial diversity be predicted from soil morphology? EGU General Assembly Conference, Vienna, Austria (oral communication).

Fournier B., Mitchell E.A.D & Guenat C. (2010). Soil morphology as an indicator of floodplain restoration success: comparison with vegetation and invertebrate diversity Swiss Society of Pedology (SSP) Annual Conference 2010, Fribourg, Switzerland (oral communication).

Fournier B., Samaritani E., Le Bayon R.C., Bullinger-Weber G., Beat Frey B., Moretti M., Gillet F., Guenat C. & Mitchell E.A.D. Impact of floodplain restoration on vegetation and soil communities. (2010). LATSIS symposium 2010, EPF Lausanne (poster).

Fournier B., Samaritani E., Le Bayon R.-C., Mitchell E.A.D (2010). Impact of floodplain restoration on earthworm communities. 9th International Symposium on Earthworm Ecology. Xalapa, Veracruz, Mexico (poster).

Fournier B., Samaritani E., Shrestha J., Le Bayon R.C., & Mitchell E.A.D. (2010). Community ecology of earthworms in a restored floodplain and potential as bioindicators of river restoration. Fifth international oligochaete taxonomy meeting 2011 (5th IOTM), Beatenberg, Switzerland (oral communication).

Fournier B., Szelecz I., Amendt J., & Mitchell E.A.D. (2010). Forensic science goes underground: the quest for new bioindicators. Annual Ph.D. students meeting 2010, Neuchâtel, Switzerland (poster).

Guenat C., Fournier B., Bullinger-Weber G., Grin K., Pfund S., & Mitchell E.A.D. (2010). Assessing floodplain restoration success using soil morphology indicators. EGU General Assembly

Conference, Vienna, Austria (Poster).

Malysheva E., Mazei Y., Fournier B., Samaritani E., & Mitchell E.A.D. (2010). Diversity and community patterns of testate amoebae (Protists) in the channelled and restored sections of river Thur (Switzerland). European Geoscience Union General Assembly Conference, Vienna, Austria (poster).

Samaritani E., Shrestha J., Frey B., Luster J., Fournier B., Vuilleumier S. & Mitchell E.A.D. (2009). Effects of environmental heterogeneity on ecosystem functioning and biodiversity. Swiss Society of Pedology Annual Conference 2009, Wädenswil, Switzerland (oral communication).

Szelecz I., Fournier B., Amendt J. & Mitchell E.A.D. (2009). Forensic science goes underground: Testate Amoebae as bioindicators of cadaver decomposition. The 5th International Symposium on Testate Amoebae, Montbéliard, France (poster).

Samaritani E., Fournier B., Frey B., Moretti M., Freléchoux F., Luster J., Vuilleumier S., Guenat C., Gillet F., Durisch-Kaiser E., Tockner K., Mitchell E.A.D. (2008). Effect of environmental heterogeneity on above- and below-ground terrestrial biodiversity in a restored river corridor: a combined field and modeling approach. Society of Wetland Scientists Annual Conference, Washington DC, USA (oral communication).

Publication list

Published: ISI

Fournier, B., Guenat C., Bullinger-Weber G. & Mitchell E. A. D. (2013). Spatio-temporal heterogeneity of riparian soil morphology in a restored floodplain. Hydrology and Earth System Sciences Discussion, 10, 4337–4367.

Fournier B., Malysheva E., Mazei Y., Moretti M. & Mitchell E.A.D. (2012). Toward the use of testate amoeba functional traits as indicator of floodplain restoration success. Eur J Soil Biol, 49, 85-91.

Fournier B., Samaritani E., Shrestha J., Mitchell E.A.D. & Le Bayon R.-C. (2012). Patterns of earthworm communities and species traits in relation to the perturbation gradient of a restored floodplain. Appl Soil Ecol, 59, 87-95.

Pellissier L., Wassef J., Bilat J., Brazzola G., Buri P., Colliard C., Fournier B., Hausser J., Yannic G. & Perrin N. (2011). Adaptive colour polymorphism of Acrida ungarica H. (Orthoptera: Acrididae) in a spatially heterogeneous environment. Acta Oecol., 37, 93-98.

Samaritani E., Shrestha J., Fournier B., Frossard E., Gillet F., Guenat C., Niklaus P.A., Pasquale N., Tockner K., Mitchell E.A.D. & Luster J. (2011). Heterogeneity of soil carbon pools and fluxes in a channelized and a restored floodplain section (Thur River, Switzerland). Hydrology and Earth System Sciences, 15, 1757-1769.

Pellissier L., Fournier B., Guisan A. & Vittoz P. (2010). Plant traits co-vary with altitude in grasslands and forests in the European Alps. Plant Ecol., 211, 351-365.

Submitted: ISI

Fournier B., Guenat C., Bullinger-Weber G. & Mitchell E.A.D. (Submitted). Spatio-temporal heterogeneity of riparian soil morphology in a restored floodplain. Hydrology and Earth System Sciences.

Fournier B., Gillet F., Le Bayon R.-C., Mitchell E.A.D. & Moretti M. (Submitted). Disentangling competition and environmental filtering in a restored floodplain using taxonomic and functional diversity. Ecology.

Jassey V.E.J., Mitchell E.A.D., Payne R., Fournier B., Chiapusio G., Binet P., Buttler A., Delarue F., Toussaint M.-L. & Gilbert D. (Submitted). Trade-off in community level-traits of microbial consumers explain the response of microbial food web structure to climate warming. PNAS.

Lara E., Roussel-Delif L., Fournier B. & Mitchell E.A.D. (Submitted). Euglyphid testate amoebae, the protists that bridge microbial and “macrobial” community ecology. ISME.

Szelecz I, Fournier B, Seppey C, Amendt J, Mitchell EAD. (Submitted). Can soil testate amoebae be used for estimating the time since death? A field experiment in a deciduous forest. Forensic Science International.

Published: non-ISI

Qin, Y., Fournier, B., Lara, E., Gu, Y., Wang, H., Cui, Y., Zhang, X., and Mitchell, E. A. D. (In press). Relationships between testate amoeba communities and water quality in Lake Donghu, a large alkaline lake in Wuhan, China, Frontiers of Earth Science.

Fournier B., Bullinger-Weber G., Mitchell E. & Guenat C. (2011). La morphologie du sol: un outil pour l’évaluation de projets de revitalisation de zones alluviales? Concept general. Bulletin de la Société Suisse de Pédologie, 31.

Fournier B., Pellissier L., Guisan A. & Vittoz P. (2010). Morphologie et reproduction des plantes le long de gradients altitudinaux. Bulletin de la Murithienne, 127.

Non academic activities

Outreach: Contributions to local natural sciences institutions (La Murithienne) & to the Swiss red lists of ferns and flowering plants

Sports & hobbies: Hiking, natural history, football, juggling

Appendix E Acknowledgements

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