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Par
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Functional responses of stream macroinvertebrate communities to hydromorphological restoration of headwater streams

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"Now to the King eternal , immortal, invisible, to God who only is wise, be honor and glory forever and ever. Amen"

1 Timothy 1:17 NKJV

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GENERAL INTRODUCTION

1.0. Ecological degradation in streams

Anthropogenic activities have altered the natural landscape of the earth leading to severe degradation of natural ecosystems worldwide (Millennium Ecosystem Assessment, 2005; Suding, 2011). Agricultural practices, industrialization, and urbanization are some of the human activities driving the degradation of natural ecosystems (Millennium Ecosystem Assessment, 2005). Man's over-reliance on the services provided by ecosystems has inspired deliberate re-engineering of those systems thereby altering the natural balance between spatial and temporal species occurrences (Dirzo *et al.*, 2014). A large chunk of the world's natural forest ecosystems has been converted for agricultural farmlands and urban settlements (Millennium Ecosystem Assessment, 2005; Mulder *et al.*, 2011). In Europe, as in other parts of the world, freshwater and coastal ecosystems have suffered severe degradation affecting rivers, their catchments, floodplains, and estuaries for centuries (Tockner, Robinson & Uehlinger, 2009); 60% of European rivers are classified as ecologically degraded (European Environmental Agency, 2018). Because of their strong connections to surrounding landscapes, the freshwater ecosystems are increasingly inundated by pressures conveyed through fluvial systems leading to eutrophication, hydrological change, habitat degradation, and alteration to the biological communities (Carpenter *et al.*, 1998; Dudgeon *et al.*, 2006). Also, increasing human demands on water resources have resulted in several pressures including pollution, modification of instream and riparian habitat, and heavy regulation of flow (Feld *et al.*, 2011).

The existential threat being faced by freshwater ecosystems, including rivers and streams, is borne out of the huge burden it bears not only for species life sustenance but also for the maintenance of the economy of many nations (Elosegi & Sabater, 2013). Despite occupying less than 1% of the Earth's surface, the freshwater ecosystems disproportionately contain as

much as 12% of all known species (Garcia-Moreno *et al.*, 2014) and provide goods and services estimated to be worth more than $4 trillion annually (Darwall *et al.*, 2018). However, the management practices employed over the years have mostly treated freshwater as a mere physical resource vital to human survival while largely neglecting it as the special and delicate habitat it provides for an extraordinary array of organisms (Lovejoy, 2019). The consequence of this is a decline in freshwater biodiversity at an alarming rate (Dudgeon *et al.*, 2006; Darwall *et al.*, 2018). It has been reported that freshwater species show decline in the order of 37% since 1970 compared to the equivalent value of 25% for terrestrial species (Loh *et al.*, 2005; Flitcroft *et al.*, 2019). This has necessitated a call for urgent attention. Elosegi and Sabater (2013) opine that the sustainable use of the resources provided by rivers can only be achieved if the rivers are maintained in good ecological health. To achieve this, conservation efforts must not only focus on species persistence but must also seek to eliminate the threats through ecosystem restoration and protection.

2.0. Physical alterations

Rivers are among the ecosystems most impacted by multiple stressors (England & Wilkes, 2018; Stefanidis *et al.*, 2020), chief among which is the alteration to their physical structures. Rivers are naturally complex and dynamic and have the capacity for self-maintenance and continuity including support for the biota (Palmer *et al.*, 2005; Postel & Richter, 2012). This natural ability in the majority of rivers has been greatly impaired as a result of the change to their physical structure. The physical structure of rivers comprises features such as channel form, current speed, flow volume, and water quality i.e. the hydromorphological component of the ecosystem (Poff *et al.*, 1997; Poff & Zimmerman, 2010). These features are functionally linked (Gomi, Sidle & Richardson, 2002) and the dynamic interactions between them at

different points and times along the river course provide the variety of habitats that support biodiversity. Alterations to these features in the form of channelization (Nakano & Nakamura, 2006) and the installation of artificial structures such as dams, weirs, and culverts alter this natural balance and remove the heterogeneity of habitats in streams with deleterious effects on biodiversity including invasive species and species loss (Cooper *et al.*, 2017). Channelization, both through riverbank modification or dredging of river channels, disconnects the lateral interactions between river channels and their riparian zones, alters channel morphology, and makes physical habitats homogeneous (Kennedy & Turner, 2011). It also straightens naturally meandered streams thus eliminating shoreline edge habitats such as backwaters and edge water usually characterized by slow current (Nakano & Nakamura, 2006).

2.1.1. Dams, weirs, and culverts

In the lotic system, hydromorphological degradation resulting from the construction of hydraulic structures has been of great concern worldwide (Gehrke, Gilligan & Barwick, 2002; Søndergaard & Jeppesen, 2007; Schilt, 2007). Over 50% of the world's rivers and streams are reported to be flow-regulated or dammed (Nilsson & Dynesius, 1994) for different purposes including hydropower generation, water supply for domestic and industrial use, irrigation for farmlands, flood control, and recreational opportunities (Bednarek, 2001). In France, there is approximately a total of 430,000 km length of streams and 121,540 obstacles of different kinds on them; this translates to approximately an obstacle at every 4 km of stream length (Eaufrance, 2021; European River Network, 2016, see Figure 1).

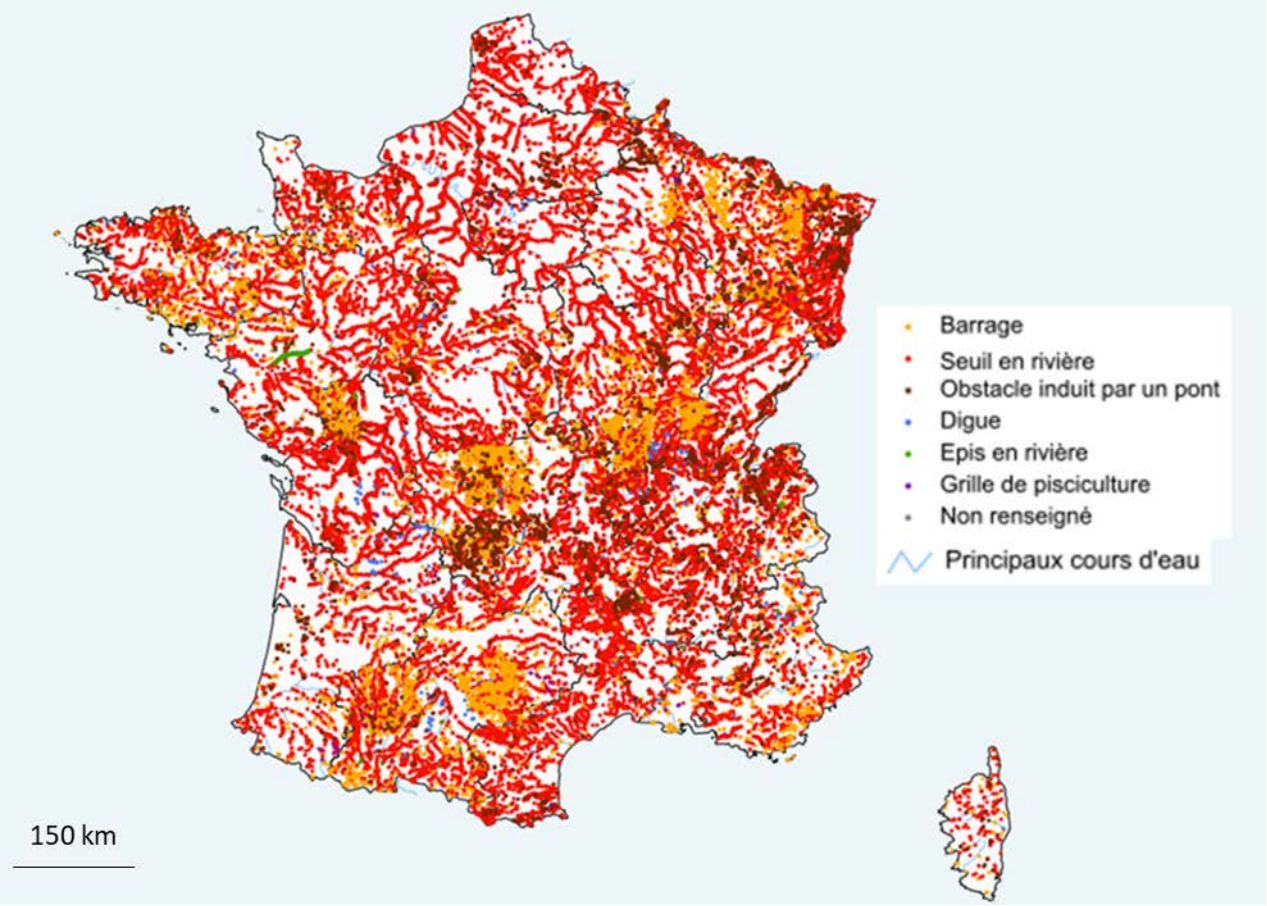


Figure 1: *Artificial obstacles on stream channels in France. There is approximately an obstacle at every 4 km of stream length. Source: Eaufrance, 2021.*

This intensive human intervention in streams affects natural flow, sediment transport, water quality, as well as biodiversity, and the general ecological health of the streams (Allan, 2004; Van Looy, Tormos & Souchon, 2014; Sabater *et al.*, 2018). Dams are usually built across mid-size to large rivers and thus vary in size and type. Small dams are defined as one having a maximum height of < 15 m and large dams > 15 m height (World Commission on Dams, 2000; Poff & Hart, 2002a). While weirs are usually smaller and of different construction (Figure 2), both weirs and dams have similar effects on the river system. Braatne et al. (2008) proposed spatial (e.g. upstream vs downstream reaches, progressive downstream patterns, dammed river

vs undammed river) and temporal (e.g. pre- vs post-dam or sequential post-dam conditions) comparisons for evaluating the impacts of barriers.

a) b)

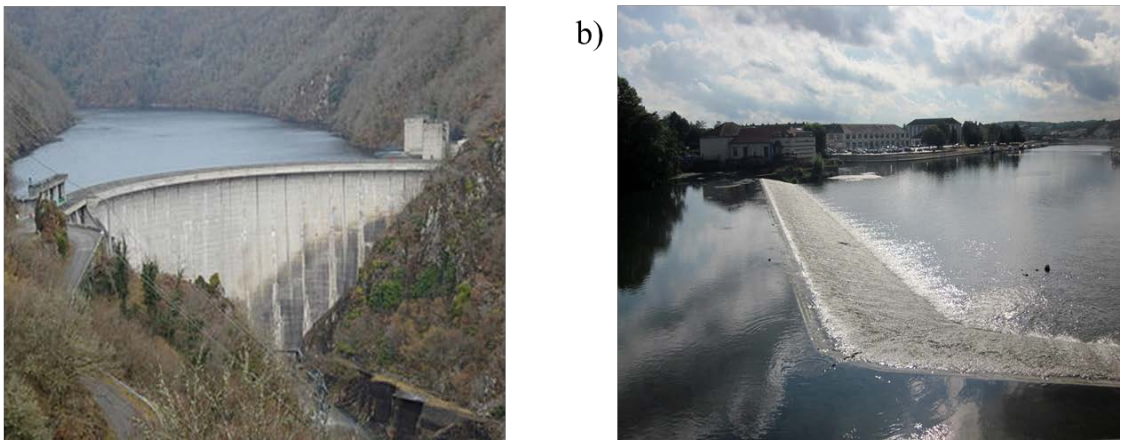


Figure 2: Examples of a) a dam (Marèges dam on Dordogne River, France) and b) a weir (Saône River, France). Though different in size, they often have similar effects on rivers, altering the natural flow and constituting an obstruction to the transport of materials and fauna migration. Source: online Wikimedia commons.

These barriers interrupt the natural continuity of a river and change the natural flow cycle (Bednarek, 2001). This has been famously dubbed the serial discontinuity concept by Stanford & Ward (2001) and Ward & Stanford (1983, 1995). This theoretical perspective of regulated lotic systems, views dams as major disruptions of the longitudinal continuum of rivers resulting in shifts in the inherent upstream-downstream biotic and abiotic patterns and processes. At the upstream, there is a dramatic transition from a flowing system to a reservoir (Nilsson & Berggren, 2000), and the effect downstream could extend to river reaches several kilometers beyond the immediate reach downstream of the dam (Rood *et al.*, 2005; Schmidt & Wilcock, 2008). The change from a river to a reservoir often shifts species composition, richness, and abundance (Cooper *et al.*, 2016; Cheng *et al.*, 2016; Rodriguez-Perez *et al.*, 2021). The increase

in the volume of water upstream could result in the inundation of the riparian areas and cause the loss of habitats and organisms (Nilsson & Berggren, 2000).

The ecological impact of dams on downstream reaches is often multi-faceted (Rood *et al.*, 2005). There is an alteration to the downstream flow regime, with the quantity and timing of flow determined by dam operations (Magilligan, Nislow & Graber, 2003; Braatne *et al.*, 2008). They constitute a blockade to the passage of alluvial materials, particularly sediment (Ligon, Dietrich & Trush, 1995) thus reducing sediment load to downstream reaches and the estuaries leading to coastal erosion and the loss of coastal habitats (Bednarek, 2001; Grant, Schmidt & Lewis, 2013). They constitute barriers to the passage of migratory fishes such as salmon, trout, eel, and sturgeon, prevent access to spawning sites (Cooper *et al.*, 2017), and may alter the structure of invertebrate and plant metacommunities (Rodriguez-Perez et al., 2021). They alter the continuum of water temperature thus changing the natural balance of bioenergetics and vital rates (Poff & Hart, 2002a; Cooper *et al.*, 2017).

Largely due to their size and the scale of impacts, these hydraulic structures mostly found in downstream reaches of streams have continued to receive a considerable level of attention since the last decade (Van Looy *et al.*, 2014). However, while the kinds of hydraulic structures usually found on headwater streams are mostly smaller, they have impacts on the ecosystems as with the large and mid-size dams and weirs on downstream reaches albeit on a smaller scale. These structures are in form of culverts and similar human interventions mostly as road crossings or for channel diversion in farmlands. In France, the national database on obstacles to water flow references 121,540 obstacles in 2021 (https://www.sandre.eaufrance.fr/). 0.5% of these have a waterfall height of more than 10 meters while 74% have a waterfall height of less than 1 meter. Despite their ubiquity, these small barriers are rarely studied both in terms of impact and in terms of response to restoration (Poff & Hart, 2002a; Liu *et al.*, 2014).

2.1.2. Channelization

The transition zone between streams and their riparian areas is marked by a lateral interaction that supports and maintains biodiversity in both ecosystems (Sabo *et al.*, 2005; Kennedy & Turner, 2011). This zone forms a hard but shifting boundary which is a key component of habitat heterogeneity mostly influenced by variability in river discharge (Malmqvist, 2002; Baattrup-Pedersen *et al.*, 2005). It also supports a continuous lateral exchange of subsidies in terms of nutrients and energy thus playing a key role in the energy balance of both ecosystems (Baxter, Fausch & Carl Saunders, 2005). Channelization alters this natural interaction with attendant implications for the ecology of the rivers and their riparian areas. Kennedy & Turner (2011) defined channelization as a form of human intervention that restricts a river to its main channel and thus disconnects it from its riparian zone. This intervention could be in the form of dredging, straightening, and realignment, snagging and clearing, levees or artificial embankments, bank protection, bed protection and river training (Gregory, 2006). These alterations often result in the loss of stream heterogeneous habitats (Lau, Lauer & Weinman, 2006); reduction of fauna diversity including aquatic macroinvertebrates (Kennedy & Turner, 2011) and fish (Lau *et al.*, 2006) and riparian biodiversity (Brooker, 1985).

3.0. What is restoration?

The European Union Water Framework Directive (WFD) requires all member states to restore streams and rivers in their respective jurisdictions to good ecological status by 2027 (European Environmental Agency, 2018). According to the report, almost 60% of European streams do not meet the criteria for good ecological status and in France, only 44.2% of streams were adjudged to be of good ecological status (Blard-Zakar & Michon, 2018; European Environmental Agency, 2018). In recent years and following the stated target of the WFD,

stream restoration has been receiving increasing attention (Ormerod, 2003; Suding, 2011; Ernst, Warren & Baldigo, 2012; Palmer, Hondula & Koch, 2014). Most projects seem to be anchored on enhancing habitat heterogeneity in degraded streams (Palmer, Menninger & Bernhardt, 2010; England & Wilkes, 2018), raising the curiosity whether restoration is aimed at improving the aesthetic view of streams and the 'beauty' they add to the general landscapes (Palmer *et al.*, 2005; Cottet, Piégay & Bornette, 2013; Walker-Springett *et al.*, 2016). It thus becomes imperative to define what restoration means and what constitutes successful river and stream restoration (Palmer *et al.*, 2005).

Sequence to the growing interest and efforts at improving the ecological conditions of degraded rivers and streams, the science of river restoration has grown tremendously at the turn of the millennium. Published articles in the Web of Science database containing the keyword 'river restoration' have approximately doubled every five years since the year 2000 (Figure 3). The evolution of restoration activities has equally followed a similar trend. Earlier efforts were focused mainly on the re-engineering of rivers and streams channels through channel re-meandering (Friberg *et al.*, 1994, 1998) and the creation of mesohabitats in streams, for example through the addition of wood debris or boulders (Andrus, Long & Froehlich, 1988). The recent years have witnessed ambitious projects like the removal of dams both small and large dams (East *et al.*, 2015; Fox, Magilligan & Sneddon, 2016) with the aims of eliminating the pressures associated with those structures and restoring key ecological processes fundamental to the health of the steams (O'Hanley *et al.*, 2013; East *et al.*, 2015). This change in the approach to stream restoration appears to be backed by ecological theories and principles underpinning the understanding of how ecosystems respond (Palmer *et al.*, 2010).

The focus on the creation of in-stream habitats in earlier restoration schemes (Bernhardt & Palmer, 2007; Smith et al., 2014) is based on the assumption that restoring habitat heterogeneity will increase biodiversity; a hypothesis which has been famously dubbed the 'field of dream'

(Palmer, Ambrose & Poff, 1997a; Miller, Budy & Schmidt, 2010; England & Wilkes, 2018), implying that if the habitats are available, the fauna will come. While most of these projects recorded success in enhancing habitat heterogeneity (Larson, Booth & Morley, 2001; Negishi & Richardson, 2003; Alexander & Allan, 2007), the majority however recorded minimal success or outright failure in improving fauna biodiversity as a result of enhanced habitat heterogeneity.

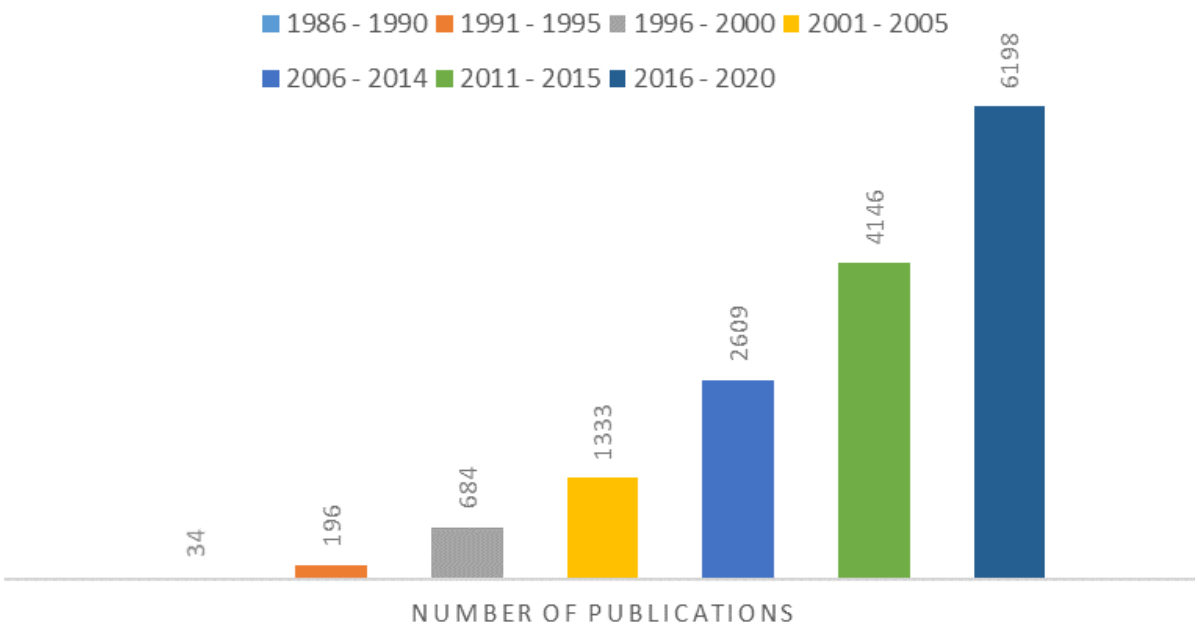


Figure 3:Published articles in the Web of Science database containing the keyword 'river restoration' and showing the growth of the science of river restoration since the turn of the millennium. Article numbers per period appear above the bars.

For example, the construction of meanders in a third-order stream in Indiana, USA improved habitat quality and had a positive effect on algal and macroinvertebrate abundance but neither macroinvertebrate diversity nor fish abundance benefitted (Moerke *et al.*, 2004; Moerke & Lamberti, 2004). Larson et al., (2001), in a study of six streams where large wood debris (LWD) were placed in disturbed stream channels, found considerable improvements in

physical habitat metrics but no detectable improvement in biological conditions using macroinvertebrate biodiversity metrics. Hence, Palmer et al., (2005) argue that restoration success cannot be adjudged to mean the same thing as ecological success in restored streams. Depending on project objectives, managers may base the assessment of restored streams on the economic, aesthetic, or enhanced social values the streams provide (Kondolf, Smeltzer & Railsback, 2001; Johansson & Nilsson, 2002) but in ecological terms, scientists believe that no restoration can be adjudged successful without ecological success (Dufour & Piégay, 2009).

The International Society for Ecological Restoration defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration, 2004). It goes further to imply that restoration seeks to return an ecosystem to its "historic trajectory". This definition is so general in application and the suggestion of a historic condition appears confusing and points towards an ambiguous end goal. Rather than attempting to return to some historic *El Dorado* or recapturing the "myth of a lost paradise" (Dufour & Piégay, 2009), the overall objective of restoration should be to improve ecosystem structure and function (Palmer *et al.*, 2005; Brierley *et al.*, 2010). Natural systems, including rivers and streams, are known to be dynamic, varying over time and space (Palmer, Hakenkamp & Nelson-Baker, 1997b; Palmer *et al.*, 2005). A healthy system is one in which the inherent spatial and temporal variabilities of its natural processes and features are within the permissible limits (Suding, Gross & Houseman, 2004) for the continued proper functioning of the ecosystem. Thus, ecologists, in practice, define restoration to broadly mean the recovery of the processes by which ecosystems work, including resource dynamics and associated biological production (Palmer *et al.*, 1997a, 2014). Therefore, an ecologically successful river restoration re-establishes hydrological, geomorphological, and ecological conditions that make the restored river a resilient one capable of self-sustainability (Walker *et al.*, 2002; Palmer *et al.*, 2005).

The emphasis on making the recovery of ecosystem processes in rivers as the overarching goal of restoration efforts (Beechie *et al.*, 2010; Palmer *et al.*, 2014) requires that the planning, design, and the activities involved in projects, as well as post-project assessment criteria, are system or site-specific (Beechie *et al.*, 2010; Batalia & Vericat, 2013). For instance, in headwater streams where organic materials from allochthonous sources occupy the base of the energy pyramid, the recovery of the processes associated with resource dynamics (e.g. connectivity with riparian vegetation, resource transport, distribution, and processing) will put the streams on the recovery trajectory where there is self-capability for physical and biological adjustments to future perturbations (Wohl *et al.*, 2005; Beechie *et al.*, 2010). The endpoint of such efforts will be a resilient, self-sustainable system capable of recovery from periodic change and stress (Beechie et al., 2010, see Figure 4).

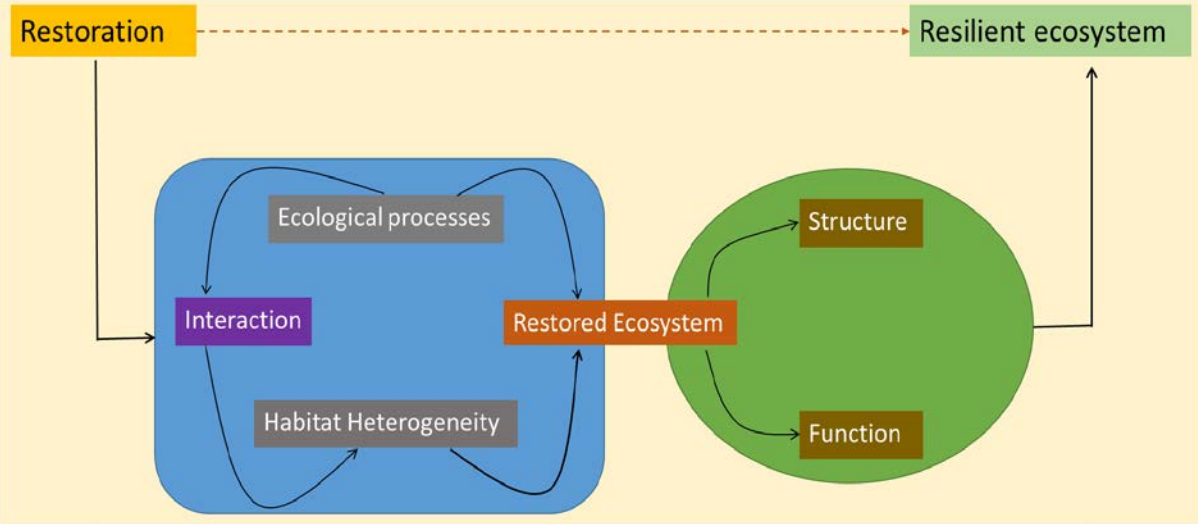


Figure 4: Conceptual pathway of ecosystem restoration. To achieve a resilient system, where there is a self-sustaining balance between ecosystem structure and functioning in restored streams, activities must be aimed at restoring key ecological processes in addition to habitat heterogeneity.

4.0. Main types of restoration in headwater streams

Restoration projects in streams seek to re-establish the processes – biological, physical, and chemical – that connect aquatic, riparian, and terrestrial ecosystems. While degraded headwater streams and larger streams down the slope have seen many restoration projects carried out on them, post-project monitoring of restoration works is scarce and largely unreported (Kail *et al.*, 2007; Al-Zankana, Matheson & Harper, 2021) and comparatively more so on small headwater streams (Figure 5). The type of activit(y)ies carried out on a river depend(s) on the kind and source of degradation, project objectives, and cost. Projects that seek to enhance biodiversity through increased habitat heterogeneity employ in-stream habitat enhancement such as the addition of large woody debris and other habitat materials (e.g. boulder, pebbles, gravels), as well as channel re-meandering. However, it is important to note that in-stream habitat enhancement alone may not produce the desired result without the restoration of natural processes (Roni *et al.*, 2002). Therefore, it is essential to identify and remove existing impairments to the natural processes in degraded streams before in-stream habitat enhancement, which should serve as a complementary measure (Roni *et al.*, 2002). In Europe (European River Network, 2016) and America (East *et al.*, 2015), the removal of artificial barriers, a primary source of pressure in lotic systems, from watercourses as a way of restoring natural processes in degraded streams has gained traction in recent decades.

