Impact of woody riparian vegetation along streams on aquatic biodiversity

Auswirkung gehölzbestandener Uferrandstreifen entlang von Fließgewässern auf
die aquatische Biodiversität

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English summary

Riparian areas are key components of riverine systems forming the transition zone connecting the terrestrial and the aquatic realm. As such an ecotone, riparian areas are naturally valuable ecosystems in their own right, providing habitat and sustaining a high biodiversity including many specialist species. Furthermore, the riparian zone is functionally linked to many physical and biotic instream processes.

In temperate regions riparian areas are vegetated naturally by a diverse plant community which is characterized by the presence of trees. Woody riparian vegetation facilitates many functions to the aquatic ecosystem such as retention of sediments, nutrients or pesticides. Additionally, canopy cover regulates light availability, therefore instream primary production, as well as water temperature, which further structures aquatic communities. Trees also provide inputs of leaves, twigs and large wood that provide food and habitat important for many adapted aquatic organisms. These functions are generally well documented suggesting that management of woody riparian vegetation is a promising tool in conservation and restoration efforts. However, some characteristics relevant for river managers still need further research.

Against this background, Kail et al. (2021) investigate changes in water temperature related to gradual variations in canopy cover along small lowland streams as well as the length of stream sections required for water temperature to adapt to new conditions. It is shown, that within lengths still relevant to river managers (ca. 400 m) and feasible lateral widths (buffer width of 10 m), woody cover can reduce maximum water temperatures by as much as 4.6°C, which is substantial.

In Le Gall et al. (2022), Palt et al. (2022) and Palt et al. (submitted) effects of woody riparian vegetation on macroinvertebrates, a biological quality element relied upon in management, are quantified. In contrast to expected trends based on evidence from literature, the impact of landuse at the catchment scale is found to far outweigh that of the riparian scale if streams from many different backgrounds across large spatial gradients are analysed. However, by disentangling landuse forms at larger scales as well as hydromorphological stressors, typical conditions emerge in which the effect of woody riparian vegetation is identified a strong driver of the ecological status of the macroinvertebrates community. This suggests that managing woody riparian vegetation can indeed be a powerful option within the appropriate context.

There is consensus in literature that wider buffers (typically > 30 m) of woody riparian vegetation are required to achieve its functions consistently. As there are competing interests

and landuse demands, Vermaat et al. (2021) therefor monetise ecosystem services for different landuse scenarios following respective shared socioeconomic pathways in four case study catchments. They find that the degree of woody cover within the floodplain has only a minor effect on overall societal benefits. However since the distribution of services varies with woody cover, a redistribution of benefits might be necessary for generating acceptance of such measures.

In conclusion, understanding of effects and functions related to woody riparian vegetation is deepened by the studies encompassed in this thesis. In doing so, potential outcomes of management activity, have become more predictable, especially pertaining to the ecological status of the macroinvertebrate community. Evidence is presented that calls for more ambitious restoration efforts, which in turn has little adverse socioeconomic trade-offs.

German summary

Gewässerränder sind wichtige Bestandteile von Fließgewässer-Ökosystemen und bilden die Übergangszone zwischen dem terrestrischen und dem aquatischen Bereich. Als sogenannte Ökotone sind Uferbereiche von Natur aus wertvolle Ökosysteme, die einer hohen Biodiversität, darunter vielen spezialisierten Arten, Lebensraum bieten. Darüber hinaus ist die Uferzone funktionell mit vielen physikalischen und biotischen Prozessen der Fließgewässer verbunden.

In gemäßigten Regionen sind natürliche Gewässerränder mit einer vielfältigen Pflanzengemeinschaft bewachsen, die durch das Vorhandensein von Bäumen gekennzeichnet ist. Diese sogenannten Ufergehölze erfüllen viele Funktionen die relevant für das aquatische Ökosystem sind, wie z. B. den Rückhalt von Feinsedimenten, Nährstoffen und Pestiziden. Außerdem reguliert das Blätterdach die Sonneneinstrahlung und damit die Primärproduktion in Fließgewässern sowie die Wassertemperatur, was die aquatische Biozönose weiter strukturiert. Darüber hinaus liefern Bäume Falllaub, Zweige und Totholz, was jeweils vielen Wasserorganismen wichtige Nahrung oder Lebensraum bietet. Diese Funktionen sind im Allgemeinen gut dokumentiert und legen nahe, dass die Bewirtschaftung der gehölzbestandenen Ufervegetation ein erfolgsversprechendes Instrument für Naturschutz und Renaturierung darstellt. Einige für die Bewirtschaftung relevante Aspekte bedürfen jedoch noch weiterer Forschung.

Vor diesem Hintergrund untersuchen Kail et al. (2021) Anpassungen der Wassertemperatur bei einer graduellen Veränderung der Baumkronenbedeckung entlang kleiner Tieflandbäche sowie die Längen der Gewässerabschnitte, die für diese Anpassungen erforderlich sind. Es zeigt sich, dass bei einer noch bewirtschaftungsrelevanten Länge (400 m), und einer realistischen Breite (Pufferbreite von 10 m) maximale Wassertemperaturen um 4,6 °C gesenkt werden können, was erheblich ist.

In Le Gall et al. (2022), Palt et al. (2022) und Palt et al. (submitted) werden die Auswirkungen der gehölzbestandenen Ufervegetation auf das Makrozoobenthos, einem biologischen Qualitätselement der Gewässerbewirtschaftung, quantifiziert. Der Einfluss der Landnutzung im Einzugsgebiet überprägt dabei bei weitem den der Gewässerränder, wenn Probestellen in einem überregionalen Datensatz mit unterschiedlicher Einzugsgebietseigenschaften analysiert werden. Es ergeben sich aber dennoch kontextspezifische starke Effekte der Ufergehölze auf den ökologischen Zustand des Makrozoobenthos, wenn zwischen typischen Landnutzungsformen auf übergeordneten Skalen differenziert wird. Dies deutet darauf hin, dass die Bewirtschaftung oder auch die Renaturierung der gehölzbestandenen Ufervegetation in einem geeigneten Kontext tatsächlich eine sehr wirksame Option sein kann ökologische Bewirtschaftungsziele zu erreichen.

Es deutet viel darauf hin, dass erst breitere gehölzbestandene Gewässerränder (typischerweise > 30 m) in der Lage sind, eine hohe Funktionalität zu gewährleisten. Aufgrund verschiedener Interessen und Konkurrenz um Flächen, monetarisieren Vermaat et al. (2021) daher Ökosystemleistungen für verschiedene Landnutzungsszenarien in vier Fallstudieneinzugsgebieten. Sie stellen fest, dass der Grad der Gehölzbedeckung im erweiterten Gewässerkorridor nur einen geringen Einfluss auf den gesamtgesellschaftlichen Nutzen hat. Da jedoch die Verteilung der Ökosystemdienstleistungen je nach Szenario variiert, scheint eine anderweite Umverteilung des Nutzens erforderlich.

Zusammenfassend lässt sich sagen, dass das Verständnis für Funktionalität und Bedeutung von Ufergehölzen durch die in dieser Arbeit aufgeführten Studien erfolgreich vertieft wird. Dadurch werden mögliche Ergebnisse von Bewirtschaftungsmaßnahmen besser vorhersehbar, insbesondere in Bezug auf den ökologischen Zustand des Makrozoobenthos. Somit wird der Nachweis erbracht, dass erforderliche ehrgeizig Renaturierungsmaßnahmen einen großen Nutzen haben ohne negative sozioökonomische Gesamtauswirkungen zu haben.

1 General Introduction

Globally aquatic freshwater biodiversity is in decline (Ceballos et al., 2017) and disproportionately more rapidly compared to other ecosystems (Grooten & Almond, 2018; He at al., 2019; Tickner et al., 2020). This is despite concerted efforts to protect and restore aquatic ecosystems in many parts of the world in recent decades (e.g. the European Water Framework Directive or U.S. Clean Water Act). These efforts seek to sustain biodiversity and enhance it where it was lost previously and do so first and foremost by maintaining and restoring habitats to more natural conditions.

In temperate regions, these natural conditions typically entail the presence of woody riparian vegetation bordering most stream types (Ellenberg, 1988). The riparian area at the transition from terrestrial to the aquatic environment has the potential to cocoon the latter from adverse effects in cultural landscapes as well as to facilitate natural instream processes. This is demonstrated by the multiple well documented, functional links between woody vegetation and aquatic habitat conditions (Section 1.1).

Natural, i.e. woody, riparian vegetation therefore is rendered potentially highly effective for achieving desired benefits for aquatic organisms targeted by river management and associated legislation. Disproportionately strong effects from standalone woody vegetation in the riparian corridor are expected to compensate losses of larger-scale natural woodland cover previously converted to other landuse forms.

Even though many of these functional linkages have been thoroughly addressed and researched, there remain main open questions. This is especially true for assessing ecological effects of woody riparian vegetation on the community level, which is crucial if the latter's ecological status targeted by restoration activity (as for the European Water Framework Directive).

Besides its effect on the well-being of the aquatic environment, riparian vegetation also has multiple implications for human endeavours. For instance, woody riparian vegetation can be either critical (e.g. potential damage to bridges) or beneficial (e.g. retention areas) in terms of flood protection. Naturally vegetated riparian areas are not available for agricultural production. Given their prominence as landscape features, rivers and associated vegetation are of recreational and cultural importance (Gregory et al., 1991) and promote also human health. However, in the context of riparian management practices, these considerations just start receiving more attention.

1.1 Functions provided by woody riparian vegetation

In this section the functions woody riparian vegetation provide to the benefit of aquatic ecosystems focus on effects from relatively narrow landscape features within the riparian corridor. Woody vegetation there is commonly dubbed woody buffer. Understanding their part in the context of aquatic ecosystem functioning is a prerequisite for planning and executing restoration measures as well as protection activities at this relevant scale.
Functions and effects achieved by woody riparian vegetation differ from those of larger-sale woodland cover in some regards. For example this is true for the effect on water temperature through regulating micro-climates (Section 1.1.4). This poses some restrictions addressing available literature. For instance, inputs of organic material from woody vegetation in general constitute textbook knowledge at this point. Nevertheless, the inputs from standalone woody riparian vegetation, albeit linked in both function and effects, are by far less well documented (Section 1.1.5). In the following, some key functions of woody riparian vegetation for aquatic ecosystems are introduced.

1.1.1 Sediment retention

The effect from woody riparian vegetation (WRV) on sediment retention has been thoroughly studied and already reviewed numerous times. Fine sediments (< 2 mm; sand, silt, clay) originate to a minor degree naturally from fluvial erosion (Belmont et al., 2011) whereas problematic heightened inputs of sediments originate from tilled agricultural areas (Russell et al., 2001; Walling et al., 2008; Foucher et al., 2015; Lamba et al., 2015) but also can stem from special landuse forms or practices such as clear-cut forests (Wenger, 1999) or roadworks (Cocchiglia et al., 2012).

Fine sediments are loaded with nutrients (Section 1.1.2) or potentially hazardous substances (Section 1.1.3) and facilitate their transport to the aquatic environment (Collins et al., 2012; Foucher et al., 2015). Additionally, inputs of fine sediments increase turbidity, reducing light availability, and therefore instream primary production, impacting in turn also higher trophic levels (Kemp et al., 2011). They further cause siltation of the stream bed, i.e. they clog the interstitial space of natural stream beds by taking up the gaps between sediments larger in size (Brunke, 1999). This results in physical blockage and crucially prohibits exchange of oxygen between the free flowing and interstitial water deteriorating habitat conditions for macroinvertebrates (Wagenhoff et al., 2012; Burdon et al., 2013; Lange et al., 2014; Elbrecht et al., 2016) prominently for larvae and eggs of lithophilic species fishes (Berkman & Rabeni, 1987). Since, inputs of fine sediments especially from agricultural areas are associated with nutrient inputs, this further can result in depletion or even a lack of oxygen (Section 1.1.2). Yet on their own already increased fine sediment inputs unloaded with nutrients have stronger negative effects on sensitive taxa in particular compared to common levels of nutrient inputs (Wagenhoff et al., 2012; Lange et al., 2014; Elbrecht et al., 2016). In several studies, an abrupt decrease in the proportion of sensitive EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) was observed when more than 10-20% of the bed was covered with fine sediment (Burdon et al., 2013).

Retention of fine sediments occurs when surface runoff from adjacent areas laterally passes through a riparian area. The roughness of the riparian vegetation determines the corresponding reduction in surface flow and velocity, reducing in turn its capacity to transport fine sediments (Muscutt et al., 1993; Yuan et al., 2009). These are then deposited in the riparian area (Dosskey et al., 2010). Initial deposition rates are very high in the first few meters (ca. 5 m) for sand and silt (Muscutt et al. 1993, Polyakov et al., 2005) however, clay particles are only retained after a sufficiently long distance (Dorioz et al., 2006; Venohr & Fischer, 2017). Therefore, effective retention of fine sediments requires a suitably wide enough riparian area, or so-called riparian buffer, depending on such factors as slope (Liu et al., 2008; Yuan et al., 2009; Zhang et al., 2010) or soil texture (Dosskey, 2001; Parkyn, 2004). Under most realistic conditions a width of > 20 m is required in order to retain ca. 80% of the sediment load in surface runoff (Sweeney & Newbold, 2014).

Riparian vegetation only consisting of woody vegetation alone, i.e. trees and no dense ground cover due to shading, is unlikely especially given lateral light penetration in often narrow riparian buffer strips. Additionally there is no (Yuan et al., 2009; Lind et al., 2019) to little (Ramesh et al., 2021) evidence that the type of riparian vegetation affects retention, despite the often expected lower retention rates due to lower assumed surface roughness under a canopy cover. Yet, trees also affect bank erosion by stabilizing banks through their root network (Muscutt et al., 1993; Wenger et al., 1999, Dosskey, 2001; Hickey & Doran, 2004) reducing inputs of fine sediments from fluvial erosion. Furthermore, large wood in streams results in localized natural sedimentation spots through diversifying flow velocities (Gurnell et al., 1995) protecting other substrates from siltation (Rice & Church, 1996) (Section 1.1.5). Therefore, a riparian buffer of shrubs and grass alone is no alternative to a diverse and complex so called woody buffer as it pertains to sediment retention.

Nevertheless, the riparian area is indeed not a uniform buffer cocooning a stream but naturally heterogeneous and patchy. Additionally, surface flow is not uniformly flowing though the riparian area along the entirety of a stream segment neither but follows preferential pathways. Here infiltration and consequently deposition and retention of fine sediments are lessened (Barling & Moore, 1994; Dosskey, 2001; Venohr & Fischer, 2017). Artificial drainage of the adjacent floodplain is an additional human-made preferential pathway and in fact can account for equal amounts of fine sediment inputs in to the aquatic environment as surface flow (Russell et al., 2001; Chapman et al., 2005; Deasy et al., 2009).

1.1.2 Nutrient retention

Similarly to sediment retention, the effect from woody riparian vegetation on nutrient retention has been extensively studied and has likewise been reviewed numerous times with even varying focus on certain key processes. The main nutrients of concern are nitrogen and phosphorous. Nitrogen occurs mostly as nitrate and also nitrite, even though other compounds exist, albeit generally in lower quantity. However, if larger concentrations of ammonium or ammonia, a fish toxin, occur, they most likely stem from point sources such as untreated waste water. Phosphorus occurs either as dissolved orthophosphate, which is directly available to plants, or as particle-bound phosphorus, which is bound to fine sediments, especially clay. Naturally, phosphorus concentrations in streams are low and traditionally had been considered the most limiting factor for instream productivity in the aquatic ecosystem, though this has been revised more recently (Elser et al., 2007).

Heightened inputs of nutrients to the aquatic environment above natural levels due to anthropocentric causes, termed eutrophication, lead to an increase in primary production by macrophytes, phytobenthos and phytoplankton. This increases competition for light among the aquatic flora resulting in a shift in community composition towards competitive species with high nutrient requirements that either grow fast and tall to obtain sufficient light or have low light requirements (Baatrup-Pederson et al., 2015; 2016). In slow flowing streams, as nutrient concentrations continue to increase, epiphytic algae colonize macrophytes, shading the latter and hindering photosynthesis. Fully submerged macrophytes are therefore replaced by emergent ones (Hilton et al., 2006; O`Hare et al., 2018). In very slow-flowing or stagnant waters, analogous to lakes, even mass abundance of phytoplankton can occur at very high nutrient concentrations, resulting in high turbidity, which suppresses macrophytes altogether (O`Hare et al., 2018).

With shifts in productivity as well as species composition of primary producers the habitat conditions for other organism groups such as fish or macroinvertebrates change accordingly albeit effects are not straightforward. For instance, a moderate increase in nutrient concentrations leads to a higher abundance of macroinvertebrates, including sensitive taxa such as Ephemeroptera, Plecoptera or Trichoptera due to higher overall productivity (Matthaei et al., 2010; Piggott et al., 2012, 2015). While these abundances do not correspond to natural water body type-specific conditions, at even higher nutrient concentrations, the species composition shifts again in favour of species that feed on the then-increased algae and detritus of dead plants. As a consequence, sensitive taxa as well as biodiversity decline (Hering et al., 2006; Johnson & Hering, 2009; Lange et al., 2014). This is due to inter-specific competition and secondary saprobic load (Gieswein et al., 2017; Sundermann, 2013) where oxygen production during the day and consumption at night cause large fluctuations in oxygen availability (Kaenel et al., 2000; Desmet et al., 2011) or even oxygen depletion (Sabater et al., 2000; Nijboer & Verdonschot, 2004).

Even in regions where nutrient inputs to streams and rivers from point sources such as wastewater discharges have been greatly reduced over recent decades, current loads are still high (Mekonnen et al., 2018). In central Europe, nitrogen in particular originates predominantly from agricultural areas, albeit municipal wastewater treatment plants, power plants, transport and industrial operations continue to play a role (UBA, 2020). Hence, there remain relevant sources of nutrients that cannot be retained by woody riparian vegetation.

Dissolved nutrients from agricultural areas enter water bodies via surface runoff, subsurface as well as groundwater flow. Particle-bound nutrient transport (crucial for phosphorous) mostly occurs in surface runoff. While woody riparian vegetation can affect transport in surface and subsurface flow it does not reliably retain nutrients form in groundwater flow, which at best partially passes its root network. Retention of nutrient inputs in surface runoff is strongly connected to sediment retention (Section 1.1.1). Velocities of surface runoff are reduced when traversing vegetation in the riparian buffer, particularly ground cover or litter, which increases residence time during which nutrients can be taken up after percolation or sedimentation (Dorioz et al., 2006; Collins et al., 2009, Stutter et al., 2019). Deposited sediments eventually become overgrown by vegetation as part of the rooted topsoil where nutrients are extracted (Dosskey et al., 2010). Nutrients in subsurface flow are directly available to be taken up by the roots of the riparian vegetation (Collins et al., 2009; Dosskey et al., 2010). Nutrient uptake is particularly high in young vegetation stands and decreases with age (Parkyn, 2004; Roberts et al., 2012). In anaerobic conditions, nitrate is additionally converted to ammonium by microorganisms, and then further metabolized, escaping to the atmosphere as nitrogen gas (denitrification) (Collins et al., 2009).

Compared to dissolved nutrients, those bound by particles are generally retained more quickly, i.e. over shorter distances of passage through riparian buffers (Dodd & Sharpley, 2016; Venohr & Fischer, 2017; Vidon et al., 2019). Most coarse soil particles (e.g. sand and silt) are deposited directly at the transition from agricultural areas to the vegetated riparian buffer (Muscutt et al., 1993) or within the first few meters (ca. 5 m) (Polyakov et al., 2005; Dorioz et al., 2006). However smaller soil particles (clay), which transport readily plant-available phosphorus (Dodd & Sharpley, 2016), are deposited only in wider riparian buffer zones (> 15 m) (Dosskey, 2001; Dorioz et al., 2006). Retention of dissolved nutrients is determined by infiltration rates of surface runoff and further by residence time (thus by slope and soil texture), i.e. the duration of time nutrients are available for uptake and denitrification (Mayer et al., 2007; Venohr & Fischer, 2017). Similar to particle-bound transport, that of dissolved nutrients also follows a pattern of strong but highly variable retention within the first few meters of traversing vegetated riparian buffers and reliably high retention rates only possible in much wider riparian buffers (ca. > 30 m).

Given the straightforward effect of grass on roughness, it is often assumed the grassy riparian vegetation retains nutrients more efficiently than woody riparian vegetation. However, differences appear to be insignificant (Mayer et al., 2007; Dosskey et al., 2010; Gericke et al., 2020; Valkama, 2018). This is because roughness due to fallen leaves and twigs as well as typical herbaceous understory (Muscutt et al, 1993) under woody vegetation is similar (Uusi-Kämppa et al, 2000; Dosskey, 2001, 2010; Dorioz et al, 2006) or sometimes even higher compared to grassy vegetation (Dosskey et al, 2010). Additionally, the amount of nutrients taken up by woody vegetation from subsurface flow is greater than for grassy/herbaceous vegetation (Hoffmann et al., 2009) and persist for longer periods of time (Dosskey et al., 2010). Hence, in some cases greater retention has been observed for buffers of woody vegetation (Fennessy & Cronk, 1997; Venohr & Fischer, 2017) and in a quantitative review Gericke et al. (2020) concluded that vegetation form is the least relevant characteristic of riparian buffer pertaining to nutrient retention. Therefore, there seems to be no evidence that non-woody riparian vegetation should be a preferred alternative regarding nutrient retention from a management perspective.

Preferential pathways reduce retention efficacy of nutrients similarly to sediment retention (Section 1.1.1) as they follow the same mechanics. Additionally, both dissolved as well as particle-bound nutrients enter water bodies to a significant degree via artificial drainage of arable land (Barling & Moore, 1994; Dosskey, 2001; Hoffmann et al., 2009; Dodd & Sharpley, 2016) which is not affected by woody riparian vegetation.

The majority of reviews conclude that, depending on local conditions (such as slope, drainage area, riparian vegetation age, and soil) a width of 15 to 30 m is necessary for effective nutrient retention (about > 80%) (e.g. Sweeney & Newbold, 2014; Gericke et al., 2020). Only in very favourable conditions some much narrower riparian (ca. 5 m wide) can achieve equal rates of retention.

1.1.3 Pesticide retention

Pesticides for plant protection are intended to promote growth of crops by suppressing or killing other undesirable plants as well as fungi and animals (especially insect species) that hinder crop growth or health. Pesticide retention by riparian vegetation has also been reviewed repeatedly although to a much lesser degree compared to sediment or nutrient retention to which it is linked functionally. This is also because much literature on pesticide retention focuses predominantly on any vegetation lining croplands and not explicitly on buffers along water bodies.

Besides impacting terrestrial flora and fauna (Feber et al., 1996; Pleasants & Oberhauser, 2012), many aquatic insects, primarily larvae, i.e. aquatic life stages, of semi-aquatic species, are susceptible especially to neonicotinoids (Anderson et al., 2015). This includes certain Culicidae, Chironomidae, Ephemeroptera, or Trichoptera, while some Plecoptera and Tipulidae are less sensitive (Roessink et al., 2013; Anderson et al., 2015; Morrissey et al., 2015; Williams & Sweetman, 2019). Multiple sub-lethal effects have been recorded such as behavioural change and inactivity (Anderson et al. 2015), reduced emergence in Chironomidae (Williams & Sweetman, 2019) and reduced abundance of shredding macroinvertebrates foraging on leafs contaminated with neonicotinoids (Cavallaro et al., 2019). Another pesticide, permethrin, is also known to cause behavioural changes resulting in increased drift of macroinvertebrates evading impaired conditions (Wurzel, 2020). Synergistic effects of different pesticides are not yet well understood but mixtures of e.g. neonicotinoids and fungicides had significantly stronger effects on non-target organisms than the application of the individual substances alone (Wernecke et al., 2019). Though the overall impact of pesticides generally remains elusive, inputs of nutrients to small lowland streams recently proofed to impair macroinvertebrates more than lack of habitat quality or nutrient inputs (Liess et al., 2021).

Documented effects on fish are rather rare (Nowell et al., 2018) and are not well studied neither with regards to event-based (i.e. ensuing heavy rainfall) nor chronic exposure (Schäfer et al., 2011). However, it has been shown that pesticides accumulate in fish, affecting animal fitness (Belenguer et al., 2014) or behaviour as observed in salmonids, resulting in reduced food intake and growth (Baldwin et al., 2009).

Inputs of pesticides to aquatic ecosystems susceptible to retention by riparian vegetation follow similar input pathways to nutrients, i.e. they enter water bodies via surface runoff, subsurface flow and groundwater (Section 1.1.2). Additionally, they can be dispersed by wind during application (drift), which, despite the relatively small contribution to overall amount of inputs, can cause short term concentration spikes in water bodies (Reichenberger et al., 2007).

Surface runoff passing through a vegetated riparian buffer starts reducing its flow depth and velocity due to the increase in ground roughness causing sedimentation of its sediment load, hence particle bound pesticides, as well as infiltration of water, hence dissolved pesticides (Krutz et al., 2005; Lacas et al., 2005). Subsurface flow has a much lower flow velocity and thus higher residence time. Dissolved pesticides can directly degrade or be bound to soil particles. Along with already bound pesticides they in turn are degraded, primarily in the topsoil rich in organic matter and therefore high microbial and enzymatic activity (Krutz et al., 2005; Lacas et al., 2005). The stronger pesticides are bound to soil particles the more they are retained with rates being as high as 76% in optimal conditions (Arora et al., 2010). The riparian vegetation may also take up pesticides to a substantial degree further enhancing retention rates in the riparian zone (Dosskey et al., 2010).

The width of vegetation filter strips serves as a proxy for retention time during which pesticides from surface and subsurface flow can be retained and degraded (Krutz et al., 2005; Collins et al., 2009). Most reviews conclude that a width of 5-10 m is sufficient for effective retention (about 80%) (Wenger , 1999; Krutz et al., 2005; Reichenberger et al., 2007 ; Zhang et al., 2010; Venohr & Fischer, 2017).

Similarly to non-riparian vegetation strips, pesticides in drift are either retained due to the reduction of wind speed already over the arable land, i.e. reducing amounts of drift to begin with, or due to deposition of droplets on the vegetation surface. Retention rates from drift can be as high as 90% (Dosskey, 2001; Reichenberger et al., 2007). High foliage density of the woody vegetation effectively reduces the necessary width of riparian vegetation for retention even at higher wind speeds.

However, diffuse surface runoff and drift do only account for some inputs of pesticides and the remaining sources cannot be mediated by riparian buffer zones. Urban sources account for substantial proportions (Tauchnitz et al., 2020) stemming from private and public gardens, as well as from green spaces along infrastructure (Gerecke et al., 2002). Along with wastewater treatment plants effluents (Gerecke et al., 2002 ; Müller et al. 2002; Münze et al, 2017) these sources may account for 40-90% of total inputs (Reichenberger et al., 2007). Additionally, if good agricultural practices are not maintained, otherwise avoidable amounts of pesticides are emitted from farmyards that are higher than those from application to arable land (Neumann et al., 2002).

1.1.4 Regulation of solar radiation

While some research has been done on the influence of riparian vegetation on water temperature, it has less frequently been the focus of reviews compared to its retaining functions (Sections 1.1.1 to 1.1.3) (but see Castelle et al., 1994; Wenger, 1999; Broadmeadow & Nisbet, 2004; Sweeny & Newbold, 2014; Lind et al., 2019). Water temperature is the result of complex energy budgeting, with main drivers being inputs of direct solar radiation as well as sensible heat transfer from the air (Caissie, 2006; Webb et al, 2008; Kelleher et al., 2012). Shading from riparian vegetation, i.e. trees, can substantially regulate these energy fluxes and thus helps preventing strong increases in water temperatures. Therefore, mainly changes to mean or maximum daily temperatures as well as daily temperature amplitudes are addressed in literature. Correspondingly shading also reduces availability of photosynthetic active radiation, which has been only been addressed in relatively fewer studies (but see Feld & Hering, 2017).

Solar radiation affects aquatic communities via two main functional links. First, it drives photosynthetic activity and hence primary production. Second, through driving water temperature it affects metabolic rates across trophic levels, while also affecting physical properties of the ambient water, crucially solubility of oxygen.
A lack of shading in streams naturally bordered by woody riparian vegetation favours aquatic autotroph organisms, which increase in abundance and biomass along with shifts in species composition. This alters the trophic web, which in small streams is naturally based on allochthonous instead of autochthonous plant matter (Vannote et al., 1980). Furthermore, aquatic plants, principally macrophytes, shape physical habitat conditions for fish and macroinvertebrates as they occur unnaturally due to a lack of shading (Grenouillet et al., 2000; Lusardi et al., 2018), causing corresponding community shifts.