4.1.1. Large Woody Debris (LWD)

There has been a depletion in the volume of LWD in rivers across the world due to persistent de-snagging and the loss of the natural source of recruitment as a result of the increasing clearance of riparian vegetation (Gippel *et al.*, 1996). LWD are riparian trees that fall into rivers flowing through forested lands and are conventionally defined as logs larger than 0.1 m in

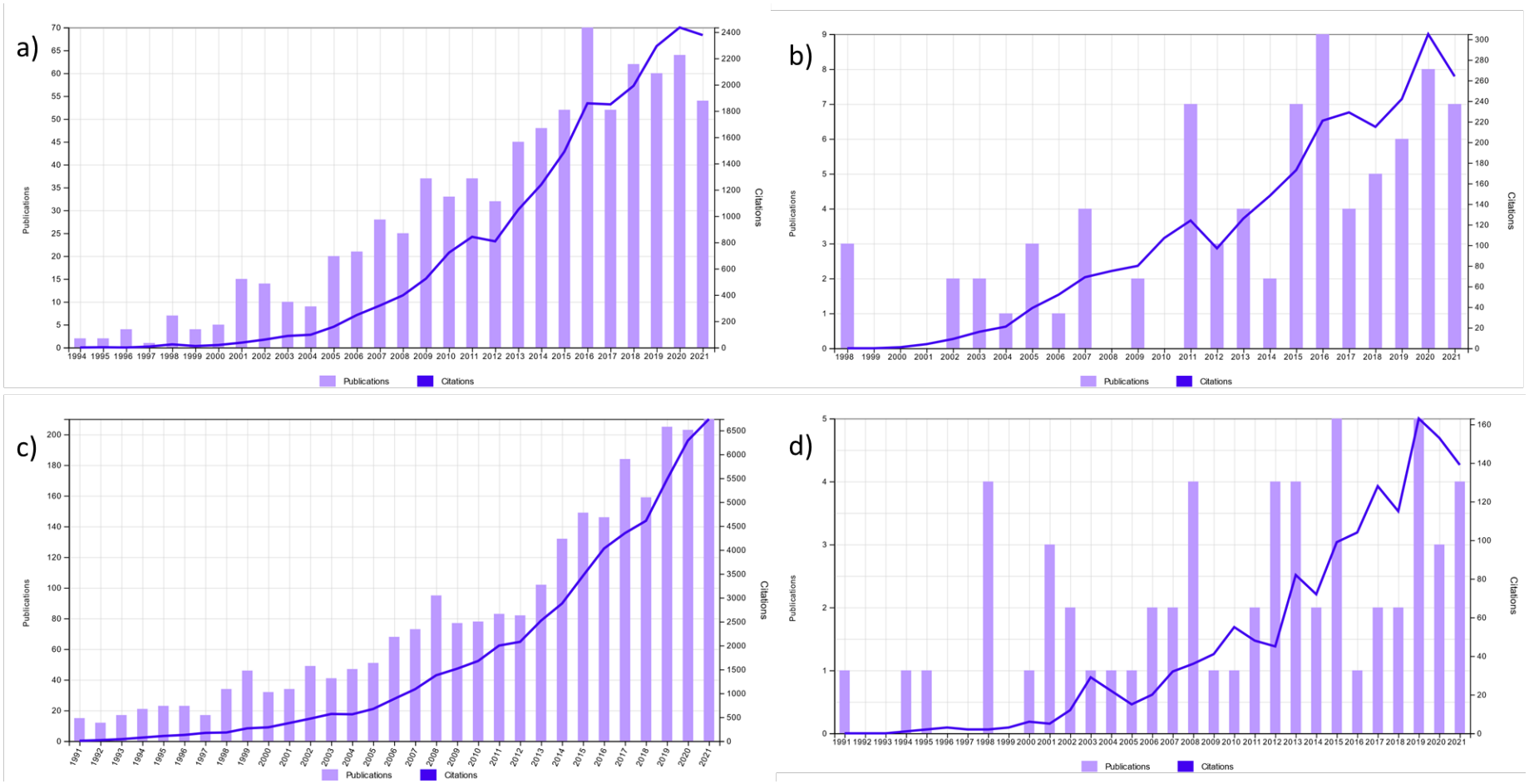


Figure 5: Publication (bars) and citation (lines) reports of river restoration in literature (1990 – 2021) from the Web of Science database using the keywords a) river restoration, macroinvertebrate; b) river restoration, macroinvertebrate, headwater; c) dam removal; and d) dam removal, headwater. Only a few of the restoration works on headwater streams are monitored or reported. Also, even though the larger majority (over 74% in France, for instance) of artificial barriers to flow occurs on headwater streams, only a few are studied for impacts and restoration compared to the volume of literature available on larger downstream reaches.

diameter and longer than 1.0 m in length (Andrus *et al.*, 1988; Kail *et al.*, 2007). The artificial installation of LWD in stream channels has the potential to increase habitat heterogeneity through alteration of geomorphological, hydraulic, and sediment retention processes (Thorp & Covich, 2001; Corenblit *et al.*, 2007). It partly obstructs and diverts streamflow; thus creating a more complex arrangement of pools, riffles, and runs and also reducing flood peaks downstream (Andrus *et al.*, 1988; Gippel *et al.*, 1996; Al-Zankana *et al.*, 2021). The resulting channel complexity can be important as spawning sites for some fish species. In a study of 50 projects in central Europe where LWD was used for restoration in streams, Kail et al. (2007) reported that only 44% of those projects were scientifically (i.e. excluding photographs and mere visual inspection) monitored for restoration success. The study observed that the overall objective of the restoration projects, which was to enhance the general hydromorphological status of the streams, was largely achieved and that the projects had positive effects on some fish species. They however opined that success would be enhanced if wood measures mimic natural wood and if non-fixed wood structures were used rather than hard engineering where fixed wood structures are employed.

4.1.2. Channel meanders

The introduction of LWD and gravel bars works at the local scale. At the intermediate scale where degraded river sections are to be restored to their natural conditions, the restoration of an entire river section is done through channel re-meandering (Fejerskov, Kristensen & Friberg, 2014), that is, the reconstruction of channels to take a form and dimensions different from those of the pre-project channel (Kondolf, 2006). This type of restoration is among the most visually striking types of restoration and it involves the creation of meanders on an existing channel whose historical bends have been lost to channel straightening or sometimes,

the establishment of new sinuous channels (Iversen *et al.*, 1993; Kondolf, 2006; Nagayama *et al.*, 2008). In an alluvial channel, the dynamic longitudinal and cross-sectional interactions between water flow and channel edges in meandering streams create a variety of in-stream habitats which include an undulating pattern of pools and riffles (Hudson, 2002; Nagayama et al., 2008, see Figure 6). This interaction has been restrained in many streams through channelization and bank straightening principally to improve flood control and to drain floodplains for urban and agricultural use with the consequent loss of in-stream habitats. As in most other types of restoration, available literature on the assessment of streams where re-meandering restoration has been carried out are few and are mostly on lowland streams. Restoration through re-meandering has shown evidence for effectiveness in the re-creation of diverse in-stream habitats in restored stream channels both longitudinally and in cross-sectional structures (Kawaguchi, Nakamura & Kayaba, 2005; Nakano & Nakamura, 2008), a remarkable change in the community composition of fish (Kawaguchi *et al.*, 2005) and improved taxon richness of macroinvertebrates (Nakano & Nakamura, 2008).

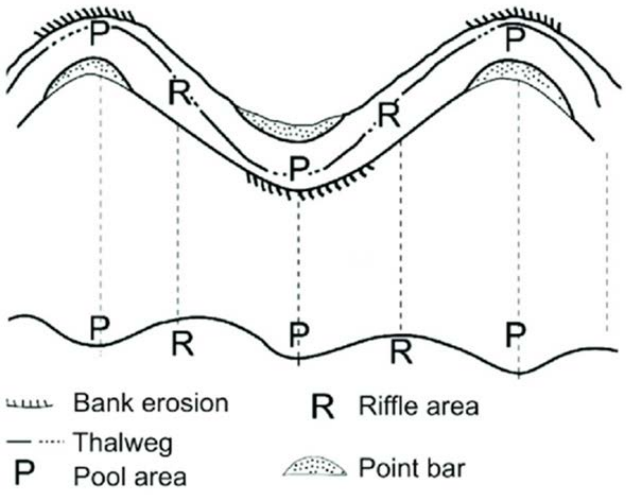


Figure 6: Undulating pool – riffle morphology of stream meanders. The bottom part represents the thalweg profile (adapted from Hudson, 2002).

4.1.3. Barrier removal

The pervasiveness of blockage on the world's river systems and its impacts on the ecological health of rivers have necessitated the call for and the implementation of mitigation measures. With the impacts of these barriers on stream networks being multi-faceted (affecting hydrology, stream temperature, channel morphology, water chemistry, hydrologic connectivity, and biological condition, Cooper *et al.*, 2016), localized and cumulative (Wang *et al.*, 2011; Van Looy *et al.*, 2014), mitigation strategies have been diverse (IUCN and UNEP, 2001). Some countries, e.g. Switzerland (Truffer, 1999), Norway, and Kenya (IUCN and UNEP, 2001) adopted policies that set aside particular river basins to be protected from the development of dams to minimize the cumulative effects of dam construction (IUCN and UNEP, 2001). In France, about 10% of the 525,000 km of watercourses are designated as "No Go" rivers where there is a strict ban on the construction of hydropower stations (European River Network, 2016). Fish passage or the so-called 'fish ladder' has also been used as a mitigation measure to allow the passage of migratory fishes across channels (Roni *et al.*, 2002; Roni, Hanson & Beechie, 2008; Fullerton *et al.*, 2009; O'Hanley *et al.*, 2013) but the structures involved have been found in most cases to constitute barriers to the passage of juvenile fishes (Roni *et al.*, 2002).

With the increasing knowledge on the harmful effects of these artificial barriers on river networks and their ecological systems, many dams and similar barrier structures have been decommissioned and removed while many more are in the process of being removed. In Europe, France has impressively led the charts for the most dams removed with over 2,900 dams (both large and small dams) removed since 1996 (European River Network, 2016). The removal is expected to restore the natural flow regime, enhance sediment transport and redistribution to downstream rivers and ultimately to the coastal waters.

Unfortunately, information on the evaluation of restored streams is limited (Bernhardt *et al.*, 2005; Alexander & Allan, 2007) either because the majority of restoration projects are not being monitored for success or those being monitored are not reported. Moreover, despite a recent increase in the volume of published information, concluding on the effectiveness of most restoration activities for improving physical habitat, water quality and biological productions remains difficult (Roni *et al.*, 2008). With most restoration projects primarily involving the enhancements of habitat heterogeneity, biota community indices have been largely used as assessment indicators. Notably, in projects adopting channel reconfiguration and addition of LWD or boulders, macroinvertebrate community has been widely used as an indicator of ecological recovery (Palmer *et al.*, 2010; Feld *et al.*, 2011; Friberg, 2014; Al-Zankana *et al.*, 2021) while fish, especially, migratory fish species have been used as biological indicators of ecological recovery in restoration projects involving the removal of artificial barriers in streams (Wang *et al.*, 2011; Cooper *et al.*, 2017). The removal of barriers from watercourses has proved very effective for migratory fish species but there is no information on the effect of dam removal on macroinvertebrate communities. In the same vein, the results of macroinvertebrate biodiversity indices recovery from in-stream habitat heterogeneity enhancement have been varied with only a few studies recording positive effects (e.g. Al-Zankana et al., 2021; Kail et al., 2015) and the majority reporting limited success (e.g. Feld et al., 2011; Friberg, 2014; Haase et al., 2013; Palmer et al., 2010).

5.0. Indicators of restoration success

The monitoring and evaluation of restoration success present a unique opportunity to treat restoration activities as experiments that can potentially enrich the understanding of the river systems and subject how managers and policymakers approach restoration to scientific

scrutiny. The knowledge gained from evaluating current projects could also aid the optimization of future projects (Woolsey *et al.*, 2007). Kondolf & Micheli, (1995) and Kondolf, (1995) were among the earlier reviews which underscore the importance of monitoring and evaluating restoration projects. Subsequent works have made practical suggestions on the approaches to post-project appraisal (Downs & Kondolf, 2002), selection of metrics and indicators for restoration (Woolsey *et al.*, 2007), and the usefulness of pre and post-project assessment as a criterion for successful projects (Palmer *et al.*, 2005). Though streams and rivers, like all ecosystems, can be characterized by their structure and function, evaluations of restored streams have mostly been limited to using the structural (both physical and biological) elements as indicators (Ferreira *et al.*, 2020). The ecosystem structure of streams includes the physical characteristics (e.g. channel morphology and water quality) and the biological communities of the ecosystem, while ecosystem functioning refers to the ecosystem-level processes (Gessner & Chauvet, 2002). Gessner and Chauvet (2002) argue that both structural and functional elements must be utilized as complementary indicators for a comprehensive assessment of ecological status in streams. In the next few paragraphs, we described some of the indicators that have been used for the evaluation of ecological success in restored streams.

5.1.1. Habitat features and biodiversity indices

Success in enhancing habitat heterogeneity and habitat features in restored streams have been well documented in restoration involving the addition of large woody debris (Larson *et al.*, 2001; Kail *et al.*, 2007; Palmer *et al.*, 2010; Al-Zankana *et al.*, 2021) and channel re-meandering (Kawaguchi *et al.*, 2005; Nakano & Nakamura, 2008). Despite the habitat success, projects often do not result in restoring biodiversity (Palmer *et al.*, 2010; Haase *et al.*, 2013). In a review of 78 stream restoration projects, Palmer *et al*. (2010) found most of the projects

successful in enhancing physical habitat heterogeneity while only two showed a statistically significant increase in macroinvertebrate biodiversity. They opined that in a restoration context, there was no evidence that habitat heterogeneity was the primary factor controlling stream invertebrate diversity. There are a few other studies that have recorded mixed results on biodiversity. Miller *et al*. (2010) reported a positive effect of in-stream restoration involving habitat heterogeneity enhancement on macroinvertebrate richness but negligible increase in density. Kail et al. (2015) in a quantitative review of existing literature on the effect of river restoration on fish, macroinvertebrates, and macrophytes, observed significant effects of instream restoration on fish and macroinvertebrates, with higher effects on abundance/biomass compared to richness/diversity. This lack of consistency in the outcome of stream restoration on macroinvertebrate community indices has necessitated the call for the complementary deployment of functional indicatoors in assessing the effectiveness of restoration efforts in stream ecology.

5.1.2. Functional indicators

The scanty evidence in support of the sensitivity of biodiversity indices to hydromorphological pressures in streams calls for complementary indicators for assessing restoration success. Following the classic model of Bradshaw (1988), an assessment incorporating both the structure and function of the stream ecosystem has been proposed for the evaluation of stream restoration (England & Wilkes, 2018; Ferreira *et al.*, 2020). Species functional traits (Verberk, van Noordwijk & Hildrew, 2013) and ecosystem process rate (Gessner & Chauvet, 2002; Ferreira *et al.*, 2020) have been nominated for this purpose. The functional traits are the attributes of a species that governs its ability to deal with environmental problems and opportunities (Verberk, 2013). They are an organism's phenotypic characteristics underpinning

its habitat and resource utilization, and its life history (Truchy *et al.*, 2015; Frainer *et al.*, 2018). In other words, the ultimate survival or otherwise of a species in an environment is a result of the combination of its traits and the interactions among the traits necessary to drive the processes responsible for the functioning of the system. Frainer et al. (2018) found that the deposition and decomposition of organic matter were significantly enhanced by stream restoration and along habitat heterogeneity gradient and that, the enhanced litter decomposition was linked with a change in the functional traits of biota and not the biodiversity metrics. Thus, monitoring evaluations incorporating species functional traits and an ecosystem process such as litter decomposition in stream restoration could provide a mechanistic and integrative understanding of the pathway of ecological recovery in restored streams. However, as promising as these functional indicators are in the evaluation and monitoring of ecology success of stream restoration, information about their utilization is still scarce (Frainer *et al.*, 2018; Ferreira *et al.*, 2020).

6.0. Study objectives and hypotheses

This work is in the context of restoration ecology of headwater streams and it seeks to deepen the science and knowledge of ecology recovery with a particular focus on achieving resilience in streams through the restoration of key ecological processes important for the proper functioning of stream ecosystems. It proposes ecosystem function, in terms of processes and species functional traits as bio-indicators of ecological recovery in stream restoration. In addition and complementary to the classical macroinvertebrate diversity metrics, we propose species functional traits, rate of leaf litter decomposition, and streambed oxygenation as indicators of ecological recovery in streams. The unique connection that headwater streams maintain with their riparian zones (Vannote *et al.*, 1980), the resulting constant mobilization

of allochthonous materials including sediment and organic matter, and the cascading effects of these materials on ecological processes in the hierarchy of the entire lotic system influenced the choice of these indicators (Gurnell *et al.*, 2016).

The spatial extent of headwater systems covers 70 to 80% of the total lotic catchment area and serves as an important source of sediment, water, nutrients, and organic matter for downstream systems (Vannote *et al.*, 1980; Gomi *et al.*, 2002) thus making the unique natural processes (hydrologic, geomorphic and biological) in headwater systems very important for the entire lotic system. As explained, the numerous restoration of degraded headwater streams are largely unreported and not being monitored. Thus, it is difficult to ascertain if the indicators that have been used for monitoring the effectiveness of restoration in larger streams will be applicable in headwater streams. In total, we investigated five headwater stream channels; three were restored by having artificial structures, which constituted a barrier to flow and sediment transport, removed from their channels while the remaining two are new channels created to put stream sections into their historical position. In each case, we adopted the Before-After-Control-Impact study design (Downes, 2002). The study answers the following questions and hypotheses.

Question 1: Will macroinvertebrate diversity indices respond differently to restoration in headwater streams than has been observed in other systems?

- **Hypotheses**: We hypothesize that for both barrier removal and in the new channels, diversity indices will improve following restoration works and that values will approach reference conditions along a temporal gradient indicative of the time needed to achieve full ecological recovery.

Question 2: Will functional indicators perform better than diversity indices as bio-indicators of ecological recovery in streams?

- **Hypotheses**: We hypothesized that functional elements in restored channels will show more closeness to reference conditions than biodiversity indices and that litter decomposition will be more related to functional traits than biodiversity indices. In the new stream channel, we hypothesized that macroinvertebrate recolonization will be driven by traits essential for dispersal and species persistence.

7.0. Organization of the thesis sections

The thesis is organized into three chapters. Chapter 1 contains the methods. Chapter 2 describes the response of macroinvertebrate community structure to barrier removal in three restored channels while Chapter 3 tests the in-stream variability of litter decomposition and the factors influencing this variability and describes leaf litter decomposition and streambed oxygenation as functional indicators of ecological recovery in restored headwater streams. All the results are discussed in a final general discussion section. A part describing macroinvertebrate recolonization of new stream channels could not be organized into a full chapter because of time. It is, however, briefly described under the discussion section. It examines if recolonization is driven by functional diversity rather than biodiversity.

CHAPTER 1: Materials and Methods

1.0.General description of study area and sites

All the streams investigated in this study are located in Brittany, north-western, France (Figure 7). The region has a mean elevation of 104 meters and a temperate oceanic climate with a relatively warm summer of an average temperature of 17.5±1.12°C and mild winter with an average temperature of 6.53±1.07°C. Precipitation in the region is evenly distributed over the year but slightly more abundant in winter (Figure 8) and with an annual value of 694±141 mm. The Brittany region is approximately 30,000 km² and is drained by numerous small coastal watersheds within the Loire-Bretagne basin.

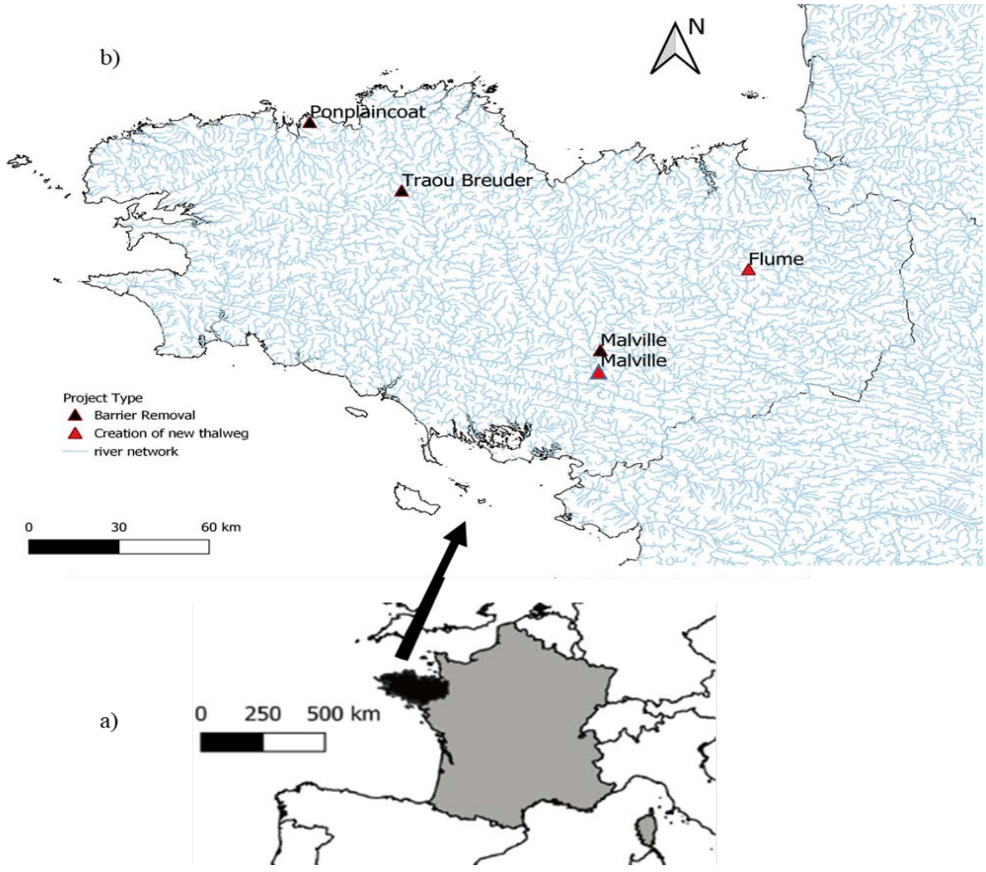


***Figure 7**: Maps of a) France and b) Brittany Region showing the three investigated streams. Streams marked with black triangles were for barrier removal while those marked with red triangles each had a new thalweg created on a section of their channels.*

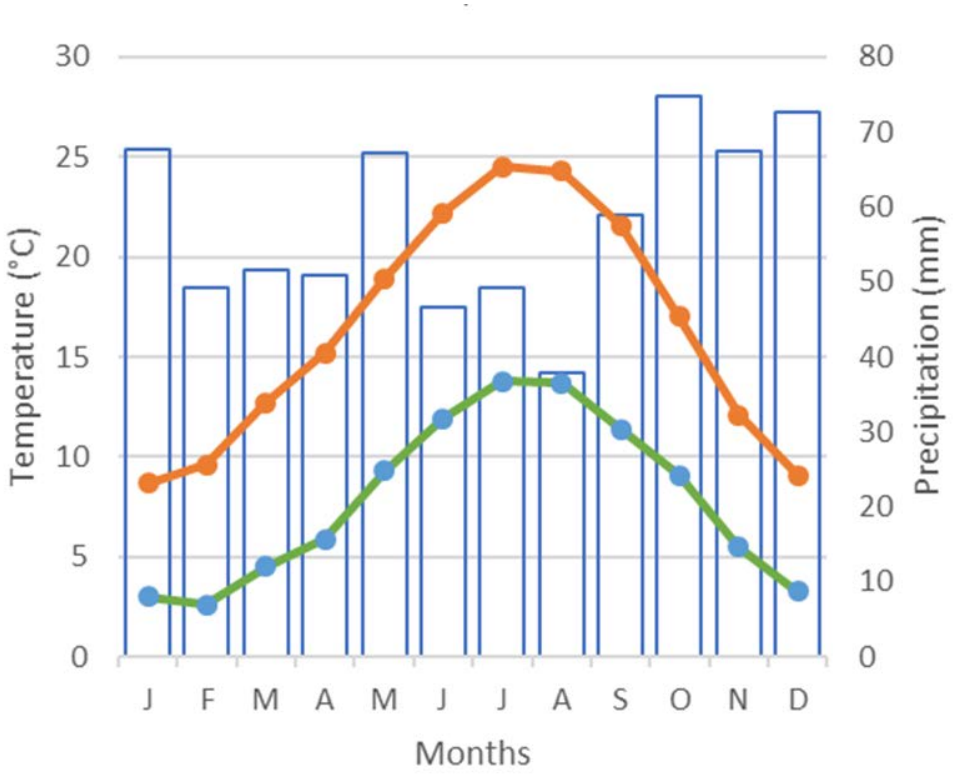


***Figure 8**: Climate diagram of Rennes, the capital city of Bretagne. Bars represent monthly rainfall in millimeters, lines depict the monthly high (in brown) and low (in green) temperature in Celsius degrees for the period 1981-2010. Data source: Météo-France.*

1.1.Sites with barrier removal

We monitored three headwater streams (Figure 7b above) sections on which artificial structures were removed. The structures were in form of concrete nozzles (Figure 9a & b) and are expected to have impacts on the streams as with other known artificial barriers. Mostly as a result of inconsistencies in slope between the artificial structure and the streambed at the point of installation, there is a damming effect upstream of the structure. The reduction in flow, coupled with the physical obstruction the structure itself constitute to sediment transport, sediment is trapped upstream, potentially leading to the clogging of the streambed. Thus, on the three streams, Traou Breuder (48°27'30.2"N 3°21'43.7"W), Malville (47°55'06.0"N 2°24'36.4"W) and Pontplaincoat (48°41'08.3"N 3°48'23.4"W), we measured streambed

oxygenation as a proxy of sediment clogging before and after the removal of the structures. We equally measured the rate of litter decomposition and assessed macroinvertebrate community and functional diversities. Land use in the catchments of the streams are different. Traou Breuder is located in a semi-natural watershed with forest trees as dominant vegetation. The landscape around Pontplaincoat is dominated by agricultural practices involving cow and pig farming while Malville is located in a mostly urbanized watershed. The restoration work on Traou Breuder was carried out in Summer 2019 while Malville and Pontplaincoat were done in Autumn 2018.

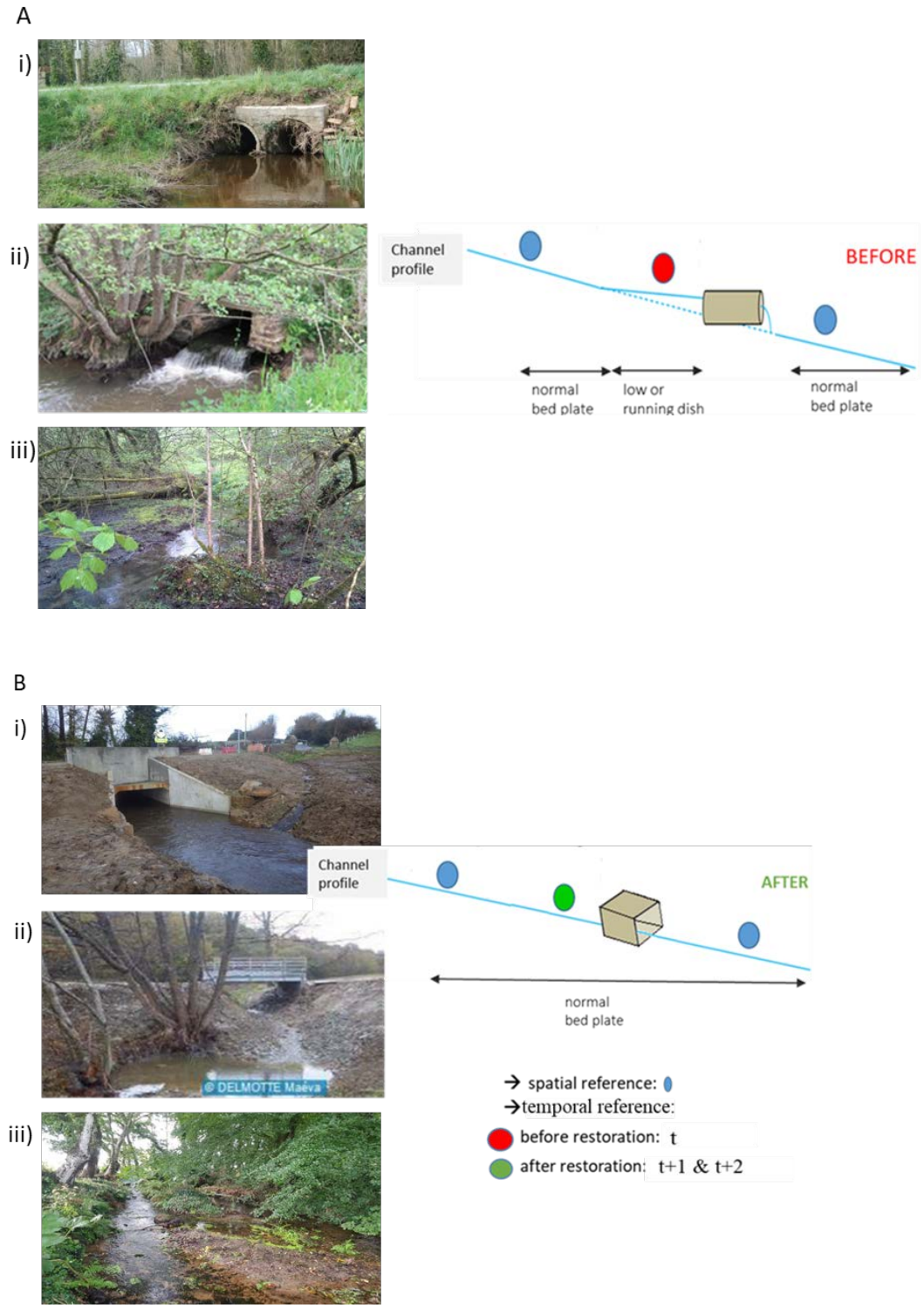


***Figure 9**: The streams A) before restoration and B) after restoration: i) Pontplaincoat; ii) Malville and iii) Traou Breuder. The damming effect of the barrier could lead to sediment accumulation and clogging of the streambed upstream. Impacts were monitored for 1 year (t) before restoration works and for two years (1st year, t+1 and year 2, t+2) after restoration works.*

1.2.Sites with new channel meanders

Two stream sections, Flume (48°14'36.8"N 1°46'43.6"W) and Malville (47°55'06.0"N 2°24'36.4"W) draining farmlands and which had previously been channeled away from their original thalwegs to create space for farmlands were restored to their original thalwegs (Figure 10). Malville (Figure 11a) was restored in summer 2019 while Flume (Figure 11b) was restored in autumn 2019. The new thalwegs were monitored for macroinvertebrate recolonization on a fine temporal scale for one year.