Different studies indicate that primary production in unshaded stream stretches, often approximated by chlorophyll-a concentrations, can reliably be as much as double that of shaded ones (Noel et al.,1986; Kiffney et al., 2003; Ghermandi et al.; 2009; Hutchins et al., 2010; Kaylor & Warren, 2018 ; Nebgen et al., 2019). It is concluded that riparian vegetation controls primary production more through shading than nutrient retention in agricultural landscapes (Hutchins et al., 2010). However, Thompson & Parkinson (2011) found that lacking riparian vegetation and consequently high amounts of fine sediment inputs also control algal growth pointing out possible trade-offs between the different functions of riparian vegetation.

The effect of shading on stream water temperature can be as much as several degrees Celsius (e.g. Johnson, 2004; Rutherford et al., 2004) and therefore it is the key determinant available to management in order to prevent excessive temperature regimes. Initially, biomass of fish and invertebrate is still favoured by slightly higher water temperatures (e.g. by speeding up egg and larval development, increased foraging opportunities on algae or macrophytes), though sensitive taxa may already be negatively affected (Haidekker & Hering, 2008). Also, already moderate water temperature increases in conjunction with other stressors such as an increase in fine sediments can result in synergistic stressors interaction (Piggott et al., 2012; 2015). Additionally, increases in daily fluctuations of water temperate have been found to be detrimental (Cox & Rutherford, 2000).

Small streams, where shading has its strongest effect on water temperature (Loicq et al., 2018), are prone to significant increases in water temperature as a consequence of the lack of riparian vegetation. This is especially true for mountain streams which are naturally cooler. Here optimum temperature ranges for fish, prominently salmonids (upper limit of 20°C; Elliott, et al. 1995) and sensitive macroinvertebrates (e.g. Stewart et al., 2013) can quickly be exceeded. For instance lethal water temperatures for more sensitive macroinvertebrates may be as low as 21°C (Dekowzlowski & Bunting, 1981; Quinn et al., 1994; Cox & Rutherford, 2000; Stewart et al., 2013).

The width of woody riparian vegetation affects its capacity to shade the streams water surface and most reviews concluded that generally 10-30 m wide buffers are effective at preventing substantial increases in water temperature also compared to a baseline in forested conditions (Wenger, 1999; Sweeney & Newbold, 2014; Lind et al., 2019). Even wider woody vegetation allow for potential benefits of woodland micro-climates controlling ambient air temperature and therefore latent and sensible heat fluxes (Barton et al., 1985; Moore et al., 2005).

The effect of shading by riparian vegetation on water temperature additionally depends on the presence of trees and a number of characteristics (.e.g. shape of tree crown, understory, and orientation in the landscape) besides its width (Sweeney & Newbold, 2014; Rutherford et al., 2018; Savoy et al., 2021). For instance, length of shaded versus unshaded stretches is key (Barton et al., 1985) as residence time in constant conditions controls settling on equilibrium temperatures as a response to changes in energy budgeting (Rutherford et al, 2004). In fast flowing mountain streams it may take shading from woody riparian vegetation multiple kilometres to reach its maximum effect (Barton et al., 1985).

Also, ambient and general water temperature levels dictate the potential response to heated stream waters (excess temperature) to shading (Moore et al., 2005; Coats & Jackson, 2020). Impounded or stagnant stream stretches, with very long residence times, can dramatically alter temperatures regimes going downstream countervailing any potential effects from woody riparian vegetation (Claeson & Coffin, 2016; Maheu et al., 2016). This makes larger-scale assessments on this function provided by the riparian vegetation very difficult (but see Beaufort et al., 2016; Loicq et al., 2018).

1.1.5 Inputs of terrestrial plant matter

The importance of inputs of leafs, twigs, i.e. coarse particulate organic matter (CPOM), and large dead wood from woody vegetation are considered textbook knowledge with regards to their effects in streams and rivers, structuring the physical environment as well as community composition of aquatic organisms. However inputs are mostly studied in the context of larger-scale woodland cover.

CPOM consist of all organic material with a diameter > 1 mm, i.e., grass, pieces of herbaceous vegetation, small woody material such as bark fragments and twigs, well as needles for conifers but most importantly it consist of fallen leaves from herbaceous vegetation (Kail & Gerhard, 2003). Especially fallen leaves are an integral allochthonous source of food and therefore energy for the aquatic ecosystem, especially in naturally shaded (Section 1.1.4) upper reaches (Vannote et al., 1980; Menninger & Palmer, 2007). Consequently, these reaches are mainly populated by shredding and gathering macroinvertebrates. If woody riparian vegetation and therefore inputs of CPOM are lacking these are replaced by grazing macroinvertebrates that feed on the thus higher biomass of primary producers, mainly algae (Section 1.1.4.), while predating macroinvertebrates dwindle, too (Wallace et al., 1997). This shift in community composition can be accompanied by in declines in macroinvertebrate abundance and biomass on the order of -90% and -80%, respectively (Wallace et al., 1999) illustrating the importance of CPOM inputs. Additionally, diversity of fallen leaves is crucial since adapted fungal communities (Lecerf et al., 2005) allow for more rapid digestion by macroinvertebrates (Leroy & Marks, 2006). Fish benefit from CPOM inputs mainly via its effects on macroinvertebrates in small upper reaches (Hicks, 1997).

CPOM is deposited to streams either directly falling into the water, potentially assisted by wind, or indirectly after lateral transport by wind and runoff through the riparian area. While grassy or herbaceous vegetation may become a substitute for leaves as an allochthonous source of coarse particulate organic matter (CPOM) in waterbodies lacking woody riparian cover (Menninger & Palmer, 2007) CPOM to forested stream reaches are 2-6 times greater in magnitude (Delong & Brusven, 1994; Gray, 1997; Stenroth et al., 2014) underlining the importance of trees.

In small streams only 10% of leaf inputs are deposited directly, whereas this proportion can be as high as 80% in larger streams enveloped by a closed canopy cover (Cillero et al., 1999; Weigelhofer & Waringer, 1994). Besides stream size (Conners & Naiman, 1984), factors affecting lateral transport rates such as slope (Weigelhofer & Waringer, 1994) determine natural levels of amounts of instream leaf litter. Also, the lateral extent of woody riparian vegetation is a key determinant for leaf inputs as the first lines of trees along the stream edge may account for just 22% of natural amounts of leaf deposits (Oelbermann & Gordon, 2000). Even much more extensive buffers more than 50 m in width fall short of leaf amounts naturally observed in woodland streams (Oelbermann & Gordon, 2000; Thomas et al., 2016).

Dead wood creates complex micro-habitats by diversifying flow conditions, both creating still water zones as well as increasing flow velocities around its edges.(Gurnell et al., 1995). In turn this diversifies substrate composition on a very small scale (Rice & Church, 1996; Buffington & Montgomery, 1999). Large wood even dictates river morphology by initiating pools (Kail, 2003), gravel bars (Abbe & Montgomery, 2003) or even side arms (Piégay & Gurnell, 1997).

Due to this higher habitat diversity in reaches with dead wood, fish of different age groups (Rabeni & Jacobsen, 1993) increase in abundance and biomass (Zika & Peter, 2002; Becker et al., 2003). Macroinvertebrate biomass and abundance is also higher on dead wood than on other substrate (Benke & Wallace, 2003) which is true for different life stages (Anderson et al., 1984) and a large number of specialist species (Hoffmann & Hering; 2000). Dead wood also offers protection from predators (Crook & Robertson, 1999; Dolloff & Warren, 2003; Zalewski et al, 2003).

Large wood is continuously supplied by woody riparian vegetation that dies off either as an entire tree, or in parts of branches and large twigs (Benda et al., 2003). Senescence in old stands contributes more material compared to young stands (Stout et al., 2018). There is general consensus that only trees growing in the streams' vicinity are prone to be deposited to the aquatic environment, with 30 m an often suggested maximum distance, as this represents a typical maximum height for riparian trees (e.g. Wenger, 1999; Gregory et al., 2003).

Yet Sobota et al. (2006) showed that in narrow valleys with associated steeper lateral slopes the amounts of dead wood could even double. Additionally, stochastically occurring events such as landslides, wind-throw, fires, or insect calamities (Benda et al., 2003) locally result in very large amounts of dead wood (Keller & Swanson, 1979; May, 2002; Reeves et al., 2003). All this suggests that in woody riparian vegetation strips maintained or established by river restoration, the often relatively young age of stands and lack of disturbances inputs of dead are below natural levels there is a potential need for purposeful introduction.

1.1.6 Terrestrial habitat and dispersal

Woody riparian vegetation as habitat for terrestrial species has only rarely been addressed in reviews (5) despite a larger number of primary studies. This already suggests that despite the implied relevance for many (semi-) terrestrial fauna and flora, generalizations are challenging due to the individual species' prerequisites. Thus, evidence here is presented much more anecdotally and less systematic than for e.g. the retaining functions (Sections 1.1.1 to 1.1.3).

This is equally true for the function of woody riparian vegetation to serve as dispersal or migration corridors, given their linear nature. While migration corridors in general have been focus of much research there has been little focus on riparian vegetation as a specific case for this (reviewed in Beier & Noss, 1998; Gilbert-Norton et al., 2010).

Woody riparian vegetation provides more diversity than grassy riparian vegetation (Lovell et al., 2006) and constitutes a natural plant community structuring trophic interactions between aquatic and terrestrial species all while providing habitat for terrestrial riparian fauna (Madden et al., 2015).

Trophic webs in riparian zones cannot be distinguished as either aquatic or terrestrial (reviewed in Baxter et al., 2005). On one hand, terrestrial invertebrates are consumed by fish if they become available and can amount to as much as half of the total uptake (Baxter et al., 2005). On the other hand birds, bats, terrestrial arachnids among others (Hering & Plachter, 1997; Paetzold et al., 2005), prey upon flying life stages of aquatic insects during events of emergence, when other food sources are scarce (Xiang et al., 2017). Bats foraging on emerging aquatic macroinvertebrates concentrate along streams with dense woody riparian vegetation (Scott et al., 2010).Additionally, predatory insects, e.g. ground beetles, concentrate at the shoreline since terrestrial life stages of aquatic insects, e.g. Ephemeroptera, Plecoptera, Trichoptera and Odonata generally stay in close proximity to the watercourse unless the riparian vegetation is lacking trees (Petersen et al., 2004; Ehlert, 2009). Yet, even grassy riparian vegetation may already favour terrestrial insects (McCracken et al., 2012). As a response to terrestrial organisms feeding on aquatic macroinvertebrates, Nakano et al. (1999) documented increased feeding pressure of fish on aquatic macroinvertebrates, which in turn benefited algal growth no longer controlled by invertebrate grazers. Thus further illustrates the close ties between the apparently distinct realms.

Besides supporting foraging of some terrestrial fauna, woody riparian vegetation also serves as habitat for many terrestrial species. For instance, plant diversity is generally higher in the large floodplains due to regular disturbances in flooding events (Naiman et al., 1993). Mallik et al. (2014) reported that already narrow 30 m wide strips of woody riparian vegetation can approximate this greater habitat diversity so that natural plant communities can be found (Spackman & Hughes, 1995; Elliott & Vose, 2016). Riparian vegetation in the floodplain also supports a relatively greater number of forest birds compared to other forests (e.g. Decamps et al., 1987; Bennett et al., 2014). Also naturalness in the bird community composition increases with woody cover (Bryce et al., 2002), and there are more species adapted to forest edges found in floodplains than in non-riparian woodlands (Pereira et al., 2014). Therefore woody riparian vegetation is a hot-spot for avian biodiversity (Hagar, 1999; Shirley & Smith, 2005) and species counts and abundances generally increase with its width (Castelle et al., 1994). Furthermore, larger mammals, such as roe deer, foxes, and badgers, concentrate in woody riparian areas with sufficient understory and width (ca. 20 m) in agricultural landscapes (Hilty & Merenlender, 2004; Dondina et al, 2016; Pelletier-Guittier et al, 2020). Yet while, the community composition of small rodents in such areas is more diverse than in open riparian zones, it does not correspond to that of woodlands, as species normally found deep within forest are missing (Darveau et al., 2001; Cockle & Richardson, 2003). Similarly, amphibians likewise generally dependent on larger forest stands. For instance salamanders, using woody vegetation as refuge, increase in abundance and species diversity along with the width of the woody buffers (0-55 m; Guzy et al., 2019). However there is also evidence that much wider woodland cover is necessary for other species such as spring frog (50-100 m distance from stream) or fire salamanders (100-400 m) (Ficetola et al., 2009).

These findings show that specific minimum buffer widths are required for certain organism groups, below which no effects from woody riparian vegetation are expected. These required minimum widths are generally smallest for terrestrial insect living on riverine substrate (< 5 m width; Hering et al., 2021), followed by plants (> 10 m; Lind et al., 2019), terrestrial stages of aquatic insects (20 m width; Hering et al., 2021), amphibians and small mammals (> 20 m; Lind et al., 2019) and finally birds (> 40 m; Lind et al., 2019). Thus, while an already relatively wide buffer of woody riparian vegetation in the realm of 30 m may suffice to account for much of the other functions it may also be adequate for demands of many species concerning the provisioning of terrestrial habitat. However, truly natural species communities of larger-scale floodplain forests, only occur in much wider woody zones or forest stands typically beyond the scope of regular management of riverine systems (Lind et al., 2019).

Woody vegetation in the riparian corridor also facilitates dispersal and migration for aquatic as well as terrestrial animals.

Regarding aquatic species this plays mainly a role for emergent adult life stages of Ephemeroptera, Plecoptera and Trichoptera, which due to their flying abilities can compensate for larval drift, colonize new stream reaches and connect meta-populations (Downes et al., 2016; Sarremejane et al., 2017). In doing so, individuals navigate along woody structures (Winterbourn et al., 2007) but dense stands of conifers, which are naturally seldom found along streams, actually impair dispersal (Hering et al., 1993). Plecoptera, in particular, move away from stream stretches without woody riparian vegetation in search for woody vegetation, whereas they remain close to the streams' edges if trees were to occur there (Petersen et al., 2004; Ehlert, 2009). It has been suggested that by reducing polarization on the water surface via shading, trees direct polarotactic insects towards the streams' centres (Farkas et al., 2016).

For terrestrial animals there has been some indication that birds preferentially fly along riparian woody vegetation yet it remains uncertain if they actually follow dispersal corridors or benefit from foraging possibilities being higher in the vicinity of streams (Mosley et al., 2006). Some research has also been conducted on certain mustelid species. For instance the pine marten primarily disperses along woody vegetation bordering streams and is negatively affected by its fragmentation (Balestrieri et al., 2015). Similarly, the European otter also migrates along continuous corridors of woody riparian cover of preferably older stands (Bedford, 2009; Van Looy et al., 2014). In otherwise agricultural landscapes other mammals such as roe deer or foxes are also more frequently observed dispersing or migrating along hedgerows or riparian strips (Pelletier-Guittier et al, 2020).

In their meta-analysis Gilbert-Norton et al. (2010) concluded that dispersal of flying insects, birds and mammals is roughly 50% higher in the presence of woody riparian vegetation than in open riparian areas.

1.2 Ensuing research motivation

As demonstrated (Section 1.1) there is overwhelming evidence detailing the functional linkages between woody riparian vegetation and aquatic ecosystems. This is not surprising, with the riparian area constituting the ecotone, i.e. transition between the aquatic and terrestrial realm, where energy fluxes, matter, and species come into contact.

Despite the considerable knowledge gathered, there remain open questions, especially from the perspective of river management. This is even true for various levels of consideration. For one the details behind some functions have not been addressed enough to predict real world consequences to maintaining or restoring woody riparian vegetation. This is even more so regarding its overarching effect on management goals, i.e. on the level of communities of biological quality elements of concern for river managers. Lastly, since there is sufficient indication that functioning woody riparian zones exceed the width currently allocated to them in cultural landscapes, the question needs to be addressed if such ambitious goals for the well-being of aquatic ecosystems are even doable from a socioeconomic perspective.

1.2.1 Potential effects of woody riparian vegetation management on water temperatures

As detailed in Section 1.1.4 shading by the canopy cover of woody riparian vegetation is a key driver of water temperature and it also regulates primary production. In doing so, shading has far reaching effects structuring trophic webs in the aquatic environment. Given practical reasons and constraints management of woody riparian vegetation is often the obvious management option to mitigate effects from further climate change.

However, there is little empirical evidence available for river managers to estimate the real world effects of changes in woody cover in the riparian area along stream sections. Most studies estimate effects from shading by comparing fully shaded to fully open stream stretches, however this is not entirely realistic. Also the longitudinal effect is often not considered, i.e. the residence time of running waters exposed to constant shading conditions. This is critical as a certain amount of time is necessary for water to adjust to changes in canopy cover.

Therefore, from a management perspective, assessing more gradual changes in woody riparian vegetation as well as gradual effects along stream stretches of a relevant length are most interesting. These would allow to define expected outcomes of planting but also loosing trees within the riparian corridor.

1.2.2 Assessing effects on biological quality elements at larger spatial scales

All functions presented in Section 1.1 have potentially large effects structuring aquatic communities. While the knowledge on these individual causal relationships is broad and much empirical evidence is available this not true for all effects taking place in concert. It is unclear if certain functions provided take precedent shaping habitat conditions and how potential trade-offs between effects are settled. This is crucial from a management perspective that often focuses on maintaining or establishing sufficiently good ecological assessments of biological quality elements, i.e. target organism groups such as diatoms, macrophytes, macroinvertebrates or fishes (e.g. European Commission; 2000) by providing the necessary habitat conditions. Therefore studies are required which can weigh functional linkages in order to inform practitioners about potential effects on target groups. With this knowledge, river managers can address specific shortcomings in community composition by mitigate impactful stressors with corresponding functions provided by woody riparian vegetation.

In addition, recently effects of woody riparian vegetation on have been studied regarding their likely scale-dependence (Feld et al., 2018). This questions the necessary spatial scale, especially the longitudinal extent that functions of woody riparian vegetation need to act on in order to generate their effect. For instance, the input of dead wood can immediately have a localized positive effect diversifying micro-habitat conditions for fish and macroinvertebrates. Changes to the canopy cover however only manifest in alterations to water temperatures after at least a few hundred meters. On an even larger scale, woody riparian vegetation might need to retain nutrients across large parts of entire catchments in order to maintain natural levels of productivity. While this may be conceptually sound empirical evidence is still lacking.

This calls for research that not only disentangles between the various functions provided by woody riparian vegetation but also addresses their context and scale dependence.

1.2.3 Socioeconomic effects of multi-functional woody riparian vegetation buffers

Much of the functions presented in Section 1.1 depend on the width, i.e. lateral extent, of riparian areas covered with woody vegetation. Despite the different processes, there is somewhat of a consensus on a minimum width required to allow for most or even all functions to become meaningfully effective.

While retention of fine sediments, nutrient or pesticide is unreliable in very narrow buffers, those 30 m in width consistently are capable of retaining around 80% of respective inputs. As buffers increase in width, added benefits to retention rates become quickly marginal. Inputs of dead wood as well providing migration corridors and even habitat for many terrestrial fauna may also already be substantial for woody riparian vegetation 30 m in width. Added benefits are possible for inputs of CPOM and habitat for amphibians or birds at much larger lateral extents exceeding even few hundred meters. Yet this effectively approaches woodland conditions no longer constituting a standalone landscape features. This excessive scale is also no longer of general concern from a river-management perspective. Since temperature regulation and habitat provisioning for most invertebrates already is achieved over the first few meters it is encompassed within a 30 m-wide corridor of woody riparian vegetation. In conclusion, from an ecological perspective it seems reasonable to suggest that this lateral width to managers as an effective option that allows to provide most of the effects to the aquatic environment while also serving the adjacent terrestrial areas.

However, this amount of lateral space is often not available due to agricultural and urban landuse encroaching upon the riparian corridor. The fact that legislation and regulations typically only set few meters of non-intensive agricultural landuse as minimum protection standards further challenges the suggestion of roughly 30 m wide buffers of woody riparian vegetation cocooning streams. Given the stark discrepancy between the ecologically desirable and widespread real world conditions this questions if such ambitious restoration goals are viable from a socioeconomic perspective

2 Published and submitted articles

The following collection of five individual studies addresses these open research motivations and questions (Section 1.2) in more detail.
In the context of this doctoral work, the following articles were published:

Kail, J., Palt, M., Lorenz, A., & Hering, D. (2021). Woody buffer effects on water temperature: The role of spatial configuration and daily temperature fluctuations. *Hydrological Processes*, *35*(1), e14008.

Le Gall, M., Palt, M., Kail, J., Hering, D., & Piffady, J. (2022). Woody riparian buffers have indirect effects on macroinvertebrate assemblages of French rivers, but land use effects are much stronger. *Journal of Applied Ecology*, *59*(2), 526-536.

Palt, M., Le Gall, M., Piffady, J., Hering, D., & Kail, J. (2022). A metric-based analysis on the effects of riparian and catchment landuse on macroinvertebrates. *Science of The Total Environment*, *816*, 151590.

Vermaat, J. E., Palt, M., Piffady, J., Putnins, A., & Kail, J. (2021). The effect of riparian woodland cover on ecosystem service delivery by river floodplains: a scenario assessment. *Ecosphere*, *12*(8), e03716.

For the readers' convenience the entailed articles published in their respective journals' layouts have been provided with additional page numbers consistent with their positioning in the text of this thesis.
Additionally, in the context of this doctoral work, the following article has been submitted:

Palt, M., Hering, D., & Kail, J. (2022). Effects of woody riparian vegetation on macroinvertebrates are context-specific and large in urban and especially agricultural landscapes. Manuscript submitted for publication in *Journal of Applied Ecology* June 13, 2022

A declaration of author contribution precedes each article, which are listed after a brief summary of them all (Section 2.1).

2.1 Summary of the entailed published and submitted articles

The articles encompassed in this thesis widen in scope of consideration of woody riparian vegetation from a single function they provide (Kail et al., 2021), to its effects on the whole macroinvertebrate community through multiple functions (Le Gall et al., 2022; Palt et al., 2022; Palt et al., submitted) and further to their role in the provisioning of ecosystem services, i.e. their socioeconomic benefit next to an ecological one (Vermaat et al., 2021).

In *Kail et al. (2021)* the effect of shading by the canopy cover of riparian trees on the aquatic environment was investigated in seven small lowland streams in western Germany. Shading is a crucial given its influence on all trophic levels directly through water temperature regulation and consequently on metabolic rates in phytobenthos, macropyhtes and poikilotherm animals; which the vast majority of freshwater aquatic animals are. Moreover, as shading limits light availability and instream primary production, it suppresses growth of autotroph organisms which structure the trophic net as well as habitat conditions for fish and macroinvertebrates.
Specifically, the effect of canopy cover on daily mean and maximum water temperatures in small lowland streams was assessed in this study in order to evaluate the effects of different lengths of shaded stream sections.
Cooling of streams previously exposed to direct solar radiation along continuously shaded sections results in a new, cooler equilibrium water temperature after 0.4 km. Streams which exit shaded sections and become exposed to direct solar radiation continue to warm for 1.6 km before reaching a new equilibrium temperature. Largest effects occurred on cloud-free days during May, where the maximum cooling effect was -4.6° and the maximum heating effect was +2.7°C. Considering the canopy cover in a 10 m wide buffer improved statistical models over using canopy cover in the 30 m wide buffer.
This implies that managing WRV in a narrow buffer and along relatively short stream sections can already offset local increases in water temperatures due to lack of canopy cover upstream to a substantial degree, which is crucial with respect to mitigating expected consequences of climate change.

In *Le Gall et al. (2022)* and *Palt et al. (2022)* woody riparian vegetation was quantified from high resolution orthoimages with the intention to investigate its effect on macroinvertebrate metrics and ecological status alongside other confounding landuse, water quality and hydromorphological variables with known effects on the macroinvertebrate community.

Specifically, woody cover was assessed at two different lengths (near upstream vs. far upstream).

All variables were arranged in structural equation models (SEM) in order to address their functional interconnectedness and statistical correlations. Besides the integrated ecological status of the community selected macroinvertebrate metrics were hypothesized to respond to certain specific functions provided by woody riparian vegetation. For instance shares of shredding organisms reflect local amounts of leaf inputs, while the share of EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) is indicative for the terrestrial habitat provisioning for flying life stages.

The respective studies for study sites in the whole of France (n = 1082; Le Gall et al., 2022) and for three federal states in Germany (n = 1017; Palt et al., 2022) found that direct effects from riparian landuse were of little importance and generally far outweighed by larger-scale stressors, i.e. catchment characteristics. While a strong effect from catchment landuse was expected for integrated measures such as ecological status or metrics related to saprobic pollution this was not hypothesized for metrics related to functions that were considered to have already localized effects (e.g. temperature or leaf inputs) independent from lager scale stressors (Feld et al., 2018).

It had to be concluded that, using these large data sets in both countries, the effects from woody riparian vegetation were marginal at best which contradicts the numerous cited literature used to derive the partially rejected hypotheses.

In *Palt et al. (submitted)* this conflict is resolved by addressing the context-dependence of functions provided by woody riparian vegetation. For instance, in agricultural landscapes the associated pressures (e.g. fertilization, soil erosion) are hypothesized to be mediated by the presence of trees in the riparian corridor, which in turn is expected to have a strong effect on the multimetric index describing the macroinvertebrate ecological status. Alternatively, pressures associated with urbanization (e.g. wastewater effluents), which do not pass through riparian zones cannot be mediated by woody vegetation there, which consequently does not have a strong effect on the macroinvertebrate community and its ecological status.

By using an approach of recursive partitioning modeling it was possible to disentangle the effects from woody riparian vegetation given catchment characteristics in the same data basis used in Palt et al. (2021) (n = 1109). This overall dataset was split into 14 subdatasets of stable relationships between the far and near upstream woody cover respectively and the multimetric index. This mirrors yet again the effect of larger-scale pressures such as catchment landuse, which indeed per-determines ecological conditions as evidenced by differing distributions of the multimetric index between the subdatasets. However, within some subdatasets there was also a significant effect of woody riparian cover and this effect differed according to catchment or local landuse as well as hydromorphological conditions.

While rural, forested catchments predictably had generally better multimetric index evaluations they did not reveal effects from woody riparian cover that could not be disentangle from general larger-scale woodland effects as expected. However, in agricultural landscapes woody riparian cover show strong significant effects on the multimetric index and can improve the ecological status by up to two classes according to the European Water Framework Directive. Unexpectedly, strong effects are also found in urban settings, where woody riparian vegetation can improve the ecological status from bad to moderate. This demonstrates that urban landuse has the expected overarching detrimental effects, however within a reduced range compared to agricultural landscapes, riparian trees still are of importance.

In conclusion, accurate assessments of the effect of woody riparian vegetation on the aquatic community are possible also in studies relying on large datasets. However, catchment characteristics need to be considered. Under certain circumstances, managing woody riparian vegetation is a powerful tool of nature conservation and restoration.

In *Vermaat et al. (2020)* ecosystem service provisioning in the floodplains of two French and two German case study catchments was assessed. Besides the present-day situation, three different degrees of woody cover in the riparian area, as part of the larger floodplain, were modeled for the year 2050. These scenarios reflect diverging future shared socioeconomic pathways (SSP; O'Neill et al., 2017). In the most extreme case the assumed variation according to SSPs resulted in changes to the mean woody riparian cover from present-day 27% to either 17% or 70% respectively.

For present-day situation as well as the pessimistic, best-practice, and ambitious future riparian management scenarios, 16 ecosystem services were calculated for spatially explicit, homogeneous segments of the river network, 500 m to 1,000 m in length, using a cascading analytical framework introduced by Mononen et al. (2016). The individual services expressed in monetary values were categorized and aggregated as provisioning, regulating, cultural as well as total ecosystem services.

In present-day conditions all services exhibited an optimum curve with regards to woodland cover in the floodplain as they were highest between 30% and 45% woodland cover. Regarding the SSPs and associated changes to woody riparian cover the total amounts of ecosystem services changed remarkably little. However there was an obvious trade-off between decreasing provision services and increasing cultural services, while regulating services (stemming from flood prevention) were rather constant. This leads to the conclusion that even the most ambitious riparian management with regards to nature conservation does not come at a premium monetary cost to overall societal benefit.