Three sampling points were established on the new thalwegs in each stream. A sampling point at least 200 meters upstream of the thalweg was established as a control or reference site in each stream. We equally established a point just downstream of the thalweg in each case for comparison (Figure 10). Macroinvertebrate samples were taken using artificial substrates enclosed in a big mesh (5cm square mesh) plastic bowl and set as a trap at the sampling point. 6 replicates were used at each sampling point and every sampling campaign. Each stream was monitored for 1 year after the creation of the thalwegs. One of the streams, Flume, was monitored at 1 week (T1), 4 weeks (T4), and 1 year (T10) after restoration. The second stream, Malville, was monitored at 1 week (T1), 2 weeks (T2), 4 weeks (T4), 6 months (T8), and 1 year (T10) after restoration.

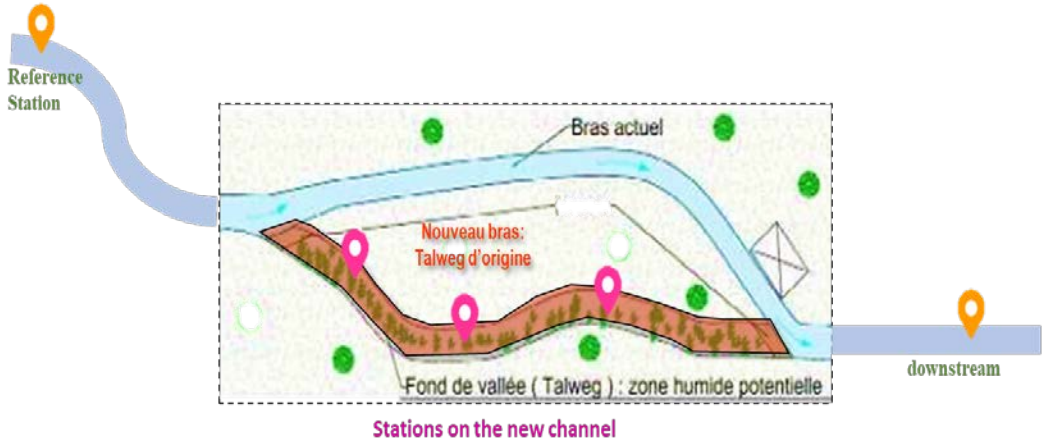
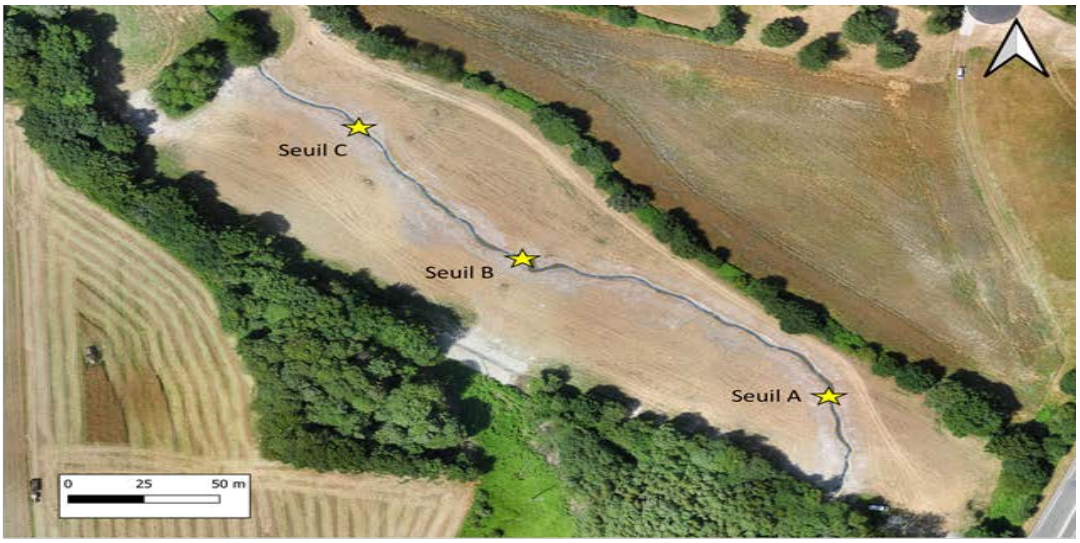


Figure 10:Ilustrative diagram showing the new channel thalwegs and our sampling points.

a)



b)



Figure 11: Aerial view through a drone photo of the new thalwegs in a) Malville and b) Flume. Yellow stars represent sampling points.

2.0.General description of the B-A-C-I design as applied in this study

For each of the indicators assessed on the sites with barrier removal, measurements were made one year (n-1) before restoration works and two years after restoration works in a Before-After-Control-Impact (BACI) design (Figure 9 above). The BACI design permits the measurement of impacts by comparing a perturbed system with a control or reference condition (Downes,

2002). A control site was located about 100 meters upstream of the impacted section on each of Malville and Traou Breuder and about 200 meters upstream of the impacted section in Pontplaincoat (Figure 12a). The selection of the control site on the same stream was to standardize for catchment variables and analyze the impact of the barrier. We also selected a site downstream on each stream to determine the extent of the impact downstream.

For streambed oxygenation, in addition to the impacted, control, and downstream sites, we also took measurements at four other transects (L1, L2, L3, and L4; Figure 12b) of about 10 meters apart in each of Malville and Traou Breuder and about 20 meters apart in Pontplaincoat to determine the spatial gradient in the depth of streambed oxygenation along the zone of sedimentation upstream of the barrier.

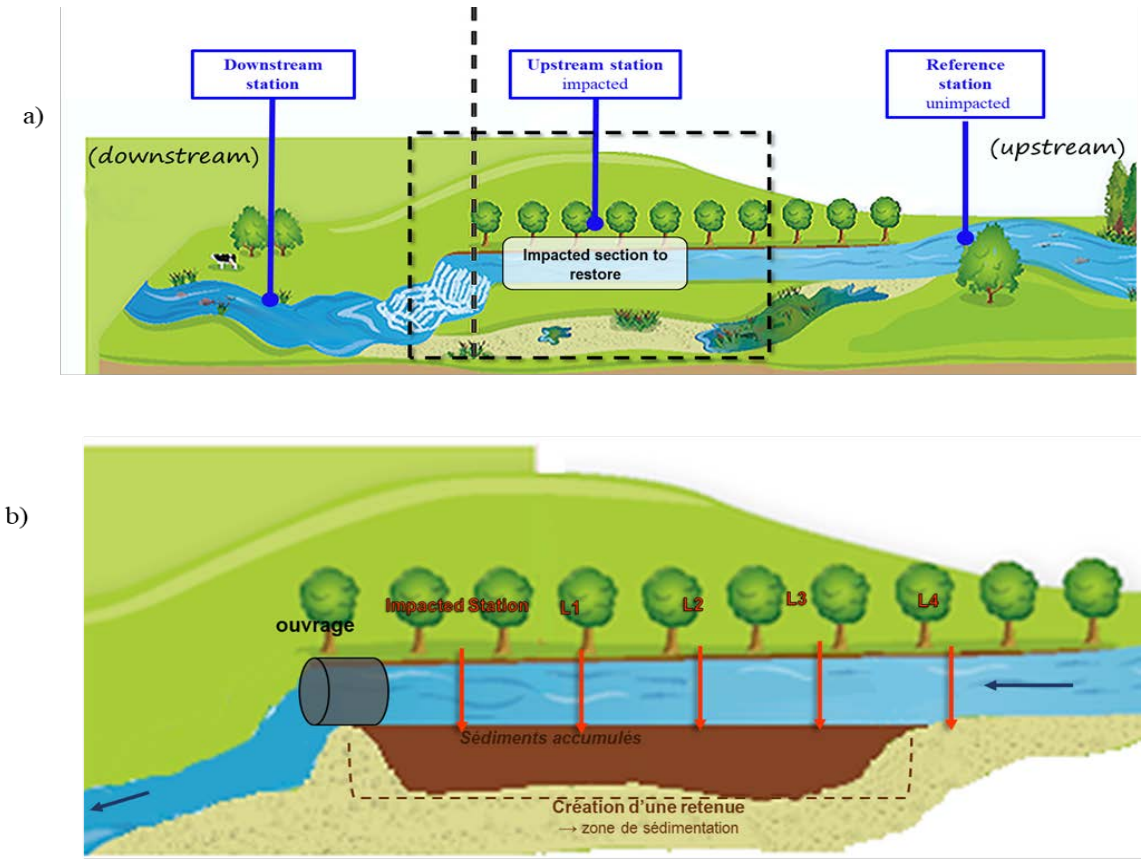


Figure 12: a) A general illustration of the sampling sites for each measurement and b) a zoom on the impacted section showing additional sampling transects (L1, L2, L3, and L4) for the evaluation of streambed oxygenation gradient along the zone of sediment accumulation upstream of barriers.

Chapter 2

CHAPTER 2: The response of macroinvertebrate community structure to barrier removal

Article 1: Responses of macroinvertebrate communities to hydromorphological restoration of headwater streams in Brittany

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Abstract

This chapter seeks to address the first question of this thesis that aims to determine the response of macroinvertebrate community indices to hydromorphological restoration. Indices of fauna communities, including macroinvertebrates, have been widely used as indicators of environmental changes in streams with great success. However, in the evaluations of in-stream restorations, results from the deployment of macroinvertebrate community indices as bio-indicators have been inconclusive with very scanty evidence for success. This study aims to determine if this will be different in headwater streams and particularly according to the type of in-stream restoration studied (i.e. suppression of nozzle). We monitored three headwater stream reaches where artificial structures (i.e. nozzle) constituting hydromorphological impairments to the streams were removed. We collected macroinvertebrate samples from the impacted sections of the streams and control sites established on the streams. Samples were collected before and after the restoration activities in a before-after-control-impact (BACI) study design. We used two macroinvertebrate-based multimetric tools (I_2M_2 and ERA) to evaluate the ecological status of the streams based on macroinvertebrate community indices and to identify the relative contributions of watershed anthropic pressures to the ecological status. We found that the removal of the artificial structures and the restoration of natural flow were successful in reducing clogging. However, only taxonomic richness shows a positive significant change in streams. Results showed that the presence of other confounding factors even after restoration may have been responsible for this minimal success in biodiversity recovery. In addition, though the multimetric assessment tools were able to differentiate between the streams and potent in disentangling the effects of the multiple pressures contributing to degradation in the streams, they showed limitations at scales below the watershed scale. Our result showed that for a better outcome on biodiversity improvement,

methods of in-stream restorations must consider the multiple pressures contributing to the degradation of fauna communities in watersheds.

Keywords: biodiversity, restoration, assessment tools, macroinvertebrate

Résumé

Ce chapitre vise à répondre à la première question de cette thèse qui cherche à analyser la réponse des indices des communautés de macroinvertébrés suite à une restauration hydromorphologique. Les indices faunistiques des communautés, notamment basés sur les macroinvertébrés, ont été largement utilisés comme indicateurs des changements environnementaux dans les cours d'eau avec succès. Cependant, dans les évaluations des opérations de restaurations des cours d'eau, les résultats basés sur des indices de communautés de macroinvertébrés en tant que bio-indicateurs sont souvent peu concluants et peu d'études montrent des résultats génralisables.

Cette étude vise à déterminer si dans les cours d'eau de tête de bassin versant les évaluations des opérations de restauration sur la base d'indice de commuanutés de macroinvertébrés présentent des réponses plus marquées, en particulier pour un certain type de restauration (i.e. le débusage). Nous avons suivi trois tronçons de cours d'eau de tête de bassin versant où des structures artificielles (des buses) constituant des altérations hydromorphologiques des cours d'eau ont été retirées. Nous avons collecté des échantillons de macroinvertébrés dans les sections impactées et dans des sections de contrôle établies. Les échantillons ont été collectés avant et après les activités de restauration dans le cadre d'une étude avant-après-contrôle-impact (BACI). Nous avons utilisé deux outils multimétriques basés sur les macroinvertébrés (I_2M_2 et ERA) pour évaluer l'état écologique des cours d'eau sur la base des communautés de

macroinvertébrés et pour quantifier les contributions relatives des pressions anthropiques des bassins versants.

Nos résultats monternt que la suppression des buses et la restauration de l'écoulement naturel ont réussi à réduire le colmatage. Cependant, seule la richesse taxonomique montrent un changement significatif positive. Les résultats montrent que la présence d'autres facteurs confondants peut avoir été responsable du peu de succès dans la récupération de la biodiversité. En outre, bien que les outils d'évaluation multimétriques aient été capables de différencier les cours d'eau et d'aider à démêler les effets des multiples pressions contribuant à la dégradation des cours d'eau, ils ont montré des limites à fine échelle, c'est à dire à une échelle inférieure de celle du bassin versant. Nos résultats monternt que pour favoriser la biodiversité, les méthodes de restauration des cours d'eau doivent considérer les multiples pressions contribuant à la dégradation des communautés fauniques dans les bassins versants.

Mots-clés: biodiversité, restauration, outils d'évaluation, macroinvertébrés

Introduction

Anthropogenic activities have resulted in widespread degradation of ecosystems worldwide with the attendant alteration to their ecological status (Vitousek *et al.*, 1997; Dobson, Bradshaw & Baker, 1997). The natural balance between spatial and temporal species occurrences is also being altered across all major ecosystems by human activities in concert with the global change in climate (Dirzo *et al.*, 2014). The lotic systems, in particular, have seen an increasingly severe impact as a result of extensive land-use changes and river modifications (Newson *et al.*, 1992; Gleick, 2003; Allan, 2004; Dudgeon *et al.*, 2006; Stoll *et al.*, 2016).

According to the European Water Framework Directive (WFD), almost 60% of river water bodies in Europe do not meet the criteria for good ecological status (European Environmental Agency, 2018). Dams and other forms of hydraulic structures built across flow channels have severely altered the natural ecology of rivers (Bednarek, 2001; Cooper *et al.*, 2017). For example, with the reduction in flow current occasioned by these structures, there is impairment to sediment transport with the consequent clogging of interstitial spaces just upstream ((Hazel Jr. *et al.*, 2006)). Migratory species are impeded and species with an affinity for high flow current are replaced by species that have a preference for low flow current (Drinkwater & Frank, 1994; Stanford *et al.*, 1996).

To reverse this trend and achieve the goal of good ecological status for European streams, the European WFD required member states of the EU to implement appropriate management and restoration programs on impacted streams (Heiring & Plachter, 1997; Voulvoulis, Arpon & Giakoumis, 2017). Consequently, the past decades have documented an increasing number of restoration works on hitherto degraded streams (Bernhardt *et al.*, 2005; Smith, Clifford & Mant, 2014; Verdonschot *et al.*, 2016).

Ecological restoration can be described as the process of assisting the recovery of damaged, degraded, or destroyed ecosystems (Hobbs & Cramer, 2008; Suding, 2011). Depending on the source of the degradation and the size (or type) of targeted stream reach, restoration activities may differ, but the primary focus of most schemes has been the in-stream restoration of habitats (Palmer *et al.*, 2005; Bernhardt & Palmer, 2007; Miller, Budy & Schmidt, 2010a; Smith *et al.*, 2014). The underlining assumption is that habitat restoration will lead to an increase in biodiversity and ultimately, the improvement of the ecological 'health' of such streams (Kail & Hering, 2009; Palmer, Menninger & Bernhardt, 2010; England & Wilkes, 2018). Consequently, biodiversity metrics of fauna have been the chief ecological indicators deployed for the assessment of restoration in streams (Mondy *et al.*, 2012; Dolédec *et al.*, 2015; Teresa & Casatti, 2017). While post-restoration assessments are generally not widespread (Bernhardt *et al.*, 2005; Miller *et al.*, 2010a), the few built on this assumption have recorded limited recovery of biodiversity (Palmer *et al.*, 2010; Friberg *et al.*, 2014).

In restored headwater streams, due to the dearth of information and the peculiarities of the nature of degradation (Levi and McIntyre 2020), the nature of ecological recovery remains uncertain (Sarriquet, Bordenave & Marmonier, 2007; Levi & McIntyre, 2020). Indeed, most post-assessment work on restored streams focused on large streams and rivers that represent only a small number of sites restored each year. For example, (Zaidel *et al.*, 2021) reported that in the United States, while there are more than 90,000 dams in the country but that when smaller dams are taken into account, the number probably reaches two million. In France, the national database on obstacles to water flow references 121,540 obstacles in 2021 (https://www.sandre.eaufrance.fr/). 0.5% have a waterfall height of more than 10 meters and 74% of them have a waterfall height of less than 1 meter. Consequently, the vast majority of hydromorphological restoration operations are carried out in the headwaters on small

structures. These operations are rarely studied both in terms of impact and in terms of response to restoration (Poff & Hart, 2002; Liu *et al.*, 2014; Fencl *et al.*, 2015).

From available records, assessment strategies have mostly relied on structural metrics as bio-indicators of the impact of environmental stressors on ecosystems (Bailey, Norris & Reynoldson, 2004; Roni, Hanson & Beechie, 2008; Barnes, Vaughan & Ormerod, 2013). Structural metrics such as indicator species, species diversity, richness or composition of communities, including those of macroinvertebrates, are frequently used for bio-assessment because species can be lost or replaced in response to environmental stressors (Miller *et al.*, 2010a; Clapcott *et al.*, 2012; Kail *et al.*, 2015; Verdonschot *et al.*, 2016). However, most assessment efforts have only reported scanty changes in diversity resulting from restoration and diversity metrics have shown little difference between restored and unrestored streams (Lepori *et al.*, 2005; Palmer *et al.*, 2010; Louhi *et al.*, 2011; Dolédec *et al.*, 2015; Verdonschot *et al.*, 2016; Stoll *et al.*, 2016). We set out to determine whether this will be different in headwater streams in response to hydromorphological restoration.

Following the European WFD, new monitoring tools emerged on macroinvertebrates (Birk *et al.*, 2012). The WFD requires that bioassessment methods implicitly evaluate the ecological status of water bodies, by comparing biological quality elements between an observed versus a reference situation (Wright, Furse & Moss, 1998; Morandi *et al.*, 2014). In France, the IBGN method (Indice Biologique Global Normalisé) has been used at the national scale since 1992 and revised in 2004. However, it was no longer satisfying due to severe inconsistencies with WFD (for further details, see Mondy *et al*. 2012). Mandated by the French Ministry of Environment (MEDDTL), Mondy *et al.* (2012) designed a new multimetric index (I_2M_2) for the invertebrate-based ecological assessment of French wadeable streams. This index should be able to identify impaired reaches for 17 anthropogenic pressure categories potentially leading to water quality alteration or habitat degradation and considering both taxonomic

characteristics and biological traits of benthic macroinvertebrates. As expected, later studies showed that this index responds efficiently to the effects of both physical, chemical, and hydromorphological stressors (Villeneuve *et al.*, 2015) as a proxy of site ecological status (Corneil *et al.*, 2018) and it is more robust than the IBGN (Wiederkehr *et al.*, 2016). This index also allows taking into account the nested spatial scales driving stream functioning in the description of ecological status by highlighting the importance of the site and reach scales in explaining stream biological condition (Villeneuve *et al.*, 2018). Today, managers urgently need tools that can support them in the decision-making process for protecting and restoring river ecosystems, either for biodiversity conservation or amelioration of anthropic pressures. It is particularly true for restoration programs concerning small artificial obstacles in headwater streams which represent the vast majority of restoration operations.

Due to multiple factors at play, the literature does not provide an overall consensus on the effect of stream restoration on invertebrates. In this context, we investigated the response of the promising I_2M_2 to the removal of small artificial hydraulic structures (i.e. nozzles) in three French headwater streams. These structures act as barriers between the stream channels and their riparian zones; impair flow connectivity between the upstream and downstream reaches, especially during base flow; and could potentially constitute a barrier to the migration of fauna; as well as causing the clogging of the substrate upstream due to fine sediment accumulation (Graf, 2005; Csiki & Rhoads, 2010; Liu *et al.*, 2014; Fencl *et al.*, 2015).

We analyzed the impact of removing these small structures in three headwater streams presenting different levels of disturbance, before and for two years after the removal of the structures. The first objective is to analyze the suitability of standard bioindicators (I_2M_2) developed for the WFD to highlight the efficiency of the hydromorphological restoration and to check if the probabilities of impact by different anthropic pressures identified by the Ecological Risk Assessment (ERA) tool (based on the biological characteristics of benthic

macroinvertebrate communities, (Mondy & Usseglio-Polatera, 2013; Mondy *et al.*, 2017) could be useful to weight multiple anthropogenic pressures influencing biotic assemblages in streams before and after restoration. The second objective is to test if the lack of consensus on the efficiency of hydromorphological restoration in literature may be related to the quality of the headwater stream before restoration (e.g. low, intermediate, or high intensity of the disturbance). More specifically, we questioned if restoration is more efficient in highly impaired streams than in streams with low impairment. To address this question, we analyzed the impact of restoration on aquatic invertebrates according to the intensity of stream disturbance (low, medium, and high intensity of disturbance). We selected three catchments: the first one, the Traou Breuder stream located in a fairly natural area with low intensity of human activities (mainly pasture); the second catchment is the Pontplaincoat stream which flows through an agricultural landscape consisting of a patchy landscape with forests, pastures, crop cultures, and farming zones which significantly impaired the nutrient content in the stream; and the third site, the Malville stream which is in a sub-urban stream affected by urbanization and nutrient loading and may be considered as the most impaired of the three. The third objective is to disentangle the impact of hydromorphological impairments from the impacts of other anthropic pressures in the response of macroinvertebrate communities. This approach presents a unique opportunity to estimate the separate role of chemical pollution and the hydromorphological degradation in the impacts of multiple stressors in streams.

Materials and Methods

Study sites

Three restored headwater stream reaches in Brittany region, north-western France were followed for this study in a before-after-control-impact (BACI) design. The region consists of

a patchy landscape with forests, pastures, crop cultures, and farming zones, exhibiting a wide range of agricultural practices (Piscart *et al*. 2009). Three reaches, belonging to 3 streams with differing anthropogenic pressures were selected (Fig. 1). Land use around each reach has been assessed through the percentage of natural and anthropic as provided for in 2018 by the Corine Land Cover database (https://www.statistiques.developpement-durable.gouv.fr/corine-land-cover-0) (Table 1).

Traou Breuder (48°27'30.2"N 3°21'43.7"W) is a first-order stream with a catchment weakly impacted by agricultural practices (mainly pasture). The site was restored in the summer of 2018 by the removal of a nozzle. The second reach is located on the Pontplaincoat stream, a second-order stream impacted by pasture, crop fields, and industrial cow and pig farming. The restoration done in autumn 2019 consisted in the removing of two successive weirs (1 and 1.5 m high) (48°41'08.3"N 3°48'23.4"W upstream and 48°41'25.7"N 3°48'54.2"W downstream). The last reach is located on the Malville stream (47°55'06.0"N 2°24'36.4"W) in a sub-urban watershed highly impacted by its hydromorphology, hydrology, and chemistry. The reach was partially restored in autumn 2018 by the removal of a nozzle. However, the restoration was incomplete because of the presence of a second nozzle downstream which cannot be removed (exit way of a motorway).

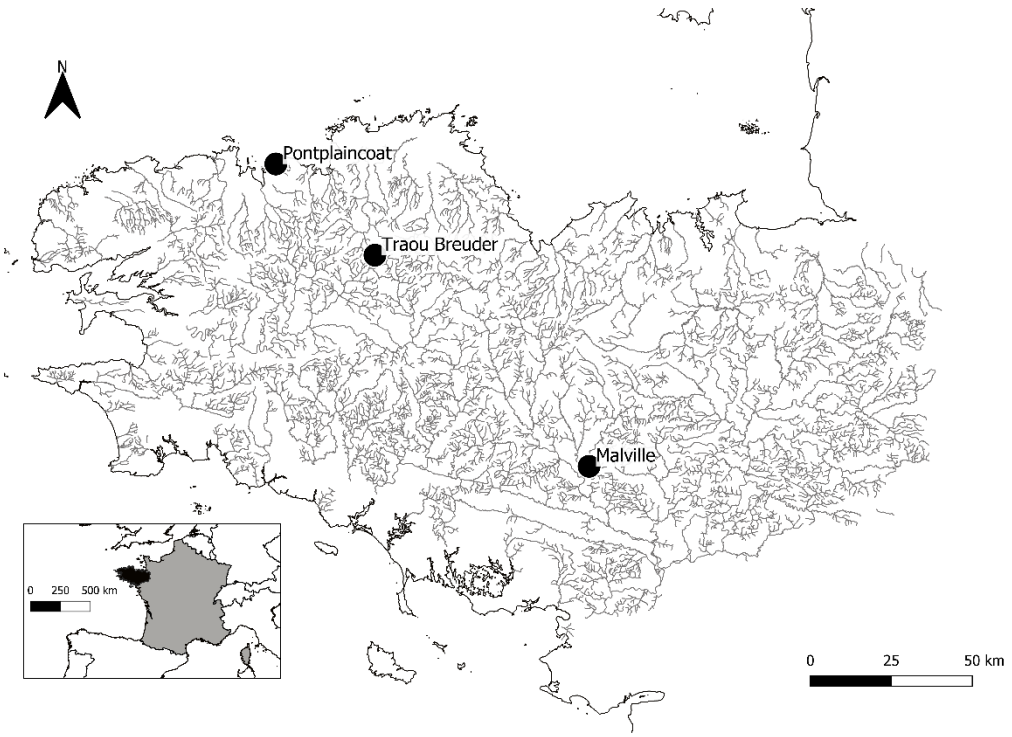


Fig 1. Maps of a) France (grey) with Brittany region (black), and b) Brittany region showing the locations of the 3 restoration sites. Grey lines represent the stream networks of the region.

Table 1. Proportion (%) of land use per watershed according to Corine Land cover 2018 data (https://www.statistiques.developpement-durable.gouv.fr/corine-land-cover-0)

Land use	Traou Breuder	Pontplaincoat	Malville
Artificial surfaces	2.59	9.48	12.50
Agricultural areas	80.03	78.32	78.22
Forest and semi-natural areas	17.38	11.75	9.28
Wetlands	0.00	0.45	0.00

We defined on each stream three sampling sites. The “impacted” site, located just upstream of the location of the artificial structure; a “control” (or reference) site, located between 30 and 200 meters upstream of the impacted site; and a “downstream” site, a few meters downstream of the artificial structure (Fig. 2).

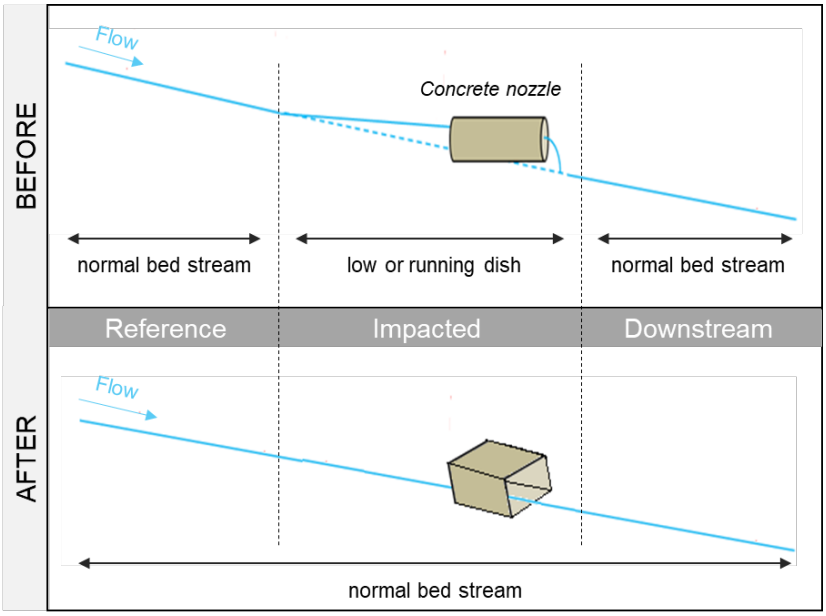


Fig. 2. Channel profile before (upper part) and after (bottom part) the replacement of the concrete nozzle. The shaded areas delimited by dotted lines represent the three sampling sites (i.e. reference, impacted, and downstream) for each stream.