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RESEARCH ARTICLE

WILEY

Woody buffer effects on water temperature: The role of spatial configuration and daily temperature fluctuations

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Abstract

Water temperature is a key driver for riverine biota and strongly depends on shading by woody riparian vegetation in summer. While the general effects of shading on daily maximum water temperature T_{max} are well understood, knowledge gaps on the role of the spatial configuration still exist. In this study, the effect of riparian buffer length, width, and canopy cover (percentage of buffer area covered by woody vegetation) on T_{max} was investigated during summer baseflow using data measured in seven small lowland streams in western Germany (wetted width 0.8–3.7 m). The effect of buffer length on T_{max} differed between downstream cooling and heating: T_{max} approached cooler equilibrium conditions after a distance of 0.4 km (∼45 min travel-time) downstream of a sharp increase in canopy cover. In contrast, T_{max} continued to rise downstream of a sharp decrease in canopy cover along the whole 1.6 km stream length investigated. The effect of woody vegetation on T_{max} depended on buffer width, with changes in canopy cover in a 10 m wide buffer being a better predictor for changes in T_{max} compared to a 30 m buffer. The effect of woody vegetation on T_{max} was linearly related to canopy cover but also depended on daily temperature range T_{range}, which itself was governed by cloudiness, upstream canopy cover, and season. The derived empirical relationship indicated that T_{max} was reduced by −4.6°C and increased by +2.7°C downstream of a change from unshaded to fully shaded conditions and vice versa. This maximum effect was predicted for a 10 m wide buffer at sunny days in early summer, in streams with large diel fluctuations (large T_{range}). Therefore, even narrow woody riparian buffers may substantially reduce the increase in T_{max} due to climate change, especially in small shallow headwater streams with low baseflow discharge and large daily temperature fluctuations.

KEYWORDS
buffer strips, riparian vegetation, riparian zone, river, stream temperature, temperate ecoregion, woody cover

1 | INTRODUCTION

In aquatic ecosystems, water temperature is a key factor for the presence and abundance of all organisms, including fish (Barton et al., 1985; Daufresne et al., 2004) and macroinvertebrates (Daufresne et al., 2004; Durance & Ormerod, 2007; Vannotte & Sweeney, 1980). Higher water temperature results in physiological stress, especially for cold-water fish. Moreover, the metabolic rate of biota and thus oxygen demand depends on water temperature. In addition, oxygen content decreases with increasing water temperature, which is most critical for heterotrophs in temperate rivers during summer when temperature is highest and oxygen contents lowest.

In summer, water temperature mainly depends on shortwave solar radiation input and emitted longwave radiation output (Webb & Zhang, 2004). Shading by woody riparian vegetation influences both of these heat fluxes and hence, is considered one of the main factors influencing water temperature in summer (Caissie, 2006; Webb et al., 2008), especially reducing daily maximum water temperature T_{max} (Bowler et al., 2012). In temperate ecoregions, most small streams would be fully shaded under natural conditions and stream restoration often includes the re-establishment of woody riparian buffers. The effect of woody riparian vegetation on T_{max} is generally appreciated. Nevertheless, several open questions remain that limit the targeted implementation of riparian restoration measures, particularly concerning the role of the spatial configuration of woody buffers. Besides the use of physical models (e.g., Beaufort et al., 2016; Loicq et al., 2018), empirical studies may help to shed light on the role of length, width and canopy cover used here to describe the spatial configuration of woody buffers.

There is limited empirical knowledge on the length or travel time needed for water temperature to adapt to a change in canopy cover and related shade level, and to reach a new equilibrium temperature. The few available studies reported contrasting results: A longer adaptation length was reported for heating due to a decrease in canopy cover (4 hr travel time corresponding to about 1.2 km river length in Rutherford et al., 2004), compared to the shorter adaptation length for cooling due to an increase in canopy cover (150 m in Zwieniecki & Newton, 1999, 0.3 km corresponding to ~1 hr travel time for a 50% downstream cooling in Davis et al., 2016). The adaptation length needed to reach new equilibrium conditions is a crucial information for river management to exploit the full potential of cooling by woody riparian buffers.

The role of woody riparian buffer width has been widely studied, indicating that even narrow buffers with a width of about 10 m provide most of the shading of forested reaches. Therefore, woody vegetation at this spatial scale is considered more relevant compared to wider buffers, but this depends on site characteristics (Sweeney & Newbold, 2014). It is highly relevant for river management to identify the most effective buffer width because buffers wider than 10 m are difficult to establish in densely populated or agricultural regions.

The level of shading increases with canopy cover in the riparian buffer. Most empirical studies compared forested, and hence fully shaded to deforested, unshaded sites, thus ignoring the gradual increase in canopy cover and shade level from fully unshaded to fully shaded conditions (Arismendi & Groom, 2019; Bladon et al., 2018; Johnson, 2004; Moore et al., 2005; Quinn et al., 2009). Only few studies considered different shade levels to establish statistical relationships with water temperature (Broadmeadow et al., 2011; Rutherford et al., 2004; Turschwell et al., 2016). Such relationships should be developed at spatial scales most relevant for water temperature, and hence, information on the effect of woody buffer characteristics like 'length' and 'width' as described above are needed. The resulting empirical relationships could be used to predict the effect of moderate changes in canopy cover and shade levels more relevant in river restoration and management because fully forested buffers are difficult to establish. Furthermore, several studies used the complement of diffuse non-interceptance to quantify shade levels (Davies-Colley & Quinn, 1998; Rutherford et al., 2004), a variable commonly used in scientific studies at the reach scale but rarely available for river management at larger scales. Empirical relationships using a simple proxy for shading like the ratio of tree height to river width or canopy cover (percentage of the buffer area covered with woody vegetation) might be more easily applicable for river managers.

Besides the spatial configuration of woody riparian buffers, shading effects on T_{max} may be affected by other factors, which rarely have been considered in empirical studies. From modelling studies, it is well known that heated water with an excess temperature T_{ex} cools until equilibrium temperature T_{eq} is reached following an exponential decay function (Jobson, 1973). As a consequence, the effect of shading increases with excess temperature, i.e. the deviation of the incoming excess water temperature from the equilibrium conditions at full shading $T_{ex} - T_{eq}$. In the context of shading by woody vegetation, excess temperature depends on solar radiation input upstream of a river segment, that is, on cloudiness and upstream canopy cover, and corresponds to T_{max} measured at the upstream start of a segment. Equilibrium temperature can be assessed but this needs data-extensive heat budget models. We hypothesized that daily minimum temperature T_{min} can be used as an easily quantifiable proxy for T_{eq} because it can be considered the maximum cooling at full shading (zero solar radiation input). There are additional energy losses during night due to for example, sensible heat and bed conduction resulting in T_{min} being lower than T_{eq}. Nevertheless, daily temperature range $T_{range} = T_{max} - T_{min}$ at the upstream start of a river section potentially is proportional and a proxy for $T_{ex} - T_{eq}$.

Against this background, the objective of our study was to derive an empirical relationship between canopy cover and summer daily maximum water temperature T_{max}. This relationship should be applicable in river management to assess how changes in shading affect T_{max}, that is, how changes in canopy cover $\Delta Cover$ (e.g., caused by river management) lead to a change in daily maximum water temperature ΔT_{max}. We first investigated the adaptation length needed to adapt to changes in canopy cover and reach equilibrium conditions, and woody buffers of different width (10 and 30 m) to identify the most relevant spatial scales (length and width). Moreover, we used percentage canopy cover as an easily available proxy for shading. In addition, we investigated how daily water temperature range T_{range} influences the change of T_{max}. More specifically, the following hypotheses were tested for small lowland streams:

1. T_{max} reaches an equilibrium within an adaptation length of a few hundred metres downstream of a sharp increase in canopy cover (cooling), and within about 1 km downstream of a sharp decrease in canopy cover (heating).
2. Changes in canopy cover in 10 m wide buffers have a significant effect on $\Delta T_{max,}$ implying that restoration of even narrow buffers can benefit water temperature in river management.

3. The effect on ΔT_{max} increases with the change in canopy cover. This effect increases with the deviation of excess temperature from equilibrium conditions, with daily temperature range T_{range} being an appropriate and easily quantifiable proxy.

2 | METHODS

2.1 | Study area

We investigated seven small sand-bed streams located in the lowlands of western Germany in the temperate forested ecoregion of the central plains (Illies, 1978) between 51 and 52 degrees North (Figure 1). At the two meteorological stations located closest to the study reaches (A and B in Figure 1), mean annual precipitation (2005–2019) was 715 and 696 mm, respectively. Precipitation in the study period in summer 2011 (May to August) was similar (310 mm, 221 mm) compared to the long-term summer mean from 2005 to 2019 (292 mm, 260 mm). Mean air temperature was lower in the summer of 2011 (16.7°C, 16.4°C) compared to the long-term summer mean (17.3°C, 16.9°C). The study reaches were 3.6–4.4 km in length with a low to moderate slope of 0.5–6.4‰ and located one to 12 km from the sources (Table 1). Catchments were 6.1–39.1 km^2 in size at the downstream end of the study reaches. Land use strongly differed, with more than 40% forest cover in catchments of reaches 1, 3, and 5, and more than 50% cropland cover in catchments of reaches 2, 6, and 7. Wetted width, depth and flow velocity during the sampling campaign typically ranged between 0.8–3.7 m, 5–32 cm and 0.01–0.43 m/s, with mean values of 2.0 m (*SD* 1.0), 14 cm (*SD* 9) and 0.16 m/s (*SD* 0.13).

2.2 | Meteorological data

For two meteorological stations run by the German Meteorological Service and located near the study reaches, daily data on cloudiness were downloaded for the measurement period 08/2010 to 10/2011 from the Climate Data Center at https://cdc.dwd.de/portal/. Data from station A (5064 Tönisvorst) was used for streams 1 and 2 and data from station B (6337 Lüdinghausen-Brochtrup) for streams 3, 4, 5, 6 and 7 (Figure 1). Cloudiness for each day was reported in eights ranging from 0 oktas (clear sky) to 8 oktas (complete overcast).

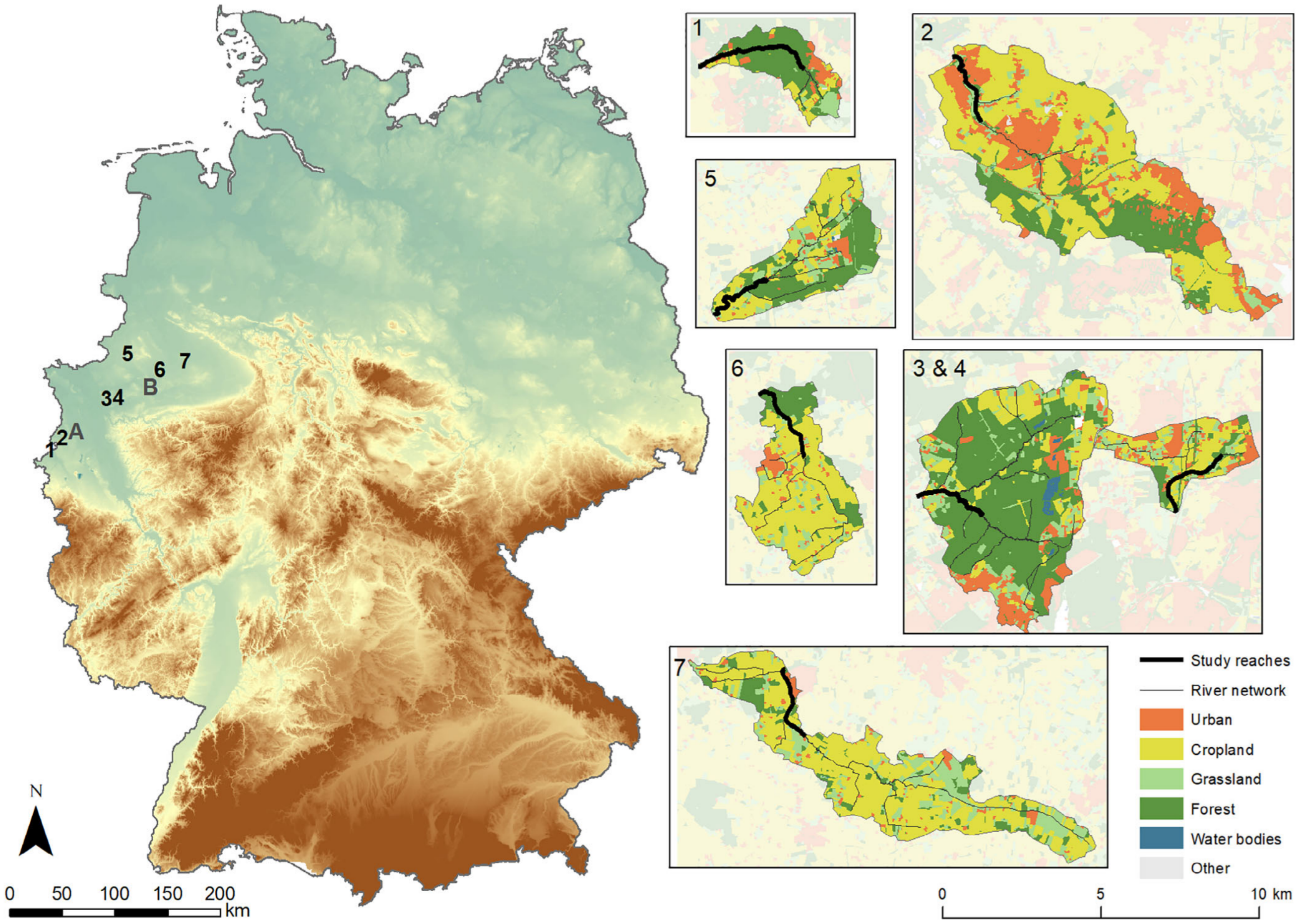

FIGURE 1 Study reaches (numbered 1–7) and meteorological stations (A, B) located in the lowlands of western Germany (left), and land use in the catchments of the study reaches (right)

TABLE 1 Characteristics of the study reaches (numbering corresponds to numbers in Figure 1), catchment size and land use were quantified for the downstream end, distance to source measured for the upstream end of the study reaches

Number	Name	Reach length (m)	Channel slope (‰)	Distance to source (km)	Catchment size (km^2)	Forest (%)	Cropland (%)	Urban (%)
1	Schaagbach	4,369	6.4	1.5	6.0	63.6	13.9	12.5
2	Kranenbach	2,709	1.7	4.0	39.1	19.3	48.2	25.0
3	Rotbach	3,426	3.6	7.9	31.9	59.3	15.8	11.2
4	Brabecker Mühlenbach	3,072	2.7	0.7	7.6	14.8	40.7	22.9
5	Felsbach	2,967	1.0	4.1	12.0	39.6	35.7	6.0
6	Dümmer	2,950	0.5	5.8	13.3	17.4	66.6	6.6
7	Mussenbach	2,646	1.1	11.8	22.9	11.5	62.9	4.5

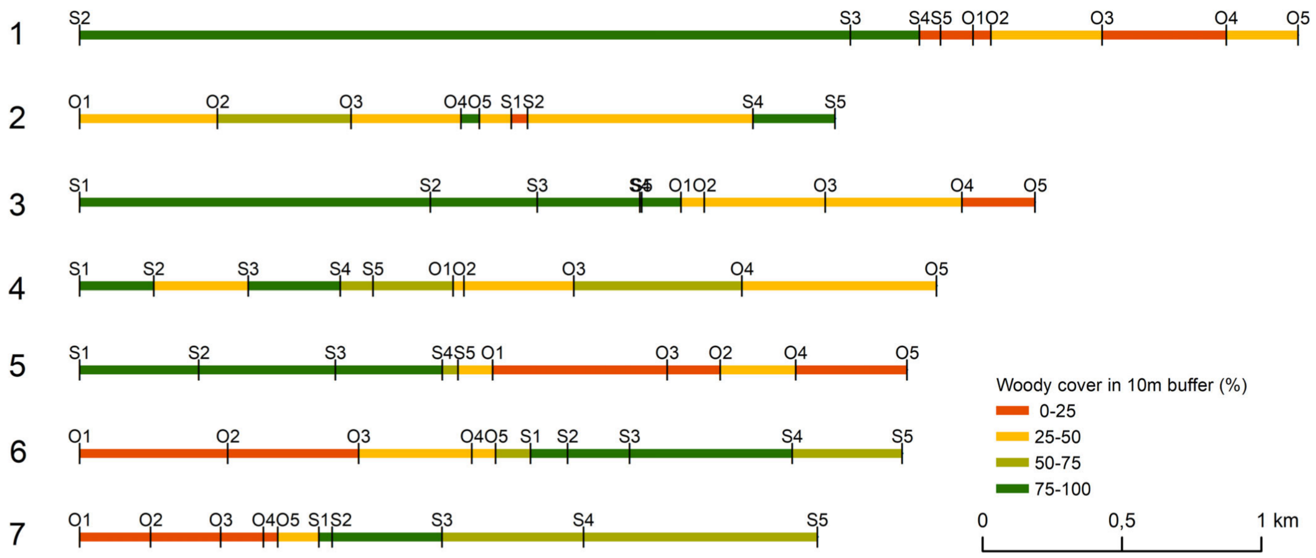

FIGURE 2 Locations of the temperature loggers along the seven study reaches (shown schematically, numbering of study reaches corresponds to numbers in Figure 1), loggers located in more open sections coded with an ‘O’, loggers in more shaded sections with an ‘S’

2.3 | Water temperature data

Water temperature was measured with HOBO Pendant Dataloggers HOBO UA-002-64 (Onset Computer Corporation) every 20 minutes between 08/2010 and 10/2011 at 10 locations in each study reach. Temperature loggers were more closely spaced around the main change in canopy cover along the reach, with five loggers placed up and downstream at distances of about 50 m, 100 m, 500 m, 1 km and 2 km, respectively (Figure 2). All loggers were placed at locations where flow velocity was representative for the section to avoid larger water temperatures at stagnant locations. Two loggers had to be excluded due to missing or incorrect GPS coordinates (S1 of stream 1 and S3 of stream 2).

The raw water temperature data were pre-processed: Days with several missing data were excluded. Obvious measurement errors of very low (e.g., −20°C) or very high (e.g., +50°C) values, records with a temperature difference >5°C between consecutive measurements, and single missing data were replaced by the mean of the adjacent values. Periods with potentially very low discharge, when loggers potentially had fallen dry or were affected by direct solar radiation warming, were identified and excluded. Time-periods when daily water temperature range suddenly increased and approximated or exceeded daily air temperature range were identified and excluded. This was true for short time periods (16–27 days) for two loggers in stream 5 (O2, S5) and one logger in stream 6 (S5) as well as for long time-periods in summer for the two most upstream loggers O1 and O2 in streams 6 and 7. Hence, these four loggers were excluded from the analysis.

The study was restricted to periods of dry weather conditions with no indication for substantial cooling by precipitation and related surface runoff, which otherwise would have masked the effect of woody vegetation on water temperature. For each stream, periods of dry weather conditions in the foliation period (May to August 2011) were identified as time-spans at which daily mean water temperature over all loggers of the reach did steadily increase or stayed constant for at least 3 days. The periods of the individual reaches occurred at similar dates, indicating that the analysis indeed identified time-periods of dry weather conditions in the region. From these periods, only days with a cloudiness of less than 7 oktas were considered, that is, excluding days with nearly complete or complete overcast, thus only including days when shading by woody vegetation potentially affects water temperature. For the selected study days of each reach, daily maximum water temperature T_{max} for each logger was calculated.

2.4 | Canopy cover

Riparian buffers along the study reaches with a width of 10 and 30 m (each side of the stream) were delineated. Woody riparian vegetation in the riparian buffers was quantified using remote sensing. Orthophotos covering the study reaches, taken during the vegetation period from May to August and as close as possible to the study period 05/2011–08/2011, were acquired from the German Federal Agency for Cartography and Geodesy. This resulted in a mix of RGB and CIR images, mostly from 2011 and 2012, with few images taken earlier (2006, 2008 and 2009) or later (2015 and 2016). The first step of an object-based image analysis OBIA – the segmentation of the orthophotos into objects – was done using the multiresolution segmentation algorithm in the eCognition Developer version 9.3 (Trimble, 2018). The resulting objects clearly distinguished between grassy/herbaceous/scrub encroachment and canopy forming shrubs/trees, given the specific small-scale shadow pattern in canopies. The second step of classifying objects as woody vegetation (canopy forming shrubs and trees) was done manually by visual inspection to minimize misclassification rates, supported by information on the Visible-band Difference Vegetation Index VDVI and Normalized Difference Vegetation Index NDVI of the objects as indicators for vegetation cover. Based on this, the percentage of the riparian buffer area covered with woody vegetation was calculated, referred to as canopy cover in the following. From visual inspection, spruce trees rarely occurred in the riparian area and deciduous trees were dominant. LiDAR data were not analysed but based on shadows of objects of known height, shrubs and trees were assessed being at least about 2 m in height but mostly >5 m.

2.5 | Statistical analysis

To address the first hypothesis on the adaptation length needed to reach equilibrium water temperature, adaptation sections were identified with a similar canopy cover along several loggers downstream of a sharp and considerable increase or decrease in canopy cover. The two adaptation sections for investigating cooling downstream of a sharp increase in canopy cover by +63 and +61 percentage points, respectively, comprised loggers O5 to S4 of stream 6 and loggers S1 to S3 of stream 7 (Figure 2). The three adaptation sections to investigate heating downstream of a sharp decrease in canopy cover by −63, −60, and −77 percentage points comprised loggers O1 to O5 of stream 3, loggers S5 to O5 of stream 5 and loggers S4 to O4 of stream 1 (Figure 2). For each adaptation section, the downstream change in T_{max} was calculated for each study day as the difference between T_{max} of the logger at the sharp change in canopy cover and each downstream logger. The loggers of the two cooling and three heating adaptation sections were pooled resulting in 6 loggers for cooling and 14 loggers for heating at different downstream distances with a total sample size of 162 cooling and 476 heating measurements.

Mixed effect models were used for the following three analyses, with streams and loggers as random effects to account for the nested experimental design, and date as an AR-1 auto-correlation structure to account for a potential temporal auto-correlation of water temperature measurements of consecutive days. First, the downstream distance of the loggers from the sharp change in canopy cover was used as the only fixed effect to test if the response variable T_{max} significantly changed in downstream direction. A generalized additive mixed model (GAMM) was used because water temperature was assumed to change non-linearly until a new equilibrium is reached, and the smooth term was used to check for a significant effect of downstream distance. Second, the additive model was compared to a linear mixed model (LMM) to test if the relationship is non-linear and T_{max} approaches a new equilibrium. Third, the slope of the fitted trend line was computed at 200 equally spaced points to identify parts of the non-linear trend, where the 90% confidence interval of its local slope did not include zero, and hence, the non-linear trend can be considered to increase or decrease significantly (Simpson, 2011).

In the following analyses, we were not interested in absolute values of T_{max} but rather how changes in canopy cover $\Delta Cover$ (e.g., caused by river management) affect ΔT_{max}. Therefore, both canopy cover and T_{max} in the study sections were compared to conditions directly upstream to investigate how the change in canopy cover in the study sections compared to upstream leads to a change in T_{max} in the study section.

To test the second hypothesis on the importance of woody vegetation in narrow buffers, loggers were grouped into 30 study sections. Loggers were combined to study sections with a length as close as possible to the adaptation length of 0.4 km identified in the previous analysis. This ensured that water temperature at the end of the sections was fully adapted to the canopy cover, resulting in a median section length of 430 m and a 10th to 90th percentile range of 338–744 m. In addition, a 0.4 km section directly upstream was demarcated for each study section. The changes in canopy cover in the 10 and 30 m buffer compared to the upstream section $\Delta Cover_{10}$ and $\Delta Cover_{30}$ were calculated, with positive values corresponding to an increase, and negative values to a decrease in canopy cover in the study section compared to upstream. In addition, the difference in T_{max} between the upstream section and the study section was calculated by comparing the loggers at the downstream end of each section, with negative ΔT_{max} values corresponding to cooling and positive values to heating in the study section. ΔT_{max} of each study section was calculated for each study day, resulting in a sample size of 930 ΔT_{max} values from the 30 study sections.

Two LMM were used, with streams and study sections as random effects, date as an AR-1 auto-correlation structure, and $\Delta Cover_{10}$ and $\Delta Cover_{30}$ as the only fixed effect, respectively. The coefficients of the fixed terms $\Delta Cover_{10}$ and $\Delta Cover_{30}$ were compared to identify the buffer width having a larger effect on ΔT_{max}. In addition, model performance as described by AIC and marginal R^2 values were compared to identify the buffer width better suited to develop the empirical relationship.

To derive an empirical relationship between canopy cover and T_{max}, and for testing the third hypothesis on the effect of daily temperature range, the 30 study sections delineated in the previous analysis were used again. The LMM with $\Delta Cover_{10}$ as the only fixed term was compared to a respective GAMM to investigate if the relationship is linear or non-linear. The third hypothesis emerged because a preliminary analysis during data pre-processing indicated a much larger effect of canopy cover on T_{max} in early summer. These seasonal differences were quantified by comparing the effect of $\Delta Cover_{10}$ on daily ΔT_{max} in two LMMs based on sub-datasets from May–June to July–August. We hypothesized that these seasonal differences were due to differences in daily temperature range as a proxy for the deviation of excess temperature T_{ex} from equilibrium conditions at full shading T_{eq}. We considered daily minimum temperature T_{min} at night as the maximum diurnal potential for cooling with zero solar radiation input and hence, daily water temperature range $T_{range} = T_{max} - T_{min}$ as a proxy for $T_{ex} - T_{eq}$. Most probably, the excess temperature of the incoming water compared to equilibrium conditions in the (shaded) river segment mainly depends on solar radiation input upstream, that is, on cloudiness and upstream canopy cover. However, besides differences in the specific weather conditions in the study period with less clouds and higher solar radiation input in early compared to late summer, there also might have been real seasonal differences in T_{range}. To test this hypothesis, all three factors potentially influencing T_{range} – cloudiness, upstream canopy cover and month – were included as fixed effects in an LMM with daily T_{range} as response variable, and tested for significance.

To finally test if the effect of canopy cover on water temperature depends on daily temperature range, T_{range} at the upstream end of the study sections was included as an additional fixed effect in an LMM besides $\Delta Cover_{10}$. The interaction term $\Delta Cover_{10}$:T_{range} as well as the two main terms were tested for significance.

In all GAMM and LMM, the maximum likelihood estimator (ML) was used to correct the degrees of freedom for nested models with the same random effects but different fixed effects to find the optimal fixed structure (Zuur et al., 2009). Each fixed effect was dropped at a time and the resulting nested model always compared to the full model using the likelihood ratio test (ANOVA) to test for significant effects of the fixed terms (significance of interaction terms was tested prior to the main terms). The final model was then refitted using the restricted maximum likelihood estimator (REML) and validated based on visual inspection of the normalized residuals plots to identify violation of normality and homogeneity. For non-nested models, where the likelihood ratio test cannot be applied, the AIC and marginal R^2 values were compared. Models with a difference in AIC values of <2, 2–5, and >10 units were considered very similar, similar, and different, respectively. All statistical analyses were performed in R, using the generic lme function for LMM, the mgcv package for GAMM as well as the R-scripts derivFun and tsDiagGamm described in Simpson (2011) to identify and visualize a significant increase or decrease in the trend lines (downloaded from the github repository at https://github.com/gavinsimpson/random_code).

3 | RESULTS

Water temperature steadily increased without reaching equilibrium downstream of the sharp decrease in canopy cover (−63 to −77 percentage points) along the 1.6 km downstream distance investigated (Figure 3). Therefore, it was not possible to derive an adaptation length for downstream heating. The non-linear smooth term of the GAMM was significant ($p < .01$) but the additive model was not significantly different from a simple LMM ($p = .36$) and only had 1.78 degrees of freedom. In the final LMM, visual inspection of the diagnostic plots showed an increasing spread of the residuals with downstream distance, indicating violation of homogeneity. This was most probably due to the study design of comparing downstream loggers to the most upstream logger of the adaptation sections (i.e., normalizing T_{max} values by setting the most upstream logger to zero). As a consequence, any differences in the study days relating to e.g. humidity or wind speed resulted in increasing differences in T_{max} and larger variance in downstream direction. Given this identifiable structure, the power of covariate variance structure was subsequently included in the LMM, allowing variance to increase with downstream distance. The resulting LMM had a significantly better variance structure ($L = 248.19$, $df = 1$, $p < .001$). Downstream distance as the only fixed effect was significant ($p < .01$) and the coefficient of 0.002 indicated that T_{max} increased by 0.2°C per 100 m.

In contrast, water temperature reached equilibrium conditions downstream of a sharp increase in canopy cover (+61 to +63 percentage points) and the adaptation length for cooling was about 0.4 km and hence, only a few hundred metres as hypothesized (Figure 4). In the GAMM with downstream distance as the only fixed effect, the non-linear smooth term was significant ($p < .01$) and the additive model was significantly different from a simple LMM according to the likelihood ratio test ($p < .01$), indicating that the relationship was non-linear. This was already implied by the 2.51 degrees of freedom of the additive model compared to 1 degree of freedom of the linear model. The slope of the fitted trend line of the smoothing curve was significantly different from zero between a downstream distance of 0–381 m. Consequently, the minimum length for the study sections used in the following analyses was set to 0.4 km.

Canopy cover in the 10 m buffer had a larger effect and was a better predictor for ΔT_{max} compared to the 30 m buffer. In each of the two LMMs, the fixed terms $\Delta Cover_{30}$ and $\Delta Cover_{10}$ were significant ($p < .01$). The coefficients of −0.019 and −0.023 indicated that a maximum change in canopy cover by ±100% in the 30 and 10 m buffer would cause a maximum change in T_{max} by ±1.9 and ± 2.3°C,

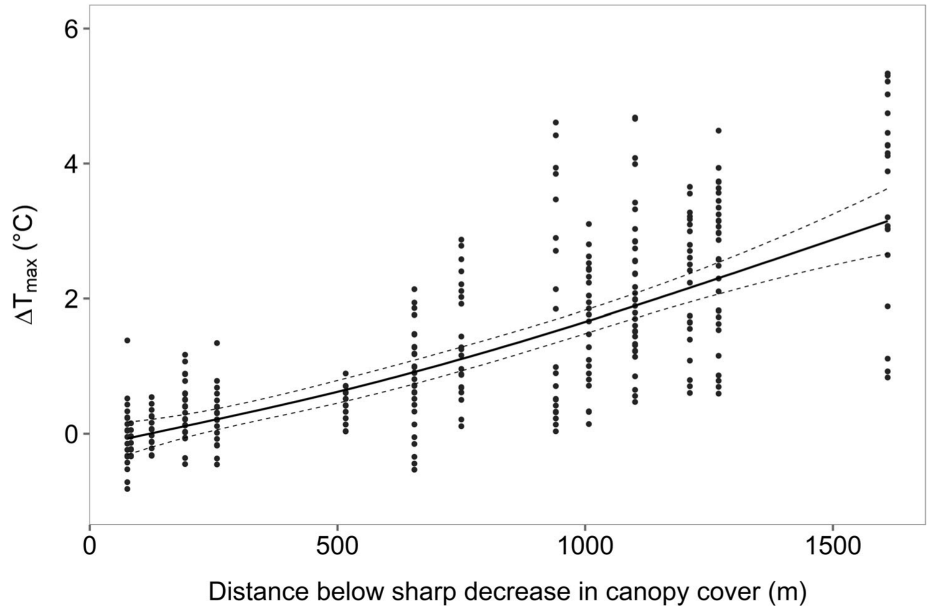

FIGURE 3 Daily maximum water temperature T_{max} downstream of loggers with a sharp and considerable decrease in canopy cover by −63 to −77 percentage points, with T_{max} at the sharp decrease in canopy cover set to zero. The graph shows the generalized additive mixed model with the smoothing curve as solid line and 95% confidence bands as dotted lines

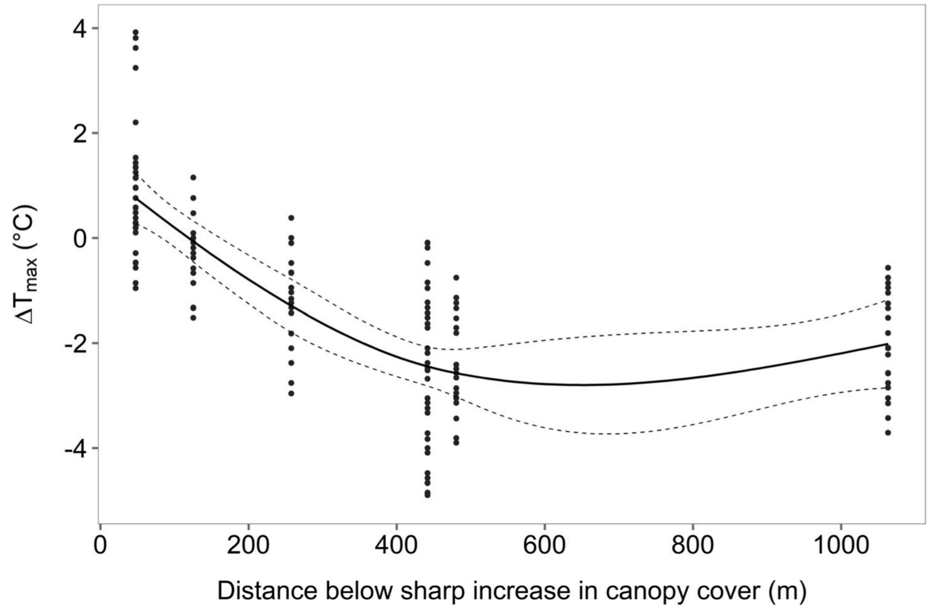

FIGURE 4 Daily maximum water temperature T_{max} downstream of loggers with a sharp and considerable increase in canopy cover by +61 to +63 percentage points, with T_{max} at the sharp increase in canopy cover set to zero. The graph shows the generalized additive mixed model with the smoothing curve as solid line and 95% confidence bands as dotted lines

respectively. Furthermore, the AIC value of the LMM with $\Delta Cover_{10}$ as the only fixed effect was −7.0 units lower compared to the $\Delta Cover_{30}$ model, indicating that models were different and $\Delta Cover_{10}$ was a better predictor. Moreover, marginal R^2 of the $\Delta Cover_{10}$ model was 23.1% and about twice the marginal R^2 of the model with $\Delta Cover_{30}$ as the only fixed effect (11.4%). Consequently, $\Delta Cover_{10}$ was used as predictor in the empirical relationship developed in the following.

The simple empirical relationship between canopy cover and water temperature with $\Delta Cover_{10}$ as the only predictor and ΔT_{max} as response was linear (Figure 5). The smooth term of the GAMM with $\Delta Cover_{10}$ as the only fixed effect was significant ($p < .01$) but the additive model was not significantly different from a simple LMM ($p = .87$) and only had 1.03 degrees of freedom. The effect of canopy cover on water temperature was much larger in early summer compared to late summer. For study days in May and June, the respective LMM with $\Delta Cover_{10}$ as the only fixed effect had a marginal R^2 of 48.8%, being about twice the marginal R^2 of the complete dataset (23.1%) and more than four times the marginal R^2 of the sub-dataset from July and August (10.7%). The coefficient of −0.036 indicated that the maximum change in canopy cover by ±100% in the early summer period (May–June) would result in a ΔT_{max} of ±3.6°C compared to a ΔT_{max} of ±1.7°C in late summer (July–August). Cloudiness was significantly lower in early summer compared to late summer (Mann–Whitney *U* test, $p < .05$). However, medians of 3.3 and 4.3 oktas were not much different given that values ranged from 0 to 5.7, quantile ranges

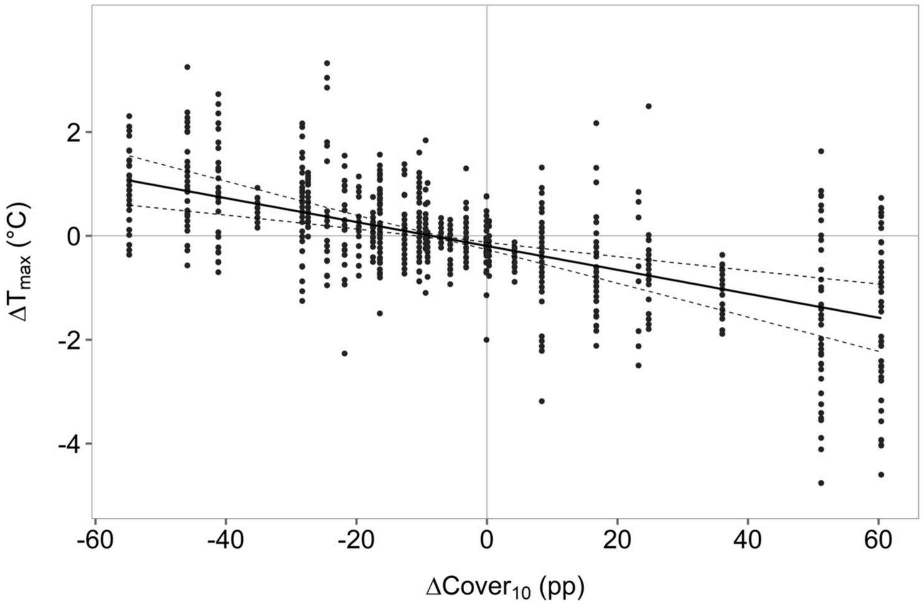

FIGURE 5 Empirical relationship between the change in canopy cover in the study sections compared to 0.4 km upstream in the 10 m buffer $\Delta Cover_{10}$ (percentage points) and the change in daily maximum water temperature in the study sections ΔT_{max} in °C. The 95% confidence bands are shown as dotted lines

overlapped, and hence cloudiness only partly explained the seasonal differences mentioned above.

Indeed, daily water temperature range T_{range} depended not only on cloudiness (*Cloud*) measured in oktas but also on canopy cover in the 10 m buffer 0.4 km upstream in percentage cover ($Cover_{10up}$), and season (*Month* from May to Aug). In an LMM with T_{range} as response variable, all three fixed effects were significant ($p < .01$) and the final model had a marginal R^2 of 48.5%. Dropping cloudiness from the full model resulted in the largest increase of +496.7 AIC units, indicating that T_{range} depended most strongly on cloudiness. But nested models without $Cover_{10up}$ (+30.9 units) and *Month* (+69.8 units) also had higher AIC values and models were significantly different from the full model ($p < .01$), indicating that these variables also increased model performance. Based on the intercept and coefficients of the final LMM, the following empirical equation was used to assess T_{range} in the study streams:

$$T_{range} = 9.79 - 0.478\,\mathrm{Cloud} - 0.028\,\mathrm{Cover}_{10up} - 0.394\,\mathrm{Month} \qquad (1)$$

with T_{range} in °C, cloudiness *Cloud* given in oktas, canopy cover upstream in a 10 m buffer $Cover_{10up}$ in percent, and *Month* from May to August coded 5–8.

Including T_{range} as a proxy for the deviation of excess temperature from equilibrium conditions improved the empirical relationship on the effect of canopy cover on ΔT_{max}. In an LMM including T_{range} at the upstream end of the study sections as an additional fixed effect besides $\Delta Cover_{10}$, the respective interaction term $\Delta Cover_{10}{:}T_{range,}$ was significant ($p < .01$), and the final model had a higher marginal R^2 of 34.6% compared to the simple model with $\Delta Cover_{10}$ as the only fixed effect (23.1%). Based on the intercept and coefficients of the final LMM, the following empirical equation was used to assess ΔT_{max} in the study streams.

$$\Delta T_{max} = 0.2706 - 0.0028\,\Delta Cover_{10} - 0.0768\,T_{range} - 0.005\,\Delta Cover_{10} : T_{range} \qquad (2)$$

with the change in daily maximum water temperature ΔT_{max} and daily temperature range T_{range} in °C, the change in canopy cover in a 10 m buffer compared to upstream $\Delta Cover_{10}$ in percent, and $\Delta Cover_{10}{:}T_{range}$ being the interaction term.

According to the final LMM and Equations (1) and (2), the largest effect in the study sections with their specific length, water width, depth, and flow velocity occurred at days with a cloudiness of 0 oktas in May. Increasing canopy cover by 100% compared to upstream would result in an upstream T_{range} of 7.9°C and a cooling ΔT_{max} of −4.6°C; decreasing canopy cover by 100% would result in an upstream T_{range} of 5.1°C and a heating ΔT_{max} of +2.7°C.

4 | DISCUSSION

In this study, we were interested in how the effect of shading on water temperature depends on the spatial configuration of the woody riparian buffers as described by buffer length, width, and canopy cover. Identifying the most relevant spatial scale for length and width was a prerequisite to develop an empirical relationship between canopy cover and summer daily maximum water temperature T_{max} for small lowland streams in temperate ecoregions.

4.1 | Woody buffer adaptation length

As hypothesized, T_{max} decreased and reached an equilibrium after a few hundred metres downstream of a sharp and considerable increase in canopy cover. The rate of cooling decreased in downstream direction very similar to the exponential decay function for excess temperature used in water temperature models (Jobson, 1973). However, there was a slight counterintuitive increase in water temperature within the first 50 m downstream of the sharp increase in canopy cover. Most probably, this reflects the conditions in the field. The loggers in the adaptation sections were approximately but not perfectly placed at the change in canopy cover. Moreover, the first logger 50 m downstream of the sharp change may still have received some higher solar radiation input compared to the more downstream loggers because there still was some transition (e.g. still direct solar radiation input in flow direction). The adaptation length of 0.4 km corresponded to a travel-time of about 45 min given the mean flow velocity of 0.16 m/s. This is in good agreement with the water temperature change predicted by the modelling approach of Davis et al. (2016). We used our empirical equation to predict the change in daily maximum water temperature ΔT_{max} for a mean summer day comparable to the temperature metric used in Davis et al. (2016) with a moderate cloudiness (3 oktas) in mid-summer (June), and for an increase in canopy cover of 60 percentage points as observed in the adaption sections. Using this ΔT_{max} of 2.3°C together with the median width (1.8 m), depth (0.12 m), and flow velocity of the study sections, the model of Davis et al. (2016) predicts a very similar exponential decrease, with about 50 and 90% of the effect reached at 100 and 350 m downstream, respectively. This indicates a wide applicability of the modelling approach and calibration setting used by Davis et al. (2016) in comparable mid-latitude temperate regions, as well as a low confounding effect of groundwater cooling in our study sections, since the model does not consider groundwater effects. Furthermore, Broadmeadow et al. (2011) only observed a marginal increase in the cooling effect of woody riparian vegetation with riparian buffer length from 0.1 to 5 km, also indicating that an equilibrium water temperature was already reached after a few hundred metres.

In contrast, T_{max} linearly increased downstream of a sharp and considerable decrease in canopy cover, not showing any non-linear trend and not approaching equilibrium conditions, at least within the 1.6 km downstream distance investigated, corresponding to a travel time of 2.8 hr. Rutherford et al. (2004) reported contrasting results. They observed a decrease in the heating rate in stream sections with a travel time of 2.7 hr and an equilibrium at about 30°C was reached after about 4 hr in their modelling study in comparable small and slow flowing streams. Possibly, the missing downstream decrease in the heating rate in our study was due to the lower absolute T_{max} values, with 90% being below 20°C and none exceeding 27°C. The heat efflux by evaporation increases with absolute water temperature as well as absolute air temperature and related vapour pressure deficit. Given the lower absolute water temperature in our study sections, evaporation loss might have been too small to compensate for the heat influx by direct solar radiation (Mohseni & Stefan, 1999; Rutherford et al., 1997). In any case, the increase of daily maximum water temperature is limited because in long unshaded sections with long travel times, water undergoes both, times of the day with positive and negative heat budgets, resulting in small net water temperature changes (Rutherford et al., 2004). The differences in the adaptation length for cooling and heating indicate that they are determined by different processes.

4.2 | Woody buffer width and the effect of narrow buffers

As hypothesized, canopy cover in the narrow 10 m buffer was a better predictor for water temperature compared to wider buffer of 30 m. This is to be expected and consistent with the modelling results of Sridhar et al. (2004) predicting largest water temperature reductions for canopies within 10 m to the stream bank. Woody vegetation in the study sections often consisted of single lines of trees directly along the river banks, resulting in large canopy cover in 10 m buffers and large reductions in T_{max} but only covering parts of the 30 m buffer. In study sections with a large percentage cover in the 30 m buffer, trees were not necessarily located directly along the river banks, not resulting in a similar large shading effect and reducing the predictive power of canopy cover at this spatial scale. Moreover, canopies of the single tree lines were overhanging the stream as described in Rutherford et al. (2018), shading the whole water surface of the small streams. These results and observations support the findings on the importance of streamside woody vegetation in narrow buffers summarized in Sweeney and Newbold (2014). However, this only holds true if woody vegetation consists of large trees because shading of course depends on vegetation height (Rutherford et al., 2018). Moreover, a dense line of trees planted at regular intervals fixes stream banks, limiting natural channel dynamics and the formation of in-channel habitats, and hence, should be avoided in stream restoration projects.

4.3 | Empirical relationships to predict the shading effect based on the change in canopy cover and daily water temperature range

The simple empirical relationship with $\Delta Cover$ as the only predictor resulted in a change in daily maximum water temperature ΔT_{max} of up to ±2.3°C when canopy cover in the 10 m buffer changes from fully unshaded to shaded or vice versa. This is a somewhat smaller effect compared to the +3.0°C heating reported in Rutherford et al. (2004) for the 45 min travel time of our study sections, and well below the cooling effect of −3.8°C and −4.0°C to −4.6°C reported in Turschwell et al. (2016) and Broadmeadow et al. (2011), respectively. Differences are most probably due to the focus on sunny days in literature. Cloudless days were excluded in Rutherford et al. (2004), maximum temperature in summer investigated in Broadmeadow et al. (2011) most probably representing cloudless days, and direct solar radiation was not a significant predictor in the statistical models of Turschwell et al. (2016), indicating that differences between days were small and solar radiation high at all study days. When looking at comparable sunny days with a cloudiness of 0 oktas in early summer, our empirical relationships predict a large daily water temperature range T_{range}, and hence, a stronger heating of +2.7°C and cooling of −4.6°C (for the study reaches with a median length of 430 m). This is very close to the values reported in the literature given above, and larger compared to the ±2.3°C predicted by the simple empirical relationship that does not include T_{range}, and hence cannot differentiate between days with different cloud cover (days with 0–6 oktas included in the dataset). In conclusion, both our results and values from literature addressing similar short reaches (~0.5–1.0 km) of small first to second order streams indicated that the heating and cooling effect of woody riparian vegetation at sunny summer days is in the range of +3°C and −4 to −5°C, respectively.

In the final empirical relationship, ΔT_{max} depended not only on the change in canopy cover $\Delta Cover$ but also on T_{range}, which in turn was governed by season besides cloudiness and upstream canopy cover. We considered T_{range} as an easily quantifiable proxy for the deviation of excess temperature from equilibrium conditions. The higher the excess temperature of the incoming water compared to the equilibrium conditions in a river section, the higher the cooling effect. This is consistent with the modelling results of Davis et al. (2016) and empirical data reported in Coats and Jackson (2020), where the cooling in a downstream shaded reach increased with water temperature in the upstream unshaded reach. It is reasonable that T_{range} at the upstream start of the study sections increased with direct solar radiation input upstream, i.e. decreased with cloudiness and canopy cover upstream, but the seasonality of T_{range} is less intuitive. Seasonal differences and a higher T_{range} in spring or early summer were also observed at a continental scale (Ferencz & Cardenas, 2017) and in other lowland streams (Łaszewski, 2018). However, our results indicate that a higher T_{range} in early summer is not due to missing foliage as speculated by Łaszewski (2018) because trees were already leafed, resulting in a significant effect of canopy cover on ΔT_{max} in May and June. Instead, a higher T_{range} in early summer might have been due to higher heat effluxes compared to late summer. Energy loss to the channel bed and bank due to heat conduction increases with the difference between water and soil temperature (Davis et al., 2016). This difference is probably larger in early summer and decreasing with higher soil temperature during summer. While solar radiation input is the same for equidistant dates from the summer solstice (20.06), soil temperature is lower start of May compared to end of August, possibly resulting in a larger T_{range} in early compared to late summer. Indeed, visual inspection of the seasonal plot of monthly mean T_{min} and T_{max} showed such a decreasing difference in T_{range}. Since the increase in T_{min} lagged behind the considerable increase in T_{max} in early summer, T_{range} was highest until June, but decreased afterwards due to a larger increase in T_{min} compared to T_{max} in late summer.

4.4 | Transferability of results

Transferability of these results is most probably limited to summer low flow in small streams. Any decrease of the water surface receiving solar radiation input compared to the water volume decreases daily maximum water temperature (Rutherford et al., 1997), T_{range}, and hence, the potential for cooling by canopy cover. In rather rectangular cross-sections typical for managed streams, water depth increases linearly with discharge, while width is rather constant. Higher discharges dampen daily water temperature fluctuations and the potential for cooling by canopy cover, because a larger volume of water has to be heated. Therefore, variation in discharge and related wetted width and depth may explain much of the scatter in the empirical relationship and might be included as explanatory variable in future studies. Furthermore, diel fluctuations usually decrease with stream size (Ferencz & Cardenas, 2017; Vannotte & Sweeney, 1980) and this decrease in T_{range} limits the potential for cooling by canopy cover in larger streams. The principles how daily water temperature fluctuations and rates of warming and cooling caused by canopy cover decrease with stream size are well established. However, so far studies have mainly focused on small streams where the largest effects can be expected and studies comparing different stream sizes or types are rare: The empirical data reported in Coats and Jackson (2020) clearly indicated that the effect of canopy cover on water temperature decreases with catchment size. The modelled effect of 60% canopy cover on daily maximum water temperature was about −3.5°C in small headwater streams (Loicq et al., 2018, which is surprisingly similar to the −3.1°C predicted by our empirical equations for 0 oktas in May) and decreased to −1°C in the lower part of the catchment about 300 km from the source.

Similar to our investigation, most studies on the effect of canopy cover on water temperature deal with reach-scale effects on daily maximum water temperature, which can be considered the peak of daily fluctuations superimposed on the general annual cycle of mean water temperature (Caissie, 2006). However, there is very limited knowledge on the large-scale and downstream effect of shading on mean water temperature (Sweeney & Newbold, 2014). A recent modelling study indicated that the cooling effect of canopy cover on mean water temperature may propagate downstream and river reaches in the downstream part of a network may benefit from restoring woody riparian vegetation in headwater streams (Beaufort et al., 2016).

5 | CONCLUSION

Based on the results and discussion, the following conclusions can be drawn for river management in mid-latitude small streams:

Woody riparian buffers should be at least several hundred metres in length (about 45–60 min travel time) and canopy openings should be avoided to exploit the full potential of cooling, which is in the range of −4 to −5°C and highest at sunny days in early summer. In contrast, the heating and increase in daily maximum water temperature in unshaded reaches is in the range of +3°C within the first few hundred metres to a kilometre downstream, water temperature continues to increase several kilometres (several hours travel time) downstream and equilibrium conditions may only be reached at high water temperature.

Developing woody vegetation (large trees) in a 10 m buffer directly adjacent to the river bank is most effective and already provides most of the effect of wider buffers. These results indicate that buffer width is less important compared to length, and woody buffers should be as long as possible to prevent the continuous heating in unshaded reaches, similar to the conclusions drawn by Stanford et al. (2020). However, wider buffers up to 30 m are known to increase other functions like nutrient retention (Gericke et al., 2020; Sweeney & Newbold, 2014).

The percentage of the riparian buffer area covered with woody vegetation mapped on orthophotos is a good and easily available proxy for shading by woody riparian vegetation and might be used for large-scale assessments. Most probably this only holds true for small streams where even small trees already shade the whole wetted cross-section. In larger streams and rivers, additional information on tree height from LiDAR data together with stream width may be used to assess the share of the cross-section shaded by woody vegetation.

The cooling effect does not only depend on canopy cover but also on the deviation of excess temperature of the incoming water from equilibrium conditions in the river section, with daily water temperature range T_{range} being an appropriate and easily quantifiable proxy. Streams with a high potential for cooling might be identified based on T_{range}.

In summary, largest effects at the reach-scale are to be expected from restoring long woody riparian buffers, which do not necessarily have to be very wide, in streams with large diel fluctuations (large T_{range}), for example, small shallow headwater streams with low baseflow discharge.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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RESEARCH ARTICLE

Woody riparian buffers have indirect effects on macroinvertebrate assemblages of French rivers, but land use effects are much stronger

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Abstract

1. Woody riparian buffers (hereafter, ‘woody buffers’) are frequently considered as important to mitigate the effects of stressors on streams and rivers. While several individual studies addressing nutrients, pesticides, water temperature and different biotic components support this conjecture, no study has addressed the effects of woody buffers on riverine biota at country-wide scales.
2. We used a comprehensive dataset from sampling sites on 1082 catchments in France, comprising samples of benthic invertebrates, along with data on river size, physico-chemistry, hydromorphology, riparian and catchment land use and woody buffers at sampling sites and upstream.
3. Using partial least square modelling, we delineated the effects of the different environmental variables on two benthic invertebrate metrics, separately for siliceous and calcareous rivers.
4. Overall, models explained 49% (calcareous) and 39% (siliceous) of the variation in benthic invertebrate metrics. Direct effects of woody buffers on benthic invertebrate metrics were marginal, while physico-chemical conditions and catchment land use explained most of the deviance. Direct and indirect effects of woody buffer together covered up to 6% (upstream scale) plus 2% (local scale) of the explained variability.
5. *Synthesis and applications*. In this national-scale study, on 1082 catchments, we investigated the potential of woody buffers to mitigate the effects of catchment-scale and local-scale stressors on macroinvertebrate biodiversity. Our results underline that the establishment of woody buffers is not necessarily a sufficient measure to solve the problem of deteriorating riverine macroinvertebrate communities, especially in catchments prone to intense land use. Nevertheless, two main outcomes included that local woody patches are not sufficient and that woody buffers should be established along longer river stretches. Also, accompanying catchment-scale measures should be promoted to reduce the effects of intense land use and pollution to a level that enables woody buffers to be effective as well.

KEYWORDS
benthic invertebrates, catchment land use, direct and indirect effects, mitigation effect, multiple spatial scale analysis, Partial least square modelling, woody riparian buffers

1 | INTRODUCTION

Rivers are embedded into the surrounding landscape and thus strongly affected by stressors acting upstream or at the catchment scale. The effects of several stressors resulting from catchment land use on riverine biota have been investigated in detail. Stendera et al. (2012) stated that land use, eutrophication and habitat destruction at the catchment scale are the major disturbances on rivers. Changing catchment land use can affect discharge (Buytaert et al., 2006), sediment transport and water quality (Miserendino et al., 2011). However, disentangling the pathways through which catchment land use affects biota remains difficult and catchment land use is frequently considered as an 'overarching stressor' or 'driver' (Death & Collier, 2010; Roth et al., 1996; Sliva & Williams, 2001; Wang et al., 1997; Weigel et al., 2000).

As land use within catchments cannot easily be changed, the riparian zone is often recognised as the most relevant scale for river management, with different measures such as grassy or woody buffers intended to prevent run-off of pesticides, nutrients and fine sediments (Lowrance et al., 1997). Additionally, the shading by woody buffers decreases water temperatures and benefits stenothermic biota (Broadmeadow et al., 2011; Ryan et al., 2013), limits the primary production and the effects of eutrophication (Gulis & Suberkropp, 2003). Furthermore, woody buffers enhance the diversity of riparian and instream habitats through the provision of woody debris (Benke et al., 1984; Wallace et al., 1995) and food sources such as leaves (Cummins et al., 1989; Wallace et al., 1997).

While all riverine organism groups can potentially benefit from woody buffers, the effects on macroinvertebrates' assemblages are supposed to be particularly beneficial. Coarse particulate organic matter (CPOM) provided by riparian trees can serve as food (e.g. leaves) or habitat (e.g. woody debris; Flory & Milner, 1999; Hession et al., 2003; McKie & Cranston, 1998; O'connor, 1991, 1992). Through shading and decreasing water temperature, primary production and periphyton growth are impacted (Bunn et al., 1997, 1999; Mackay & Marsh, 2005), thus changing the availability of food sources for different feeding types. For macroinvertebrate species having an aerial life stage, woody buffers act as terrestrial habitat for reproduction, migration or resting. In particular, sensitive groups such as Ephemeroptera, Plecoptera and Trichoptera (EPT) may benefit from the lower temperatures and thus higher oxygen due to shading effect and from improved water quality due to riparian filtration (Jerves-Cobo et al., 2017).