Macroinvertebrate sampling

For an efficient quantitative assessment and to ensure that cryptic species are not left out, a standardized Surber net sampler (0.05 m² and 0.5 mm mesh size) was used for benthic macroinvertebrates sample collection on all sites both before and after restoration works. Samples were collected in autumn and spring before restoration work and for 2 years in each case after the restoration. Twelve sample units per site (i.e. reference, impacted, downstream, Fig. 2), following a standardized multi-habitat sampling protocol (Multi-Habitat Sampling, norm XP T 90-333 in AFNOR (2009) with consideration for the relative coverage and fauna-hosting capacity of substrates, were performed during every sampling campaign. All invertebrates were stored in 96% alcohol and later sorted and identified to the least taxonomic level possible, which for most groups is the genus level except Oligochaeta and Diptera, which were identified to the family/subfamily level.

Data analyses

We estimated the ecological status of the streams using the French multimetric index (I_2M_2) for the invertebrate-based ecological assessment of French wadeable streams (Mondy *et al.*, 2012). We used the I_2M_2 because it fulfills the European Water Framework Directive requirements. It significantly improves the detection of impaired reaches when compared to other multimetric indexes and it takes into account pressure–impact relations for a high number of pressure categories (including both water quality and habitat degradation of reaches) and considers both taxonomic characteristics and biological traits of benthic macroinvertebrate assemblages (Mondy *et al.*, 2012). The I_2M_2 expresses ecological status in terms of the Ecological Quality Ratio (EQR). The EQR corresponds to the difference between the observed situation and the reference situation. This ratio is a number between zero and one, with values from 'reference' conditions close to one and values from impacted reaches with 'bad' ecological status close to zero (Mondy *et al.*, 2012). The I_2M_2 integrates a suite of physico-chemical and hydromorphological pressures by assigning weight based on the specific pressure-type combination of five taxonomy-based and trait-based metrics of macroinvertebrates. The five taxonomy-based and trait-based metrics are the ASPT (Average Score Per Taxon) score (Armitage *et al.*, 1983), the taxonomic richness (calculated at the reach level following taxonomic identification levels recommended by (Gabriels *et al.*, 2010), the Shannon diversity index (Shannon 1948), the relative abundance of ovoviviparous species and the relative abundance of the polyvoltine species (Dolédec & Statzner, 2008). We tested if the I_2M_2 score and the five taxonomy-based metrics differed significantly between streams, sampling session (i.e. before restoration, the first and the second year of monitoring after restoration), sites (i.e. reference, impacted, and downstream section), and their interactions. We performed a type III analysis of variance (ANOVA) using the package 'car' due to the presence of the interaction factor (Fox & Weisberg, 2019). The normal distribution of the residuals of

the model was checked using the Shapiro-Wilk test of normality. When a factor was significant, we performed Tukey posthoc tests for pairwise comparisons. To illustrate the impact of the restoration, we also computed the deviations of the mean values of the taxonomic metrics at each site from the mean values at the control site for each sampling date.

To study the changes in macroinvertebrate community structures between the "control", "impacted" and "downstream" sites, we performed type III PERMANOVAs under a reduced model for each stream with Bray Curtis similarities and "site" as the fixed factor and "restoration" as the second factor (with 2 modalities "before" and "after" restoration).

We also used the ecological risk assessment (ERA) tool of Mondy et al. (Mondy & Usseglio-Polatera, 2013; Mondy *et al.*, 2017) to establish the probabilities of impact by different anthropic pressures from the biological characteristics of benthic macroinvertebrate communities before and after restoration. This diagnostic tool aims to identify the potential weight of individual anthropogenic pressures influencing biotic assemblages in streams under a multiple pressure scenario (Mondy & Usseglio-Polatera, 2013). Models were built for different types of pressures related either to water quality (based on the (SEQ-Eau Version 2) assessment grids) or to the quality of the physical habitat at the level of the watercourse and its watershed. Models were constructed following the procedure described in (Mondy *et al.*, 2017). The water quality degradation pressure categories considered are organic matter, nitrogen compounds (except nitrates), nitrates, phosphorous compounds, pesticides, and polycyclic aromatic hydrocarbons. The habitat degradation pressure categories considered are transportation facilities, riverine vegetation, hydrological instability, urbanization, clogging risk, and catchment anthropization. All the details about pressure categories are provided in (Mondy *et al.*, 2012). The ERA tool retains the anthropic pressures with satisfactory performance among the 17 (Mondy *et al.*, 2017).

To investigate the different anthropic pressures identified by the ERA tool before and after the restoration, we firstly conducted a Principal Component Analysis (PCA) on the anthropic pressures retained among the 17 by the ERA tool as variables with the 'ade4' package (Dray, Dufour & Thioulouse, 2020). The PCA enabled us to give a first descriptive approach since we also projected the I_2M_2 index and factors related to the five taxonomy-based metrics as supplementary variables (which do not influence the PCA). We also did a pairwise comparison of the I_2M_2 index and factors related to the five taxonomy-based metrics with the different anthropic pressures identified by the ERA tool using Spearman correlation analysis to test the relationship between the ecological status of the streams, macroinvertebrate community structure, and the environmental pressures respectively.

To analyze the effect of restoration for each site, we decided to work on the PCA coordinate projections on the PC1 and PC2 axes. We tested if the projection of the points on the two first dimensions differed significantly between session (i.e. before restoration, the first and the second year of monitoring after restoration), sampling site (i.e. reference, impacted, and downstream sites), and their interactions. We performed a two-way analysis of variance (ANOVA) with site as random effect using the 'lmer4' package (Bates *et al*., 2015) followed by a normal distribution check of the residuals of the model using Shapiro-Wilk test of normality. Due to the presence of random effect, when a factor was significant, we performed Tukey posthoc tests using 'emmeans' package (Lenth, 2021) to characterize the differences.

Results

Efficiency of bioindicators

I_2M_2 and associated metrics confirmed the difference and the intensity of stress between the three streams (Figure 3). The Traou Breuder stream is the stream with the highest EQR for all metrics. Malville stream presents the lowest EQR for I_2M_2, ASPT, and richness and similar values to Pontplaincoat for Shannon diversity, ovoviviparity, and polyvoltinism. The Pontplaincoat has intermediate values of EQR. Moreover, before restoration, the ecological status of streams, as assessed through the values of I_2M_2 ranged from poor (Malville and Pontplaincoat streams) to moderate (Traou Breuder) (Table 2).

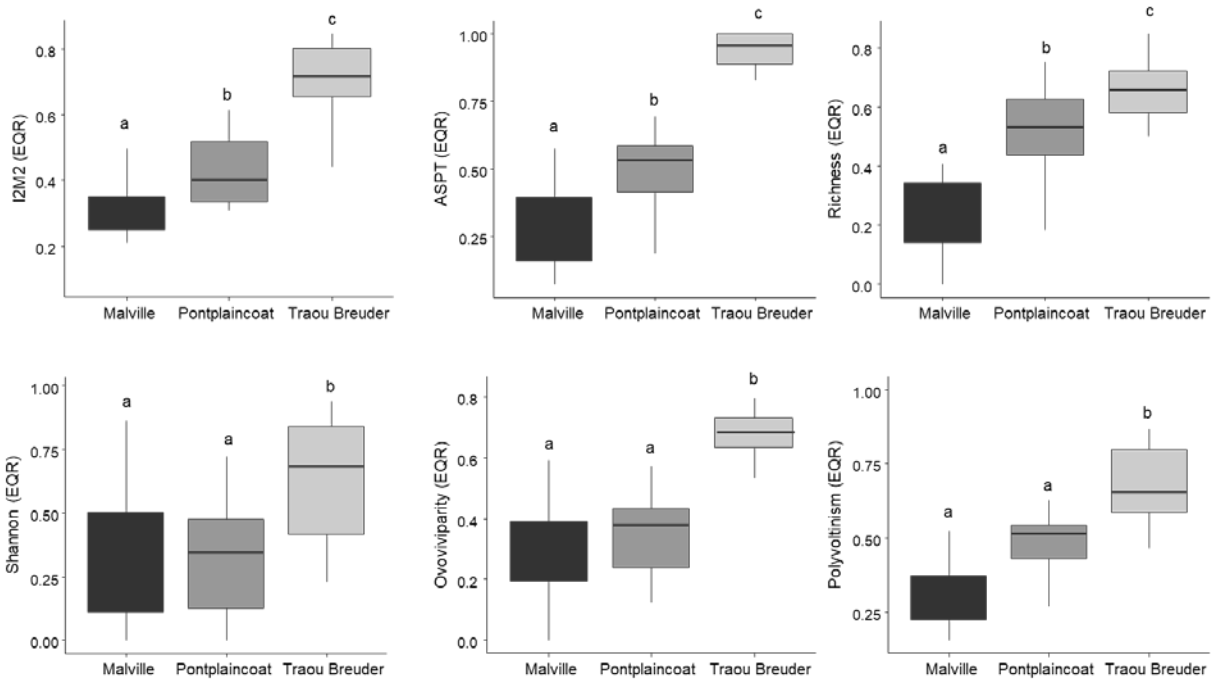


Figure 3. Boxplots representing the I_2M_2 and the five taxonomy-based metrics in terms of Ecological Quality Ratio (EQR) in the three streams. Different lower case letters represent significant differences according to the results of Tukey's posthoc tests (ASPT: Average Score Per Taxon; Richness: taxonomic richness and Shannon: Shannon's diversity index; Ovoviviparity: relative abundance of ovoviviparous species; polyvoltinism: relative abundance of the polyvoltine species).

Table 2. Ecological status (I_2M_2) of the three sites before and after restoration (Before: before restoration; after1: first year of monitoring after restoration; after2: second year of monitoring after restoration) according to the five taxonomy-based and trait-based metrics. The threshold values used to define the ecological status classes are those from (Mondy et al., 2012). These threshold values are respectively: 0.870; 0.733; 0.488; 0.244. Values are expressed as mean ± variance in terms of Ecological Quality Ratio (EQR)

Site	Session	I_2M_2 (EQR)	Ecological status
Malville	Before	0.325±0.001	Poor
	After1	0.426±0.024	Poor
	After2	0.217±0.005	Bad
Pontplaincoat	Before	0.462±0.017	Poor
	After1	0.448±0.014	Poor
	After2	0.405±0.011	Poor
Traou Breuder	Before	0.706±0.013	Moderate
	After1	0.666±0.001	Moderate
	After2	0.814±0.000	Good

After restoration, the overall results per stream are strongly heterogeneous (Table 2). Traou Breuder presented a slight increase from moderate to good ecological status after two years (Table 2) whereas Malville changed from poor to bad also after two years and Pontplaincoat had no change of ecological status by remaining classified as poor.

ANOVA results showed a significant stream effect on the I_2M_2 and the five taxonomy-based metrics (Table 3). Except for the richness which presented a significant difference according to the session, no significant difference for the I_2M_2 and the five taxonomy-based and trait-based metrics according to the session, the sampling period, or their interaction (Table 3).

Table 3. Results of the ANOVA for the effects of stream, session, the sampling site and their interaction on the I2M2 and the five taxonomy-based metrics (Df = degree of freedom; F: F value; p: p-value; ASPT: Average Score Per Taxon; Richness: taxonomic richness and Shannon: Shannon's diversity index; Ovoviviparity: relative abundance of ovoviviparous species; polyvoltinism: relative abundance of the polyvoltine species)

		I_2M_2		ASPT		Richness		Shannon		Ovoviviparity		Polyvoltinism	
	Df	F	P	F	p	F	p	F	p	F	p	F	p
Stream	2	45.63	**<0.001**	109.20	**<0.001**	36.94	**<0.001**	8.02	**<0.001**	24.42	**<0.001**	10.17	**<0.001**
Session	2	1.26	0.29	1.31	0.28	3.55	**0.04**	2.54	0.09	1.19	0.31	0.21	0.81
Sampling site	2	0.14	0.87	0.59	0.56	0.91	0.41	0.25	0.78	0.48	0.62	0.001	0.99
Session × sampling site	4	0.51	0.73	0.71	0.59	0.75	0.56	0.37	0.83	0.62	0.64	0.58	0.67

For the taxonomic richness, the values showed a significant difference (Table 3; p = 0.05) between the before restoration session (0.61±0.03) and the two years after restoration session (0.37±0.05). There was no significant difference between the one year after restoration session (0.45±0.04), the before restoration session, and the two years after restoration session. The deviation from the mean taxonomic richness of the control site significantly changed between streams (Figure 4; p < 0.001), sites (p = 0.040), and the hydromorphological restoration significantly increased the number of species (p = 0.002). However, we did not observe any significant interaction between the restoration and any other factors, neither with stream (p = 0.194) nor with site (p = 0.336). Moreover, the deviation from the control site was the highest in Pontplaincoat in comparison with Traou Breuder and Malville (p < 0.001 and p = 0.033, respectively).

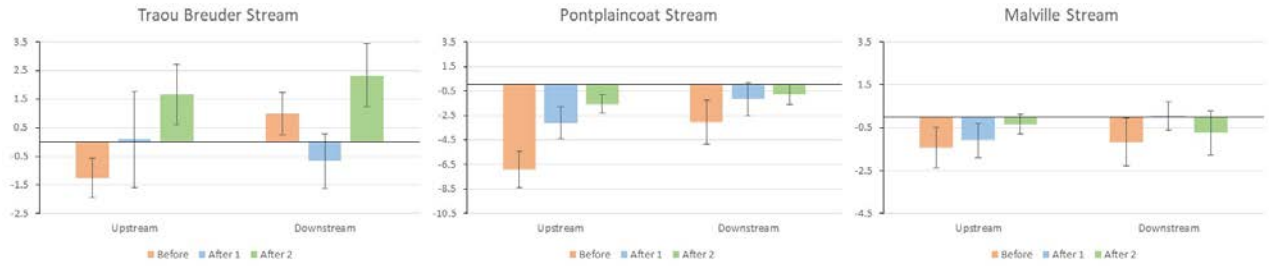


Fig 4. Annual mean deviation (± SE) from the mean taxonomic richness in the "control" sites before and after restoration (Before: before restoration; after1: first year of monitoring after restoration; after2: second year of monitoring after restoration).

Assessment of community structure

The results of Bray-Curtis similarities of macroinvertebrate communities between each sampling site in the streams were very heterogeneous before restoration and after restoration (Table 4). Before restoration, in Traou Breuder, there was no difference in the Bray-Curtis similarities between the macroinvertebrate community in the control and the upstream ($p = 0.185$) or downstream sites ($p = 0.084$) but a weak difference between the upstream and the downstream section ($p = 0.034$). In the Pontplaincoat, the upstream section was significantly different from the control ($p= 0.001$) and downstream section ($p = 0.001$) but control and downstream sections were similar ($p = 0.064$). In the Malville Stream, control and upstream sections were similar ($p= 0.117$) but the downstream section significantly differed from the other sections (p values = 0.001).

After restoration, all differences between sites disappeared after two years, remained similar in Pontplaincoat but slightly increased in Traou Breuder (Table 4).

Table 4. Results of PERMONAVAs on the Bray-Curtis similarities between macroinvertebrate communities before and after restoration (Before: before restoration; after1: first year of monitoring after restoration; after2: second year of monitoring after restoration).

		Traou Breuder Stream		PontPlaincoat Stream		Malville Stream	
		t	p	t	p	t	p
Before	Control / upstream	1.304	0.084	2.621	**0.001**	1.245	0.117
	Control / downstream	1.152	0.185	1.368	0.064	2.380	**0.001**
	Upstream / downstream	1.368	**0.034**	2.370	**0.001**	2.621	**0.001**
After 1	Control / upstream	1.141	0.214	1.573	**0.02**	1.073	0.304
	Control / downstream	1.276	0.136	1.324	0.085	1.637	**0.003**
	Upstream / downstream	1.529	**0.027**	2.017	**0.002**	1.172	0.16
After 2	Control / upstream	1.386	**0.040**	1.631	**0.009**	0.914	0.577
	Control / downstream	1.000	0.379	1.362	**0.051**	1.077	0.296
	Upstream / downstream	1.496	**0.033**	1.769	**0.003**	1.208	0.155

Ecological Risk Assessment (ERA) tool

The ERA tool identified 12 anthropic pressures: transportation facilities, organic matter, nitrogen compounds, phosphorous compounds, hydrological instability, urbanization, pesticides, polycyclic aromatic hydrocarbons (PAH), clogging, nitrates, catchment anthropization, and riverine vegetation.

The first two principal components of the PCA explained respectively 55.5% and 25.5% of the total variance (Fig. 5A). The first component was mainly explained by six anthropic pressures: clogging at 13.20%, catchment anthropization at 12.06%, nitrates at 11.73%, PAH at 11.44%, pesticides at 9.93%, and urbanization at 9.88%. The second component was mainly explained by five other anthropic pressures: transportation facilities at 21.29%, organic matter at 21.06%, nitrogen compounds at 17.33%, phosphorous compounds at 7.29%, and riverine vegetation at 8.76%. The first principal component of the PCA is related to watershed chemical perturbations

and sediment clogging whereas the second principal component is related mainly to riparian vegetation and nutrients (Fig. 5B).

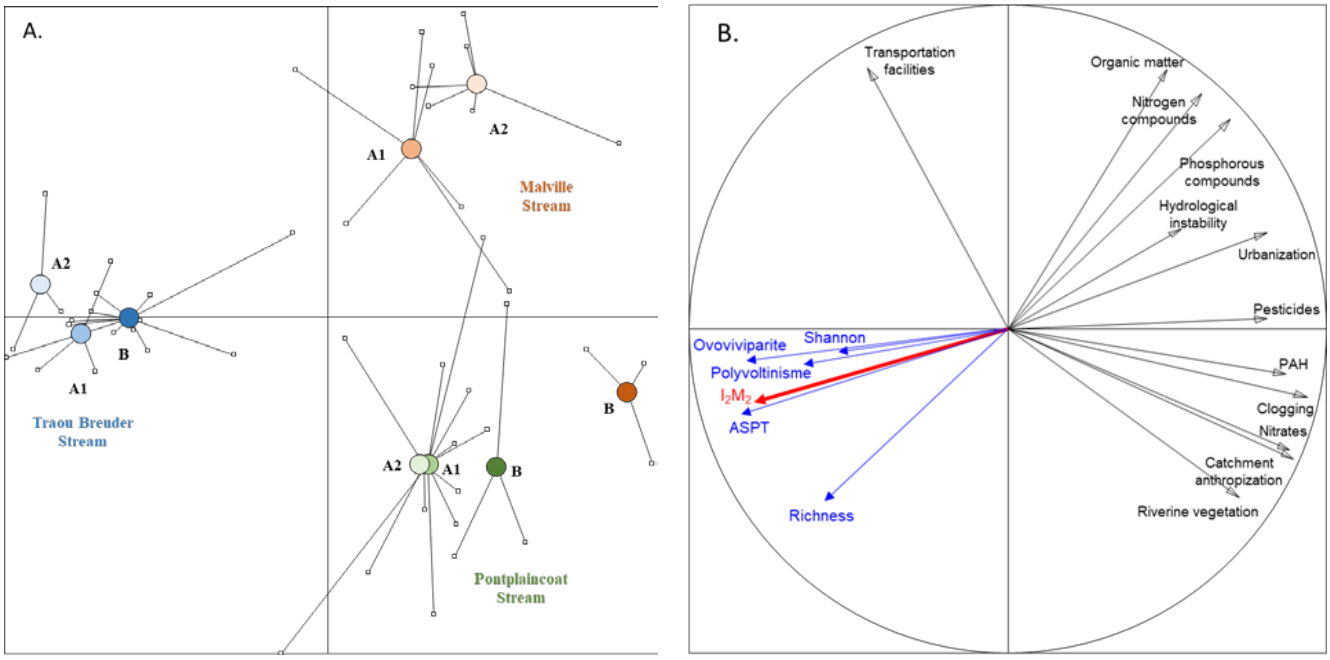


Figure 5. A. Principal Component Analysis (PCA) of the three sites according to the different anthropic pressures identified by the ERA tool. The colored circles represent the barycenters of the sessions (A: after restoration, B: before restoration). B. Correlation circle showing correlations among the 12 water quality and habitat degradation pressure categories retained (PAH: polycyclic aromatic hydrocarbons). The I_2M_2 (red arrow) and the five taxonomy-based metrics (blue arrows) are projected as quantitative supplementary variables (ASPT: Average Score Per Taxon, Richness: taxonomic richness, Shannon: Shannon's diversity index, Ovoviviparity: relative abundance of ovoviviparous species, polyvoltinism: relative abundance of the polyvoltine species).

These results were confirmed by the Spearman correlation tests (Fig. 6). The I_2M_2 and the five associated metrics were significantly positively correlated. The six main anthropic pressures explaining the first axis of the PCA were also significantly positively correlated. Among the five main anthropic pressures explaining the second axis of the PCA, the organic matter, nitrogen compounds, and phosphorous compounds were highly positively and significantly correlated, riverine vegetation and transportation facilities were significantly negatively correlated.

The I_2M_2 and the five associated metrics showed significant negative correlations with the 11 anthropic pressures; only 2 non-significant relations occurred (top right part of Fig. 6). richness and Shannon index did not correlate with the degradation from riverine vegetation and organic matter respectively, and the transportation facilities, without any correlation except with the ovoviviparity.

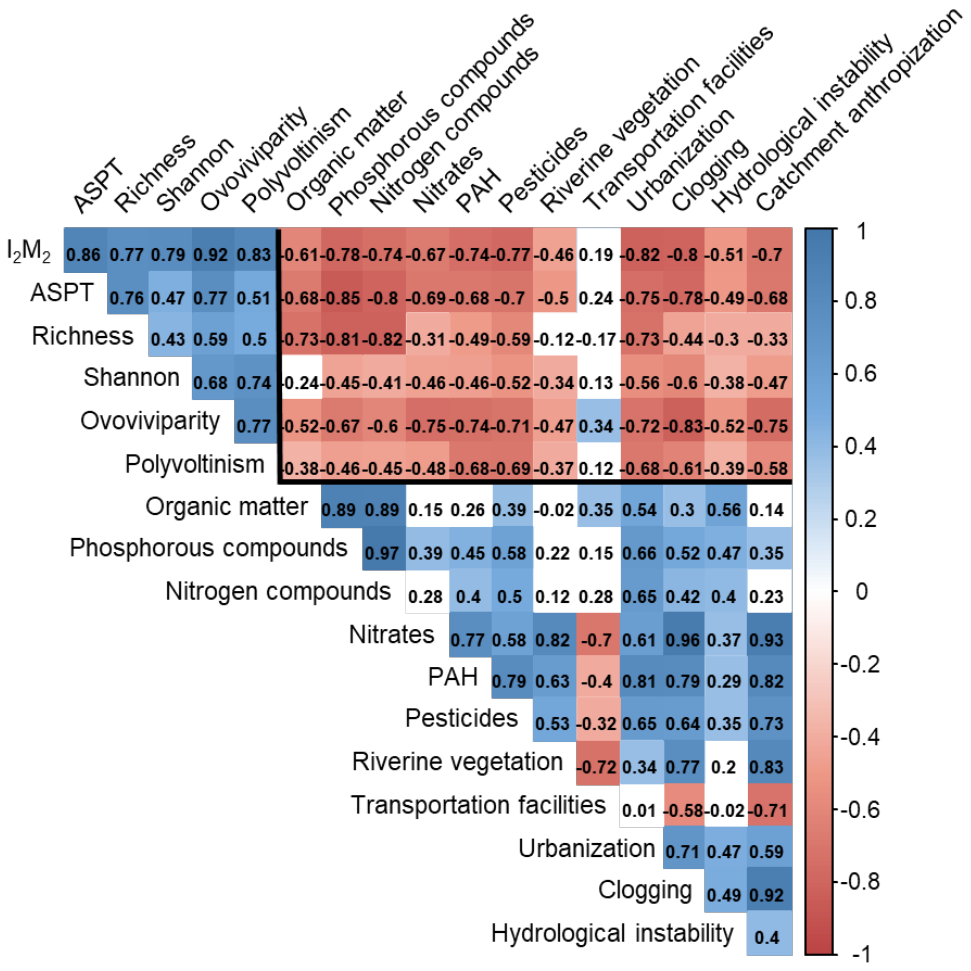


Figure 6. Spearman correlations between the I_2M_2, the five taxonomy-based and trait-based metrics in terms of Ecological Quality Ratio (ASPT: Average Score Per Taxon, Richness: taxonomic richness, Shannon: Shannon's diversity index, Ovoviviparity: relative abundance of ovoviviparous species, polyvoltinism: relative abundance of the polyvoltine species) and the 12 water quality and habitat degradation pressure categories (PAH: polycyclic aromatic hydrocarbons). The values represent the correlation coefficients. The colored squares represent the significant coefficients (red or blue, p-value <0.05) according to the scale of the values indicated on the right of the correlogram. The black lines are used to visually separate the I_2M_2, the five taxonomy-based and trait-based metrics from the 12 water quality and habitat degradation pressure categories.

Before restoration, the probabilities of impact by the different anthropic pressures at Traou Breuder was relatively low compared to the other two streams and presented the highest ecological status as suggested by the values of I_2M_2 and other metrics (Fig. 5A). Pontplaincoat was located in the lower right/down part of the PCA, mainly characterized by a high probability of clogging, catchment anthropization, strong nitrates inputs, and degradation of riverine vegetation. Finally, Malville, located at the right side of the axis, was characterized by a high probability of PAH, clogging, nitrates, catchment anthropization, and pesticides.

No significant effects of sampling sites (i.e. control, upstream and downstream section) and their interactions (Table 5). Tukey posthoc tests showed that the position of points significantly shifted one year after restoration and remained stable after two years.

Table 5. Results of the two-way ANOVA with random effects for the stream, the session, the sampling site, and their interaction on the two first dimensions of the PCA (Df = degree of freedom; F: F value; p: p-value)

		PC1		PC2	
	Df	F	p	F	p
Session	2	8.10	**0.001**	2.89	0.07
Sampling site	2	0.01	0.99	0.20	0.82
Session × sampling site	4	0.41	0.80	0.43	0.78

After restoration, the position of Traou Breuder and Pontplaincoat slightly shifted toward the left side of the first axis, confirming a decrease in the probabilities of the impacts of anthropogenic pressures on the two streams. Malville was the most influenced watershed with a strong shift in the probabilities of the different anthropic pressures before and after restoration. After restoration, the points highly shifted toward the top right part of the factorial

plan which indicated that a high probability of nutrient, organic matter compounds, and hydrological instability and a reduced probability of clogging, PAH, and anthropization.

Discussion

Irrespective of the complexity of restoration projects (Morandi *et al.*, 2014), assessing the outcome of river restoration projects is vital for adaptive management, evaluating project efficiency, optimizing future programs, and gaining public acceptance (Woolsey *et al.*, 2007). Although subjective criteria exist (Jähnig *et al.*, 2011), the development of indicators now makes it possible to evaluate the effects of restoration programs (Pander & Geist, 2013). In France, the I_2M_2 was built on more than 1700 sites, designed to identify impaired reaches, and to be compliant with the European WFD (Mondy *et al.*, 2012; Mondy & Usseglio-Polatera, 2013) as it can be used as a proxy to assess the ecological status of rivers (Corneil *et al.*, 2018). In this study, we go a step further and ask whether this index is also able to detect hydromorphological impacts on headwater streams under multiple pressures and the change in their ecological status after restoration. Associated to the I_2M_2, we also used the ecological risk assessment (ERA) tool (Mondy & Usseglio-Polatera, 2013; Mondy *et al.*, 2017) to establish the probabilities of impact by different anthropic pressures from the biological characteristics of benthic macroinvertebrate communities before and after restoration. The goal is to identify the potential weight of individual anthropogenic pressures influencing biotic assemblages in streams under multiple pressure scenario (Mondy & Usseglio-Polatera, 2013) in order to address the question of the efficiency of hydromorphological restoration widely used in headwaters.