Thus, woody buffers may simultaneously mitigate various stressors acting on benthic invertebrates and significantly contribute to enhancing biodiversity. However, despite the multitude of individual studies at the reach scale, the effects of woody buffers on benthic invertebrates have only recently been considered in large-scale analysis by studying the effect of losing woody buffers in tropical regions (Dala-Corte et al., 2020). In Europe, where large parts of the riparian areas have been used for agriculture or converted to build-up area, national or regional scale, including multiple catchments, studies investigating the effects of catchment-scale land use and of the remaining woody riparian buffers on biodiversity are missing. Such an investigation needs to consider several anthropogenic disturbances that act simultaneously, from catchment to site scales, including their interactions (Munns, 2006). Structural equation modelling is increasingly used and has proven efficient in identifying the pathways through which land use impacts the functional structure of fish assemblages, necessary to inform managing decisions at the right level (Leitão et al., 2018). However structuring such models requires many data often not available on a larger regional scale. Thus, finding trade-offs between precise pathways and assessing general relationships at a national scale remain challenging.

Here, we used a large dataset of 1082 sampling sites from French rivers to investigate both the direct and indirect (e.g. through modified river hydromorphology or physico-chemistry) effects of woody buffers on macroinvertebrate metrics with PLS-pm. We related the effects of woody buffers to the effects of a wide array of stressors at the catchment, riparian and local scales. Against their well-documented beneficial effects at the local scale, we expected a strong positive effect of woody buffers on macroinvertebrate metrics, both direct and indirect, in particular on the share of EPT. Furthermore, we aimed to determine if local woody buffers offer a sufficient solution or if continuous afforestation is needed to mitigate human pressures. Calcareous and siliceous rivers differ in their overall nutrient conditions (Krueger & Waters, 1983), siliceous rivers being generally poorer and more sensitive to physico-chemical disturbances (Villeneuve et al., 2018). As several of the pathways relating to catchment land use, as well as woody buffers and biota, depend on physical and chemical conditions within the catchment, we further expected differences in the effects of the different stressors between calcareous and siliceous river types and therefore considered both river types separately.

2 | MATERIALS AND METHODS

2.1 | Data source

The dataset used in this study was extracted from the French nationwide survey network database (RCS, in Naïades) storing standardised macroinvertebrate samples' results for the surveyed sites (short river reach on which macroinvertebrates are sampled). This study, therefore, did not require any ethical approval. We used data recorded between 2007 and 2013, excluded sites in ecoregions with highly specific character, such as the Mediterranean or high mountain regions (all sites considered are located at altitudes below 450 m a.s.l.), and limited the analysis to sites located in small- and medium-sized rivers (Strahler order 1–6). The resulting dataset is composed of 1082 sites (mostly one site per stream), 613 of which are in calcareous rivers and 469 in siliceous rivers (Figure 1).

In the French survey process, macroinvertebrates were sampled according to a standardised protocol (AFNOR, 2009). Twelve sample units were defined per site, based on predefined mesohabitat types, and sampled with a standardised Surber net. Macroinvertebrates were sorted, counted and identified to a predefined taxonomic level, that is, genus level except for Oligochaeta, some Diptera (mainly family), Trichoptera Limnephilidae, Coleoptera Dytiscidae and Hydrophilidae (subfamily). From the resulting taxa lists, the following metrics were calculated: abundance (i.e. share in the community) and diversity (i.e. taxa number) of EPT, and the I2M2 index (Mondy et al., 2012). The multimetric I2M2 index is the official French system to assess the ecological quality of streams for the Water Framework Directive. To avoid rare species effects in raw counts of taxa, we used the average value of the metrics.

For each site, several environmental data were compiled. The woody buffers were extracted from BD TOPO® (IGN) at two scales: The woody buffer at the local scale corresponds to the share of woody vegetation within an area of 30-m width and 500-m length (i.e. 250-m upstream and 250-m downstream of the studied site). The woody buffer at the upstream scale corresponds to the share of woody vegetation within an area of 30-m width and 5,000-m length upstream of the studied site, including tributaries. The 30-m width is a commonly used buffer for the riparian forest (Van Looy et al., 2013).

Land use data were extracted from the 2006 Corine Land Cover database (European Environment Agency, 2007). We used five pooled categories: urban areas (i.e. urban elements and roads), wetlands (i.e. lakes, ponds and rivers), croplands, grasslands and forests. For each study site, we computed the land use at two scales: to assess the site-scale riparian land use (hereafter local land use) possibly affecting sites' physical and chemical characteristics (Allan et al., 1997), we used a 30-m radius buffer around the sampling site; at the catchment scale, the land use within the subcatchment from river source to the sampling site was calculated.

Physico-chemical data were obtained from the French surveillance network RCS. We considered the monthly measurements of concentrations (mg/L) of suspended matters, ammonium, nitrite, nitrate, phosphorus and dissolved oxygen. We calculated the average concentrations over the 11 months preceding the macroinvertebrates sampling.

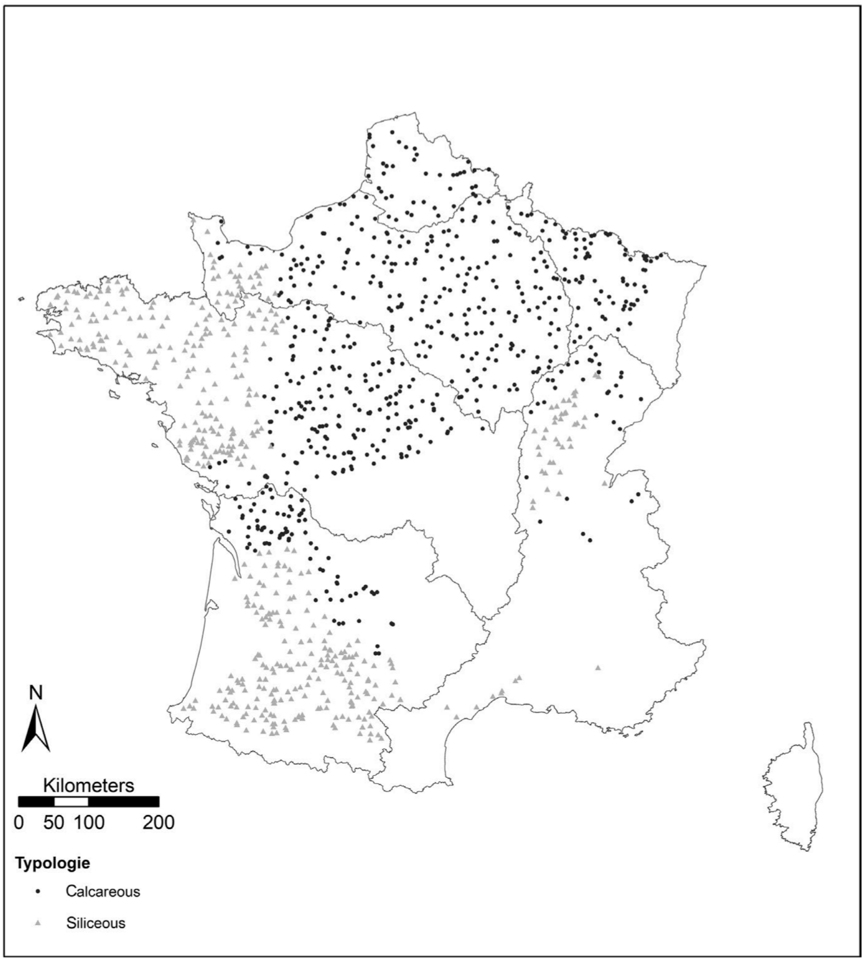

FIGURE 1 Map of the studied sites in France

We considered hydromorphological variables potentially affecting the hydromorphological functioning of the river: straightness rate of the watercourse, the number of crossings (e.g. bridges), the mean number of dams and weirs per kilometre and the number of pumping facilities per catchment surface unit (km²). There is no database on individual hydromorphological modification or impact on every river; therefore, all of these variables are considered as proxies (e.g. crossings are usually protected with embankments) for these modifications and were calculated from the BD TOPO® (3D vector description of the elements of the territory and of its infrastructures, of metric precision, exploitable on scales ranging from 1:5000 to 1:50000; IGN).

In addition to the pressure data, we included Strahler order and the subcatchment size upstream of the sampling site into the analysis.

2.2 | Data analysis

Different methods have emerged recently to study the relative stressor effects on macroinvertebrate communities (Damanik-Ambarita et al., 2018), among which partial least square path modelling (PLS-pm; Wold, 1982, see Appendix S1 in Supporting Information for a short description) has proven efficient to consider the hierarchy of scales in linking land use to environmental variables and eventually to biodiversity (Riseng et al., 2011), and to classify the importance of links and interactions between these groups of variables (Lange et al., 2014). PLS models were computed in the XLSTAT software (v. 2019.2.1, https://www.xlstat.com).

Based on this method, we developed models (Figure 2) linking the latent variables of (a) land use at the catchment scale, (b) land use at the local scale, (c) share of woody buffers at the upstream scale, (d) share of woody buffers at the local scale, (e) physico-chemical conditions, (f) hydromorphological alterations and (g) the river's characteristics to macroinvertebrate metrics.

These latent variables represent the main factors proven to have effects on macroinvertebrates' communities. Land use and local land use are usually considered as 'overarching stressors' (Death & Collier, 2010) as they drive different stressors such as increased run-off (Buytaert et al., 2006), sediment inputs and water quality deterioration (Miserendino et al., 2011). Urban cover and cropland particularly generate an overall degradation of biotic integrity indices (Marzin et al., 2013). Woody buffers are hypothesized to have positive effects on stream ecology by controlling water warming and dissolved oxygen concentration through shading effects, or to limiting suspended matters and nutrients incomes. They also provide food and habitats for macroinvertebrates. The alteration of hydromorphological processes at the reach scale directly effects macroinvertebrates' communities by degrading their physical habitats (Dahm et al., 2013; Lamouroux et al., 2004). Lastly, the physico-chemical parameters have a strong direct effect, especially on sensitive taxa, such as EPT (Dahm et al., 2013). Catchment size and Strahler index were used as natural landscape predictors of the biodiversity metrics.

Interactions between these different stressors were considered, introducing indirect effects for the different latent variables when data were available to inform the underlying mechanisms. Catchment land use and local land use explain a part of the observed variations of all the other latent variables (e.g. woody buffer structure depends on agricultural practices, part of the hydromorphological alterations is related to crossing protection, water quality is highly related to land use at the catchment scale) and are therefore considered to have indirect effects on macroinvertebrates through all the other variables. Woody buffers are hypothesised to explain a part of the physico-chemical variables' variations, due to retention effects (Gericke et al., 2020), and of the hydromorphological conditions, due to riparian stabilization. Last hydromorphological conditions influence the physico-chemical conditions, as a modification of the stream morphology can modify the residence time of substances, the self-purification capacity of streams and other internal processes (Baker et al., 2012). All of the necessary data to describe the underlying mechanisms were not available in regional/national-scale databases. Therefore, we maintained the remaining undocumented pathways as the direct pathways. The statistical inference of the PLS-pm allowed then to differentiate the weights of the different pathways. Separate models were run for the two metrics (I2M2 and abundance diversity of EPT) and for calcareous and siliceous rivers. In contrast to I2M2 as a single variable, abundance diversity of EPT final node is built as a latent variable, therefore constructed from the two manifest variables: the abundance and the diversity of EPT. As the different sites belong to different catchments, we considered these as spatially uncorrelated.

3 | RESULTS

The models well explained the variability of the two macroinvertebrate metrics (Table 1). Validation index values ranged from 49% (calcareous rivers; I2M2) to 21% (siliceous rivers; abundance diversity of EPT), with the other two models having a validation index of nearly 40% (siliceous; I2M2: 39%/calcareous; abundance diversity of EPT: 39%). All the Q^2 values were positive, indicating a good predictive capability.

The by far most important direct influence on both metrics was posed by the physico-chemical conditions (35%–60%) and by catchment land use (23%–37%; Table 1), followed by hydromorphology (3%–17%). Physico-chemistry was a particularly good predictor for I2M2 in siliceous rivers (60%), while the effects of catchment land use were most pronounced for EPT in siliceous rivers (37%). Direct effects by woody buffers were generally minor, with both the effects of upstream woody buffers and of local woody buffers, ranging between 1% and 4%. Effects were most pronounced for EPT in calcareous rivers (4% each for local and upstream woody buffers).

In contrast to the direct effects, catchment land use was generally more important than physico-chemical conditions for the

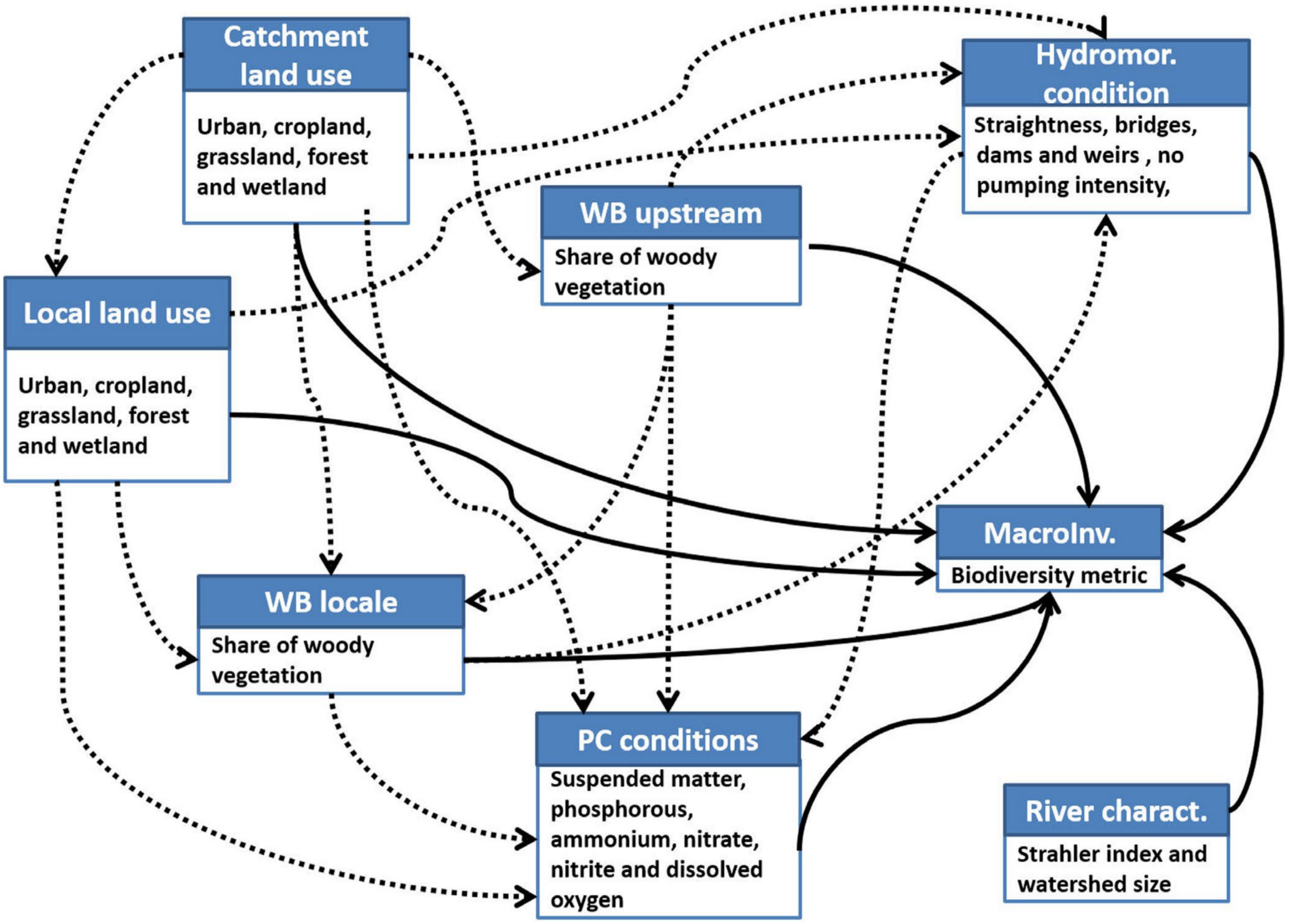

FIGURE 2 Design of the multiscale and multi-stressors structural model. Each latent variable is represented by a coloured box and each direct effect from this latent variable to another is represented by a solid arrow. Indirect effects on the biological response variables are represented by dotted arrows. Each latent variable is a linear combination of the manifest variables listed in the box frame

total effects (direct and indirect effects). For all four models, the total effect of land use ranged between 34% and 48%, while the total effect of physico-chemical conditions dropped to 23%–34%. Hydromorphological conditions remained in the same order of magnitude (5%–15%) than for the direct effects. The total effects of woody buffers ranged between 1% and 6% (woody buffers upstream), and between 1% and 2% (woody buffers local). As for the direct effects, the total effects of woody buffers were strongest for EPT in calcareous rivers (6% each for upstream woody buffers, 2% for local woody buffers).

4 | DISCUSSION

4.1 | General effects of woody buffers on macroinvertebrates

We expected strong positive direct and indirect effects of woody buffers on macroinvertebrate metrics. This was not confirmed. In line with the large catchment analysis from Burdon et al. (2020) showing a positive but weak link between woody riparian integrity and macroinvertebrates communities' integrity, the effects of woody buffers were smaller than expected, with the effects of the upstream woody buffers slightly exceeding the effects of local woody buffers. However, the effects of catchment land use and of physico-chemistry superimpose the effects of woody buffers greatly. Thus, our results somehow contradict the majority of local-scale studies on the effects of woody buffers on macroinvertebrate communities (Couceiro et al., 2007; Iñiguez-Armijos et al., 2014; Lorion & Kennedy, 2009; Nessimian et al., 2008; Rios & Bailey, 2006). At the local scale, there is overwhelming evidence that reducing the width of woody buffers promotes generalists over specialists, such as EPT (Braun et al., 2018; Li & Dudgeon, 2008; Mc Conigley et al., 2017; Tomanova et al., 2006). The reasons for the weak effects of woody buffers in our study remain controversial. Potentially, we could have omitted an important explanatory factor when building the PLS model or have implemented unsuited relationships between the woody buffers' latent variables and the other latent variables. We consider this as unlikely, as the structure has been designed to be in line with the above-cited references. However, a reach-scale study

TABLE 1 Results of PLS model for I2M2 and abundance diversity of EPT for calcareous and siliceous rivers. The first line provides the R^2 of the individual models; other lines show the direct and total effects of the different latent variables on I2M2 and abundance diversity of EPT. Values are percentages of explained variance

	I2M2		Abundance diversity of EPT	
	Calcareous rivers	Siliceous rivers	Calcareous rivers	Siliceous rivers
Validation of the structural model, R^2	49	39	39	21
Direct effect of the latent variables				
Land use (catchment)	24	27	23	37
Land use (local)	7	8	5	< 1
Woody buffers (upstream)	1	< 1	4	< 1
Woody buffers (local)	1	< 1	4	1
Physico-chemical conditions	44	60	35	38
Hydromorphological alterations	16	3	17	13
River's characteristics	7	1	12	11
Total effect of the latent variables				
Land use (catchment)	37	48	33	44
Land use (local)	8	9	6	2
Woody buffers (upstream)	2	1	6	2
Woody buffers (local)	1	1	3	2
Physico-chemical conditions	29	34	23	25
Hydromorphological alterations	15	5	16	13
River's characteristics	7	2	12	11

often uses dedicated observed explanatory variables that do not exist as national-scale databases. Thus, in our model, we included the indirect pathways that were possible to populate with existing databases (e.g. physical and chemical local variables result from land use and woody buffer). The remaining effects not accessible in indirect pathways (e.g. not observed temperature, connectivity, hydrology) could not simply be ignored and were summarised as the remaining direct effects between catchment-scale land use or woody buffers and macroinvertebrates. By construction, this gives more explanatory weight to the highest level of latent variable in the hierarchy. A second option is that the variability of conditions in the spatially broadly distributed dataset has masked the effects of woody buffers. However, the variability of conditions was not reflected in the Strahler order and the sub-catchment size, both of which had only minor effects on the targeted metrics. A third possible explanation is that the gradient in the share of woody buffers might have been too short for significant effects on macroinvertebrates. In other words, the woody buffers present along the vast majority of river sections might not have been sufficiently broad or have covered a sufficiently long river stretch to show large effects on the benthic fauna. This conjecture is in line with several studies highlighting the relevant buffer width required for effects on rivers; for example, a meta-analysis of 222 studies recommends a width of 100 m for high land-use intensity, 70 m for moderate intensity and 40 m for low intensity (Hansen et al., 2010). Fourth, we have not introduced potential legacy effects into the models, due to the lack of historical land use datasets at this very large scale. Legacy effects potentially limit the explanatory power of current catchment and riparian land use, in line with results from Greenwood et al. (2012). Some currently forested catchments in France were not forested in the 1950s (Koerner et al., 2000), which may still affect recent aquatic biota as observed by Harding et al. (1998). This is most frequently relevant for siliceous hilltops (e.g. Brittany), and siliceous plains (e.g. the Landes), providing a possible rationale for the smaller effects of riparian buffers in for siliceous rivers. Fifth, we considered the extent of woody riparian buffers but ignored woody buffer quality and functioning. Beneficial effects of woody riparian buffers on the retention of nutrients, on fine sediments and pesticides and on water temperatures were mainly reported by reach-scale or experimental studies on well-functioning woody buffers that did not consider or even actively excluded confounding factors (Dosskey, 2001; Feld et al., 2018). However, it is well known that preferential flow or drainages bypassing the woody buffers limit retention effects (Dorioz et al., 2006; Dosskey, 2001; Polyakov et al., 2005). As a consequence, the overall effects of woody buffers at the catchment scale, that inevitably include woody buffers of varying quality and limited functionality, are much lower compared to reach-scale or experimental studies (Hill, 2019). Finally, recent afforestation often involved coniferous trees (Koerner et al., 2000) with potential acidification effect and detrimental effect on aquatic communities (Harriman et al., 2003; Ormerod et al., 1989) that can obstruct the recovery of invertebrates' communities (Malcolm et al., 2014). As land use did not differentiate between deciduous and coniferous trees, we were not able to consider this potential confounding effect. Despite these various limiting factors, we detected small positive effects of riparian forest on aquatic invertebrates' communities and on specific sensitive taxa, comforting the overall potential of riparian buffers as managing measure.

4.2 | Riparian buffers can mitigate a small proportion of catchment-scale land use impacts

The overarching effect of catchment land use on macroinvertebrates, as resulting from our analysis, echoes many studies determining the ecological functioning of rivers by hierarchical ordination of possible pressures (e.g. Allan, 2004; Poff et al., 1997; Roth et al., 1996; Thorp, 2014; Wasson et al., 2002). Concerning EPT, effects at the catchment scale are often more important than effects at the local scale (Burt et al., 2010; Miserendino et al., 2011). High shares of grassland, forest and wetland favour EPT taxa, while high shares of cropland and urban area are detrimental. Numerous studies have shown that land use pressures like agriculture and urbanization have a negative impact on water quality at the reach scale (Allan, 2004; Hering et al., 2013; Lorenz & Feld, 2013; Robinson et al., 2014), for example, through reducing oxygen contents (Ding et al., 2017). In contrast, forested catchment has a positive effect. Death and Collier (2010) showed that rivers having a catchment covered with 40%–60% of forests conserved 80% of freshwater macroinvertebrate diversity. The catchment-scale forest has also an impact on local water temperature and Dohet et al. (2015) showed that some cold stenothermic Trichoptera species were only detected in forested catchments. Finally, forest can reduce the loadings of suspended matters like fine sediments, a benefit to sensitive EPT taxa (Feld, 2013). Nevertheless, our results show that even though land use effect remains clearly dominant on explaining the observed biodiversity, implementing riparian buffers should have a positive effect on both the general quality index and specialised taxa.

4.3 | An ideally continuous woody riparian corridor has higher positive effects and longer buffer stretches should be implemented

We observed that the total effect of upstream woody buffer cover is more important than the effect of local woody buffers. Several beneficial effects of woody buffers are likely to act only on longer river stretches, while the effects of very local buffers might be superimposed by the stressors acting upstream. Orlinskiy et al. (2015) found that upstream woody buffers limited the effects of pollution on downstream freshwater macroinvertebrate populations. Likewise, upstream woody buffers have an impact on the water temperature downstream and a 100-m section of woody buffers can reduce temperature by up to 1°C compared to an open river (Kristensen et al., 2013). Thus, it appears that managing woody buffers at the catchment scale and maintaining or enabling a large proportion of wood cover in the 30-m corridor over longer upstream stretches (ideally a full cover), limiting the impact of pollution and preventing its spread (Osborne & Kovacic, 1993), is preferable for macroinvertebrates, rather than local woody buffers in unforested upstream reaches.

4.4 | Riparian buffers are more efficient for calcareous river types

We expected differences in the effects of woody buffers (as well as in the effects of stressors) between river types. This expectation was confirmed. Catchment land use and physico-chemistry had the highest total effects on both I2M2 and EPT for siliceous rivers. These results are in line with Villeneuve et al. (2018), who observed similar differences between calcareous and siliceous rivers. Calcareous and siliceous rivers differ fundamentally in ecological functioning and the effects of pressures. Calcareous rivers are more productive (Hill & Webster, 1982). Conversely, a lower primary production evokes a lower secondary production for siliceous rivers (Cross et al., 2006). This often results in more nutrient-poor conditions in siliceous rivers, which are therefore more vulnerable to physico-chemical disturbances while calcareous rivers with a higher primary production and a more stable secondary production are more resistant to physico-chemical disturbances (Villeneuve et al., 2018). In this study, the total effects of local and upstream woody buffers were higher for calcareous rivers, especially for EPT diversity but remained rather low at this broad scale. Our results underline that woody buffers are not able to mitigate catchment disturbances, especially for the most sensitive siliceous river ecosystem, which should therefore be managed at the catchment scale to reduce the overall upstream impacts. Woody buffers have a higher potential to mitigate impacts in calcareous rivers, and the establishment of woody riparian corridors should therefore be prioritized in calcareous regions.

4.5 | Conclusion and management summary

Our results indicate that the establishment of local woody buffers is not necessarily a sufficient measure to solve the problem of deteriorating riverine macroinvertebrate communities, at least not at large (i.e. country-wide) scales and in intensively used agricultural landscapes. If macroinvertebrate communities are strongly affected by pollution or by intense catchment land use, the establishment of local woody buffers is likely to have minor effects. This does not preclude, however, that woody buffers may be beneficial for macroinvertebrates at the local scale, as there is an overwhelming support in the literature for this conjecture.

Therefore, our study identified two main rules in order to enhance the local effects of woody buffers on macroinvertebrates biodiversity: (1) Effects of upstream woody buffers are larger than those of local woody buffers, and woody buffers should be established continuously along longer stretches of rivers. (2) The establishment of woody buffers needs to be accompanied by measures targeting the effects of intense land use and of pollution, to decrease them below a level that continuous woody buffers can mitigate, especially for the most sensitive siliceous river ecosystems.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors jointly conceptualised the study. M.L.G. compiled and analysed the data with support from M.P. and J.P. The manuscript was written by M.L.G., with support of J.P. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the data INRAE repository https://doi.org/10.15454/QY4UVN (Piffady, 2020).

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A metric-based analysis on the effects of riparian and catchment landuse on macroinvertebrates

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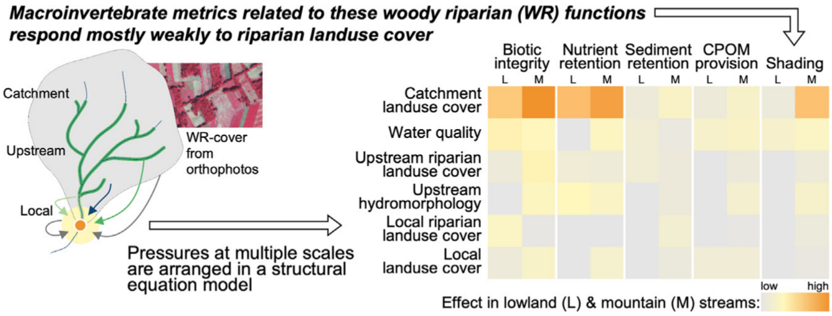
HIGHLIGHTS

- Woody riparian vegetation facilitates multiple functions benefitting river biota.
- These functions are thought to either be affected by large-scale stressors or not.
- This concept was tested with high-resolution woody riparian cover data.
- Large-scale stressors even affect functions thought to be independent from them.
- Riparian restoration cannot occur in a vacuum and must consider catchment context.

GRAPHICAL ABSTRACT



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ABSTRACT

Woody riparian vegetation along rivers and streams provides multiple functions beneficial for aquatic macroinvertebrate communities. They retain fine sediments, nutrients and pesticides, improve channel hydromorphology, control water temperature and primary production through shading and provide leaves, twigs and large wood.

In a recent conceptual model (Feld et al., 2018), woody riparian functions were considered either independent from large-scale landuse stressors (e.g. shading, input of organic matter), or dependent on landuse at larger spatial scales (e.g. fine sediment, nutrient and pesticide retention).

We tested this concept using high-resolution data on woody riparian vegetation cover and empirical data from 1017 macroinvertebrate sampling sites in German lowland and mountain streams. Macroinvertebrate metrics indicative for individual functions were used as response variables in structural equation models (SEM), representing the hierarchical structure between the different considered stressors at different spatial scales: catchment, upstream riparian, local riparian and local landuse cover along with hydromorphology and water quality.

The analysis only partly confirmed the conceptual model: Biotic integrity and water quality were strongly related to large-scale stressors as expected (absolute total effect 0.345–0.541), but against expectations, fine sediments retention, considered scale-dependent in the conceptual model, was poorly explained by large-scale stressors (absolute total effect 0.027–0.231). While most functions considered independent from large-scale landuse were partly explained by riparian landuse cover (absolute total effect 0.023–0.091) they also were nonetheless affected by catchment landuse cover (absolute total effect 0.017–0.390).

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While many empirical case studies at smaller spatial scales clearly document the positive effects of restoring woody riparian vegetation, our results suggest that most effects of riparian landuse cover are possibly superimposed by larger-scale stressors. This does not negate localized effects of woody riparian vegetation but helps contextualize limitations to successful restoration measures targeting the macroinvertebrate community.

1. Introduction

River biota are affected by multiple stressors at multiple spatial scales that are hierarchically nested (Allan et al., 1997; Poff et al., 1997; Aschonitis et al., 2016; Villeneuve et al., 2018). At the catchment-scale, built-up areas or agriculture increase runoff resulting in hydrological alterations to the river network (Arnold and Gibbons, 1996; Booth and Jackson, 1997; Gordon et al., 2008). Furthermore, nutrient and pesticide pollution from e.g. agricultural or urban areas deteriorates water quality (Paul and Meyer, 2001; Schäfer et al., 2016). At the river network scale, flood prevention, navigation, and hydropower generation drive the regulation of channel morphology and hydrology. These alterations reduce longitudinal connectivity, impairing sediment transport along with migration of biota, and additionally affect thermal regimes (Bunn and Arthington, 2002; Elosegi and Sabater, 2013; Kail et al., 2021). The removal of natural riparian woody cover causes an increase in summer water temperature and exposes the river to adjacent, detrimental landuse forms (Broadmeadow and Nisbet, 2004; Bowler et al., 2012). At the reach scale, the aforementioned drivers and stressors locally reduce channel morphodynamics (Tokeshi and Arakaki, 2012) as well as lateral and vertical connectivity through bed and bank fixation, reducing habitat diversity and availability (Schinegger et al., 2012).

Despite the overarching effects of stressors acting at larger scales, the majority of restoration measures are implemented at the reach scale (Bernhardt and Palmer, 2011; Muhar et al., 2016). While these projects had an overall positive effect on riverine biota (Kail et al., 2015), especially aquatic macroinvertebrates showed little or no response in a large number of restoration projects (Jähnig et al., 2010; Verdonschot et al., 2013; Hering et al., 2015; Nilsson et al., 2015). The low effectiveness of reach-scale restoration was often attributed to stressors acting at the river network or catchment scales (Death and Collier, 2010; Lorenz and Feld, 2013; Leps et al., 2016). However, stressors stemming from catchment or floodplain landuse can hardly be addressed at these large scales given the economic and social costs. Restoration actions at the riparian corridor scale remain the prime management option bridging the gap between the catchment-scale stressors and feasible local restoration measures.

Natural riparian corridors in temperate regions are generally covered by woody vegetation, with few exceptions such as above the tree line or in some wetlands (Ellenberg, 1988). Trees provide many functions benefiting aquatic biota: The retention of nutrients, fine sediment, and pesticides has been extensively studied (Dosskey, 2001; Broadmeadow and Nisbet, 2004; Hoffmann et al., 2009; Orlinskiy et al., 2015; Hill, 2019; Gericke et al., 2020). Similarly, the cooling effect of shading by woody riparian vegetation is well studied and might mitigate the increase in water temperature caused by climate change (Caissie, 2006; Broadmeadow et al., 2011; Bowler et al., 2012). In addition, shading limits growth of phytobenthos and macrophytes and thereby keeps instream primary production at a natural level (Hill et al., 1995). It also limits the growth of herbaceous bank vegetation that otherwise would fix stream banks, hindering natural channel dynamics, resulting in unnaturally narrow, straight, and incised streams (Gurnell, 2014). Additionally, woody riparian vegetation provides leaves, twigs, and large wood that are important food sources and habitats (Cummins et al., 1989; Wallace et al., 1997). Natural riparian vegetation also directly provides habitat for terrestrial life-stages of aquatic insects, or terrestrial invertebrates, birds, and mammals (Pearson and Manuwal, 2001; Marczak et al., 2010; Lind et al., 2019). Given their linear shape, woody riparian vegetation enhances migration and dispersal along the riparian corridor, connecting populations and allowing new habitats to be colonized (Machtans et al., 1996; Beier and Noss, 1998; Winterbourn et al., 2007; Van Looy et al., 2014). These functions of woody riparian vegetation for instream processes and the aquatic community are well documented and summarized in numerous studies and reviews (e.g. Broadmeadow and Nisbet, 2004; Sweeney and Newbold, 2014). Therefore, re-establishing woody riparian vegetation is considered an adequate restoration measure, mitigating several stressors while not requiring large areas (Bernhardt et al., 2005; Stutter et al., 2012). However, the vast majority of studies documenting the functions of woody riparian vegetation were conducted at the reach scale. There is limited knowledge on the effect of woody riparian vegetation at the river network scale in the context of large-scale stressors, limiting their applicability as a restoration tool at the catchment scale. Understanding the stressors and processes affecting impaired sites, river reaches or even larger parts of a riverine network that can be mitigated by woody riparian vegetation is a prerequisite to appropriately plan and evaluate restoration measures centred on woody buffers.

In a conceptual model, Feld et al. (2018) linked catchment scale stressors and functions of woody riparian vegetation to environmental variables and river biota, i.e. biomass of primary producers and diversity metrics for macroinvertebrates and fish. Especially macroinvertebrates are proven indicators of stream health and a core component of many assessment schemes (Poff et al., 2006). Their taxonomic and trait composition respond to local habitat conditions as well as water quality or hydrological regime which in turn are affected by catchment-scale conditions. Therefore, metrics and indices based on macroinvertebrates' taxonomic or trait composition reflect local as well as large-scale stressors. Based on a literature review, Feld et al. (2018) argued that some functions of woody riparian vegetation depend on stressors at larger spatial scales, e.g. nutrient retention depends on diffuse nutrient pollution at the catchment scale. In contrast, other functions were found independent from stressors at larger spatial scales, e.g. shading and water temperature regulation as well as provisioning of coarse particulate organic matter (CPOM) and large wood. This implies that restoring woody riparian vegetation at the reach scale can already be beneficial for macroinvertebrate communities through functions independent from large-scale stressors. In contrast, functions depending on stressors at larger scales may not be restored by solely developing woody riparian vegetation locally. This concept of functions and effects being independent and dependent on large-scale stressors has not been rigorously tested yet. Studies investigating the effect of woody riparian vegetation on biota at multiple spatial scales are still rare (but see Le Gall et al., submitted). This may partly be due to the fact that high resolution data on woody vegetation in narrow riparian buffers are required, which is not part of conventional landuse datasets, especially at large spatial scales such as entire catchments.

Against this background, this study aimed at testing the concept of large-scale stressor dependence of woody riparian vegetation functions using empirical data. We developed a comprehensive structural equation model (SEM) representing the causal links between landuse cover at different spatial scales (catchment, river network, local) as proxy for stressors, environmental variables (water quality, hydromorphology) and their effects on macroinvertebrate metrics. The SEM allows distinguishing between the direct effects of landuse cover at the different scales and their indirect cascading effects through landuse and environmental variables at smaller spatial scales. For each individual function, we selected representative macroinvertebrate metrics that are considered indicative for the respective function. We hypothesized that macroinvertebrate metrics related to functions dependent on large scale stressors (nutrient and fine sediment indication and biotic integrity) are affected by large-scale landuse cover both directly and indirectly by causal links through riparian landuse cover. In contrast, macroinvertebrate metrics related to functions independent from large scale stressors (water temperature preference and feeding types) were expected to directly respond to riparian landuse cover, but not directly to large-scale landuse cover. This requires high resolution data on woody riparian vegetation down to single lines of trees which were previously missing from landuse data and field mapping protocols. We quantified this data from orthophotos, and are therefore for the first time capable to address these hypotheses.

2. Material and methods

2.1. Macroinvertebrate community

Macroinvertebrate data from 4235 sites in the three German federal states of Hesse, North Rhine-Westphalia, and Saxony-Anhalt were provided by state authorities. The sampling sites are located in lowlands (16–186 m MSL) and mountain ranges (59–567 m MSL) with varying catchment landuse and river types (Fig. 1). Sites are located in the drainage basins of the Meuse, Rhine, Vechte (Ijssel), Ems, Weser, and Elbe. Macroinvertebrates were collected between 2004 and 2013 by state authorities using multi-habitat sampling protocols in compliance with the Water Framework Directive (WFD) to obtain quantitative taxa lists on species level (Meier et al., 2006). Taxa lists were processed using the online tool PERLODES (https://www.gewaesser-bewertung-berechnung.de/index.php/perlodes-online.html), which calculates an exhaustive set of taxonomic, functional, and diversity metrics.

Specifically, the multimetric index (MMI) was used to assess the overall influence of riparian landuse on macroinvertebrate community composition. The MMI is the standard method for the river-type specific ecological quality assessment in Germany and provides an estimation on how stressors affect water management goals. The shares of taxa with preferences for psammal (sand), pelal (mud), and argyllal (loam) were chosen as indicators for the function of woody riparian vegetation to retain and reduce fine sediment inputs from adjacent, especially agricultural, areas. The saprobic index was selected as an indicator for the function of woody riparian vegetation to retain manure and nutrient inputs from adjacent, especially agricultural, areas. The share of taxa with habitat preference for particulate organic matter (POM) and the share of shredders were chosen to reflect the input of coarse particulate organic matter (CPOM) like leaves and twigs. The index for the community's temperature tolerance (KLIWA-Index$_{MZB}$; Halle et al., 2016) and the share of grazers were chosen as indicators for the function of woody riparian vegetation, either to shade the streams, regulating water temperature or to allow growth of aquatic autotrophs. Selected metrics are shown in stream-type specific pairwise scatter plots with Pearson's correlation coefficient in Fig. 2.

The dataset was filtered to exclude data of insufficient quality and sites where the influence of landuse scales is masked by other stressors, and to ensure strong landuse cover gradients. We excluded samples with less than 5 taxa and all samples not taken between December 1st and April 30th, to guarantee reliability and comparability between samples. We further excluded samples with a saprobic index >2.7, corresponding to the national threshold for polluted streams, which potentially are affected by point sources. Furthermore, all sites with

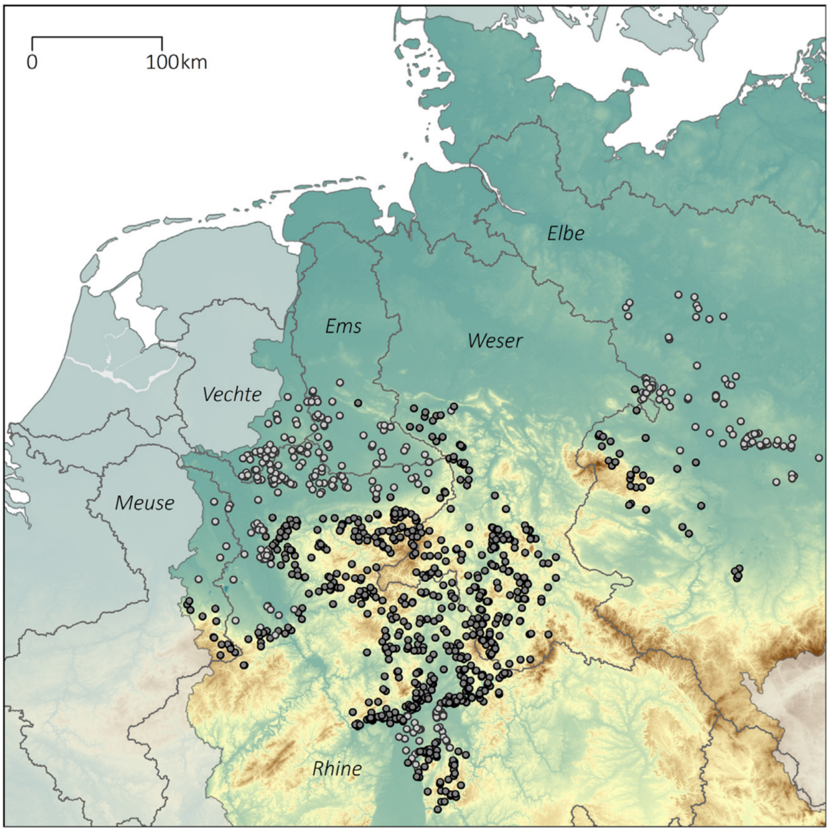

Fig. 1. Location of the macroinvertebrate sampling sites in central and western Germany differentiated according to river typology: Light dots denote lowland sites and dark dots denote mountain sites. Drainage basins are shown and labelled in the map. The Meuse and Rhine share a common estuary system. Topography outside Germany less saturated.

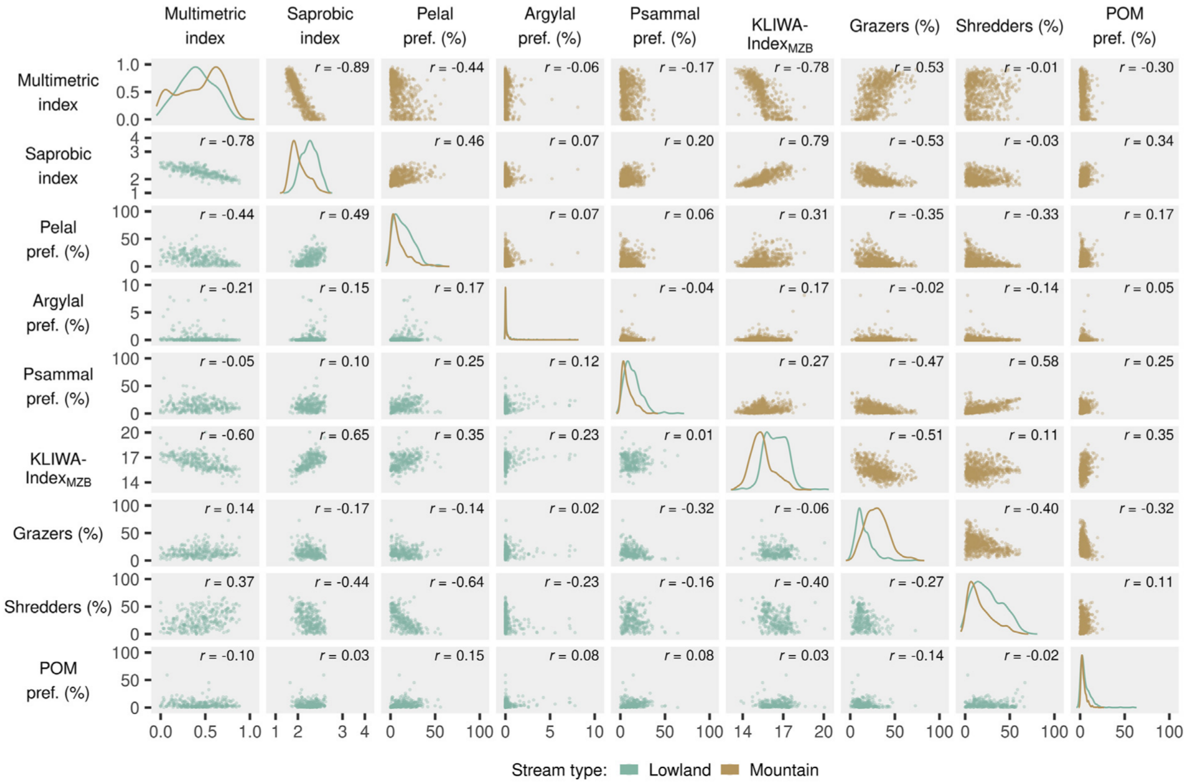

Fig. 2. Pairwise scatter plots for macroinvertebrate metrics. The top half (brown) is for mountain streams and the bottom half (green) is for lowland streams. In the diagonal the respective density distribution are shown with the scaled density estimation on the y-axis. Pearson's *r* is given as correlation coefficient. POM is particulate organic matter.

barriers within 5000 m upstream of the sampling site were excluded, since these act as sediment traps and alter the thermal regime, thus potentially masking the effects of sediment retention and shading by woody riparian vegetation. Sites with less than 20% agricultural catchment landuse and more than 80% forest catchment landuse were not considered to exclude near-natural or catchments fully covered by forest, where no strong landuse effects can be expected. Minimum catchment area was 10 km^2, since larger streams are not expected to respond strongly to local riparian conditions, as they have already aggregated stressors from larger catchment areas. The resulting dataset

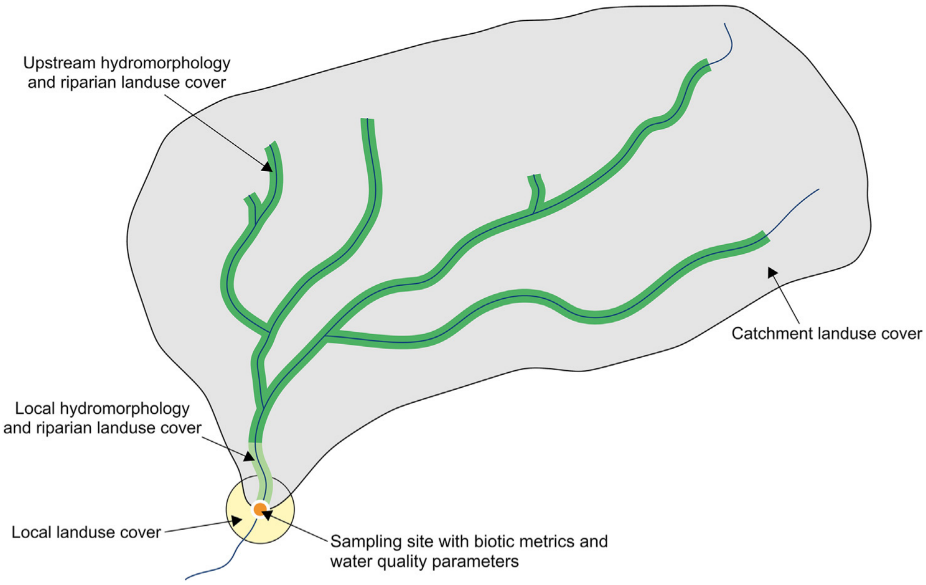

Fig. 3. Spatial scales combined for the biological data at the sampling site (red dot). Landuse was assessed in the (1) catchment, i.e. the basin draining to the sampling site, in the (2) upstream riparian buffer, i.e. a corridor 30 m to either side and 5000 m upstream the sampling site (dark green band), (3) locally in a 250 m circle around the sampling site (black circle) and (4) in the local riparian buffer, i.e. a corridor 30 m to either side and 500 m upstream the sampling site (light green band). For the lengths in the upstream and local riparian buffers available hydro morphological mappings were aggregated to local hydromorphology and upstream hydromorphology. For the sampling site, physico-chemical parameters were modelled based on catchment geometry.

was split according to river type, i.e. small mountain streams (n = 715) and small lowland streams (n = 302).

2.2. Spatial scales

Multiple stressors were quantified, using the following four spatial scales: (1) the catchment scale, i.e. the entire basin draining to a sampling site, (2) the upstream riparian buffer, i.e. the corridor 30 m to either side of the stream 5000 m upstream of the sampling site, (3) the local scale, i.e. a circle around the sampling site with 500 m diameter, and (4) the local riparian buffer i.e. the corridor 30 m to either side of the stream 500 m upstream of the sampling site (Fig. 3).

For each sampling site, the upstream catchment was delineated using a digital elevation model (DEM, 10 m resolution) and visually checked. The local scale was a circular buffer with 500 m diameter around the sampling sites encompassing some areas downstream the sampling site and aiming to account for more general effects of local landuse that affect macroinvertebrate metrics also on the community level. The upstream river network including tributaries was delineated on official river networks which had been manually corrected up to 5000 m and 500 m, respectively, in ESRI ArcView (Version 3.3). These river segments were buffered 30 m to either side to get the upstream (5000 m) and local (500 m) riparian buffers. In order to exclude the streams' own water surface the river segments for both upstream distances were buffered latterly with 30 m from the stream edge. The streams' water surface was either given in the official ATKIS landuse dataset or, for small streams not represented as water surface areas in this dataset, the water surface was approximated by buffering the river network lines using a mean stream width measured on orthophotos (n = 30 measurements for each Strahler order). Subsequently, the percentage cover of the different landuse types described in Section 2.3 was quantified at these four spatial scales. River habitat survey results described in Section 2.5 were aggregated in both the upstream and local riparian buffer. Nutrient loads and toxic indices were calculated given the catchment geometry and sampling site location.

Where not specified otherwise, GIS work was carried out in ESRI's ArcMap (ArcGIS Desktop 10.8) software.

2.3. Landuse data

Official ATKIS landuse data were available for the entire study region. The landuse classes were grouped into seven categories, (1) “arable land”, (2) “grassland”, (3) “natural vegetation”, (4) “urban green space”, (5) “urban”, (6) “water surface”, and (7) “woodland”, with some very specific and rare landuse classes excluded (e.g. quarries or harbours). The category “urban” includes all built-up areas and infrastructure.

For landuse in the riparian buffers and locally around the sampling site, these data were complemented by woody vegetation identified on orthophotos obtained from the German Federal Agency for Cartography and Geodesy covering the entire width of the 60 m-wide corridor. Only orthophotos taken during the extended vegetation period from April to August were used and the closest once to the year of 2010 selected to match with the macroinvertebrate samples. Orthophotos were mostly colour-infrared (CIR) and partly RGB, which were processed separately. Spatial resolution of the orthophotos was 0.20 m for CIR and the great majority of RGB photos with some older photos having a resolution of 0.40 m. Orthophotos were segmented and resulting objects classified in an object-based image analysis (OBIA) consisting of image segmentation and object classification.

Multiresolution segmentation of the orthophotos into objects of homogenous pixel patches was done in Trimble's eCognition software (Version 9.3.0) based on the pixel values of the colour bands of the RGB and CIR images, respectively (i.e. red, green, blue, and near-infrared). These objects were then classified, distinguishing woody vegetation, other forms of vegetation (grassland, cropland), and non-vegetated areas (built-up areas or bare soil) based on the following characteristics: geometric shape (rectangular fit, compactness) plus means, standard deviations and standard deviations of the means of sub-objects for the respective colour bands, brightness, as well as the Visible-band Difference Vegetation Index (VDVI, RGB images) or Normalized Difference Vegetation Index (NDVI, CIR images). To develop a classifier for these objects, a training dataset was compiled using an individual supervised nearest neighbour classification (NNC) on 40 representative orthophotos (n = 14 RGB, n = 26 CIR) in eCognition. On each of the orthophotos, a small set of representative objects was manually selected for each class. The remaining objects are assigned in the NNC to the class of the representative object that is nearest in the multidimensional space of the variables listed above. The results of the supervised NNC was visually checked, and manually corrected if necessary. This training dataset was used to set up a Support Vector Machine classifier (SVM) that divides the multidimensional space into sectors of most homogenous classifications. This SVM classifier was then applied to the remaining orthophotos using .the R package e1071 (version 1.7-3). General accuracy of segmentation and classification was assessed visually. In addition, accuracy of the SVM classifier was assessed using cross-validation. Woody vegetation objects identified in the OBIA overwrote landuse in the official landuse data from the categories, ‘arable land’, ‘grassland’, ‘natural vegetation’, ‘urban green space’, and ‘urban’. Hence, we included the typically small patches of woody vegetation that occur along streams and that are not large enough to be covered in official landuse datasets. Improving the spatial resolution of landuse data in close proximity to the river was a prerequisite to correctly quantify the percentage cover of woody vegetation at the local, upstream riparian, and local riparian scale.

Landuse cover was used as a proxy for processes taking place at all the respective scales (Section 2.2). While the OBIA was able to distinguish woody from non-woody vegetation in the riparian scales, it could not account for different types of woody riparian vegetation nor was information on e.g. vegetation height available (i.e. LiDAR data). Therefore, it was not possible to remotely assess qualitative aspects like species composition, vertical and lateral structure as well as connectivity. Field data was not available and hardly can be mapped at lager scales. Therefore, this large-scale study was restricted to quantitative landuse cover.

The subsequent analysis was limited to agricultural, grassland, urban, and woodland landuse cover to express landuse gradients and their effect on riverine macroinvertebrates. Agricultural areas are cultivated, fertilized, and subject to pesticide application rendering them potential sources of fine sediments, nutrients, and toxic substances, respectively. Grassland, while managed and fertilized, is deemed less harmful and therefore river management plans favour grassland over agricultural areas in the riparian corridor. Urbanization has localized adverse effects on stream biota from the catchment (e.g. sewage) down to the local riparian scale (e.g. light pollution). In temperate regions, the potential natural vegetation generally is woodland and therefore this landuse is the most natural form of land cover as opposed to agriculture and urbanization.

2.4. Nutrients and toxic substances

Increased nutrient inputs to streams favour macrophytes growth causing a chain of effects towards reduced oxygen supply and water quality that negatively affects macroinvertebrate communities. Nutrient pollution at the sampling sites was assessed using the annual loads of nitrogen and phosphorous modelled for the upstream catchments of the sampling sites. These data were derived from Venohr et al. (2014). Modelling was done using MONERIS, a semi-empirical conceptual model to assess nutrient emissions for entire catchments and to analyse their retention and transport in the river system (Venohr et al., 2011). MONERIS accounts for natural background emissions, diffuse nutrient input such as atmospheric deposition, surface runoff, erosion, and groundwater inflow, as well as point sources like wastewater treatment plants and industrial discharges.

Toxic substances also deteriorate water quality and therefore a variant of mixture toxic pressure metrics, the multi-substance potentially affected fraction of species (msPAF; De Zwart and Posthuma, 2005) was included in the analysis. Specifically the msPAF-EC50 calculated by Lemm et al. (2021) using mixture toxic pressure data from Lindström et al. (2010) was already available and has been proven to be indicative of biological integrity (Lemm et al., 2021). They had calculated the msPAF-EC50 for river sub-catchment units not being congruent with the sampling sites' catchments. Therefore, the sampling sites were assigned to the sub-catchment they are located in and the respective msPAF-EC50 value used.

Modelled data on nutrient loads and the msPAF-EC50 were used because measured data were not available. The models were based on catchment landuse without explicitly considering nutrient and pesticide retention in riparian buffer strips (but see recent developments of MONERIS in Gericke et al., 2020). Therefore, the causal relationship between riparian landuse and water quality was not fully captured in this dataset and this has to be considered when interpreting results.

2.5. Hydromorphology

River hydromorphology was assessed using data mapped by regional authorities. The mapping and assessment method essentially corresponded to the one described in Gellert et al. (2014). Twenty-five parameters are recorded for 100 m river segments, compared to natural reference conditions, and assessed on a seven-point ordinal scale ranging from unchanged (only minor deviations from the reference conditions, class 1) to heavily degraded (class 7). The assessment scores of the 25 parameters are aggregated to assess the 6 main parameters (1) ‘channel pattern’, (2) ‘longitudinal profile’, (3) ‘channel bed features’, (4) ‘cross section’, (5) ‘channel bank features’, and (6) ‘floodplain conditions’. Main parameters 1–5 describe instream habitat quality for macroinvertebrates. For each sampling site, the mean assessment scores were calculated based on all stream sections in the upstream or local riparian buffer, respectively.