Macroinvertebrate communities and the ecological status of headwater streams impacted by hydromorphological impairments

There is a clear difference in the overall ecological status at the watershed scale as depicted by the I_2M_2 which categorizes two streams (Malville and Pontplaincoat) as “poor” and Traou Breuder as “moderate”. The five macroinvertebrate metrics also differ from stream to stream. Three of these metrics; Shannon diversity index, Average Score Per Taxon (ASPT), and taxonomic richness are taxonomic metrics considered as the simplest measure of diversity (Stirling & Wilsey, 2001; Mendes *et al*., 2008). However, within the streams (i.e. at the reach scale), neither the ecological status nor the macroinvertebrate metrics have any important difference between sampling sites. These results indicate that the I_2M_2 and its associated metrics failed to highlight the impacts of physical impairments such as nozzles and weirs at the reach scale as there is no differentiation between “control”, “upstream”, and “downstream” sites before restoration. This is contradictory to a previous study showing that I_2M_2 was negatively influenced by variables describing hydromorphology at the reach scale (Corneil *et al*., 2018). This difference may be explained by the fact that while in their study, Corneil *et al*. considered hydromorphological factors at the reach scale, these factors are mostly different from the factors associated with the artificial structures responsible for the hydromorphological impairments in the streams investigated in our study. Also, our study focused on small impairments affecting watersheds over a few meters (from 30 to 200 meters long reaches). At this small scale, dispersal of invertebrate by drift or by flight remains possible and likely compensate for physical impacts (Piscart *et al.*, 2009).

Ecological status and biodiversity indices in response to hydromorphological restoration

We expected an improvement in the ecological status of restored sites after restoration (Hypothesis 1) and more specifically, we expected that the ecological status of the restored sites will be comparable to the reference conditions at the control sites. The ecological status of the streams changed positively only in Traou Breuder from “Moderate” to “Good”, but the status in Pontplaincoat remained “Poor” after restoration and changed from “Poor” to “Bad” in Malville. This result indicates that the estimation of the I_2M_2 -based ecological quality ratio in each stream is dependent on the totality of the factors (water quality, nutrient, hydromorphological, etc.) in the streams and not just only on the hydromorphological impacts of the artificial structures. Corneil *et al*. (2018) made a similar observation and concluded that the I_2M_2 was more strongly influenced by physical and chemical pressures than by hydromorphological impacts.

Also, the I_2M_2 based taxonomic metrics show that only richness has a positive change after restoration with the mean values of the impacted sites closest to reference conditions in each stream 2 years after restoration and even exceeding the reference condition in Traou Breuder in the second year after restoration while there is no observable change in diversity and other taxonomic indices. Miller *et al*. (2010) also observed positive effects of in-stream restoration on macroinvertebrate richness and inconclusive effects on density. In addition, the PERMANOVA on the Bray-Curtis similarities indicates that there is no consistent pattern in the overall similarities in macroinvertebrate community structure between the control sites and the impacted sites in the streams both before and after restoration. This scanty and inconsistent response of macroinvertebrate communities to in-stream restorations has been observed in previous studies (e.g. Palmer *et al.*, 2010; Miller, Budy & Schmidt, 2010b; Kail *et al.*, 2015). Even in the stream where there is an observable improvement in the ecological status after restoration, only taxonomic richness has a corresponding significant increase with other indices showing only minimal changes. One possible reason to explain this lack of robust response by

macroinvertebrate communities to in-stream restorations is the presence of other stressors which are not simultaneously addressed by most restoration strategies (Palmer *et al.*, 2010; Leps *et al.*, 2015). The removal of the artificial structures in the investigated streams in this study is expected to restore natural flow and enhance sediment transport thus improving the habitat conditions in the restored reaches. This strategy, however, has minimal to no effect on the other anthropic pressures (including water quality and nutrient load) present in the watersheds. This point is supported by our findings from the ERA tool which reported the presence of multiple anthropic pressures in the three watersheds both before and after restoration. In Malville, for example, the ERA result reported a reduced probability of clogging after restoration but a higher probability of nutrient and organic matter loading.

Disentangling the impacts of multiple anthropic pressures on the ecological status and the response of macroinvertebrate communities to hydromorphological restoration

Every stream is subject to natural variations of both the biotic and abiotic components (Palmer, Hakenkamp & Nelson-Baker, 1997; Palmer *et al.*, 2005). The ability to maintain this variation at the permissible level for the continuous functioning of the system is inhibited in degraded streams usually due to the presence of multiple stressors (Vörösmarty *et al.*, 2010). The unbundling of these stressors will be key to the proper and sustainable restoration of such a system. The simultaneous use of the ERA tool and the I_2M_2 multimetrics in our analyses presents a potential to be able to disentangle the impacts of the artificial structures from other anthropic pressures. Using the ERA tool, we identified 12 anthropic pressures: transportation facilities, organic matter, nitrogen compounds, phosphorous compounds, hydrological instability, urbanization, pesticides, polycyclic aromatic hydrocarbons (PAH), clogging, nitrates, catchment anthropization, and riverine vegetation present at the watersheds at different

probabilities of impact before and after restoration. This is in addition to the impacts of the presence of the artificial structures before their removal. We found that the I_2M_2 and associated metrics generally have a negative relationship with 10 of these anthropic pressures indicating that their presence adversely affects the ecological status of the streams and consequently the macroinvertebrate communities (Mondy, Muñoz & Dolédec, 2016). Moreover, the most important impacts suggested by the analysis of the probability of impacts for each stream are consistent with the supposed impacts relating to the land use as a proxy for watershed-scale conditions (Piscart *et al.*, 2009; Miller *et al.*, 2010b; Piscart *et al.*, 2011). We equally found differentiation between the probability of impacts before and after restoration. Before restoration, the ERA tool clearly separates Traou Breuder from Malville and Pontplaincoat and highlights a gradient of anthropic pressure as the main factors discriminating streams. This is consistent with the nature and intensity of stress observed on those streams. After restoration, the probabilities of impact by different anthropic pressures identified by the ecological risk assessment (ERA) tool decreased in Traou Breuder and Pontplaincoat, suggesting that hydromorphological restoration can increase the overall quality of a watershed even if other pressures (ie. nutrient or chemical pollution) are still present. In Malville, there is a drastic change in the main anthropic pressures identified by the ERA tool. Before restoration, the main pressures identified were clogging, alteration of riverine vegetation, and anthropization of the catchment. After restoration, the main pressures are hydrological instability and organic matter. These changes are consistent with our observation on the stream after restoration which had strong impacts of erosion and increased summer drying. The ERA tool is hence able to highlight not only the main visible pressure but also unexpected negative consequences of hydromorphological restoration. In addition, the results from the ERA tool indicate that the removal of the artificial structures in the streams is generally successful in removing the impact of clogging which was the main identified impact of the presence of the structures (Beschta &

Jackson, 1979; Gayraud & Philippe, 2001) and this is most visible in Malville. However, the persistence of the impacts of chemical compounds and nutrient load in the watersheds even after restoration may have been responsible for the scanty improvement in macroinvertebrate biodiversity indices. Water quality has been shown to have more influence on the community structure of macroinvertebrates than other factors including habitat availability (Roy *et al.*, 2003; Moerke & Lamberti, 2004; Kail, Arle & Jähnig, 2012).

Conclusions

The prediction and distinction of the effects of multiple potential stressors represent a serious practical need for prioritizing management options to efficiently enhance river reach ecological quality (Ippolito *et al.*, 2010). Our study highlights that the presence of these confounding factors can potentially limit the gains from hydromorphological restoration. Like in most other restoration activities in streams, the restoration works monitored in this study were done at the reach scale whereas most available macroinvertebrate-based assessment tools, including the I_2M_2 and the ERA, for measuring the impacts of multiple pressures on the ecological status of streams are most effective at the watershed scale (Friberg, Sandin & Pedersen, 2009). Hence, despite observing significant differences between streams in most of the metrics, the contributions of the reach scale changes to these differences were not detected.

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Chapter 3

CHAPTER 3: Ecological processes as functional indicators of ecological recovery

Summary

The previous chapter reports on the evolution of macroinvertebrate community structure in the restored streams. The current chapter proposes two ecological processes – leaf litter decomposition and streambed oxygenation as indicators of ecological recovery in headwater streams following hydromorphological restoration. It mainly addresses question 2 of this thesis and it contains two articles i.e. articles 2 and 3. Article 2 has been published in the journal *Water* with the digital object identifier: https://doi.org/10.3390/w13162246 while article 3 is still a draft.

Leaf litter decomposition is an integrative ecosystem-level process that forms the base of the energy pyramid in forested streams where energy from autotrophic sources is limited by forest shading. It is mediated by a combination of biotic and abiotic actors in the ecosystem and has been used extensively to monitor the ecological status of terrestrial and aquatic ecosystems at different spatio-temporal scales. However, information about the factors influencing the rate of litter decomposition at the riffle mesohabitat scale in streams remains scarce and thus its variability at this scale remains largely sketchy. In article 2, the litter bag experiment was conducted in six successive riffles in 9 streams to determine the natural variability of decomposition rate and the factors influencing this at the riffle scale. The result of this experiment shows that in-stream variability could be as high as variability between streams and that this variability is sensitive to local factors at the riffle scale, with streambed roughness being negatively related to decomposition rate and was the most important factor at the riffle scale. This observation confirms the sensitivity of the litter bag assay to local habitat factors and can thus potentially be useful in monitoring ecological response at such local scale as the riffle to environmental perturbations - including restoration activities in headwater streams.

In article 3, leaf litter decomposition rate and an abiotic ecological process – streambed oxygenation depth are defined as functional indicators of ecological recovery following restoration activities involving the removal of artificial barriers in headwater streams. The artificial structures which constituted partial barriers on three degraded headwater stream sections were removed and we followed the two indicators on each stream before and after the removal of the structures. We hypothesized that the barriers will have negative impacts on litter decomposition rate and streambed oxygenation as a result of sediment clogging. For each of the indicators, we compared values, both before and after the restoration works, on the impacted sections of each stream with values from the control sites that were established on the streams.

We observed a significant impact of the artificial structures on streambed oxygenation and only a slight impact on litter decomposition rate. We also observed that time could be very important in the recovery dynamics of restored streams as decomposition rates in the restored stream sections approached reference values only in the second year after restoration while streambed oxygenation progressively approached reference values from the first year after restoration. Litter decomposition rate also shows a stronger affinity with species life-history traits than to biodiversity indices.

Résumé

Le chapitre précédent rapporte l'évolution de la structure de la communauté des macroinvertébrés et des traits des espèces dans les cours d'eau restaurés. Le chapitre actuel propose deux processus écologiques - la décomposition des feuilles et l'oxygénation du lit du cours d'eau - comme indicateurs du rétablissement écologique dans les cours d'eau de tête de basin versant après une restauration hydromorphologique. Il répond principalement à la question 2 de cette thèse et il contient deux articles, à savoir les articles 2 et 3. L'article 2 a été

publié dans la revue *Water* (https://doi.org/10.3390/w13162246), l'article 3 est sous forme de draft.

La décomposition des feuilles est un processus intégratif au niveau de l'écosystème qui forme la base de la pyramide énergétique dans les cours d'eau forestiers où l'énergie provenant de sources autotrophes est limitée par l'ombrage de la forêt. Elle est médiée par une combinaison de facteurs biotiques et abiotiques dans l'écosystème et a été largement utilisée pour surveiller l'état écologique des écosystèmes terrestres et aquatiques à différentes échelles spatio-temporelles. Cependant, les informations sur les facteurs influençant le taux de décomposition de la litière à l'échelle du mésohabitat du radier des cours d'eau restent rares et donc sa variabilité à cette échelle reste largement méconnue. Dans l'article 2, l'expérience sacs de décomposition a été menée dans six radiers successifs au sein de 9 cours d'eau afin de déterminer la variabilité naturelle du taux de décomposition et les facteurs d'influence à l'échelle du radier. Les résultats de cette expérience montrent que la variabilité au sein des cours d'eau peut être aussi élevée que la variabilité entre les cours d'eau et que cette variabilité est sensible aux facteurs locaux à l'échelle du radier. La rugosité du lit du cours d'eau étant négativement liée au taux de décomposition et représentant le facteur le plus important à l'échelle du radier. Cette observation confirme la sensibilité de la decomposition de la litière aux facteurs locaux et peut donc être un indicateur utile dans le cadre du suivi de la réponse écologique des cours d'eau à une échelle aussi locale que celle du radier dans un context de perturbations environnementales comme les activités de restauration dans les cours d'eau de tête de basin versant.

Dans l'article 3, le taux de décomposition de la litière et un processus écologique abiotique (la profondeur d'oxygénation du lit du cours d'eau) sont définis comme des indicateurs fonctionnels de la restauration écologique des cours d'eau de tête de bassin versant suite à une restauration impliquant la suppression des barrières artificielles. Les structures artificielles qui

constituaient des barrières partielles sur trois sections de cours d'eau dégradés ont été retirées et nous avons suivi les deux indicateurs sur chaque cours d'eau avant et après le retrait des structures. Nous avons émis l'hypothèse que les barrières ont un impact négatif sur le taux de décomposition de la litière et sur l'oxygénation du lit du cours d'eau en raison du colmatage des sédiments. Pour chacun des indicateurs, nous avons comparé les valeurs sur les sections concernées de chaque cours d'eau avec les valeurs des sites de contrôle qui ont été établis sur les cours d'eau avant et après les travaux de restauration.

Nous avons observé un impact significatif des structures artificielles sur l'oxygénation et seulement un faible impact sur le taux de décomposition de la litière. Nous avons également observé que le l'aspect temporel pouvait être important dans la dynamique de restauration des cours d'eau, car les taux de décomposition dans les sections de cours d'eau restaurées ne se sont rapprochés des valeurs de référence qu'au cours de la deuxième année après la restauration. L'oxygénation du cours d'eau s'est, elle progressivement rapprochée des valeurs de référence dès la première année après la restauration. Le taux de décomposition de la litière présente également une plus grande affinité avec les traits du cycle de vie des espèces qu'avec les indices de biodiversité.

Article 2: In-stream variability of litter breakdown and consequences on environmental monitoring

In-stream variability of litter breakdown and consequences on environmental monitoring

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Abstract

Energy derived from leaf litter decomposition fuels food webs in forested streams. However, the natural spatial variability of the decomposition rate of leaf litter and the relative contributions of its drivers are poorly known at the local scale. This study aims to determine the natural in-stream variability of leaf litter decomposition rates in successive riffles and to quantify the factors involved in this key ecosystem process at the local scale. Experiments were conducted on six successive riffles in nine streams in north-western France to monitor the decomposition rate in fine (microbial decomposition, k_f) and coarse (total decomposition, k_c) mesh bags. We recorded 30 ± 2% (mean ± S.E.) variation in k_c among riffles and 43 ± 4% among streams. k_f variability was 15 ± 1% among riffles and 20 ± 3% among streams. However, in-stream variability was higher than between-stream variability in four of the nine streams. Streambed roughness was negatively related to decomposition and was the most important factor for both total and microbial decomposition. Our study shows that the natural variability of the decomposition rate resulting from the local morphological conditions of habitats could be very important and should be taken into consideration in studies using leaf litter assays as a bio-indicator of anthropogenic impacts in streams.

Keywords: Organic matter recycling; natural variability; leaf litter decomposition; geomorphological factors

Introduction

Energy deficit resulting from canopy shading in forested streams is partly compensated by allochthonous inputs of leaf litter from riparian vegetation [1-4]. Energy from leaf litter is incorporated following a sequence of interdependent processes that include leaching by flowing water, conditioning by aquatic microbes, physical abrasion, and consumption by macroinvertebrate shredders [5]. Colonization of litter by microorganisms reduces its toughness [6-8], increases leaf quality and nutrient content [9], and thereby litter palatability for macroinvertebrate shredders [7,10-11]. Macroinvertebrate shredders turn coarse particulate matter into fine particulate matter and dissolved organic matter that is later consumed by other aquatic invertebrates [10,12-14] and microbes [15,16].

Litter breakdown has been proposed [17] and is widely used as an indicator tool of the ecological status of streams with evident results [18-27] because of the relative ease of implementing the leaf litter assay and the fundamental role leaf litter plays in the trophic structure of headwater streams. Nevertheless, litter breakdown is a complex process influenced by both internal (in-stream) and external (climatic and anthropogenic) environmental factors. This makes it difficult to disentangle the effects of anthropogenic stressors from those of natural variability in impacted systems [17]. In the latter study, authors suggested standardization of the assessment procedure and a possible stream classification and/or comparative approach as means of untangling the effects of internal environmental factors from those of anthropogenic stressors. However, these factors also react at different temporal and spatial scales (mesohabitat, reach, catchment, and region) [28-31], hence, it is important to determine not only the factors involved but also the scale at which they respond [28]. At the global and regional scales, climatic and geological factors are very important for water quality

and hydrological conditions [32]. For instance, previous research has found that the decomposition rate is low and mostly driven by microbial activity in tropical streams with warmer waters where invertebrate detritivores are less diverse [33] than in temperate streams. Furthermore, nutrient concentrations resulting from geological formation influence the heterotrophic microbial biomass available for decomposition [34]. At the catchment scale, where climatic and geological conditions are more homogeneous, stream size (or stream order), land use, and other related factors impact litter breakdown rates [23,29,35]. The range of habitats at the reach scale and the different substrate structures and sizes influence the litter trapping efficiency of those mesohabitats [36,37]. At the riffle mesohabitat scale, flow [38] could combine synergistically with substrate roughness to increase physical abrasion [39] and thereby increase the litter breakdown rate. Finally, at the litter patch scale, the composition of leaves [7] and leaf litter mixing [40] may deeply change the breakdown rate.

While the factors at play in the ecosystem function are hierarchical, the actual sites where these processes take place are the mesohabitats, and local factors may drive the processes at this very fine scale. Some authors hence chose the riffle as the primary habitat to examine the spatial trend of decomposition rates across nested habitats [29]. However, and surprisingly to the best of our knowledge, very few studies have addressed the natural instream variability, and no studies focussed on riffles.

In this context, our study aimed to quantify the natural variability of decomposition rates over the few meters corresponding to the distance between successive riffles. Significant in-stream variability may indeed strongly impair the efficiency of monitoring programs using litter decomposition as a bio-indicator. We hence selected sites in similar and weakly altered watersheds to standardize external environmental factors including anthropogenic stressors i) to determine the natural in-stream variability of decomposition rates at the local scale, ii)

quantify the interacting factors that drive the process, and iii) compare the magnitude of this variability with the between-stream variability.

Our experiment was conducted in nine streams and 6 successive riffles per stream, all located in natural watersheds. We expected riffles located within any given watershed over a short distance (i.e. few meters) to be identical in terms of water chemistry and temperature, but their hydrological conditions could strongly vary according to other physical factors (e.g. stream slope and width). Based on this physical heterogeneity, we predicted that in-stream variability in small heterogeneous streams may be in the same range as between-stream variability [41]. Secondly, we predicted that the in-stream variability of the rates of decomposition by microorganisms would be higher than the rates of decomposition by invertebrates. Microbial activities in streams are indeed mediated at the microhabitat scale, while the activities of macroinvertebrates are less impacted at this scale because of their ability to swim or drift over a few meters, which may reduce the spatial heterogeneity at the reach scale [22]. Lastly, we predicted that several physical factors mediating the variability of litter breakdown would be the same for invertebrate litter breakdown as in microbial decomposition. Though microorganism activities are mainly regulated by sediment organic content, sediment size, nutrient content, and temperature [22,23], the distribution of these abiotic factors and invertebrate communities are both influenced by flow, among other factors [42].

Materials and Methods

Study sites

A leaf litter decomposition experiment was carried out in nine streams (Figure 1) ranging from the 1st to the 3rd orders in Strahler's classification and located in north-western France. We established six successive riffles on each stream, selected in the same reach and a

few meters apart in the first-order streams, and located up to 30 meters apart in the third-order streams. The sites were selected to standardize anthropogenic stressors (nutrient loading, land use, canopy cover, industrial and domestic seepage, etc.). Consequently, the riffles were sited in natural watersheds without dense canopy cover by riparian trees and were similar in terms of physicochemical parameters such as temperature, pH, conductivity, and oxygen saturation (Table 1) and also had similar riparian vegetation mainly composed of deciduous tree species (oak, alder, and chestnut) and grassland to avoid any strong effect of these factors. The riffles were examined visually to ensure that the stretch of microhabitats was as highly diverse as possible and adequately representative of the streams.

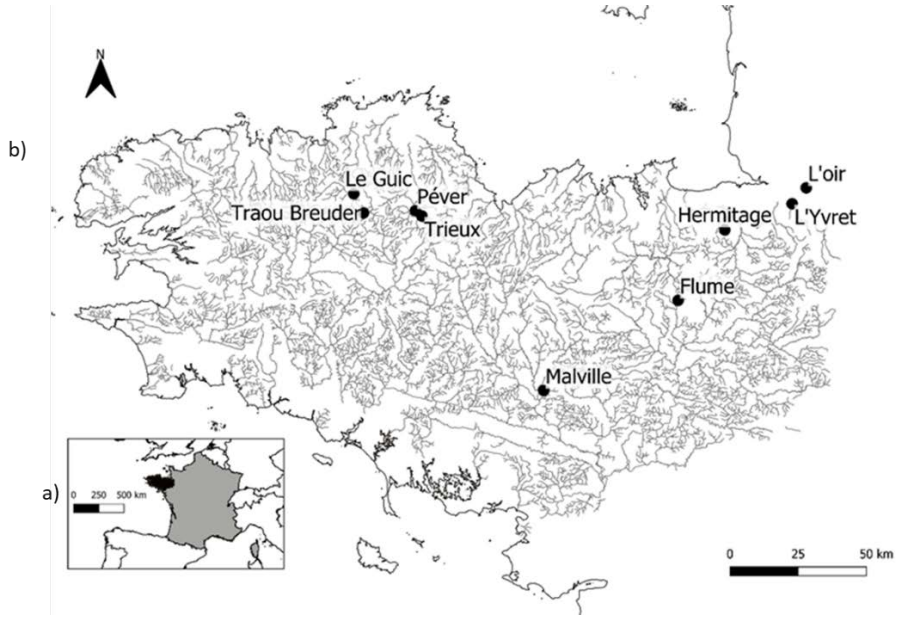


Figure 1. Maps of a) France with administrative regions, and b) the study area showing the localizations of the 9 streams. Black lines represent stream networks.

Table 1. Mean (±SE) values of the physico-chemical characteristics of the 9 streams (number between brackets corresponds to the stream order) during the leaf litter experiment.

Streams (Strahler order)	O_2 saturation (%)	Temperature (°C)	pH	Electrical Conductivity (µs/cm)
Trieux (3)	99.3±3.0	7.8±0.5	8.4±0.8	205±3
Hermitage (1)	93.4±0	13.2±0.3	9.3±1.0	152±2
Le Guic (3)	94.2±0.3	9.7±0.7	8.7±1.8	113±4
Traou Breuder (1)	90.5± 0	10.8±0	8.7±1.1	178±1
Malville (2)	88.2±7.6	9.9±0.3	7.9±0.5	305±43
L'oir (2)	100.4±0.9	9.2±0.5	7.2±0.3	194±8
Flume (2)	113.8±10.6	11.9±1.0	8.9±1.1	356±18
Péver (2)	92.4± 0	9.4±0.6	9.0±1.5	233± 0
L'Yvret (1)	97.5± 0	10.0±0.4	7.5±0.3	240±5

Litter decomposition

Freshly abscised alder leaves (*Alnus glutinosa* (L.) Gaertn) collected between mid-November and mid-December 2018 were air-dried at room temperature in the laboratory. Known weights – W_o (2.06 ± 0.001 g) – of dried leaves were remoistened and enclosed in coarse-mesh (5 mm mesh size) 10 x 10 cm plastic bags or fine-mesh (0.5 mm mesh size) 10 x 10 cm nylon bags. The coarse bags allow access to shredders and microbes, while the fine bags only allow access to microbes. This way, total decomposition (k_c) and contribution from microbial conditioning and other background variables such as leaching, physical abrasion, sediment loads and other hydraulic factors (k_f, later referred to as microbial decomposition) can be estimated, respectively [22]. In total, 540 bags (2 types of bags x 5 replicates x 6 riffles

x 9 streams) were exposed at the same dates in all the sites in the spring of 2019. The bags were staked at random locations throughout each riffle in pairs of coarse and fine mesh bags to the stream bed using an inverted J-shaped iron rod. The anchored edges of the two bags were placed at a right angle to each other so that the bags did not overlap but rather rested on the substrate. The bags were retrieved after 14 days, transported, and sealed in zip-lock bags in a box for storage in the laboratory at -20°C for further treatment.

In the laboratory, the remaining leaf material was thawed, gently rinsed with tap water to remove any accumulated debris and mud. The leaf residue was air-dried to constant weight (generally 3 days at room temperature), weighed, and incinerated at 550°C for 4 hours to obtain the Ash Free Dry Mass, AFDM (W_t). Decomposition rates, k_c (coarse-mesh bags), and k_f (fine-mesh bags) were calculated using the negative exponential decay model as shown in Equation 1 [1]:

$$k = [\ln(Wt/Wo)]/t \quad (1)$$

where t is the exposure time in days.

The litter fragmentation rate – λF – was calculated from values of k_c and k_f according to Lecerf [43] (Equation 2):

$$\lambda F = kc - \frac{kf - kc}{\ln(kf) - \ln(kc)} \quad (2)$$

We also computed the ratio *kf* : *kc* as a descriptor of the relative contributions of microorganisms to the total decomposition rate and the ratio λF : k_c as a descriptor of the relative contributions of macroinvertebrates in the total decomposition rate.

Morphological factors

Stream width was estimated using the mean values of four transects established on each riffle. Width represents the distance between the tops of the left and right banks. Depending on the width of each transect, at least 12 points of equal interval were established on each transect to estimate the mean water depth ($N \geq 48$). This measurement was repeated at each of three visiting dates. We defined the depth-width ratio, a dimensionless factor, to avoid entering the two collinear factors in the same model [25]. For each of the 48 points, the water depth (i.e. the height between the surface of the water and the top of the substrate) was measured (± 5 mm) using a digital level (Leica Sprinter 250m Digital Level) in order to estimate the magnitude of bed roughness. The substrate roughness was estimated as the standard deviation of the 48 measured water depth. Indeed, previous studies found that at low relative depths, the blocking of flow area by roughness elements is shown to be related to the standard deviation of local bed surface heights [44].

The slope of each riffle was also measured using a digital level (Leica Sprinter 250m Digital Level) between the top of the riffle and the deepest part of the pool downstream riffle. We also estimated other physical factors such as shear stress as ρghs, where $h \equiv$ mean depth, $\rho \equiv$ weight density of water (1,000 $kg.m^{-3}$), $g \equiv$ gravity (9.81 $m.s^{-2}$), and $s \equiv$ water slope.

Water depth was very low in most of the streams (generally less than 15 cm) and turbulence was very high (minimum Reynolds' number 6,300) so that the measurement of flow velocity with a velocimeter was not possible. Consequently, we shot short videos of the water flow to estimate the surface flow velocity on each riffle and at each visit. The videos were analyzed using TracTrac PTV software developed in our laboratory [45]. The program tracks every moving object on the water surface and provides its mean displacement in pixels *per* frame. Mean displacement was converted into mean velocity in meters *per* second by multiplying each measurement by the frame rate of the camera and by a video scale determined on each riffle.

Macroinvertebrate sampling

Macroinvertebrate samples were collected using a Surber net sampler (0.05 m² and 0.5 mm mesh size). Surber sampler is efficient for quantitative measurements and in catching cryptic species. Substrate composition in each riffle was assessed visually, and four replicate samples of macroinvertebrates representing substrate composition were taken from each riffle. The samples were fixed in 96% ethanol in situ. In the laboratory, macroinvertebrates were separated from other materials, and debris was discarded. Among macroinvertebrates, shredders (mostly amphipods, trichopteran, and plecopteran larvae) were determined according to Tachel *et al*. [46], and their abundance was enumerated at the species level.

Statistical analyses

We performed a three-factor two-way nested ANOVA using decomposition rates as response variables, with riffles nested in streams and treatment (coarse and fine mesh bags) blocked within riffles to test the variability of decomposition rates among streams, riffles, and treatment. Coefficients of variation (CVs) computed either with the mean values *kc* and *kf* of each riffle (i.e. in-stream variability) or with the mean values *kc* and *kf* of each stream (i.e. between stream variability) were used to estimate the natural instream and between stream variabilities of leaf litter decomposition rates.

To analyze how physical factors measured at the riffle scale influence leaf litter (*kc* and *kf*), generalized linear models (GLMs) were performed. The mean riffle values of *kc* and *kf* were the response variables, while the mean riffle values of the physical factors were the explanatory variables in models. To avoid having two collinear factors in the same model [25], we conducted a collinearity check of the predictors using Spearman's rank correlation. High collinearity was assumed for r spearman ≥ 0.7 [47]. Thus, GLMs with Gaussian family were run for both *kc* and *kf*, with non-collinear physical factors as predictor variables. Model

selection was performed using the step function in the lmer package [48]. The models with the lowest Akaike's information criterion (AIC) score were considered as the best-fit models, and the amount of accounted deviance (D2) was estimated using the Dsquared function in the modEva package [49].

All data analyses were performed using R software, version 3.6.2. [50].

Results

In-stream and between-stream litter breakdown rates

The nested ANOVA showed that the mean value of *kc* (0.069 ± 0.007 $g.d^{-1}$) was significantly higher (Table 2) than the mean value of *kf* (0.021 ± 0.0004 $g.d^{-1}$).

Similarly, the CV of *kc* was significantly higher than the CV of *kf* ($F_{1,106} = 45.07$, $p < 0.001$).

Table 2. Results of the nested ANOVA testing decomposition rate according to the streams, riffles nested within streams; treatments (coarse and fine mesh bags) within riffles

	Degree of freedom	Sum of squares	Mean squares	F	P
Stream	8	0.34	0.04	41.85	<0.001
Riffle	5	0.005	0.001	1.04	0.395
Stream | Riffle	40	0.10	0.002	2.45	<0.001
Riffle | Treatment	6	0.28	0.05	16.94	<0.001

Decomposition rate significantly varied among riffles nested with streams (Table 2), with *kc* which presents a mean in-stream CV of 30 ± 2% (Figure 2), and between streams (Table 2), with a mean between streams CV of 43 ± 4%. Moreover, the in-stream CV of *kc* was higher than the between-stream CV in four of the nine streams (Péver, Guic, Trieux, and Flume) (Figure 2).

kf was also significantly different between streams (CV = 20 ± 3%), and to a lesser extent among riffles (CV = 15 ± 1%) (Table 2).

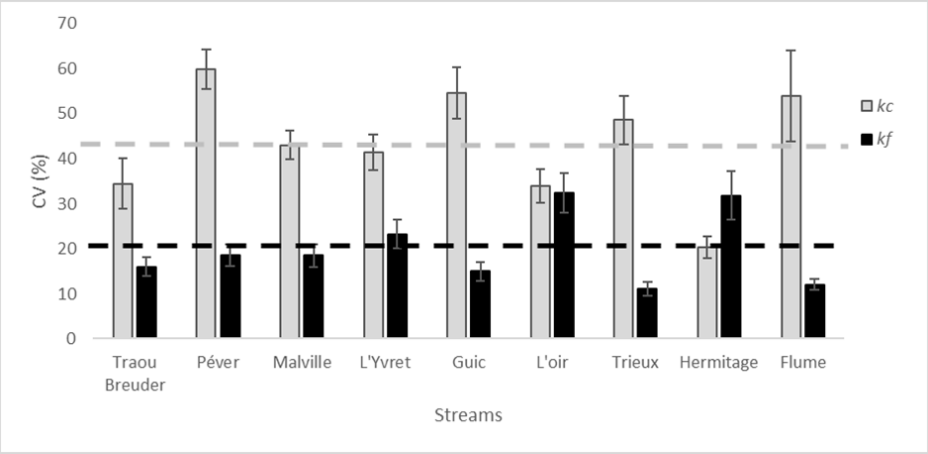


Figure 2. Mean ± SE in-stream variability measured by the coefficients of variation (CVs) of *kc* and *kf* for the 9 streams.

The between-riffle variability of *kc* was very high, and so was the decomposition rate among streams (Figure 3), whereas *kf* variability was more similar within streams than it was among streams (Figure 3).

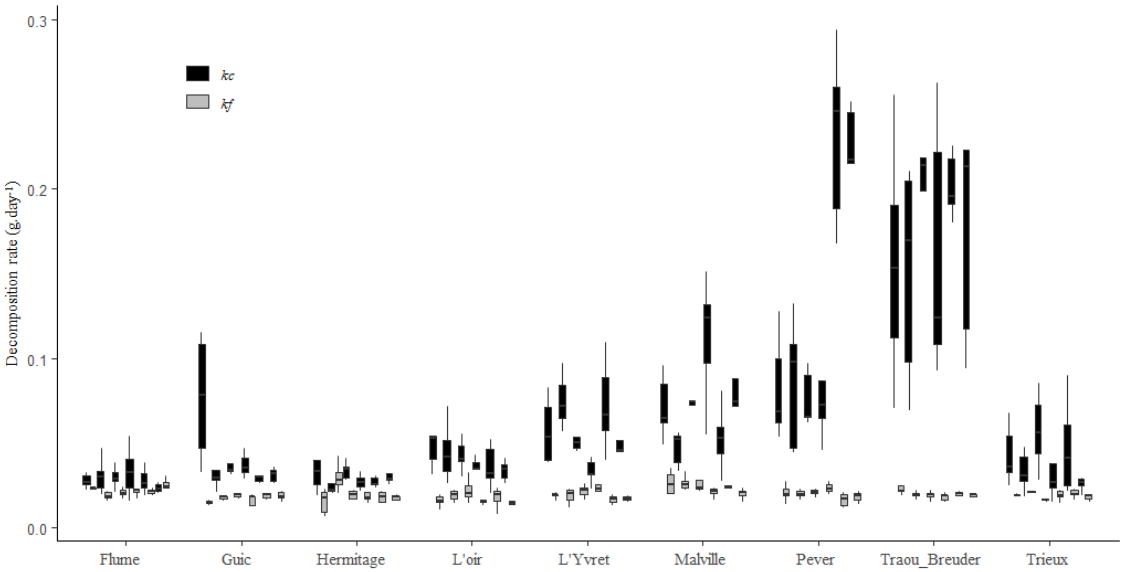


Figure 3. Mean values (± SE) of a) total decomposition (*kc*), and b) microbial decomposition (*kf*) in each riffle for the 9 streams

The ratio *kf* : *kc* was higher than the ratio λF : *kc* in five streams (Le Guic, L'oir, Trieux, Hermitage, and Flume Figure 4). This suggests that microbial activities in these streams contribute more to litter decomposition than invertebrate shredders.

We recorded a total of 12,320 shredders comprising 86% of crustaceans (mainly Amphipods and few Isopods), 11% of Plecoptera, 3% of Trichoptera (mainly Limnephilidae), and less than 1% of tipulid Dipterans. There was a positive correlation between kc and shredder abundance (rspearman = 0.48, $F1_{106} = 3.93$, $p<0.001$).

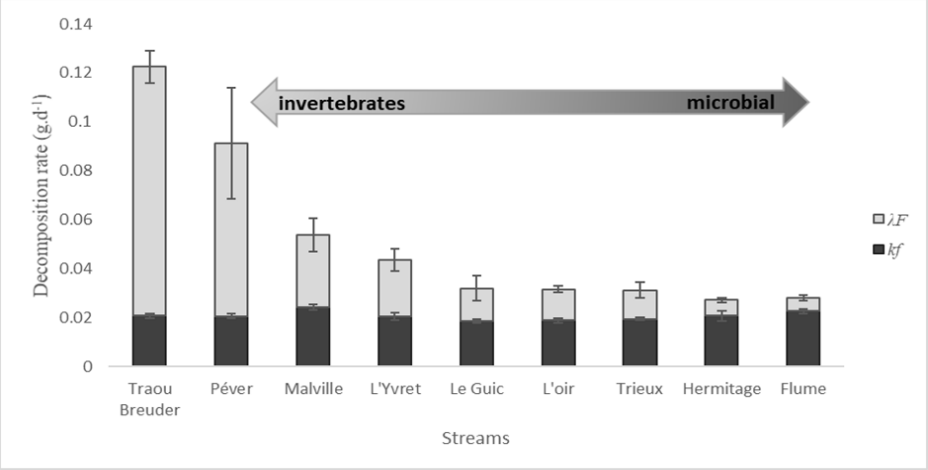


Fig. 4 Mean ± SE proportions of k_f and λ_F in total decomposition rate (k_c). Bars are ordered along the gradient of shredders' contribution to decomposition rates

Physical factors

The mean values and CVs of physical factors are presented in Table 3. There was high collinearity (rspearman ≥ 0.7) among physical factors (Table 4).

Table 3. Mean values (±SE) and coefficient of variation (CV) of morphological factors.

Site	*Depth (cm)*	*Slope*	*Bankfull Width (cm)*	*Roughness (cm)*	*Flow Velocity ($m.s^{-1}$)*	*Depth/Width*	*Shear Stress ($kg.m^{-1}s^{-2}$)*
Traou Breuder	4.7±0.3	-0.01±0.001	194±5	2.9±0.3	0.25±0.03	0.02±0.001	45.1±2.42
CV (%)	13.0	30.5	6.2	27.7	27.6	14.1	13.2
Péver	5.8±0.7	-0.01±0.004	308±19	4.7±0.49	0.26±0.04	0.02±0.003	56.1±6.8
CV (%)	28.9	37.8	15.3	25.6	36.8	35.3	29.7
Malville	10.7±0.9	-0.002±0.01	227±20	4.0±0.4	0.20±0.03	0.05±0.01	104±9.62
CV (%)	22.5	38.8	21.7	21.4	37.8	34.2	22.6
L'Yvret	7.6±0.6	-0.03±0.01	322±31	5.8±0.2	0.11±0.04	0.03±0.003	73.0±5.9
CV (%)	18.3	68.6	23.2	9.8	80.3	29.2	19.8
Le Guic	48.7±3.1	-0.003±0.002	1157±55	15.8±1.36	0.25±0.02	0.04±0.003	476.3±29.9
CV (%)	15.7	91.3	11.6	20.9	19.1	19.7	15.4
L'oir	8.3±0.1	-0.02±0.004	233±4.5	5.6±0.6	0.27±0.06	0.04±0.001	80.3±1.1
CV (%)	2.9	49.5	4.8	27.5	53.5	4.4	3.3
Trieux	30.9±3.7	-0.04±0.04	1069±52	14.1±1.2	0.26±0.04	0.03±0.004	294.8±39.8
CV (%)	29.1	209.5	11.9	21.1	32.6	32.6	33.0
Hermitage	8.0±0.4	-0.01±0.01	254±17	5.0±0.6	0.35±0.03	0.03±0.004	77.7±4.2
CV (%)	13.5	96.4	16.1	30.9	17.3	27.4	13.1
Flume	4.0±0.5	-0.03±0.01	278±15	4.0±0.6	0.29±0.07	0.01±0.001	37.9±4.7
CV (%)	29.0	68.4	13.2	33.9	54.4	23.2	30.4

Table 4. Spearman correlation coefficients (rspearman>0.7 in bold) between morphological factors

	Depth	*Slope*	*Bankfull Width*	*Roughness*	*Flow Velocity*	*Depth/Width*	*Shear Stress*
Depth	1.00						
Slope	-0.10	1.00					
Bankfull Width	**0.90**	0.03	1.00				
Roughness	**0.89**	0.02	**0.92**	1.00			
Flow Velocity	-0.05	-0.09	-0.03	0.04	1.00		
Depth/Width	0.47	-0.22	0.15	0.27	-0.13	1.00	
Shear Stress	**0.99**	-0.15	**0.90**	**0.89**	-0.05	0.47	1.00

The GLMs for *kc* and *kf* included four factors (slope, roughness, flow velocity, and depth/width ratio) preselected based on the correlation coefficient. There were no significant differences in the AIC scores of the selection models for either *kc* or *kf*, so the initial models containing the four preselected factors were retained as the best-fit models. D^2 was 0.18 and 0.13 for *kc* and *kf*, respectively. Among the morphological factors, only roughness was significantly related (negatively) to both *kc* and *kf* (Table 5).

Table 5. Results of the GLM of predictor variables on *kc* and *kf*

	P-value (*kc*)	**Estimate ± SE**	**P-value (*kf*)**	**Estimate ± SE**
Slope	0.41	-0.20 ± 0.24	0.77	-0.004 ± 0.01
Roughness	0.03	-0.003 ± 0.001	0.01	-0.0002 ± 0.0001
Flow velocity	0.19	-0.04 ± 0.03	0.10	-0.003 ± 0.002
Depth/Width	0.58	-0.32 ± 0.58	0.96	-0.001 ± 0.03

Discussion

In-stream and between-stream variability of decomposition rates

About in-stream and between-stream variabilities of decomposition rates, firstly we predicted that in-stream variability in small heterogeneous streams would be in the same range as between-stream variability [40]. Secondly, we predicted that the in-stream variability of the rates of decomposition by microorganisms would be higher than the rates of decomposition by invertebrates.

We highlighted that natural in-stream variability could be very high at the reach scale (in-stream CV up to 60%) even if chemical factors remain stable along our selected watersheds. This result confirmed our first prediction that in-stream variability may be in the same order or even higher (in four of the nine streams in our case) than between-stream variability. Tonin *et al*. suggested that such variability might be related to the canopy [51]. They reported a higher variability of decomposition rates among reaches than among watersheds along a canopy cover gradient where the area covered by canopy decreased from stream reaches to watersheds. However, in streams that present similar and low canopy coverage, as is the case in our study, the variability of litter breakdown rates could also be very high. Other morphological factors at the riffle scale such as geomorphology could strongly drive the leaf litter decomposition process in such systems [29,31]. In bio-assessment studies of impacted streams, this could constitute a natural source of variation difficult to account for and isolate from the variability due to anthropogenic stressors. One way to overcome this limitation could be a comparative approach of impacted versus unimpacted systems exhibiting similar natural characteristics, this condition being rarely encountered in most cases.

Secondly, we expected the variability of decomposition rates by microorganisms to be higher than the variability of the total litter breakdown rates. Microbial activities are indeed driven by local factors such as temperature [52], stream nutrient content [22,53,54], and fine sediment load [22]. While these factors are mostly temporal, they are largely spatially heterogeneous at the small, local scale at which this experiment was conducted. On the other

hand, total litter breakdown is (in addition to microbial conditioning) mediated by heterogeneous hydraulic factors as well as variable geomorphological habitat parameters, thus making the process patchy within stream riffles [55,56]. However, and contrary to our expectations, we found higher variability of the total litter breakdown (*kc*) than of microbial decomposition (*kf*). Moreover, in our study sites, the proportion of microbial decomposition in total breakdown was also less variable than breakdown by invertebrate shredders (λF). The fact that the variability of the decomposition rate was mostly due to the variability of the invertebrate breakdown could be due to the patchiness of detritivore distribution [57,58] and their sensitivity to hydromorphological parameters [58] that has been found in previous studies [22,29,60,61]. To explain the unexpected low microbial decomposition variability, one plausible reason for this may be the transport and distribution of fungal spores in streams by the water flow [62], resulting in the homogenization of leaf colonization by fungi. Secondly, the sites were mostly located in small natural watersheds, with minimal impacts of anthropogenic activities such that the chemical heterogeneity in terms of nutrient and sediment influx from the catchment basin was negligible. Therefore, our results are rather congruent with the observation of Colas *et al.* [25], who found that microorganisms react mainly at the catchment scale and less at the reach scale.

Explaining factors of decomposition rates

We expected that physical factors mediating the variability of litter breakdown would be the same for invertebrate litter breakdown as in microbial decomposition. Accordingly, with this assumption, we found that the physical factors mediating breakdown rates were the same for the total breakdown and microbial decomposition rates. The physical factors describable in riffle mesohabitats are largely responsible for resource retention and distribution [63] and consequently for the community structure of macroinvertebrates and microbes in riffles

[29,64]. Therefore, although the mechanisms and magnitude of interactions may not be the same, the hydromorphological factors influencing the two biotic agents (microbes and macroinvertebrates) of litter decomposition in streams appear to be the same. Although this is largely expected, it is noteworthy that only a small fraction of decomposition (<20% of deviation) can be explained by physical factors only. This suggests that invertebrate shredders likely remain the chief drivers of litter breakdown in streams. However, microorganisms, in half of our streams, mainly drove litter breakdown. Even though we did not measure the stream microbial load concentration, elevated microbial concentrations in streams are known drivers of litter decomposition [65-67].

More precisely, we found that among morphological factors, the most important factor for both total litter breakdown and microbial decomposition rates was the streambed roughness. The negative relationship between bed roughness and decomposition rates suggests a reduced decomposition rate when bed roughness is high. In lowland streams as in Brittany, and natural conditions, bed roughness is positively correlated with particle size and in turn to flow velocity. When bed roughness increases, leaf litter stocks are easily and quickly washed off [63], and cannot serve as habitats and feeding resources for shredders. In the same vein, shredders are generally less adapted to high flow velocity and prefer low velocities [46]. Whereas in riffles with low bed roughness, substrates can be smaller and more similar in size (mainly sand and gravel). This condition could be more suitable for litter storage. According to Bovil *et al*. [37], reaches dominated by gravels retain the highest stocks of coarse organic particulate matter, while the lowest retention is found in reaches dominated by cobbles; these authors suggested that channel retentiveness does not increase with channel roughness. It could also be more suitable for conditioning by microbes and colonization by shredders, and explain a faster decomposition rate by both invertebrates and microbes. This realization could have profound implications for the management of headwater streams where leaf litter stocks from

allochthonous sources occupy the base of the energy pyramid. Secondly, restoration efforts in impacted streams mostly involve activities that enhance habitat heterogeneity through the alteration of the geomorphological composition of the systems with post-project assessments of restored streams largely relying on biodiversity as a bio-assessment tool. The sensitivity of leaf litter assay to geomorphological factors within the habitats, as observed in this study, suggests it can serve a complementary role as an integrative ecosystem-level bio-assessment tool in restored systems.

Conclusions

This study highlights that the natural in-stream variability of leaf litter breakdown rate could reach or even overreach the between-stream variability. Our study underscores the importance of local factors such as roughness as drivers of ecological processes and in turn overall ecosystem functioning. The sensitivity of this important ecological process to hydromorphological factors in stream mesohabitats has significant implications for stream management and the deployment of litter decomposition assays as a bio-indicator tool. One of the advantages of using ecosystem-level processes such as leaf litter assays as a bio-assessment tool is that it provides an integrative measure of ecosystem integrity, but protocols need to be adapted to disentangle the influence of natural habitat conditions on decomposition rates from the effects of external environmental stressors. This is by no means an easy task in most cases. As a consequence, natural variability at the riffle scale must be taken into account in the assessment of anthropogenic impacts. One solution to integrate this very strong variability is to measure the breakdown rate on several successive riffles to obtain a good estimate of the mean values of the decomposition rates on each site, which is not the case in many studies. Further studies on the relationship between hydraulic factors, litter storage, and the presence

of shredders are required to understand this complex relationship between morphological and biological factors explaining the spatial heterogeneity of the breakdown process.

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Article 3: The recovery of key ecological processes in headwater streams following hydromorphological restoration: the examples of litter decomposition and streambed oxygenation

The recovery of key ecological processes in headwater streams following hydromorphological restoration: the examples of litter decomposition and streambed oxygenation

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Abstract

Evaluations of restoration success in streams have mostly been limited to structural elements with results riddled with uncertainties. Consequently, there has been a growing call for a more robust assessment protocol that integrates ecosystem functioning into the assessment of ecological recovery in streams. We proposed leaf litter decomposition rate and streambed oxygenation depth as potential indicator tools for the assessment of both the impacts of hydromorphological alterations and ecological recovery after restoration in headwater streams. Using a BACI study design, we monitored the two indicators on designated control sites and at the altered sections of three headwater streams in Brittany, Northwest France for one year before and two years after restoration works. The restoration works involved the removal of artificial obstruction to flow. Before restoration, streambed oxygenation depth in the three streams and litter decomposition rate in one stream were lower in degraded sections than in control sites. After restoration, oxygenation depth in restored sites became significantly higher than values before restoration and progressively approached reference values at the second year after restoration. The significant dip in litter decomposition rate immediately after restoration was reversed in the second year with values significantly comparable to reference values two years after restoration. Our results show the sensitivity of ecological processes such as leaf litter decomposition and streambed oxygenation to hydromorphological restoration and can therefore serve as useful indicators of ecological recovery in restored streams.

Keywords: Streambed oxygenation, sediment clogging, litter decomposition, stream restoration.

Introduction

The restoration of degraded streams to achieve good ecological status has received tremendous attention in recent years (Suding, 2011; Ernst *et al.*, 2012; Palmer *et al.*, 2014). While the European Water Framework Directive states ecological status as an assessment of the quality of the structure and functioning of surface water ecosystems, it suggests only the structural elements for the assessment of the ecological status of streams and rivers (European Environmental Agency, 2018). Therefore, most evaluations of restoration success in streams have been limited to structural elements. Ecosystem structure refers to the spatiotemporal patterns in the physical and chemical characteristics (e.g. water quality, nutrients, pH, Hydrological regime, habitat features, and channel form) and in the composition of the biological communities (plankton, benthic macroinvertebrates, fish, aquatic plants) of the ecosystem, while ecosystem function refers to the ecosystem processes mediating the services provided by the ecosystem (Gessner & Chauvet, 2002; Truchy *et al.*, 2015; Ferreira *et al.*, 2020). These two components (that is, the structure and the function) define the ecological status of stream ecosystems (Feckler & Bundschuh, 2020), are both sensitive to environmental changes (Sandin & Solimini, 2009), and can take different trajectories in response to changes in the ecosystems (Jackson *et al.*, 2016; Verdonschot & van der Lee, 2020) including hydromorphological restorations. Thus, a comprehensive and complete evaluation of the ecological success of stream restoration must view structural and functional elements as complementary indicators. While fauna community structures have been popular as bio-assessment indicators, functional indicators based on ecological processes are not considered (Gessner & Chauvet, 2002; Ferreira *et al.*, 2020).

Headwater streams are mainly affected by widely distributed physical barriers altering flow (Poff & Hart, 2002b; Liu *et al.*, 2014) and sediment transportation (Liu *et al.*, 2014). These

barriers are in form of different types of physical structures such as weirs, bridge foundations, nozzles, etc. but exert similar impacts on flow velocity causing a huge disparity between the upstream and the downstream of the barriers and a physical clogging of the sediment upstream (Waters, 1995). To measure the impacts of barriers on stream channels, different functional indicators can be used. The streambed oxygenation can serve as a proxy of sediment clogging using woody stakes embedded in the streambed (Marmonier, 2004) before and after the removal of barriers. The leaf litter breakdown rate can also be used to measure the ecological consequence on invertebrate communities (Piscart *et al.*, 2009).

A purely abiotic process that can be used for evaluating stream restoration is the depth of streambed oxygenation (Marmonier, 2004). The hyporheic zone is marked by continuous interaction and mixing between stream and pore waters due to spatiotemporal variations in channel characteristics including sediment transport and deposition (Tonina, 2012). The hyporheic zone depends on this hyporheic exchange for the essential elements required for the many biogeochemical reactions it sustains (Tonina, 2012). In streams impacted by the artificial blockade to flow and sediment transport, there is excessive deposition of fine sediment on the streambed which could lead to a reduction in sediment porosity (Gayraud & Philippe, 2001), permeability (Beschta & Jackson, 1979; Schälchli, 1992) and the clogging of the interstitial spaces (Schälchli, 1992) and thus inhibiting the exchange between the hyporheic zone and the water column. This is particularly so for the level and depth of oxygenation needed for microbial activities within the streambed. When there is a low level of oxygenation due to clogging by fine sediment deposition, aerobic respiration by microbes is replaced by denitrification (Skiba, 2008) with the attendant impact on the environment. Marmonier *et al*. (2004) developed a simple method for measuring the depth of oxygenation in the streambed. This method involves inserting woody stakes in the streambed for some days. Due to microbial activities occasioned by anoxic conditions, the stake changes colour from brown to pale grey

or black occurring at the transition between oxygenated and anoxic interstitial environments (Zehnder, 1988; Harvey & Fuller, 1998; Marmonier, 2004). The drastic colour change is typically observed at the transition zone and the depth of oxygenation in the streambed, to the nearest 0.5cm, is taken as the length from the top of the stake to the first appearance of the colour band.

In headwater streams, leaf litter decomposition is also a key ecosystem process that is sensitive to environmental changes at different spatiotemporal scales (Chauvet *et al.*, 2016; Tiegs *et al.*, 2019; Omoniyi *et al.*, 2021). It represents energy subsidy from riparian vegetation in forested headwater streams and has shown sensitivity to environmental stressors in headwater catchments as well as in-stream conditions (Ferreira *et al.*, 2016; Jackson *et al.*, 2016; Omoniyi *et al.*, 2021). It is mediated by both biotic (microbes and macroinvertebrate shredders) and abiotic (climatic, hydrologic, hydraulic, and morphologic) agents in streams following a sequence of usually over-lapping processes: leaching of soluble compounds in water; colonization and conditioning by heterotrophic microbes; and fragmentation by macroinvertebrate shredders and physical abrasion (Abelho, 2001). It can, therefore, provide an integrative understanding of the ecological recovery pathway in restored streams. Unlike benthic macroinvertebrates, heterotrophic microorganisms are not commonly considered in bio-assessment programs, incorporating litter decomposition into the ecological evaluation of restored streams can thus provide useful information on the changes in microbial community structure following restoration in streams (Ferreira *et al.*, 2020). Additionally, litter decomposition can allow the comparison of ecological recovery over a large spatial scale because litter fragmentation is not dependent on the presence of a specific taxon but is rather mediated by the shredder functional group (Bunn & Davies, 2000; Gessner & Chauvet, 2002). Furthermore, litter decomposition is also influenced by watershed events such as nutrient and chemical loading (Ferreira *et al.*, 2015, 2016) and land use (Piscart *et al.*, 2011) and can thus

provide insights into how these factors influence the recovery time of restored streams in inundated watersheds. With the apparent lack of consistent evidence for the responsiveness of biodiversity indices to stream restoration, leaf litter decomposition can potentially serve as a sensitive functional indicator for assessing the success of restoration practices in streams (Ferreira *et al.*, 2020). Therefore, we assessed ecological recovery in three restored headwater streams using the leaf litter experiment before and after the restoration works and compared these evaluations with reference conditions.

In this study, we deployed the two indicators mentioned above, by measuring the depth of oxygenation in the streambed and the leaf litter decomposition in three headwater streams in Brittany. We hypothesized that: 1) artificial blockade of flow and sediment will impact negatively on the depth of oxygenation 2) the removal of the artificial structures will unclog interstitial spaces and enhance streambed oxygenation 3) the rate of litter decomposition in the impacted sections before restoration will be lower than reference values, and 4) there will be an increase in the rate of decomposition after restoration and values comparable to reference conditions.

Materials and Methods

Study sites

This study was conducted on three headwater streams in Brittany, north-western France (Figure 1, Table 1). The region has an average summer temperature of 17.5±1.12°C, average winter temperature of 6.53±1.07°C, and an annual rainfall of 694±141 mm. The restoration works carried out on the sections of the streams involved the removal of artificial structures. Before the removal, the restored sections each had a concrete nozzle installed across their channels to

control flow and in effect, constituted a barrier between the stream channel and the adjoining riparian zone as well as an obstruction to the transport of materials downstream. The nozzles were removed to reconnect the sections to the riparian zones and enhanced flow connectivity between the upstream and downstream reaches.

Table 1. Information on the three streams investigated in this study and the dates restoration works were carried out on each stream.

Site	Longitude	Latitude	Date restored
Malville	47°55'06.0"N	2°24'36.4"W	Autumn 2018
Pontplaincoat	48°41'08.3"N	3°48'23.4"W	Autumn 2018
Traou Breuder	48°27'30.2"N	3°21'43.7"W	Summer 2019

Study design

We adopted the Before-After-Control-Impact (BACI) design in monitoring the impacted site, a site downstream, and a reference site on each stream. This approach allows the measurement of impacts by comparing a perturbed system with a control or reference condition (Eberhardt, 1976; Green, 1979; Downes, 2002). In each case, the control site was situated on the same stream but at least 100 meters upstream of the restoration point (hereafter referred to as the upstream site) to standardize for other environmental factors and in effect, isolate the impacts due to the artificial structure. Each site was monitored for one year before restoration and two years after restoration.