2.6. Structural equation models

A structural equation model (SEM) was developed for each of the nine macroinvertebrate metrics (Section 2.1), separately for mountain and lowland streams, to model the relationship between macroinvertebrate metrics as indicators for functions of woody riparian vegetation and stressors at different spatial scales. SEMs allow linking a set of predictors to a response variable through multiple paths. Furthermore, predictors can be directly linked to the response and/or indirectly by pathways via other predictor variables. Thus, the SEM allows introducing and distinguishing between direct effects of landuse cover at the different scales, and their indirect cascading effects through landuse and environmental variables at smaller spatial scales (Fig. 4). For example, catchment landuse as a large-scale stressor directly predicts macroinvertebrates at the sampling sites, as well as the upstream riparian landuse, which in turn predicts macroinvertebrates too. Each introduced causal link in the model structure is quantified using a univariate regression model to assess if it is supported by empirical data. Direct and indirect pathways can be combined to calculate the variables' total effect on the model's response by simple addition and multiplication of standardized path coefficients in the individual regression models.

SEMs also allow including variables that cannot be directly measured like landuse pressure, habitat or water quality at the different spatial scales. These composite variables are constructed through weighted additions of several measured manifest variables. Weights were derived from multiple linear regression models of the manifest predictor variables and the respective macroinvertebrate metric as response variable. The use of composite variables based on multiple linear regression models allowed reducing the number of variables in the conceptual model while maximising their predictive power. For each of the four spatial scales (Section 2.3), a statistical composite landuse variable was constructed using shares of agricultural, grassland, woodland and urban landuse cover as manifest variables. Similarly, a statistical composite variable for water quality was constructed using phosphorous and nitrogen loads as well as the msPAF-EC50 (Section 2.4) as manifest variables. Finally, a statistical composite variable for hydromorphological habitat quality was constructed using the assessments of ‘channel pattern’, ‘longitudinal profile’, ‘channel bed features’, ‘cross section’, and ‘channel bank features’ (Section 2.5) as manifest variables. To ease interpretation of the results, the resulting composite variables express expected beneficial conditions for the aquatic community. Therefore, if necessary, landuse cover composite variables were inverted so that they correlate positively to woodland whereas water quality was ensured to correlate negatively with phosphorous loads and hydromorphology scales to correlate negatively with ‘channel bed features’ as higher scores indicate degradation.

For the technical implementation, a piecewise SEM approach to local estimation was selected (Shipley, 2009) which allowed accounting for the spatial structure of the dataset, i.e. random effects, since all causal pathways were linear mixed-effects models (Lefcheck, 2016). This would not have been possible in a standard, globally estimated SEM. Random effects considered were latitude, longitude, and a grouping based on river typology, elevation above sea level, and location in the major catchments. All significant ($p < 0.05$) pathways were considered to calculate direct, indirect and total effects. Path coefficients were standardized to allow comparing the effects of different predictor variables and expressed as direct, indirect, or total path coefficients. The larger the respective effect, the larger the influence on the macroinvertebrate metric. Models for the different biological responses were compared using the Fisher's C statistic as a measure of overall model fit as well as the share of explained variance using conditional pseudo-R^2, which is the total share of variance explained including the share of variance explained by random effects, and marginal pseudo-R^2, which only covers the variance explained by the predictors. In addition to the proposed causal links between the variables in the SEM, two correlated errors, i.e. non-causal but statistically relevant links, were included in the SEM between upstream riparian landuse and local landuse and also between upstream hydromorphology and local riparian landuse. Including these correlated error terms relieves the assumed causal structure from having to account for the covariance between two variables lacking an assumed directed relationship. The only remaining independence claim in the model is therefore between upstream hydromorphology and local landuse.

All calculations were carried out in R, more specifically with the piecewiseSEM package (version 2.1.2) for SEM calculation, the nlme package (version 3.1-151) for linear mixed-effects model and the MuMIn package (version 1.43.17) for calculation of shares of explained variances using pseudo-R^2 for generalized mixed-effect models according to Nakagawa et al. (2017).

3. Results

3.1. Overall model fit

The results showed that the structural equation models (SEMs) reflected the main causal relationships between landuse and other stressors to predict the macroinvertebrate metrics from a statistical point of view. All modelled SEM fits were satisfactory as all Fisher's C-statistics were non-significant, i.e. the hypothesized structure was supported by the data and no extra pathways were falsely omitted (Table 1). The correlated error between upstream riparian landuse cover and local landuse cover was significant in all models, while the one between upstream hydromorphology and local riparian landuse cover was only significant in seven~~7~~ of the 14 models. The unaccounted

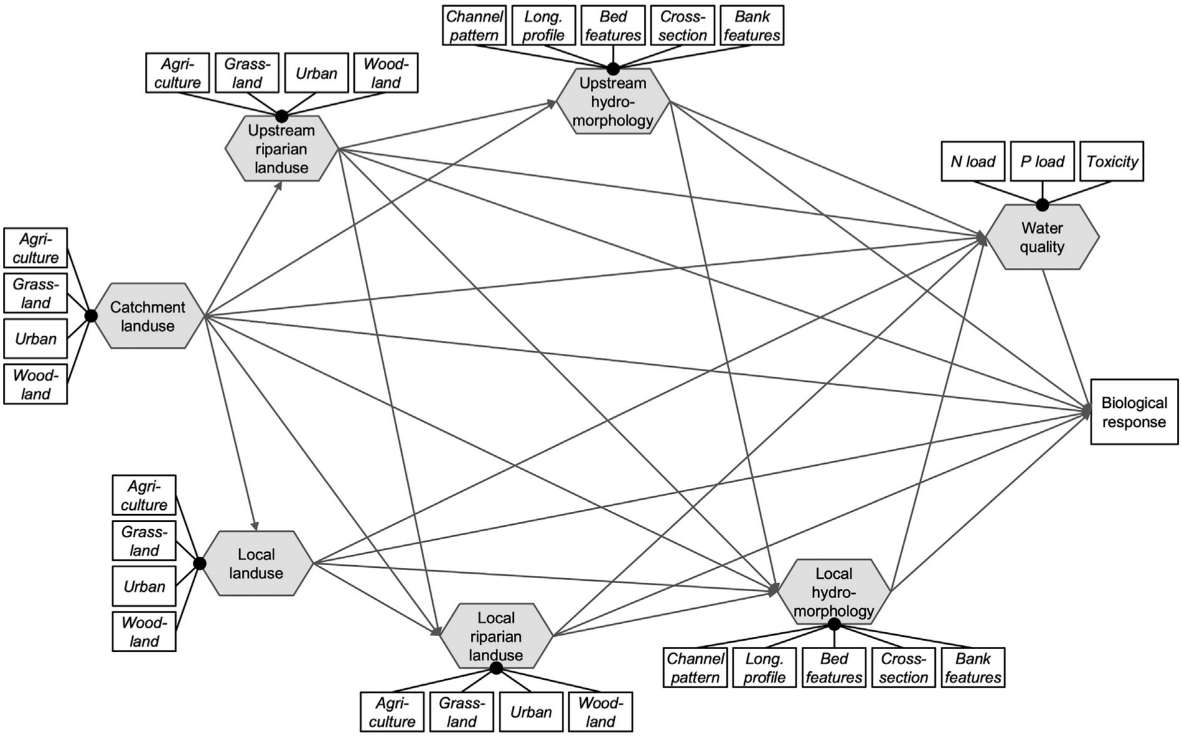

Fig. 4. Structure of the structural equation model applied to nine macroinvertebrate metrics as biological response in both mountain and lowland streams. Landuse categories, hydromorphological and water quality parameters were measured or modelled and are shown in rectangles. “Urban” landuse is comprised of all built-up areas, “Toxicity” is the mixture toxic pressure metric. Measured or modelled variables inform composite variables shown in dark hexagons. Correlated errors between “Riparian landuse upstream” and “Landuse local” as well as “Hydromorphology upstream” and “Riparian landuse local” were fit in the model but are not depicted for clarity of the hypothesized effect pathways.

for independence claim between upstream hydromorphology and local landuse cover was never significant which was therefore justifiably not incorporated into the model as another correlated error.

3.2. Woody riparian functions dependent on large-scale stressors

Macroinvertebrate metrics related to large-scale stressor dependent functions (saprobic index, multimetric index, psammal, pelal and argyllal preferences) were expected to be directly affected by large-scale landuse cover, and indirectly by pathways through riparian landuse cover. Full depictions of the SEMs' paths can be found in the supplementary material (Figs. S.1–S.5).

For the multimetric index (MMI) there were direct effects both in mountain (marginal pseudo-$R^2 = 0.505$) and lowland streams (marginal pseudo-$R^2 = 0.305$) by catchment landuse cover along with water quality (Table 2). In mountain streams, upstream riparian landuse cover, upstream and local hydromorphology additionally had direct effects. Both riparian landuse scales were part of indirect cascading pathways between catchment landuse and the MMI (Fig. S.1). In lowland streams the local riparian landuse cover additionally had a

Table 1
SEM fits for all metrics in either river type: Fisher's C-statistic from SEM fit local estimation is reported along with *p*-Value and degrees of freedom. Shares of explained variances in the biological responses are pseudo-R^2s; given the random effects structure in the SEM both marginal and conditional are listed.

Metric	Type	R^2 biological response		Fisher's C statistic	Degrees of freedom	*p*-Value
		Marginal	Conditional			
Multimetric index	Lowland	0.295	0.305	0.900	2	0.638
	Mountain	0.457	0.505	2.248	2	0.325
Saprobic index	Lowland	0.386	0.420	1.294	2	0.524
	Mountain	0.429	0.462	2.583	2	0.275
Pelal pref. (%)	Lowland	0.174	0.174	3.477	2	0.176
	Mountain	0.143	0.186	4.371	2	0.112
Argyllal pref. (%)	Lowland	0.035	0.046	2.505	2	0.286
	Mountain	0.041	0.041	3.477	2	0.176
Psammal pref. (%)	Lowland	0.074	0.074	0.722	2	0.697
	Mountain	0.048	0.149	1.247	2	0.536
KLIWA-Index$_{MZB}$	Lowland	0.258	0.300	1.247	2	0.536
	Mountain	0.322	0.349	0.900	2	0.638
Grazers (%)	Lowland	0.050	0.063	2.583	2	0.275
	Mountain	0.165	0.180	0.840	2	0.657
Shredders (%)	Lowland	0.210	0.220	0.840	2	0.657
	Mountain	0.086	0.141	2.505	2	0.286
POM pref. (%)	Lowland	0.040	0.040	4.371	2	0.112
	Mountain	0.059	0.069	0.722	2	0.697

direct effect on the MMI. This relationship was also part of an indirect cascading effect from catchment landuse, through the local landuse cover and the local riparian landuse on the MMI. The total effect of catchment landuse was stronger compared to the total effect of upstream riparian landuse in both mountain (≈2.7-fold) and lowland streams (≈6.6-fold) (Table 2). It was also stronger than the total effect of local riparian landuse in both mountain (≈38.6-fold) and lowland streams (≈2.3-fold).

Similarly, for the saprobic index there indeed were direct effects from catchment landuse both in mountain (marginal pseudo-$R^2 = 0.462$) and lowland streams (marginal pseudo-$R^2 = 0.420$). There were also indirect cascading effects on the saprobic index from catchment landuse, through the upstream riparian landuse and upstream hydromorphology in both stream types (Fig. S.2). Additionally, there was another indirect cascading effect from catchment landuse, through the upstream riparian landuse, upstream hydromorphology and water quality in mountain streams. However, there was no direct effect from either riparian landuse scale on the saprobic index. The total effect of catchment landuse was stronger compared to the total effect of upstream riparian landuse in both mountain (≈8.3-fold) and lowland streams (≈5.7-fold) (Table 2).

Macroinvertebrate metrics related to fine sediment habitat preferences were less unambiguous and poorly explained by the SEM (Table 1). Only conditional shares of explained variance for psammal habitat preference in mountain streams were meaningful while marginal and conditional shares of explained variance for pelal habitat preference were meaningful in both stream types. Argyllal habitat preferences were poorly explained in both stream types.

For pelal habitat preference in mountain streams there was a direct effect from catchment landuse along with multiple indirect cascading effects through both riparian scales as expected (marginal pseudo-$R^2 = 0.143$; Fig. S.3). Here local riparian landuse was the only other direct effect besides catchment landuse and upstream hydromorphology. The total effect of catchment landuse was stronger than that of both upstream riparian landuse (≈2.8-fold) and local riparian landuse (≈2.0-fold) (Table 2). Contrary to expectation, there was no direct effect from catchment landuse on pelal habitat preference in the SEM for lowland streams (marginal pseudo-$R^2 = 0.174$; Fig. S.3). However, there exist two indirect cascading effects from catchment landuse through upstream riparian landuse and water quality, both of which have direct effects. The total effect of upstream riparian landuse was slightly stronger than the total effect of catchment landuse (≈1.3-fold) (Table 2).

For psammal habitat preference in mountain streams there was a direct effect from catchment landuse without any other direct or indirect cascading pathways identified (marginal pseudo-$R^2 = 0.048$, conditional pseudo-$R^2 = 0.149$; Fig. S.4). Contrary to expectations, there were no direct and thus total effects at all for psammal habitat preference in lowland streams as explained variance was very low (marginal pseudo-$R^2 = 0.074$).

3.3. Woody riparian functions independent on large-scale stressors

Metrics related to water temperature (KLIWA-Index$_{MZB}$), feeding types (shares of grazers and shredders) and share of taxa preferring particulate organic matter as substrate (POM) were expected to directly respond to riparian landuse cover but not directly to large-scale landuse cover in both mountain and lowland streams. Full depictions of the SEMs' paths can be found in the supplementary material (Figs. S.6–S.9).

In lowland streams, this expectation was not met as no direct nor indirect effects from neither riparian landuse scale were identified for the KLIWA-Index$_{MZB}$, share of shredding and grazing feeding types, POM habitat preference. Both the KLIWA-Index$_{MZB}$ (marginal pseudo-$R^2 = 0.300$) and share of shredders (marginal pseudo-$R^2 = 0.220$) were explained reasonably well, but the sole effect was from water quality and the associated cascading indirect effect from catchment landuse

Table 2
Direct standardized path coefficients for all landuse or stressor gradients are listed along with their statistical significance levels (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$) whereas total effects, i.e. the sums of direct and all indirect pathways are only listed if some significant effect was identified between the landuse or stressor gradient and the biological response metric.

Metric	Type	Landuse catchment		Landuse local		Riparian landuse upstream		Riparian landuse local		Hydromorphology upstream		Hydromorphology local		Physico-chemical conditions	
		Direct	Total	Direct	Total	Direct	Total	Direct	Total	Direct	Total	Direct	Total	Direct	Total
Multimetric index	Lowland	0.217 *	0.345	0.036	0.051	0.057	0.052	0.147 *	0.147	0.120		0.013		0.202 *	0.202
	Mountain	0.294 ***	0.541	0.110 **	0.129	0.122 **	0.197	0.013	0.014	0.103 **	0.162	−0.074 *	−0.074	0.172 ***	0.172
Saprobic index	Lowland	−0.311 ***	−0.385	−0.068		−0.119	−0.067	−0.023		0.179 *	0.179	−0.026		0.149	
	Mountain	−0.330 ***	−0.491	−0.106 **	−0.106	−0.084	−0.059	−0.022		0.123 **	0.136	0.020		0.155 ***	0.155
Pelal pref. (%)	Lowland	0.039	−0.165	−0.069		−0.208 **	−0.220	−0.024		0.100		−0.088		0.222 *	0.222
	Mountain	−0.167 **	−0.235	−0.077	−0.060	−0.002	−0.083	−0.116 **	−0.116	0.113 *	0.113	0.030		0.050	
Argyllal pref. (%)	Lowland	−0.071		−0.041		−0.098		0.016		−0.140		0.139		0.051	
	Mountain	−0.002	0.027	0.011	−0.057	−0.053	−0.049	−0.144 **	−0.144	−0.032	0.014	0.015		0.085 *	0.085
Psammal pref. (%)	Lowland	−0.077		0.075		−0.019		0.118		0.052		−0.028		0.100	
	Mountain	−0.136 **	−0.136	−0.046		−0.009		0.032		0.058		−0.095		0.058	
KLIWA-Index$_{MZB}$	Lowland	−0.153	−0.092	−0.034		−0.086		−0.081		0.115		0.038		0.222 *	0.222
	Mountain	−0.273 ***	−0.390	−0.067		−0.075	−0.058	−0.031		0.117 **	0.130	0.004		0.167 ***	0.167
Grazers (%)	Lowland	−0.059		−0.097		0.081		−0.050		−0.036		0.070		0.021	
	Mountain	0.273 ***	0.348	0.078	0.047	−0.061	0.050	0.091 *	0.091	0.096 *	0.096	0.048		0.124 **	0.124
Shredders (%)	Lowland	0.117	0.081	0.107		0.125		−0.012		0.085		0.072		0.230 **	0.230
	Mountain	−0.105 *	−0.179	−0.122 *	−0.135	−0.007	0.037	0.000	0.023	−0.078	0.104	−0.109 *	−0.109	0.174 ***	0.174
POM pref. (%)	Lowland	0.060	−0.017	0.137 *	0.137	0.057		0.061		−0.038		−0.030		0.109	
	Mountain	−0.088	−0.058	−0.040		0.037	−0.051	−0.081		0.167 **	0.096	−0.125 **	−0.125	0.093 *	0.093

cover through water quality (Table 2). The share of grazers and POM habitat preference were not explained meaningfully (Table 1).

In mountain streams, for the KLIWA-Index$_{MZB}$ there was only an indirect effect from upstream riparian landuse cover through upstream hydromorphology but no direct effects from the riparian landuse scales as expected (marginal pseudo-$R^2 = 0.349$). However, there was a direct effect and multiple indirect cascading effects from catchment landuse on the KLIWA-Index$_{MZB}$ (Fig. S.6). The total effect of catchment landuse was stronger than that of the upstream riparian landuse (≈6.7-fold).

Contrary to our expectations, for the share of shredders in mountain streams there were no direct effects from neither riparian landuse scale but there were both direct and indirect effects from catchment landuse. There was, however, an indirect cascading effect from the upstream riparian landuse through upstream hydromorphology and water quality (Fig. S.8). Another indirect effect on the share of shredders was observed from the local riparian landuse cover through local hydromorphology, yet model explanatory power was weak (marginal pseudo-$R^2 = 0.141$). The total effect of catchment landuse was stronger than the total effect of both upstream riparian landuse (≈4.8-fold) and local riparian landuse (≈7.8-fold).

As expected, the share of grazers in mountain streams was affected directly by the local riparian landuse but unexpectedly also by catchment landuse in mountain streams (marginal pseudo-$R^2 = 0.189$). Additionally, there were two separate indirect pathways: from upstream riparian landuse through upstream hydromorphology and water quality (Fig. S.7). The total effect of catchment landuse was stronger than the total effect of both upstream riparian landuse (≈7.0-fold) and local riparian landuse (≈3.8-fold).

POM habitat preference was not explained meaningfully in mountain streams (Table 1).

4. Discussion

The vast majority of studies targeting the effects of local riparian landuse in general and of woody riparian buffers in particular addressed small spatial scales. They frequently relied on the comparison of paired sites (e.g. Davies-Colley and Quinn, 1998; Moraes et al., 2014) or even followed near-experimental BA/CI designs when surveying restoration activities (e.g. Kiffney et al., 2003; Parkyn et al., 2003; Clews and Ormerod, 2010; Lecerf and Richardson, 2010). There is almost consensus in the respective literature on the multiple beneficial effects of woody buffers over other landuse forms (e.g. Broadmeadow and Nisbet, 2004; Sweeney and Newbold, 2014). In particular nutrient and fine sediment retention, water temperature regulation, and the provision of organic material like CPOM and large wood are functions that clearly have the potential to benefit macroinvertebrate assemblages. At the same time, there is overwhelming evidence that macroinvertebrates are strongly affected by catchment-scale stressors (Lorenz and Feld, 2013; Leps et al., 2015). The approach by Feld et al. (2018) was, therefore, to separate catchment and riparian scale effects on macroinvertebrate assemblages, with each of the scales expected to influence different species and metrics. While the individual components of the conceptual model suggested by Feld et al. (2018) are supported by multiple literature references, the overall model has not yet been rigorously tested with a large data set. The results of our study support certain parts of the model suggested by Feld et al. (2018), in particular the overarching role of catchment-scale landuse on metrics such as the saprobic index and the MMI, while other parts were not supported, in particular the hypothesized strong role of riparian landuse cover on metrics indicating water temperature and feeding types. Overall, our results support to the conjecture that macroinvertebrate assemblages are more strongly determined by catchment landuse, while the effects of riparian vegetation, although measurable for some combinations of stream types and metrics, is limited.

Individually, the results for the multimetric (MMI) and saprobic indices both well reflect the expected dependence on catchment landuse cover. The MMI was designed to evaluate biotic integrity, i.e. to integrate the effects of various stressors, and is composed of several metrics that mainly reflect the impacts of catchment landuses (Hering et al., 2004; Böhmer et al., 2004). While the MMI was developed with a limited data source of heterogeneous quality, our results, which are based on a large and homogeneous dataset, clearly support its applicability and its relation to catchment landuse. The relative strength of influence decreases from larger to smaller scale landuse. This demonstrates that large-scale stressors surmount smaller scale stressors by pre-setting environmental conditions in entire river networks. This aligns with previous studies (Leps et al., 2016; Berger et al., 2017; Brettschneider et al., 2019).

The saprobic index and the MMI are correlated ($R^2 = 0.79$ in mountain, $R^2 = 0.61$ in lowland streams), as they have been calculated with the same site-specific taxa lists and the taxas' indicator values for catchment landuse (MMI) and organic pollution (saprobic index) are often quite similar (Fig. 2). Nonetheless, insight can be garnered from the comparison of the respective SEMs: Whereas explained shares of variance are greater for the MMI than the saprobic index in mountain streams, the opposite is true for lowland streams. The difference in explained shares of variances between stream types is also more pronounced for the MMI and more scales contribute significantly to the model in either type. This underlines that the saprobic index, designed to capture organic pollution, is in fact mainly influenced by water quality, which is determined by catchment-scale landuse in our data set, as sites strongly affected by point-source pollution have been excluded. In contrast, the MMI, while mainly impacted by catchment-scale stressors as well, does also capture effects of local landuse and riparian cover.

In contrast to our expectations, sediment related metrics were not found to consistently depend on catchment landuse. Specifically, shares of explained variance where negligible for habitat preference for argyllal (loam) in both types and for psammal (sand) in lowland streams. Also the marginal share of explained variance for psammal habitat preference in mountain streams was negligible, while its conditional counterpart was much higher. This means that psammal habitat preference is more spatially clustered in mountain streams compared to lowland streams, where sandy sediments are more evenly distributed as they in fact can be ubiquitous. Psammal is in fact the dominant substrate type in lowland streams, also under near-natural conditions, while sand accumulations in mountain streams are often related to sediment inputs from adjacent lands, i.e. to the lack of buffer strips.

The only habitat preference that the SEMs captured well in both stream types was for pelal sediment, i.e. mud of organic origin. This may partly be indicative for sediment retention, but could also be due to its relation to diffuse pollution and to local hydromorphological modifications. Yet, the strongest observed effect of the upstream riparian landuse cover in lowland streams is on pelal habitat preference and that effect is more than twice of the effect on the SI. Therefore, the results suggest that riparian landuse along the river network has a more immediate effect on reducing mud accumulation in the river bed than it has on the SI, which is also driven by point sources not subject to riparian retention. Furthermore, mud can be covered by leaves in streams accompanied by woody buffers. As a result, the effect upstream riparian landuse has on pelal habitat preference is larger than that of catchment landuse, suggesting that the SEMs disentangled the functions associated with these two metrics successfully.

Contrasting to our expectations, the metrics supposed to reflect local riparian conditions (KLIWA-Index$_{MZB}$, share of taxa with habitat preference for POM, shares of shredders and grazers) were also mainly impacted by the catchment scale and less consistently and to a minor degree by the local scale. While the relationship between water temperature and shading from upstream riparian vegetation (Caissie, 2006; Bowler et al., 2012; Kail et al., 2021.) and the influence of water temperature on macroinvertebrates (Haidekker and Hering, 2008) are well documented, the results in this study did not detect direct effects of upstream or local riparian landuse cover on the KLIWA-Index$_{MZB}$, which reflects temperature preferences of the macroinvertebrates taxa. Strong effects on this index came from water quality, suggesting a possible stronger link of that metric to oxygen availability, which is affected by both water temperature and enrichment of nutrients and organic substances.

Preference for particulate organic matter (POM) is merely a proxy for inputs of leaves and twigs from riparian woody vegetation. It was not successfully captured by the analysis. Most likely this was due to the small gradient across the dataset (Fig. 1), suggesting that there are no streams with medium to high degrees of POM preferring species no matter the riparian configuration. The data exclusively originate from streams with a catchment area larger than 10 km^2. Hence, small streams where POM can strongly accumulate due to strong input of leaves and low discharge have not been included. This may contribute to the small gradient. Additionally in lowland streams, local landuse cover, which extends beyond riparian corridor considered in this study, had the strongest effect on POM habitat preference. This suggests that the lateral extent of the riparian landuse scales in this study is too small to capture all inputs of leaves and twigs from adjacent areas (Oelbermann and Gordon, 2000; Thomas et al., 2016).

Grazers respond to local riparian landuse directly, but other than expected. As indicated by the positive path coefficient and the orientation of the composite variables, an increase in woody riparian cover leads to an increase in grazer abundance. At first glance this seems counterintuitive as one would expect less grazers in shaded streams due to suppressed periphyton growth. However, the observed pattern may relate to the overall modification of substrate composition in streams lacking woody buffers. Grazers require coarse substrates (e.g. stones, gravel), on which periphyton can grow. Increased input of fine sediments tends to cover stones and gravel, while suspended sediment decreases light attenuation; both pathways can reduce periphyton abundance and thus the food source for grazers.

While model performance for grazers in lowland streams was marginal, shredders in either type show no direct effect of riparian landuse but are most strongly determined by water quality, large scale and, in mountain streams, local landuse. Again, this is contrasting to our expectations that the provision of leaves by the riparian vegetation support shredder abundance. However, already the share of POM preferring species showed a limited gradient in the dataset. Based on our results, we conclude that shredder abundance is less impacted by POM availability, but more by the conditions for POM processing. Under low oxygen concentrations, many of the shredding species cannot survive, in particular in leaf packs, where contact to the turbulent surface water is limited. Also here, diffuse pollution at the catchment scale seems to overrule the effects of the local riparian conditions. In mountain streams, local landuse cover had an effect similar in strength to these stressors potentially affecting POM processing. This suggests again, that areas beyond the considered lateral extent of the riparian landuse scales are of relevance for leaf inputs. This is in line with previous studies which concluded that even extensive woody riparian buffers do not reach same nature-like levels of leaf inputs as woodlands do (Oelbermann and Gordon, 2000; Thomas et al., 2016; Stutter et al., 2020). Therefore the concept of riparian vegetation may be too narrow despite considering a buffer width that would be generous for management purposes.

Overall, the effects of riparian landuse, i.e. of woody riparian buffers, on macroinvertebrate assemblages were limited. They were measurable with direct effect in case of the MMI, the saprobic index, pelal habitat preference and grazers in at least one stream type. Indirect effects were in fact measured for all metrics in at least one out of the two stream types except for psammal habitat preference. In all of these cases, however, the effects of catchment landuse overruled the effects of local riparian buffers. This is in line with the results obtained by Le Gall et al. (2021), who observed similar patterns for streams in France or Burdon et al. (2020). The question remains, however, why the effects of woody riparian buffers in these large-scale datasets are so much smaller in comparison to the multitude of local-scale studies. Local field studies usually rely on comparative experimental designs between different reaches of the same catchments, with a pronounced gradient of characteristics of riparian buffer, such as extent, composition or structure. This tends to maintain large-scale stressors constant and thus effects of woody riparian vegetation area become more apparent not being masked by other stressors due to common catchment characteristics. In our study, we consider both a gradient in catchment and riparian landuse and address their relationship in jointly affecting the macroinvertebrate community. Objectives are therefore different. While we proved that woody riparian buffers have some effect even across diverse landscapes, this is superimposed by constraining large scale conditions. Since environmental conditions in river networks are so strongly determined by catchment landuse aquatic restoration cannot hope to achieve restoration goals by effects from managing riparian landuse alone.