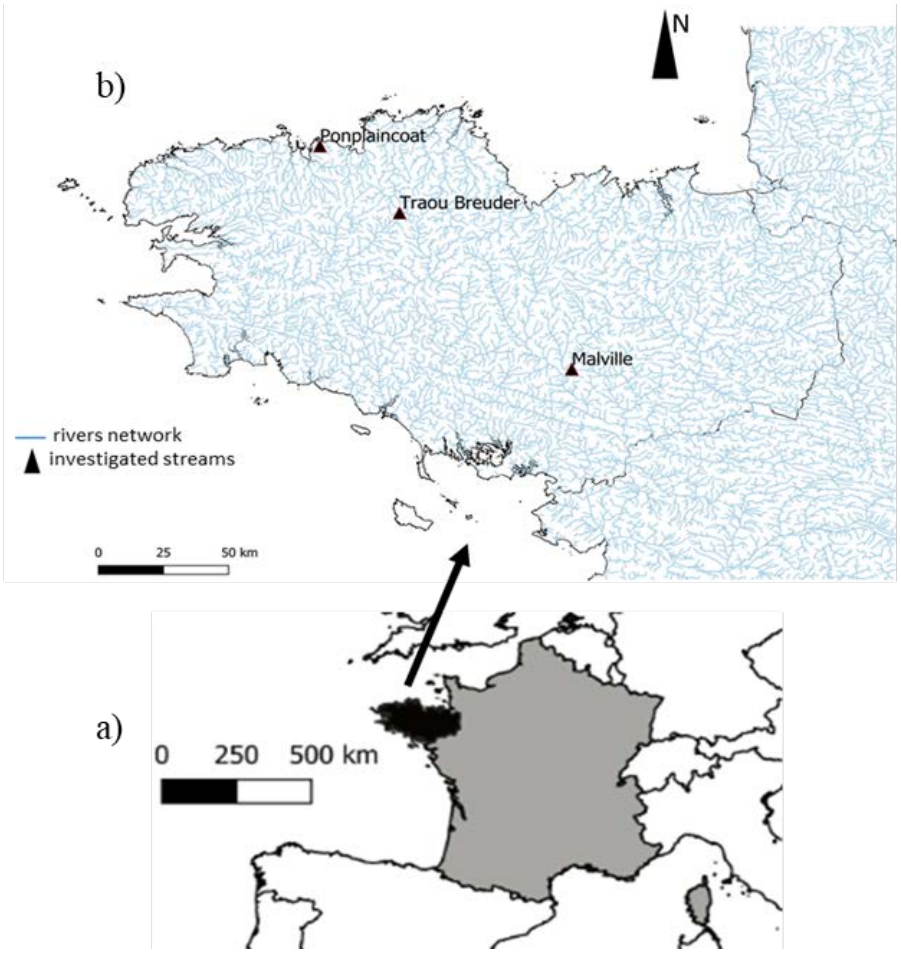


Figure 1. Map of a) France and b) river network of Brittany region showing the localization of studied streams (black triangles).

Streambed oxygenation

For the measurement of the depth of streambed oxygenation, we used untreated (natural) white woody stakes (9 x 9 mm in dimension) cut into 28 ± 0.2 cm length (Marmonier, 2004). Each stake was pierced at approximately 1 cm from one end and a piece of coloured wire was inserted for easy location in water and to help with the retrieval of the stakes.

In addition to the three sites on each stream, we also established four successive transects, L1, L2, L3, and L4 upstream from the impacted site to determine the spatial gradient of oxygenation depth along the channel of the streams in relation to the impacted sites. Ten replicate stakes were inserted into the streambed at each site with the aid of an iron bar and a mallet. The entire length of each stake was completely immersed in the streambed. After 30

days, the stakes were retrieved and the distance from the top of the stake to the first appearance of a dark band/spot on the stake was measured. The average of this measurement on all the stakes at each site was taken as the depth of oxygenation. This was done four times a year for one year before restoration and two years after restoration.

Litter decomposition

Litter bags (10 x 10 cm in dimension and 5 mm mesh size) containing a known weight of freshly abscised alder leaves (*Alnus glutinosa* (L.) Gaertn.), air-dried in the laboratory at room temperature, were installed at each site fixed to the stream substrate for 15 days (Omoniyi *et al.*, 2021). Five replicate litter bags were deployed at each site every winter for two years before restoration and two years after restoration. At the end of 30 days in each campaign, bags were retrieved and transported to the laboratory in a cool box at -20°C for further treatment. In the laboratory, after thawing the litter bags, the leaves were individually rinsed under a flowing tab to remove sand and other debris. The remaining leaves were thereafter air-dried to constant mass and weighed. The rate of litter breakdown was estimated as the mass of leaf degraded per day.

Statistical analyses

We evaluated values of parameters in stepwise temporal scale of before restoration (t), one year after restoration (t+1), and two years after restoration (t+2). The mean values of measurements at each site were centered around the values for reference sites to evaluate the impact of the artificial structure before removal and to see how values compare with reference conditions after restoration. We fitted an ANOVA model with either decomposition rate or oxygenation depth as the response variable and, site (upstream, downstream, and control sites) and temporal

scale (t, t+1, and t+2) as treatment variables. The interaction between site and temporal scale was also tested. Subsequently, we performed a Tukey HSD posthoc test at 95% family-wise confidence level to determine all possible pair-wise combinations of the variables.

Results

Streambed oxygenation

There were significant site and temporal scale effects on streambed oxygenation in each of the three streams and a significant effect of the interaction between site and temporal scale on streambed oxygenation in both Malville and Pontplaincoat (Table 2). The depth of oxygenation in the downstream sites in two streams (Traou Breuder and Pontplaincoat) was comparable with the oxygenation depth in their respective reference sites as there was no significant difference (Tukey HSD tests; Figure 2a and c). Downstream oxygenation was, however, slightly lower than in the reference site at Malville. As shown in Figure 2, oxygenation depth before restoration at all the impacted sites in the three streams was generally lower than the reference values indicative of an impact of the artificial structures on the depth of oxygenation in the streambeds.

In the three streams, the values of oxygenation following the removal of artificial structures were significantly higher than the values before removal with values approaching reference values in year 2 after removal. In Traou Breuder values became significantly comparable (i.e. $p<0.001$significant difference between t+1 and t) to reference values just immediately (i.e. t+1) after the removal of the artificial structure and progressively so at two years (t+2) after restoration (i.e. t+2 was significantly higher than t but only slightly higher than t+1).

Additionally, along the spatial gradient of the four transects, L1 to L4, on each stream, there was generally a steady increase in oxygenation depth from the impacted point to transect L4.

*Table 2. Result of the ANOVA model with streambed oxygenation depth as response variable and site and temporal scale as treatment variables. T, M, and Pt represent Traou Breuder, Malville, and Pontplaincoat respectively while *, **, and *** represent the threshold of the p values p<0.05, p<0.01, and p<0.001 respectively, Df represents the degree of freedom and F value represents the F-statistics.*

	Df			F value			P-value		
	T	M	Pt	T	M	Pt	T	M	Pt
Site	5	5	5	19.546	12.659	45.14	***	***	***
Temporal scale	2	2	2	9.568	10.229	11.76	***	***	***
Interaction	10	10	10	0.758	9.259	4.60		***	***

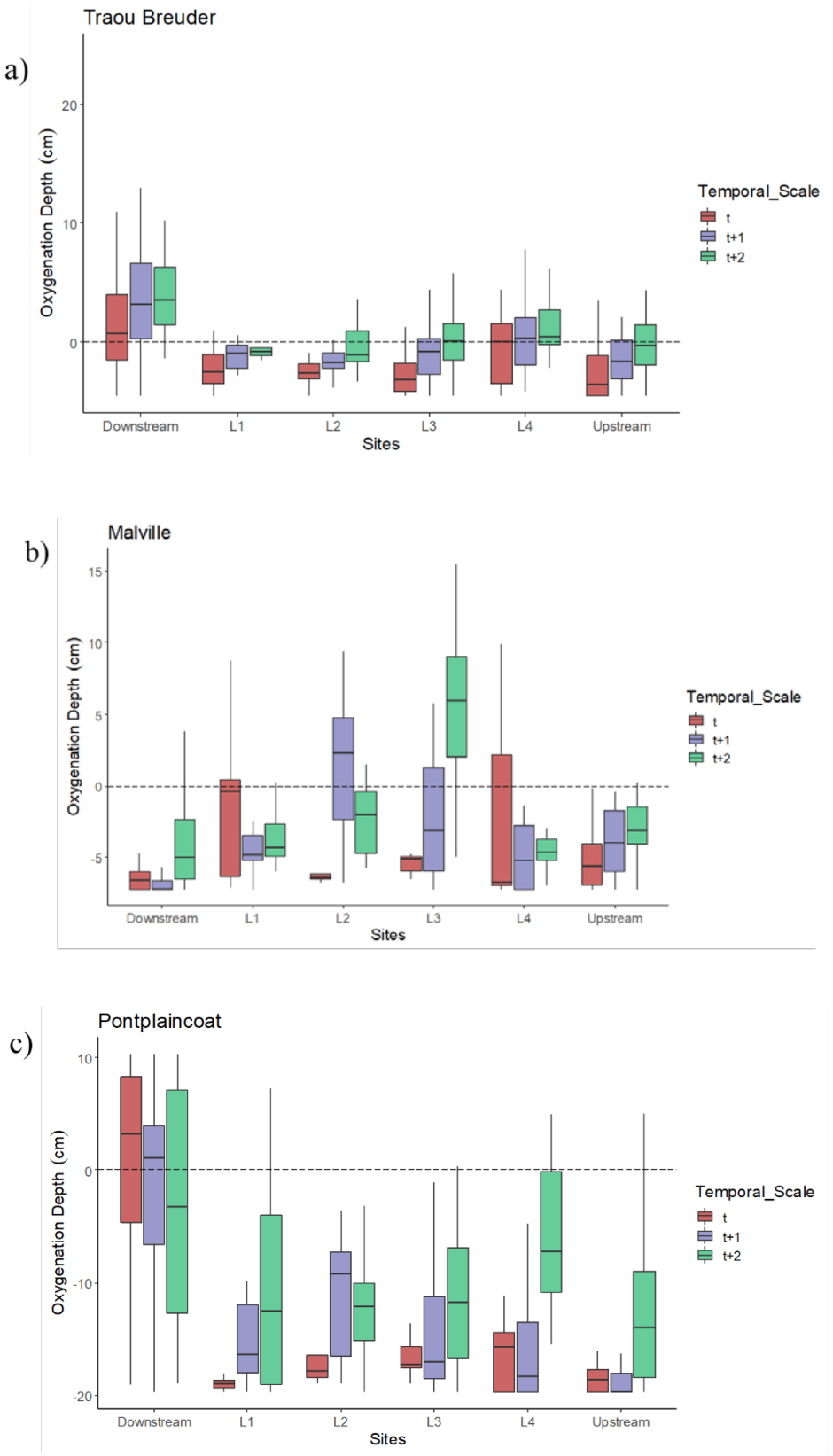


Figure 2a, b, and c. Mean ± standard error streambed oxygenation depth in the three restored streams. Values at each site were normalized around the mean values of the reference site represented by the dotted line). t represents pre-restoration while t+1 and t+2 represent one and two years post-restoration respectively.

Litter decomposition

The ANOVA result with litter decomposition rate as response variable shows significant site and temporal scale effects on decomposition rate in Traou Breuder while in Malville, only the temporal scale was highly significant (Table 3). The rate before restoration in both downstream and upstream sites was lower than the reference value in Traou Breuder (Figure 3a) while in Malville and Pontplaincoat, the rate before restoration at the downstream and upstream sites was slightly higher than the values at the reference sites (Figures 3b and c).

There was a dip in decomposition rates immediately after restoration in Malville and Pontplaincoat with the rate in the first year after restoration (t+1) being significantly lower ($p<0.001$) than the rate before restoration (t) in Malville (Figure 3b) but only slightly in Pontplaincoat (Figure 3c). However, this condition was reversed in the second year after restoration (t+2) in the two streams with t+2 being significantly higher ($p<0.001$) than t+1 in Malville. Decomposition rates in t+1 and t+2 at the upstream sites in the three streams were progressively comparable to reference values with t+2 comparatively higher than t+1 in each case.

*Table 3. Result of the ANOVA model with litter decomposition rate as response variable and site and temporal scale as treatment variables. T, M, and Pt represent Traou Breuder, Malville, and Pontplaincoat respectively while *, ** and *** $p<0.05$, $p<0.01$, and $p<0.001$ respectively, Df represents the degree of freedom and F value represents the F-statistics*

	Df			F value			P-value		
	T	M	Pt	T	M	Pt	T	M	Pt
Site	1	1	1	4.127	1.403	0.071	*		
Temporal scale	2	2	2	5.235	11.21	0.228	*	***	
Interaction	2	2	2	0.216	0.419	0.085			

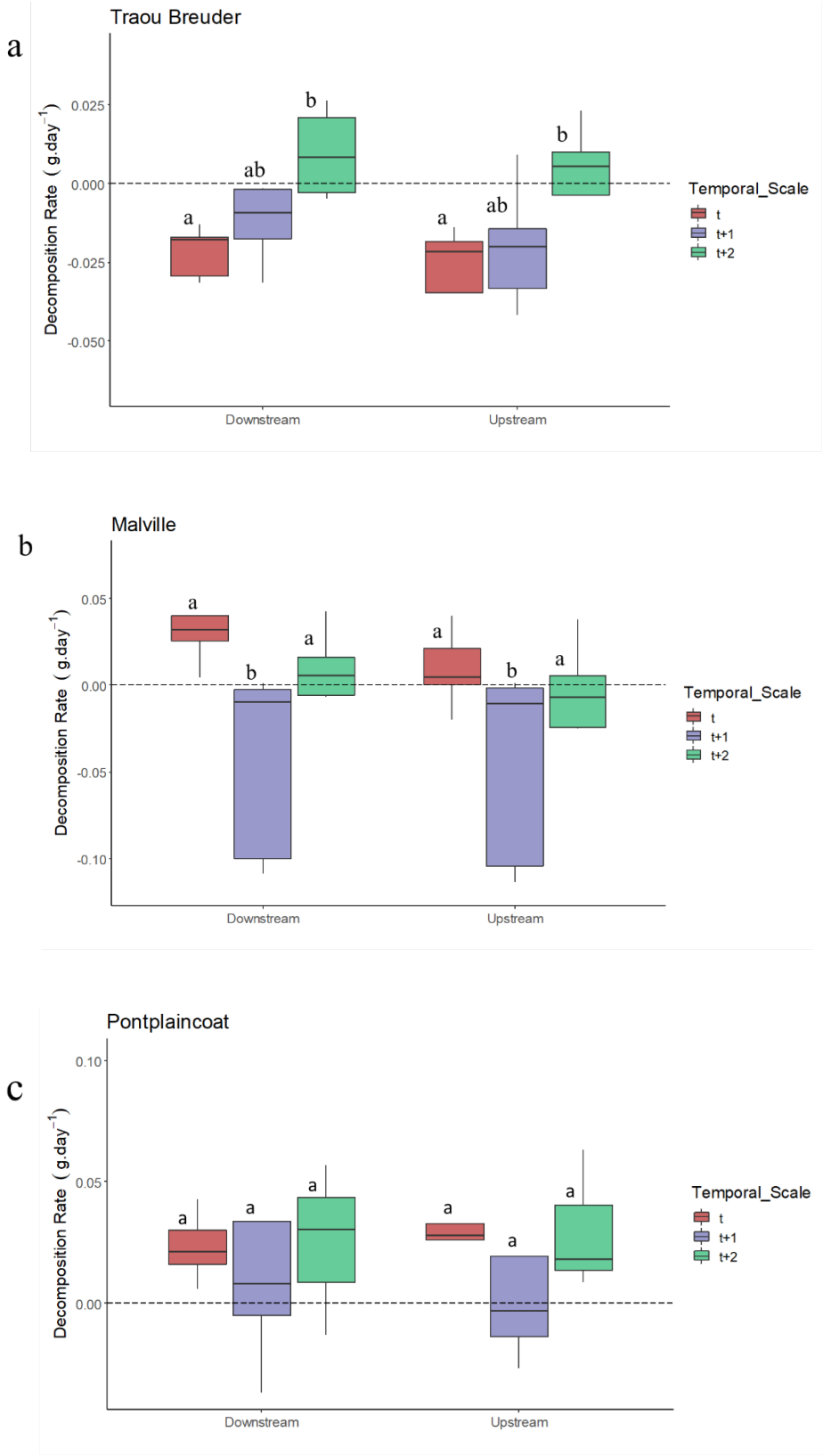


Figure 3a, b, and c. Mean±s.e. litter decomposition rate in the three restored streams. Values at each site were normalized around the mean values of the reference site (represented by the dotted line). t represents pre-restoration while t+1 and t+2 represent one and two years post-restoration respectively. Letters represent significant differences between modalities.

Discussion

Streambed oxygenation

We hypothesized that streambed oxygenation depth will be low in impacted sites as a result of low flow and due to the deposition of fine sediment upstream of the blockade by the artificial structures. This is confirmed in our result as oxygen depth in impacted sites was lower than in reference sites before the removal of the artificial structures. Fine sediment particles are either deposited on the surface of the streambed or transported downstream upon entering the fluvial system (Salant & Hassan, 2008). Deposited fine sediment particles may be retained or recruited back into the water column. However, flow stagnation caused by channel blockade such as those investigated in our streams often leads to the accumulation and subsequent infiltration of accumulated fine sediment particles into the streambed via the interstices (Salant & Hassan, 2008). This clogging of the interstices could potentially limit the interaction between the water column and the interstitial spore water through which inter-exchange of materials including nutrients and dissolved oxygen usually takes place (Tonina, 2012) thus leading to low oxygen depth in the streambed. The reduced interstitial spores and the consequent low oxygen regime in the streambed or hyporheic zone could have profound consequences for the general ecology of the stream. The degree of interaction and exchange of materials between channel surface and subsurface is dependent on sediment particle size and the rate of exchange decreases as particles become smaller (Metzler & Smock, 1990). In addition, in forested headwater streams, for instance, a substantial part of the allochthonous plant materials entering the streams may end up buried in the streambed (Herbst, 1980; Metzler & Smock, 1990; Cornut *et al.*, 2012, 2014), insufficient availability of oxygen may hamper the activities of heterotroph microorganisms involved in the decomposition of these materials in the sediment.

Our result also shows that there is an improvement in streambed oxygenation after the removal of the artificial structures and that values progressively approach reference values over the two years of investigation following barrier removal. This is indicative of the effectiveness of the removal of the artificial structures in restoring flow and enhancing sediment transport and distribution within stream channels and confirms our second hypothesis that barrier removal will unclog interstitial spaces and enhance streambed oxygenation. Moreover, it also highlights the importance of time in the ecological recovery of restored streams. The time it takes to attain full recovery (i.e. states similar to reference or undisturbed conditions) in restored streams has been a subject of discussion and varies widely in monitored restoration projects and techniques. The restoration of habitat heterogeneity has been reported to be almost instantaneous in projects and techniques which have this as the main objective (Friberg *et al.*, 1994, 1998). For the restoration of benthic communities, Muotka *et al.* (2002) reported a recovery period of 4 to 8 years in streams that were restored to their pre-channelized states. Our study suggests that for barrier removal, the recovery of such ecological indicators as the health of the hyporheic zone could be as rapid as within 2 years.

Litter decomposition

We hypothesized that the impact of the artificial barrier will make the rate of litter decomposition in the impacted sites (i.e. immediately upstream of the artificial structure) lower than the rates in the reference sites. This was confirmed in one of the streams investigated in this study. Sedimentation at the impacted sites caused by the partial blockage of sediment transport by the artificial structure may have led to the 'burial' of leaf packs. Metzler *et al.* (1990) reported that 'buried' leaves are processed slower than leaves on the sediment surface. This can be explained in several ways: (1) the inundated leaves are compacted together by the

weight of the substrates, thus reducing the effective surface area for microbial and invertebrate actions; (2) coupled with reduced flow, the 'burial' of leaves reduces the abrasive actions of current (or turbulence) and suspended particles. Physical abrasion is very important in aiding litter breakdown in lotic systems (Dobson, Dobson & Frid, 2009); and (3) the anaerobic conditions created by the 'burial' may have resulted in decreased processing rate. Decomposition rates are generally thought to be reduced in anoxic conditions (Reddy & Patrick, 1975). In addition, excessive deposition of fine sediment on streambeds causes homogenization and degradation of habitats for stream fauna including macroinvertebrates (Waters, 1995; Salant & Hassan, 2008). Aquatic macroinvertebrates are known to inhabit varied habitats (Piscart *et al.*, 2007); habitat homogenization would cause a shift in community structure and could result in a reduction in the abundance and richness of detrital herbivores essential for litter breakdown (Ryan, 1991). In a finding of another part of this thesis (see article 2), we reported that physical characteristics of streambed especially bed roughness are among the factors influencing litter breakdown rate in streams (Omoniyi *et al.*, 2021).

Overall, there is an improvement in litter decomposition rates over the two years monitored after restoration. However, in two streams, Malville and Pontplaincoat, rates in the first year after restoration were lower than before restoration. There are two possible explanations for this. One, restoration works on the two streams were carried out in late autumn 2018 and the litter decomposition experiments were done in winter that same year. Restoration activities themselves have been described as a form of immediate disturbance in streams (Dyste & Valett, 2019). The substantial earth movement, the sudden surge in flow, sediment upwelling and transport, and other activities involved in the restoration technique may have created an immediate shock in the ecosystem and possibly displaced macroinvertebrates detrital herbivores. To put ecological recovery time into the proper perspectives, Dyste and Valett (2019) suggested a phased approach to ecological monitoring and to consider a restoration

activity as an immediate disturbance that initiates succession over a long time frame. Secondly, there was a flooding episode in the two watersheds shortly before the rate measurement was done. This may have had some effects on the shredders community mainly dominated by free-swimming gammarid amphipods (refer to article 1) which could be swept downstream by flood current thus reducing the density of shredders in the investigated reaches. This highlights how important stochastic watershed events could be in the recovery of ecosystems following restoration.

However, it is noteworthy that in the three streams, process rate values after two years had approached the values for reference sites confirming our hypothesis that the rate of litter decomposition will increase after the removal of the artificial structure and that values will be comparable to reference values over time. While the leaf litter assay has been widely used as a functional indicator of stream ecological health, its usefulness in assessing ecological recovery in restored streams has been underexplored. Our result shows that this ecosystem function can serve as an integrative functional indicator of ecological recovery in restored headwater streams.

Conclusions

Despite the huge potentials for being effective and efficient tools for assessing the ecological status of streams, functional indicators are rarely included in the bio-assessment of hydromorphological restoration in streams. Our study shows that process-based functional elements such as litter decomposition and streambed oxygenation are not only able to detect the impacts of anthropogenic perturbations in streams but can also be effective as indicators of ecological recovery in restored headwater streams. With the increasing popularity of hydromorphological restoration in headwater streams coupled with the inconsistency that has

been noted in the response of community indices, these functional indicators present managers and stream ecologists with integrative alternatives which could provident insights into the responses of both the biotic and abiotic components of the ecosystem. In addition, one of the reasons why most restoration activities are not being monitored is the cost of such monitoring. The leaf litter assay and the woody stake method of measuring streambed oxygenation are cost-effective and easy to be implemented.

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Supplementary Note 1

Supplementary Analysis and Result

To answer a key part of our hypotheses that states that "***litter decomposition rate would be more related to taxa traits than to biodiversity indices***", we determined the relationship between litter decomposition rate, macroinvertebrate biodiversity indices (see article 1), and taxa traits.

We defined a total of 30 trait modalities comprising both biological and ecological traits of the benthic macroinvertebrates of the three restored streams and performed Spearman correlation analysis to compare litter decomposition rate, biodiversity indices (abundance, species richness, and diversity indices of EPT, shredders, and macroinvertebrate communities), and the 30 trait modalities.

Out of the 30 traits, 19 had strong positive correlations with litter decomposition rate (Figure xx) while macroinvertebrate richness, abundance, shredders abundance, and EPT abundance were only weakly correlated to litter decomposition rate (Figure A1). This suggests that while biodiversity indices may not drastically improve immediately after restoration in streams, the selection and combination of traits in the system are such that are necessary for resource optimization and continuation of the key processes important for the functioning of the ecosystem. In this case, the 19 traits are mostly life-history traits indicative of relative ease of dispersal and species persistence. They include passive aquatic dispersal, adult aquatic life stage, respiration by gills, and multiple reproductive cycles in a year. The relative ease of dispersal mostly through drifting with water current from connected upstream reaches highlights the importance of ensuring proximity of restored streams or stream sections to colonist pools.

A.

B.

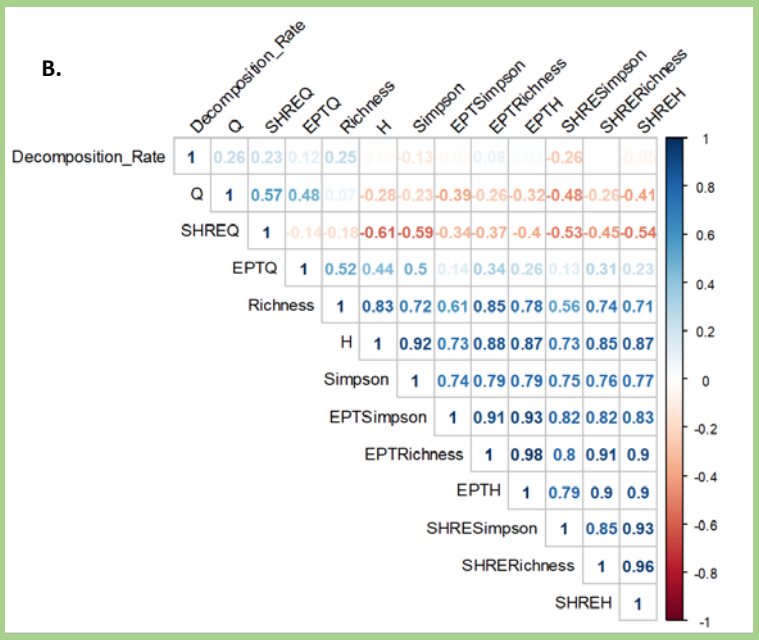


Figure A1: Spearman correlation between litter decomposition rate and A.) species traits and B.) community indices (Q: abundance; H: Shannon diversity; Simpson: Simpson diversity, Richness: species richness; EPTQ, EPTH, EPTSimpson, EPTRichness: abundance, Shannon, Simpson index and richness of EPT functional group respectively; SHREQ, SHREH, SHRESimpson, SHRERichness: abundance, Shannon, Simpson index and richness of shredders functional group respectively).

GENERAL DISCUSSION

Biodiversity response to hydromorphological restoration in headwater streams

In this thesis, we studied three headwater streams for the impacts of artificial strictures on two key ecological processes - leaf litter breakdown and streambed oxygenation in headwater streams and proposed that these ecological processes can serve as functional indicators of ecological recovery in addition to the classical macroinvertebrate community structure following hydromorphological restoration. Existing literature suggests the ineffectiveness of in-stream restoration at improving fauna community metrics. We aimed to determine if this would be different in headwater streams and equally proposed the two ecological processes as functional indicators for monitoring restoration success in headwater streams.

First, we hypothesized that, contrary to what has been observed in other systems, biodiversity indices will respond positively to hydromorphological restoration in headwater streams. Of the five benthic macroinvertebrate biodiversity indices we evaluated, only species richness has a significant increase after restoration in the streams (Chapter 2). While this result partly negates our hypothesis, it is, however, in agreement with the inconsistent outcomes that have been reported for biodiversity recovery following restoration in other types of the lotic system. Miller *et al.* (2010) reported an increase in macroinvertebrate richness but negligible effect on density; Kail *et al*. (2015) observed significant effects on fish and macroinvertebrate abundance and biomass but not on richness and diversity while Verdonschot *et al.* (2016) recorded no overall positive effects on macroinvertebrate metrics. Some of the reasons that have been theorized in literature for this lack of community response to in-stream restoration include (i) the probable inadequacy of some sampling designs to detect restoration effects (Vaudor *et al.*, 2015), (ii) the failure of most restoration activities to simultaneously address all the multiple stressors affecting communities thus limiting recovery (Palmer *et al.*, 2010; Leps *et al.*, 2015), (iii) the difference in the spatial scales of environmental stressors and restoration projects (Lake, Bond & Reich, 2007; Roni *et al.*, 2008; Feld *et al.*, 2011), and (iv) the low recolonization

potential or inadequacy of colonist pool near restored reaches (Stoll *et al.*, 2014; Tonkin *et al.*, 2014). Though restoration activities in headwater streams are mostly targeted at enhancing habitats at the reach scale, the local communities at this scale are part of and connected by dispersal to a metacommunity (Stoll *et al.*, 2016) that is influenced by the totality of the environmental factors at a much higher scale (Leibold *et al.*, 2004; Brown *et al.*, 2011). This argument is supported by our observation which found that in the Traou Breuder watershed where anthropic pressures were considerably lower and of minimal impacts than in Malville and Pontplaincoat, the ecological status and biodiversity indices were significantly higher after restoration than before restoration with the ecological status changing from moderate to good. This highlights the influence of watershed stochastic factors on biodiversity and the overall ecological status of streams. Palmer *et al*. (2010) opine that there is no evidence to support that habitat heterogeneity is the only or primary factor controlling stream invertebrate diversity. While hydromorphological restoration resulting in habitat improvement is theoretically expected to improve biodiversity, natural and anthropogenic watershed events may alter the trajectory and the dynamics of this improvement. Therefore, the greater focus of restoration should be on enhancing the resilience of streams to withstanding stochastic environmental factors and maintain a self-sustainable natural variability.

Functional elements as complementary indicators to community indices

With the apparent unreliability of biodiversity indices as indicators of ecological recovery in streams, we proposed function-based indicators as complementary tools for the assessment of ecological recovery in restored streams. Because ecological functions are mediated by multiple factors which could include both biotic and abiotic entities, ecological functions and structural elements (e.g. invertebrate community structure) can respond in similar, complementary, or

different magnitude and direction to changes in the system (Verdonschot & van der Lee, 2020; Ferreira *et al.*, 2020). Additionally, the EU WFD recognizes the quality of both the structure and functioning of aquatic ecosystems as components of the ecological status. Therefore, we opine that evaluating ecological recovery in restored streams solely based on structural indices may be inaccurate and misleading. Thus, in chapter 2 (comprising of Articles 2 and 3), we examined leaf litter decomposition and streambed oxygenation as potential functional indicators of ecological recovery in restored headwater streams and hypothesized that these indicators will perform better than biodiversity indices as indicators of ecological recovery in restored streams.

In Article 2, litter decomposition experiments comparing the variability in decomposition rate at the riffle scale (which is the scale at which the restoration activities in our study were carried out) to the variability in rate between streams were performed in nine streams to ascertain the sensitivity of the litter bag experiment to the local factors at this scale. The result of this experiment confirms the sensitivity of the litter bag experiment to the factors at the riffle scale with an in-stream variability of litter decomposition rate comparable to the variability between streams and streambed roughness the most important factor influencing this variability. In Article 3 and the addendum thereof, litter decomposition rate, as well as the depth of streambed oxygenation were examined as functional indicators in the three restored streams monitored. Streambed oxygenation was measured as a proxy of sediment clogging arising from the partial blockage to flow and sediment transport by the artificial structures along the impacted sections of the streams. Our results indicate a significant impact of the structures on streambed oxygenation depth in the three streams while the impact on litter decomposition rate was minimal in two streams but significant in one stream. Additionally, in agreement with our hypothesis, the two indicators show a remarkable improvement after the removal of the

structures with values, in each case, approaching reference conditions two years after the removal.

Based on these results, macroinvertebrate diversity responses and the responses of the functional indicators we examined appear to be complementary rather than different in indicating the direction of ecological recovery after hydromorphological restoration. While a few studies have reported unidirectional responses of structural and functional indicators to environmental changes (e.g. Smucker, Drerup & Vis, 2014; Burson *et al.*, 2018), some others, in agreement with our findings, have found that structural and functional metrics were complementary and can be used in concert to provide a better and broader understanding of the effects of environmental changes on the ecosystem. For example, in a study of the relationship between water quality and leaf breakdown rates, Pascoal, Cássio & Gomes, (2001) found that in response to nutrient concentrations, macroinvertebrates increased in density but decreased in taxon diversity, while there was a substantial increase in leaf breakdown rates. In the same vein, Friberg *et al.*, (2009) found a decrease in diversity, an increase in density of invertebrates as well as an increase in organic matter breakdown rates in response to temperature increase. With the removal of the artificial structures in the streams investigated in this study, natural flow is restored enhancing sediment transport and redistributing accumulated fine sediment downstream, thus declogging the streambed for enhanced interstitial oxygenation. The cumulative effect of flow restoration and bed heterogeneity would immediately increase hydraulic abrasion compared to the time that may be required for noticeable recovery in biodiversity. Uehlinger, Kawecka & Robinson, (2003) observed that there are differences in the recovery time for structural and functional metrics. They found that even though metabolism and periphyton assemblage were both altered by a flood event, metabolism recovered relatively quickly compared to the continuous shift in periphyton assemblage. Therefore, combining the indices of community structure with functional indicators such as

streambed oxygenation and litter breakdown rate in monitoring hydromorphological restoration in streams may provide complementary information on the dynamics, trajectory, and pattern of ecological recovery over time. It also has the potentials of providing an integrative understanding of an ecosystem response to hydromorphological restoration. Litter decomposition, for instance, is mediated by leaching in water, microbial actions, physical abrasion and invertebrate shredders. Therefore, its combination with biodiversity metrics would give a complementary insight into the responses of both the biotic and abiotic components of the system and help to disentangle the effects of the multiple factors influencing ecological recovery.

Our result also indicates the effect of the time factor in the recovery dynamics of restored streams (Article 3). Streambed oxygenation was progressively comparable to reference values from the first year after restoration while litter decomposition rate took two years after restoration to show significant semblance to reference values. Friberg *et al*. (1994 & 1998) reported an immediate improvement in habitat conditions in a restoration scheme with channel re-meandering while Muotka *et al*. (2002) reported a recovery time of 4 to 8 years for macroinvertebrate communities. Generally, taxa richness had a slight improvement during the two years post-restoration assessment in this study, nevertheless, we cannot convincingly conclude that two years is enough to attain full recovery and stability of fauna communities. We would recommend a long enough monitoring program to be able to evaluate the short-term and long-term recovery status of restored streams macroinvertebrate communities.

Implications for the science of restoration and management of restored streams

These results have implications for both scientists and managers of streams. Narrowing the objectives of river restoration to only biodiversity recovery informs the emphasis on habitat

heterogeneity in most restoration schemes. However, in this thesis, only the stream with minimal watershed and anthropic pressures post-restoration had some improvement in biodiversity and ecological status. This underscores the importance of considering all the components of an ecosystem both in the planning of restoration schemes and in the evaluation of the success of such schemes. While biodiversity may remain a key end-goal of in-stream restorations, focusing restoration activities only on enhancing habitat heterogeneity as the magic wand for improving biodiversity may be insufficient. Friberg, Sandin & Pedersen, (2009b) and Kail *et al*. (2012) opined that water quality could be more limiting than habitat availability for biological conditions.

Additionally, there is a need for the planning and application of restoration type or activity to be system-specific. In the place of the blanket approach of the addition of large woody debris, channel re-meandering, and similar methods of enhancing stream habitat conditions, our results indicate that for headwater streams, the restoration of natural flow and sediment transport through the removal of artificial barriers could have profound ripple effects on the health of the interstitial zone and improve streambed heterogeneity. These will in turn enhance the rate of litter processing as well as the recovery and stability of the fauna community over time.

However, it is important to recognize that, due to the life span of a doctoral study, the post-restoration monitoring in this study only lasted for two years. We expect that full recovery in the system would require a much longer time (Muotka *et al*., 2002). Also, it will be interesting to see the change in channel form over time as a result of the restoration of natural flow and alluvial connection with the riparian area. Hodson (2002) alluded to the idea that the planform morphology of rivers with natural banks is in a state of continuous 'migration' as a result of the scouring effect of flow and the alluvial mobilization of inorganic materials from the riparian area. In addition, alongside the restoration activities, a layer of vegetation was removed along the riparian area. It will be interesting to know how the return of riparian vegetation combines

with the change in channel form and bed heterogeneity to affect the dynamics of resource availability, retention, distribution, and processing over time. Organic materials from riparian vegetation form the base of the complex food webs in headwater streams (Vannote *et al.*, 1980) and channel features could have controlling effects on the retention (Webster *et al.*, 1994; Larrañaga *et al.*, 2003) and the processing (Omoniyi *et al.*, 2021) of the materials.

Supplementary Note 2

Macroinvertebrate recolonization of new stream thalwegs

As part of this thesis, the macroinvertebrate recolonization of two new stream thalwegs created to reconnect the upstream and the downstream sections of the two streams was followed at a very fine temporal scale. The purpose of the projects was to restore these sections of the streams which were previously lost as a result of diversions to create space for farmlands. They were restored to their original channel restoring the sinuosity of the sections through the creation of meanders.

The overall goal of the study was to monitor the recolonization dynamics of macroinvertebrates and to study the succession pattern in the new channels. We also set out to determine whether this succession pattern is better explained by taxonomic indices or by species traits. We are also interested in what local factors (e.g. channel form, hydrological parameters, nutrient elements, and water quality) influence recolonization and as well as trait selection and succession in the new channels. Necessary measurements and samples were taken for these determinations. All the data have been obtained, but we lack time to do a full analysis and organize the findings here in a full chapter. However, a quick outlook of the macroinvertebrate communities in the two streams are presented in the charts below.

A.

Macroinvertebrate recolonization of new thalwegs. Bars represent the mean taxonomic richness while T1, T2, T4, T8, and T10 represent 1 week, 2 weeks, 4 weeks, 6 months, and 1 year after restoration respectively.

Main results:

- Richness is similar between the upstream and the downstream control sites
- Richness is lowest at T1 in each riffle and each stream but increases gradually up to T10, that is, one year after restoration. However, the rate of increase in Riffle A in each stream is faster than in other riffles. Riffle A is the closest to the upstream section. This suggests the importance of proximity to a colonist pool. It will be interesting to see what dispersal method aided this quick arrival from the upstream of the watershed and what traits ensure the persistence of the 'seed' individuals and species.
- And finally, the difference between the control sites and the riffles gradually becomes negligible 1 year (T10) after restoration suggesting a macroinvertebrate community similar

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CONCLUSIONS

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The headwater stream is a very important section of the lotic system and provides key ecosystem services as part of the entire river network. It also has its share of the widespread degradation affecting the ecosystem and thus we were able to show that it cannot be neglected in the current drive to restore the lotic system to good ecological status able to sustain biota and maintain ecosystem services.

Like has been reported in other systems, we found that macroinvertebrate community indices do not have a robust response to in-stream restoration of headwater streams as only species richness improved significantly following hydromorphological restoration. Our findings suggest that this might be due to the scale of the projects and the presence of other limiting factors not considered in the restoration projects. We then concluded that the planning of stream restoration needs to be re-appraised and be site-specific to provide insight into when, where, how, and what method to apply in restoring a site considering all the factors contributing to the degradation of the site.

Furthermore and interestingly, we found that functional elements of the ecosystem can serve as complementary indicators of ecological recovery in combination with fauna community indices. In headwater streams, for instance, key ecosystem-level processes like litter decomposition and streambed oxygenation were found sensitive to the impacts of the presence of artificial barriers and also to their removal. We believe that this can be juxtaposed to other sections of the lotic system and processes like respiration, metabolism, and autotrophic production should be studied for this purpose.

PERSPECTIVES

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Global climate change is set to worsen the problem of degradation in the lotic system. With increasing drying and competition for resources by growing populations, streams and rivers will be exposed to more pressures leading to widespread degradation. As scientists collaborate with policymakers and political leaders to arrest the decline, more funds will be pumped into restoration projects. To ensure maximum benefits from the increased attention and resources, the approach to stream and river restoration must be tailored towards efficiency and the self-sustainability of ecosystem services.

All the results suggest that the current approach needs to be reappraised for optimization. In the headwater system where the presence of small dams, weirs, and other artificial structures constitute a major source of degradation, we found that their removal, which appears to be the prevailing mode of restoration at the moment, is not enough for the desired recovery of fauna communities. In the other sections of the lotic systems as well, methods such as the addition of large woody debris, boulders, and other habitat materials have been prevalent. Like in our findings, existing literature has also shown similar limitations from these approaches. To achieve better results beyond the enhancement of habitat heterogeneity, the scale of restoration projects in streams must be broadened beyond the reach scale. This will ensure that other watershed pressures than habitat conditions are equally addressed in restoration efforts.

Furthermore, we found that ecological processes could serve as complementary functional indicators of restoration success in streams. Ferreira *et al*. (2020) also made similar observations. In headwater streams where leaf litter decomposition is the primary source of energy, we found that litter breakdown rate and streambed oxygenation depth are potent for this purpose. In the other sections of the lotic system downstream, further studies are needed to determine what ecological processes could be deployed as functional elements in monitoring

restoration success. Primary productivity, ecosystem metabolism, and respiration are integrative ecosystem-level processes that could be potent candidates in this regard.

In addition, macroinvertebrate-based multimetric tools that are currently available for the assessment of the ecological status of streams appear to be limited at scales below the watershed scale and thus not suitable for assessing hydromorphological restoration at these local scales. Since habitats and the conditions prevailing in them are responsible for species traits and the combination of traits that confer the ability to adapt and ultimately survive on species (Southwood, 1977; Verberk *et al.*, 2013), we believe that comparing faunal traits (biological and ecological) before and after restoration with reference conditions may provide a mechanistic understanding of the trajectory of ecological recovery following restoration. Further studies are needed to confirm this.

Finally, environmental degradation is ubiquitous and the African landscape and indeed Nigeria are not left out. The incessant crisis among riparian communities in the lower Niger basin has been traced, among other causes, to the degradation of the Niger River and its tributaries. Countries surrounding the Chad basin are collaborating to pull resources together for the restoration of shared water bodies. Most rivers and streams in the delta of Nigeria have been severely degraded over the years from resource exploration and other anthropogenic activities. Recently, the government, with technical support from United Nations Environmental Programme, UNEP, has begun planning for the restoration of these ecosystems. My training in the course of this thesis will put me in a position to contribute meaningfully to these efforts. I will be seeking opportunities to collaborate with other scientists to increase advocacy and raise awareness among decision-makers to the need to do more in restoring degraded water bodies. And for restoration projects being planned or that have been commissioned, I will be advocating for scientific monitoring of these projects, developing and using suitable indicators and measuring tools for project appraisal.

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Traduction

EXTENDED SUMMARY IN FRENCH

Objectifs et hypothèses.

Ce travail s'inscrit dans un contexte d'écologie de restauration des cours d'eau de tête de bassin versant et vise à approfondir les connaissances sur les conséquences de programmes de restauration. Il met l'accent sur la résilience des cours d'eau étudiée par le prisme de processus écologiques clés caractérisant le bon fonctionnement des écosystèmes aquatiques. Il propose d'analyser la fonctionalité des écosystèmes, en termes de processus et de traits fonctionnels des espèces, comme bio-indicateurs de la restauration écologique des cours d'eau. En complément des mesures classiques sur la diversité des macro-invertébrés, nous proposons d'étudier les traits fonctionnels des espèces, le taux de décomposition de la litière et l'oxygénatio du lit du cours d'eau comme indicateurs de la restauration écologique des cours d'eau. Le lien entre les cours d'eau de tête de bassin versant et leurs zones ripariennes (Vannote et al., 1980), la mobilisation de matériaux allochtones comme les sédiments et la matière organique, et les effets en cascade de ces matériaux sur les processus écologiques sur l'ensemble du système lotique ont influencé le choix de ces indicateurs (Gurnell et al., 2016).

Les cours d'eau de tête de bassin versant couvrent spatialement 70 à 80 % de la superficie des bassins versants et constituent une source importante de sédiments, d'eau, de nutriments et de matière organique pour les systèmes plus en aval (Vannote et al., 1980 ; Gomi et al., 2002). De fait, les processus naturels (hydrologiques, géomorphologiques et biologiques) résultant des cours d'eau de tête de bassin versant sont importants pour l'ensemble du système lotique. Les nombreuses actions de restauration sur les cours d'eau de tête de bassin versant ne sont généralement pas renseignées et ne font généralement pas l'objet de suivi. Il est donc difficile de déterminer si les indicateurs qui ont été utilisés pour contrôler l'efficacité de la restauration des grands cours d'eau seront applicables aux cours d'eau de tête de bassin versant.

Dans le cadre de cette thèse, nous avons étudié des rivières de tête de bassin versant; trois d'entre elles ont été restaurés en retirant des structures artificielles qui constituaient une barrière à l'écoulement et au transport des sédiments, tandis que les autres sont caractérisées par un travail sur le cours d'eau principal afin de replacer le lit de la rivière dans sa position historique. Dans chaque cas, nous avons adopté le plan d'étude Avant-Après-Contrôle-Impact (BACI, Downes, 2002). L'étude répond aux questions et hypothèses suivantes.

Question 1: Les indices de diversité basés sur les macroinvertébrés répondent-ils à la restauration des cours d'eau de tête de bassin versant différemment de ce qui a été observé dans d'autres systèmes ?

- **Hypothèses**: Nous émettons l'hypothèse que, tant pour la suppression des barrières que dans les nouveaux chenaux, les indices de diversité s'amélioreront après les travaux de restauration et que les valeurs de ces indices se rapprocheront des conditions de référence au cours du temps, permettant de définir à quelle est l'échelle temporelle nécessaire pour atteindre l'état de référence.

Question 2: Les indicateurs fonctionnels seront-ils plus performants que les indices de diversité en tant que bio-indicateurs de la restauration écologique des cours d'eau ?

- **Hypothèses**: Nous avons émis l'hypothèse que les indicateurs fonctionnels des tronçons restaurés seront plus proches des conditions de référence que les indices de diversité et que la décomposition de la litière sera plus liée aux traits fonctionnels qu'aux indices de diversité. Dans les tronçons restaurés, nous avons émis l'hypothèse que la recolonisation des macroinvertébrés sera déterminée par les traits essentiels à la dispersion et à la persistance des espèces.

Organisation de la these.

La thèse est organisée en trois chapitres. Le chapitre 1 contient les méthodes. Le chapitre 2 décrit la réponse de la structure de la communauté des macroinvertébrés à la suppression d'obstacles dans trois rivières restaurées tandis que le chapitre 3 teste la variabilité de la décomposition de la litière dans le cours d'eau et les facteurs influençant cette variabilité. Il dérit également si la décomposition de la litière et l'oxygénation du lit du cours d'eau peuvent constituer de bons indicateurs fonctionnels rendant compte de la restauration écologique dans les cours d'eau de tête de bassin versant. Tous les résultats sont discutés dans une discussion générale. La partie décrivant la recolonisation par les macroinvertébrés des tronçons de cours d'eau restaurés n'a pas pu faire l'objet d'un chapitre complet en raison du manque de temps. Elle est brièvement décrite dans la discussion. Elle examine si la recolonisation est motivée par la diversité fonctionnelle plutôt que par la diversité taxonomique.

Résumé du Chapitre 2. La réponse de la structure de la communauté des macroinvertébrés à la suppression d'obstacles.

Ce chapitre vise à répondre à la première question de cette thèse qui cherche à analyser la réponse des indices des communautés de macroinvertébrés suite à une restauration hydromorphologique. Les indices faunistiques des communautés, notamment basés sur les macroinvertébrés, ont été largement utilisés comme indicateurs des changements environnementaux dans les cours d'eau avec succès. Cependant, dans les évaluations des opérations de restaurations des cours d'eau, les résultats basés sur des indices de communautés de macroinvertébrés en tant que bio-indicateurs sont souvent peu concluants et peu d'études montrent des résultats génralisables.

Cette étude vise à déterminer si dans les cours d'eau de tête de bassin versant les évaluations des opérations de restauration sur la base d'indice de commuanutés de macroinvertébrés présentent des réponses plus marquées, en particulier pour un certain type de restauration (i.e. le débusage). Nous avons suivi trois tronçons de cours d'eau de tête de bassin versant où des structures artificielles (des buses) constituant des altérations hydromorphologiques des cours d'eau ont été retirées. Nous avons collecté des échantillons de macroinvertébrés dans les sections impactées et dans des sections de contrôle établies. Les échantillons ont été collectés avant et après les activités de restauration dans le cadre d'une étude avant-après-contrôle-impact (BACI). Nous avons utilisé deux outils multimétriques basés sur les macroinvertébrés (I_2M_2 et ERA) pour évaluer l'état écologique des cours d'eau sur la base des communautés de macroinvertébrés et pour quantifier les contributions relatives des pressions anthropiques des bassins versants.

Nos résultats monternt que la suppression des buses et la restauration de l'écoulement naturel ont réussi à réduire le colmatage. Cependant, seule la richesse taxonomique montrent un changement significatif positive. Les résultats montrent que la présence d'autres facteurs confondants peut avoir été responsable du peu de succès dans la récupération de la biodiversité. En outre, bien que les outils d'évaluation multimétriques aient été capables de différencier les cours d'eau et d'aider à démêler les effets des multiples pressions contribuant à la dégradation des cours d'eau, ils ont montré des limites à fine échelle, c'est à dire à une échelle inférieure de celle du bassin versant. Nos résultats monternt que pour favoriser la biodiversité, les méthodes de restauration des cours d'eau doivent considérer les multiples pressions contribuant à la dégradation des communautés fauniques dans les bassins versants.

Résumé du Chapitre 3. Les processus écologiques comme indicateurs fonctionnels de la restauration écologique.

Le chapitre 2 rapporte l'évolution de la structure de la communauté des macroinvertébrés et des traits des espèces dans les cours d'eau restaurés. Le chapitre actuel propose deux processus écologiques - la décomposition des feuilles et l'oxygénation du lit du cours d'eau - comme indicateurs du rétablissement écologique dans les cours d'eau de tête de basin versant après une restauration hydromorphologique. Il répond principalement à la question 2 de cette thèse et il contient deux articles, à savoir les articles 2 et 3. L'article 2 a été publié dans la revue *Water* (https://doi.org/10.3390/w13162246), l'article 3 est sous forme de draft.

La décomposition des feuilles est un processus intégratif au niveau de l'écosystème qui forme la base de la pyramide énergétique dans les cours d'eau forestiers où l'énergie provenant de sources autotrophes est limitée par l'ombrage de la forêt. Elle est médiée par une combinaison de facteurs biotiques et abiotiques dans l'écosystème et a été largement utilisée pour surveiller l'état écologique des écosystèmes terrestres et aquatiques à différentes échelles spatio-temporelles. Cependant, les informations sur les facteurs influençant le taux de décomposition de la litière à l'échelle du mésohabitat du radier des cours d'eau restent rares et donc sa variabilité à cette échelle reste largement méconnue. Dans l'article 2, l'expérience sacs de décomposition a été menée dans six radiers successifs au sein de 9 cours d'eau afin de déterminer la variabilité naturelle du taux de décomposition et les facteurs d'influence à l'échelle du radier. Les résultats de cette expérience montrent que la variabilité au sein des cours d'eau peut être aussi élevée que la variabilité entre les cours d'eau et que cette variabilité est sensible aux facteurs locaux à l'échelle du radier. La rugosité du lit du cours d'eau étant négativement liée au taux de décomposition et représentant le facteur le plus important à l'échelle du radier. Cette observation confirme la sensibilité de la decomposition de la litière aux facteurs locaux et peut donc être un indicateur utile dans le cadre du suivi de la réponse

écologique des cours d’eau à une échelle aussi locale que celle du radier dans un context de perturbations environnementales comme les activités de restauration dans les cours d'eau de tête de basin versant.

Dans l'article 3, le taux de décomposition de la litière et un processus écologique abiotique (la profondeur d'oxygénation du lit du cours d'eau) sont définis comme des indicateurs fonctionnels de la restauration écologique des cours d’eau de tête de bassin versant suite à une restauration impliquant la suppression des barrières artificielles. Les structures artificielles qui constituaient des barrières partielles sur trois sections de cours d'eau dégradés ont été retirées et nous avons suivi les deux indicateurs sur chaque cours d'eau avant et après le retrait des structures. Nous avons émis l'hypothèse que les barrières ont un impact négatif sur le taux de décomposition de la litière et sur l'oxygénation du lit du cours d'eau en raison du colmatage des sédiments. Pour chacun des indicateurs, nous avons comparé les valeurs sur les sections concernées de chaque cours d'eau avec les valeurs des sites de contrôle qui ont été établis sur les cours d'eau avant et après les travaux de restauration.

Nous avons observé un impact significatif des structures artificielles sur l'oxygénation et seulement un faible impact sur le taux de décomposition de la litière. Nous avons également observé que le l’aspect temporel pouvait être important dans la dynamique de restauration des cours d'eau, car les taux de décomposition dans les sections de cours d'eau restaurées ne se sont rapprochés des valeurs de référence qu'au cours de la deuxième année après la restauration. L'oxygénation du cours d'eau s'est, elle progressivement rapprochée des valeurs de référence dès la première année après la restauration. Le taux de décomposition de la litière présente également une plus grande affinité avec les traits du cycle de vie des espèces qu'avec les indices de biodiversité.

Conclusions.

Les cours d'eau de tête de bassin versant représentent une proportion importante du réseau hydrologique et fournit des services écosystémiques clés. Soumis à de forte dégradations affectant l'ensemble de l'écosystème, nous avons pu montrer qu'il est important de considérer avec attention et d'étudier le fonctionnement des cours d'eau de tête de bassin versant afin de maintenir leur bon état écologique et les services écosystémiques associés.

Comme cela a été rapporté dans d'autres systèmes, nous avons constaté que les indices de diversité des macroinvertébrés n'ont pas une réponse équivoque à la restauration des cours d'eau de tête de bassin versant. Seule la richesse des espèces s'est améliorée de manière significative après restauration hydromorphologique. Nos résultats suggèrent que cela pourrait être dû à l'échelle de considération des projets et à la présence d'autres facteurs limitatifs non pris en compte dans les projets de restauration. Nous avons conclu que la planification de la restauration des cours d'eau doit être réévaluée et être spécifique au site afin de fournir un aperçu du moment, de l'endroit, de la manière et de la méthode à appliquer pour restaurer un cours d'eau en tenant compte de tous les facteurs contribuant sa dégradation.

En outre, et de manière intéressante, nous avons constaté que certains éléments fonctionnels de l'écosystème peuvent servir d'indicateurs complémentaires pour le suivi d'opréations de restauration écologique en combinaison avec des indices plus classique caractérisant les communautés de macroinvertébrés. Dans les cours d'eau de tête de bassin versant, par exemple, les processus clés au niveau de l'écosystème comme la décomposition de la litière et l'oxygénation du lit du cours d'eau se sont avérés sensibles aux impacts de la présence d'un obstacle artificiel et sa suppression. Des études sur d'autres tronçons de cours d'eau impactés et d'autres processus comme la respiration, le métabolisme et la production autotrophe pourraient être complémentaires.

UNIVERSITÉ DE RENNES 1

Titre : Réponses fonctionnelles des communautés d'invertébrés à la restauration hydromorphologique des cours d'eau

Mots clés : cours d'eau, restauration, indicateurs fonctionnels, biodiversité, oxygénation

Résumé : La dégradation généralisée d'origine anthropique du système lotique a nécessité la restauration de nombreux cours d'eau dans le monde entier. En Europe, la Directive Cadre sur l'Eau de l'Union européenne impose à tous les États membres de restaurer les cours d'eau pour qu'ils atteignent un bon état écologique et propose une évaluation basée sur les éléments structurels de l'écosystème pour surveiller l'état écologique des cours d'eau restaurés. Cependant, les composantes de l'état écologique des cours d'eau comprennent des éléments structurels mais également fonctionnels. En raison de la non homogénéité des résultats issus des évaluations de la biodiversité en tant qu'indicateurs de l'état écologique des cours d'eau restaurés, un besoin croissant de protocoles d'évaluation plus adaptés et inclusifs sont requis. Nous proposons l'oxygénation du lit du cours d'eau et le taux de décomposition de la litière comme indicateurs fonctionnels en plus des indices classiques basés sur les communautés de macro-invertébrés pour surveiller le succès de la restauration de cours d'eau situés en tête de bassin versant. Nous avons montré que les indicateurs fonctionnels proposés sont complémentaires aux indicateurs relatifs à la diversité biologique pour suivre la restauration écologique. Nous avons également constaté qu'en combinaison avec les indices de biodiversité, ces indicateurs fonctionnels sont utiles pour démêler les effets d'autres facteurs des impacts des activités de restauration sur la santé des cours d'eau. Cette thèse souligne également l'importance d'élaborer un programme de surveillance suffisamment long pour dissocier les effets à court et à long terme des opérations de restauration.

Title : Functional responses of macroinvertebrate communities to hydromorphological restoration in headwater streams

Keywords : headwater streams, restoration, functional indicators, biodiversity, oxygenation, leaf litter decomposition

Abstract: The widespread anthropogenic degradation of the lotic system has necessitated the restoration of many rivers worldwide. In Europe, the EU WFD mandates all member states to restore rivers to good ecological status and proposes an assessment based on the structural elements of the ecosystem for monitoring the ecological status of restored streams. However, the components of the ecological status of streams comprise both structural and functional elements. Therefore, consequent on the inconsistent outcomes from the assessments of biodiversity as indicators of the ecological status of restored streams, there has been a growing call for better and more inclusive assessment protocols. We proposed streambed oxygenation and litter decomposition rate as functional indicators in addition to the classical macroinvertebrate community indices for monitoring restoration success in headwater streams. We found that these functional indicators complemented biological diversity in tracking the trajectory of ecological recovery in headwater streams. We also found that in combination with biodiversity indices, these functional indicators are useful in disentangling the effects of other confounding factors from the ipacts of restoration activities on the health of the streams. This thesis also highlights thei mperativeness of a long enough monitoring program to determine the short and long-term effects of restoration activities in streams.