We relied on riparian landuse cover as a proxy for management, dynamics, composition and structure of riparian vegetation. Similarly, considering landuse cover at the catchment scale as a proxy for large-scale stressors conditions has greatly contributed to explaining the macroinvertebrate community (Feld and Hering, 2007; Marzin et al., 2013; Kuemmerlen et al., 2014), as it integrates many processes relevant for invertebrates. In contrast to catchment landuse, however, riparian landuse does not necessarily reflect all processes relevant for macroinvertebrates at this scale; especially, the lack of data on dynamics and spatial configuration (e.g. gaps, width) of woody riparian vegetation may limit the explanatory power for benthic invertebrate community composition. Remote sensing of riparian vegetation is a continuously developing field of research and additional and important qualitative information provided by a more sophisticated remote sensing analysis could give a better insight in the functioning and effect of woody riparian vegetation. However, some challenges persist (Congalton et al., 2002; Goetz, 2006; Huylenbroeck et al., 2020). Landscape metrics, e.g. from FAGSTATS (McGarigal and Marks, 1995), could be used to more accurately depict the relevance of riparian landuse for the aquatic community (but see Kupfer (2012) for limitations). These would still enable the use of larger datasets through remote sensing rather than being limited to smaller data sets acquired in field studies. Large datasets better reflect landuse variability to allow for more general management recommendations. With respect to these recommendations it also must be noted that in Feld et al. (2018) literature was sourced globally whereas the data here stems from a distinct geographical region in Central Europe only.

Another promising approach for better disentangling the effects of riparian landuse, and in particular of woody riparian vegetation, on aquatic biota is to focus on more homogeneous groups of streams (e.g. Corneil et al., 2018). While effects of woody riparian vegetation might be masked by large-scale landuse, they might be most obvious for streams with homogeneous catchment landuse. Identifying the conditions under which riparian cover has the strongest effects would also be of great management relevance.

5. Conclusion

The development of woody riparian buffers is not the one-size-fits-all solution in river restoration. While the findings of this study do not negate the generally accepted functions of woody riparian vegetation, they suggest that benefits of riparian vegetation are context dependent. In the majority of catchments, where intense landuse and its legacy determines environmental conditions and macroinvertebrates assemblages of entire river networks, the benefits of riparian landuse cover can be limited. If a stream is affected by diffuse pollution and fine sediment inputs, local riparian landuse cover and even that of 5000 m upstream can only partly affect the situation: instream habitats created by woody riparian vegetation might be covered by transported fine sediments; sensitive species, which may find habitats in streams accompanied by riparian buffers, are restricted by oxygen depletion or toxic substances. Thus pressures form catchment landuse can clearly persist despite locally favourable riparian conditions even though at the same time, the overall conditions in the river network are improved by riparian buffers. This is also underlined by this study which, despite riparian cover being utilised as a proxy for more complex relationships, nonetheless finds a limited effect from riparian vegetation on the macroinvertebrate community. In conclusion, riparian buffers remain a cornerstone of catchment-scale restoration approaches, but need to be accompanied by measures addressing landuse practices to unfold their full benefits.

CRediT authorship contribution statement

Martin Palt: Conceptualization, Methodology, Formal analysis, Investigation, Writing, Writing - Review & Editing, Visualization **Mickaël Le Gall:** Conceptualization, Methodology, Writing - Review & Editing **Jérémy Piffady:** Conceptualization, Methodology, Writing - Review & Editing, Funding acquisition **Daniel Hering:** Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition **Jochem Kail:** Conceptualization, Methodology, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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Effects of woody riparian vegetation on macroinvertebrates are context-specific and large in urban and especially agricultural landscapes

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Running headline: Large woody buffer effects in agricultural landscapes

Abstract

(1) Woody riparian vegetation (WRV) benefits benthic macroinvertebrates. However, in recent large scale studies, the effects of WRV on macroinvertebrates were small compared to catchment landuse, raising the question about the relevance of WRV in restoration. Limited effects of WRV might be due to context specificity: While some functions are provided by WRV irrespective of catchment landuse, others depend on the landscape setting.

(2) Recursive partitioning modelling was used to identify context dependent effects of WRV on streams macroinvertebrates' ecological status in small lowland (n = 361) and mountain streams (n = 748). WRV cover was quantified from orthophotos along the near (500 m) and far (5,000 m) upstream river network and used to predict the site's ecological status. Agricultural, urban and woodland cover at the local and catchment scales along with hydromorphology were considered as partitioning variables.

(3) In rural agricultural landscapes, the effect of WRV on the ecological status was large, indicating that establishing WRV can improve the ecological status by as much as two classes.

(4) In streams impacted by catchment urbanization, effects of WRV were largest, but WRV cover and ecological status were both low, indicating practical limitations of WRV restoration in urban catchments.

(5) *Synthesis and applications:* Independent effects of WRV on macroinvertebrates' ecological status can be discerned from catchment landuse. While WRV can also improve the ecological status in urban settings, it is especially relevant for river management in rural agricultural catchments, where developing WRV potentially are effective measures to reach good ecological status.

Key words: agricultural landuse, urbanisation, macroinvertebrates, river restoration, woody riparian vegetation

1. Introduction

Woody riparian vegetation (WRV) benefits aquatic ecosystem health in temperate regions, where most streams and rivers are naturally bordered by trees (Ellenberg, 1988). This notion is supported by a large number of studies demonstrating functional links between WRV and ecosystem processes in the riparian and aquatic environment (reviewed e.g. in Broadmeadow & Nisbet, 2004; Sweeney & Newbold, 2014).

Several of these functions are provided irrespective of landscape settings while others are context-specific and linked to adjacent landuse in the floodplain. Independently from adjacent landuse, WRV provides organic material like leaves, twigs, and large wood that serve as food and habitat for different aquatic organisms (Oelbermann & Gordon, 2000) and redirect flow, creating higher flow- and substrate-diversity and channel features like pools, bars and undercut banks (McBride et al., 2010). Moreover, herbaceous bank vegetation is supressed, promoting natural channel patterns and dynamics (Parkyn et al., 2005). Finally, WRV serves as habitat and as migration or dispersal corridor for terrestrial invertebrates, birds, mammals and terrestrial life-stages of aquatic insects (e.g. Petersen et al., 2004; Van Looy et al., 2014). In principle, these functions depend on the presence of trees alone. In contrast, retention of nutrients, fine sediments, and pesticides is also related to inputs from adjacent agricultural areas and strongly increases with WRV width (Arora et al., 2010; Gericke et al., 2020; Ramesh et al., 2021). Moreover, some functions of WRV are more relevant in specific contexts. For example, shading limits primary production and reduces water temperature, which is especially relevant if elevated nutrient levels would otherwise result in excessive phytobenthos and macrophyte growth (Kiffney et al., 2003; Nebgen et al., 2019). Besides landscape setting, these effects also depend on the length of WRV patches. While shading by WRV causes lower equilibrium water temperatures within few hundred meters (Kail et al., 2021), the positive effect of reducing inputs of nutrients, fine sediment and pesticides rather accumulates over long distances. Since several functions depend on landscape setting and length of the WRV patches, these should be considered when investigating the effect of WRV on river biota. Based on these reasons, higher effects are expected in agricultural catchments, as well as from wider and longer WRV sections along the riparian corridor.

A large number of reach-scale empirical studies have found positive effects of WRV on functional traits and community composition of benthic macroinvertebrates while limited effects were evident in some recent, larger-scale empirical studies. In reaches bordered by WRV, shares of shredding macroinvertebrates were higher than in open reaches (ZumBerge et al., 2003; Thomas et al., 2016; Turunen et al., 2019), indicating the role of WRV to provide leaves as a food source (Lecerf & Richards, 2010). Biomass and abundance of macroinvertebrates were lower in shaded stream reaches due to lower water temperature and light availability (Smith, 1980; Noel et al., 1986; Kaylor & Warren, 2018), limiting instream primary production (Parkyn et al., 2003; Feld et al., 2011). With decreasing canopy cover, the abundance of tolerant taxa like Chironomidae and Oligochaeta strongly increased on the expense of sensitive taxa like Plecoptera and Ephemeroptera (Kiffney et al., 2003; Thompson & Parkinson, 2011). The decline of sensitive taxa also reflects the associated increase in fine sediment input and substrate siltation (Davies & Nelson, 1994). Additionally, sensitive taxa benefit especially from the retention of pesticides by WRV (Bunzel et al., 2014).

These reach-scale studies usually compare differing configurations of WRV and often follow a BA/CI design. This implies that larger-scale stressors originating from the catchment are similar. However, recent studies, which analysed a larger number of reaches from different catchments, indicate that catchment landuse as a proxy for larger-scale stressors superimposes on the effects of riparian landuse cover on benthic macroinvertebrate traits (Le Gall et al., 2021; Palt et al., 2022). Therefore, catchment landuse must be considered when investigating the effect of WRV on benthic macroinvertebrates. From a management perspective, these studies imply that establishment of WRV would not substantially raise the ecological status if catchment landuse remains unchanged.

Most of the studies mentioned above investigated the effect of reach scale WRV on functional traits and community composition, yet there is limited knowledge of the effect on the ecological status according to the EU’s Water Framework Directive (LeGall et al., 2022; Palt et al., 2022; Tolkkinen et al., 2021). The few studies using comparable indices of macroinvertebrate communities’ naturalness like the Index of Biotic Integrity (IBI) or a Quantitative Macroinvertebrate Community Index (QMCI) found however better conditions in reaches with WRV compared to those lacking it (e.g. Newbold et al., 1980; Parkyn et al., 2003; ZumBerge et al., 2003; Aschontis et al., 2016).

Yet, besides aforementioned large-scale stressors superimposing on the effects of riparian landuse, also the low effectiveness of reach-scale restoration is often attributed to stressors acting at the catchment scale (Jähnig et al., 2010). This raises the question, under which conditions WRV, a widely used restoration measure, can significantly improve the ecological status of macroinvertebrate communities. Most studies on the effect of reach scale WRV on macroinvertebrates quantified landuse on low-resolution data, covering forested areas but not including small patches of WRV like single lines of trees along rivers (Dahm et al., 2013; Lorenz and Feld, 2013; Tolkkinen et al. 2021). Moreover, riparian corridors investigated in these studies were wide (50 – 100 m), rather reflecting forest cover in the whole floodplain and adjacent hillslopes. Many functions like shading mainly depend on WRV directly adjacent to the river banks (Kail et al., 2021) and wide strips of WRV can hardly be established in densely populated regions or areas intensively used for agriculture. Therefore, studies are missing that include small woody patches and focus on WRV effects in a narrow riparian corridor which is important from an ecological and management point of view.

Against this background, this study aims at identifying conditions, under which WRV in a narrow riparian corridor has significant effects on the ecological status of macroinvertebrates using high resolution data on WRV. We hypothesise that the effect of WRV is context-specific and differs with catchment and local landuse, length of the considered riparian corridor and hydromorphology. More specifically, we expect WRV having its largest effects in agricultural landscapes, because several of its functions described above are mainly linked to agricultural landuse in the floodplain. WRV even far upstream is expected being important, since positive effects of some functions potentially accumulate downstream. Meanwhile, stressors related to urban catchment landuse like point source pollution and stormwater runoff are expected to limit effects of WRV.

2. Material and Methods

2.1. Biological data

Data on macroinvertebrate samples from small lowland (n = 361; 18–189 m MSL) and small mountain streams (n = 748; 58–594 m MSL), taken between 2004 and 2013, were acquired from three German federal state: Hesse, North Rhine-Westphalia, and Saxony-Anhalt (Fig. 1). Sites in lowlands and mountains were analysed separately due to assumed differences in the interaction of aquatic and terrestrial environments based on factors such as topography, discharge, slope and consequently flow velocity and stream morphology.

Macroinvertebrate samples were taken according to the multi-habitat sampling method described in Haase et al. (2004). The species-level taxa lists were processed using the online tool PERLODES (https://www.gewaesser-bewertung-berechnung.de/index.php/perlodes-online.html), which amongst others computes the river-type specific multimetric index (MMI). The MMI is the core component of the ecological status assessment according to EU Water Framework Directive in Germany. The MMI reflects the impact of various stressors like hydromorphological degradation, altered hydrology and impacts of landuse (Böhmer et al., 2004).

The dataset was pre-processed to exclude data of insufficient quality: Only samples with at least 5 taxa and samples taken between December 1st and April 30th were included to guarantee reliability and comparability. For the same reason samples with a saprobic index > 2.7 were excluded, as theses correspond to polluted streams affected by point sources. Sites with barriers within 5,000 m upstream of the sampling site were excluded, since these trap sediments, alter the thermal regime to varying degrees, and therefore potentially mask sediment retention and shading by WRV.

2.2. Riparian landuse

Upstream riparian buffers were demarcated for each sampling site at two spatial scales, starting at the sampling site and extending for 500 m and 5,000 m upstream length, respectively (Fig. 2), referred to as near upstream and far upstream in the following. Riparian buffers were delineated using ESRI ArcView (Version 3.3) and included tributaries. Laterally, they covered 30 m to either side starting from the stream banks, hence excluded the water surface, quantifying terrestrial landuse only. Water surfaces were taken from official ATKIS landcover data (www.adv-online.de/Products/Geotopography/ATKIS). For small streams not included as water surfaces in ATKIS, the wetted width was approximated by a mean width measured from orthophotos for all different Strahler orders (n = 30 each). The rather small buffer width of 30 m was chosen, as it is relevant in river management and restoration and because many functions like shading mainly depend on woody riparian vegetation (WRV) directly adjacent to the stream.

WRV was quantified from ATKIS data. Its detailed landuse classes were grouped into seven categories: (1) “arable land”, (2) ”grassland”, (3) ”natural vegetation”, (4) ”urban green space”, (5) ”urban”, (6) ”water surface”, and (7) ”woody vegetation”, with some rare landuse classes excluded (e.g. quarries, harbours). Given the minimum size of woody vegetation patches in ATKIS is 0.1 ha, smaller landscape features, like single lines of trees along rivers, were missing. Therefore, ATKIS data in the riparian corridor were complemented by WRV, down to single trees, identified on orthoimages. These were obtained from the German Federal Agency for Cartography and Geodesy and were mostly CIR and some RGB images with a 0.2 m resolution (0.4 m for some few older RGB images). Only orthoimages taken between April and August and closest to 2010 were used to match the vegetation period and macroinvertebrate samples respectively.

Orthoimages were processed in an object-based image analysis (OBIA), consisting of image segmentation and classification of resulting objects. The multiresolution segmentation into objects of homogenous pixel patches was carried out in Trimble’s eCognition (Version 9.3.0) based on the pixel values of the colour bands. For their classification a support vector machine (SVM) classifier was developed based on a training dataset of 40 representative orthophotos (n = 14 RGB, n = 26 CIR), which had been classified in a supervised semi-manual nearest neighbour classification approach. The SVM classifier distinguished woody vegetation, other forms of vegetation (grassland, cropland), and non-vegetated areas (built-up areas or bare soil) based on shape, colour and brightness of the objects, as well as the Visible-band Difference Vegetation Index (VDVI, RGB images) or Normalized Difference Vegetation Index (NDVI, CIR images). This SVM classifier was applied to the orthophotos using the R package e1071 (version 1.7-3). General accuracy of segmentation and classification was assessed visually. Additionally, accuracy of the SVM classifier was assessed using cross-validation on the training dataset. Woody vegetation objects identified on the orthoimages replaced ATKIS landuse patches of the categories, “arable land”, “grassland”, “natural vegetation”, “urban green space”, and “urban”. Improving the spatial resolution of landuse data in close proximity to the river was a prerequisite to correctly quantifying the percentage cover of near and far upstream WRV.

2.3. Catchment and local landuse

For each sampling site, landuse outside the riparian corridor was quantified at two spatial scales (Fig. 2). (1) The catchment, i.e. drainage basin to the sampling site, was delineated on a digital elevation model (DEM, 10 m resolution) and visually checked. (2) The local surroundings of the sampling site were a circular buffer with a radius of 250 m.

Percentage cover of the three landuse categories “urban”, “agriculture”, and “woodland” was quantified for each scale with ESRI’s ArcGIS Desktop 10.8. Urban landuse comprises all built-up areas and infrastructure. It has detrimental effects on stream biota from catchment (e.g. impervious surfaces) to local scale (e.g. light pollution). Agricultural areas are subject to tillage, fertilization, and pesticide application, which respectively may result in inputs of fine sediments, nutrients, and toxic substances. Woodlands are the predominant potential natural vegetation in temperate regions and should cause the least detrimental effects approximating natural instream conditions. Quantifying woodland cover at catchment and local scale allows distinguishing the effect of woody riparian vegetation in the riparian buffer from adjacent woodland cover, i.e. forest cover in general.

2.4. Hydromorphology

Stream morphology pre-sets the potential of transport of sediment or detritus, as well as the thermal regime. Therefore, the effect of woody riparian vegetation (WRV) might further depend on instream hydromorphology.

Hydromorphology mappings and assessment results following Gellert et al. (2014) were provided by regional authorities. Twenty-five individual hydromorphological parameters are mapped for 100 m river segments and compared to natural reference conditions. Their deviation from reference conditions is assessed on an ordinal scale ranging from unchanged with just minor deviations (class 1) to heavily degraded (class 7). Scores of the 25 parameters are aggregated to main parameters: (1) “channel pattern”, (2) “longitudinal profile”, (3) “channel bed features“, (4) “cross section“, (5) “channel bank features“, and (6) “floodplain conditions“. For each sampling site, mean assessment scores for main parameters 1 to 5 were aggregated based on all available assessment segments 500 m and 5,000 m upstream of the sampling sites (Fig. 2). Main parameter “floodplain conditions” was omitted not to duplicate information on riparian vegetation.

2.5. Statistical analysis

Model-based recursive partitioning (Zeileis et al., 2008) was used to test the hypotheses. Its core was a linear regression model (*lm*) for the macroinvertebrate multimetric index (MMI) given the percentage cover of woody riparian vegetation (WRV) in the near upstream and far upstream riparian buffer, which is fitted per maximum likelihood estimation. The other variables in the data set, namely urban, agricultural and woodland cover at both the local and catchment scale, as well as the hydromorphological assessment results at the near and far upstream scale, were incorporated as candidate partitioning variables.

The recursive approach first tests for the entire dataset if the estimates of the *lm* show any significant parameter instability towards the gradients of any candidate partitioning variable. If statistically significant instability is found (Andrews’ sup*LM* test; Zeileis, 2005), the optimal split in the gradient of the partitioning variable causing the highest parameter instability is calculated. This split point optimizes the maximum likelihood for the core model fitted to the resulting child datasets. The process is reiterated until no more parameter instability with respect to the candidate partitioning variables in the *lm* is found for the thus final subdatasets.

The recursive splitting of the entire dataset can be intuitively displayed in a tree-diagram similar to other CART approaches. However, this method differs from most of these as it does not partition the data into groups of observations with similar response values. Rather it splits the data into groups of observations with similar model trends between the response (MMI) and core predictors (WRV) not used for partition (Garge et al., 2013).

Spearman's ρ correlation coefficient between WRV and woodland cover in the catchment were calculated in order to assess if potential effects of WRV on the MMI were independent or rather a proxy for effects of larger-scale forest cover.

3. Results

3.1. Lowland streams

The lowland sampling sites were split into three subdatasets (LL.1 – LL.3) by recursive partitioning based on two partitioning variables (Fig. 3).

In the lowlands, near upstream woody riparian vegetation (WRV) had the largest effect on macroinvertebrates' ecological status in rural, agricultural catchments (n = 34; regression coefficient = 0.415). This subdataset LL.1 was characterized by low urban (≤ 6.3%; median = 4.9%; 75th-percentile = 5.7%) and low woodland cover (≤ 18.9%; median = 12.4%; 75th-percentile = 15.5%) in the catchment. Consequently, agriculture cover was high in the catchment (median = 70.3%, 25th-percentile = 65.1%) but also at the local scale (median = 55.9%; 75th-percentile = 81.9%).

Near upstream WRV had an intermediate effect on the MMI in rural, forested catchments (LL.2; n = 100; regression coefficient = 0.329) with low urban (≤ 6.3%; median = 3.1%; 75th-percentile = 4.0%) but much high woodland (> 18.9; median = 49.0%; 75th-percentile = 64.6%) cover in the catchment. Additionally, local woodland cover was slightly higher compared to subdataset LL.1 (median = 13.5%; 75th-percentile = 38.0%).

WRV had the smallest effect on the MMI (LL.3; n = 227; regression coefficient far upstream = 0.160) in catchments with high urban cover (> 6.3%; median = 16.4%; 75th-percentile = 26.0%). Local urban cover was equally high, also compared to the other two subdatasets (median = 10.7%; 75th-percentile = 33.8%). Local woodland cover was similar to subdataset LL.1 (median = 12.6%; 75th-percentile = 29.9%) and woodland at the catchment scale was intermediate (median = 21.1%; 75th-percentile = 35.0%).

Since near upstream WRV was virtually un-correlated (and even negatively) with catchment woodland cover in subdataset LL.1 (Spearman's ρ = -0.086; Table 1), the observed positive effect on the MMI was not simply due to sampling sites being located in forested areas. Conversely, near upstream WRV in LL.2 correlated moderately with catchment woodland cover (Spearman's ρ = 0.404), implying that the smaller effect on the MMI might be partly due to positive effects of larger-scale forest cover. Finally, far upstream WRV in LL.3 correlated just weakly with catchment woodland (Spearman's ρ = 0.291).

3.1 Mountain streams

Sites in mountain streams were split into eleven subdatasets (M.1 – M.11) by recursive partitioning based on four different partitioning variables (Fig. 4). Significant effects were found in seven of these subdatasets, with regression coefficients ranging from 0.149 to 0.995:

Woody riparian vegetation (WRV) had a similarly large effect on the multimetric index (MMI) in two rural, agricultural subdatasets compared to lowland streams: Subdatasets M.5 (n = 65) and M.6 (n = 45) were characterized by low urban (≤ 11.4%; pooled median = 6.1% and 75th-percentile = 7.9%) and high agricultural cover (> 34.3%; pooled median = 49.2% and 75th-percentile = 61.2%) in the catchment. They were partitioned from each other using near upstream hydromorphology, which was substantially altered in M.5 (≤ 5.1; median = 4.2; 75th-percentile = 4.7), but even strongly degraded in M.6 (> 5.1; median = 5.8; 75th-percentile = 6.1). Besides these habitat conditions, the two subdatasets also differed in local woodland cover, which was intermediate in M.5 (median = 17.4%; 75th-percentile = 43.4%) and notably lower in M.6 (median = 8.7%; 75th-percentile = 20.1%). In subdataset M.5 with worse hydromorphology and higher local woodland cover, near upstream WRV had a positive effect on the MMI (regression coefficient 0.381). In subset M.6 with the less severe hydromorphological degradation and lower local woodland cover, far upstream WRV had a similar positive effect on the MMI (regression coefficient 0.420). Catchment woodland cover was moderate for both subdatasets (pooled median = 29.6%; 75th-percentile = 37.9%).

WRV also had a significant but smaller effect on macroinvertebrates' ecological status in rural, non-agricultural catchments, with a regression coefficients of 0.255 and 0.149 in subdatasets M1 and M2, respectively. These two subdatasets M.1 (n = 132) and M.2 (n = 149) were both characterized by low urban (≤ 11.4%; pooled median = 5.0% and 75th-percentile = 6.9%) and moderate agricultural cover in the catchment (≤ 34.3%) as well as very low agricultural cover locally (≤ 17.6%, pooled median = 0.0% and 75th-percentile = 5.0%). Consequently, local woodland cover was high in both subdatasets (M.1: median = 53.1%; M2: median = 42.6%).

Far upstream WRV had the largest effect on macroinvertebrates' ecological status in urban catchments as observed in subdatasets M.8 (n = 54), M.9 (n = 30), and M.10 (n = 60). These three subdatasets were characterized by high catchment urbanisation (> 11.4%; pooled median = 16.2%; 75th-percentile = 23.6%). Sites in subdataset M.8 and M.9 where further characterized by low local agricultural cover (≤ 8.9) that was even completely lacking in M.8, which in turn featured intermediate catchment agriculture cover (> 6.9%; median ^= 20.3%; 75th-percentile = 33.9%). Rather high shares of local agriculture (> 8.9%; median = 45.1%; 75th-percentile = 65.2%) and less than strongly altered near upstream hydromorphology (≤5.5; median = 4.26; 75th-percentile = 4.72) characterized subdataset M.10. Far upstream WRV had exceptionally strong significant effects on the MMI in two of these subdatasets (regression coefficient M.8 = 0.949; M.9 = 0.995) where local urbanization was very high (pooled median = 42.9%; 75th-percentile=78.3%) while catchment (pooled median = 33.3%; 75th-percentile=54.5%) and local woodland (pooled median = 13.5%; 75th-percentile=39.5%) were intermediate at best. The third urban subdataset M.10, was the only one with significant effects from both near (regression coefficient -0.499) and far upstream (regression coefficient 0.794) WRV as well as the only with a negative effect (near upstream). Local (median = 16.2%; 75th-percentile = 26.6%) and catchment (median = 32.4%; 75th-percentile = 42.6%) woodland cover were both intermediate. Despite the highest amounts of catchment urbanisation of any subdataset with significant effects, local urbanisation was barely moderate (median = 5.1%; 75th-percentile = 14.4%).

In the two rural, agricultural subdatasets M.5 and M.6, the effects of near and upstream WRV were considered independent from large-scale woodland cover. Near upstream WRV was even negatively correlated with catchment woodland in M.5 (Spearman's ρ = -0.114; Table 1), while far upstream WRV was positively but weakly related to catchment woodland in M.6 (Spearman's ρ = -0.300).

In contrast, in the rural, non-agricultural subdataset M.1, far upstream WRV strongly correlated with catchment woodland (Spearman's ρ = 0.614), indicating that the effects of WRV might be at least partly due to larger-scale forest cover. Yet in the second rural, non-agricultural subdataset (M.2), near upstream WRV correlated negatively with catchment woodland (Spearman's ρ = -0.103).

In two of the urban subdatasets (M.8, M.9), far upstream WRV was also negatively correlated with catchment woodland cover, and only weakly positively correlated with catchment woodland cover in the third urban subdataset (M.10).

4. Discussion

This study aimed to identify conditions, under which woody riparian vegetation (WRV) in a narrow buffer has the largest effects on the ecological status of macroinvertebrates (multimetric index, MMI). Despite using, to our knowledge the most detailed data on WRV in a large-scale study to date, there exist limitations to the approach. First, only percentage cover of certain landuse forms was assessed, which simplifies characteristics of more complex landscape elements (e.g. tree species, type of built-up area) and neglects temporal dynamics (e.g. forest development phase) as well as spatial arrangement. For instance, gaps in WRV are not accounted for and neither is it possible to perfectly distinguish WRV from wider forest cover by just comparing the narrow riparian corridor to local landuse and the entire catchment.

4.1 Rural landscapes

As hypothesized, WRV had a large positive effect on the ecological status of macroinvertebrates (multimetric index; MMI), in rural, agricultural landscapes. Results were consistent and regression coefficients similar in one subdataset in lowland (LL.1, regression coefficient 0.415) and two subdatasets in mountain streams (M.5 and M.6, regression coefficients 0.381 and 0.420). As the MMI ranges from 0 to 1 and is discretized evenly into five ecological status classes (high, good, moderate, poor or bad status), these coefficients imply that by managing woody riparian cover between 0 and 100%, without accompanying measures, the macroinvertebrate ecological status could be improved by as much as two status classes. This confirmed that woody riparian buffers are indeed a powerful tool for restoration in streams impacted by agricultural stressors. Given low catchment (median: 12.4 – 31.0%) and local (median: 8.6 – 17.4%) woodland cover and the lack of strong correlations between woodlands and WRV, the observed significant positive effects can be considered independent from larger-scale forest cover.

Other than expected, far upstream WRV was less important than near upstream WRV in agricultural landscapes. There was only one significant effect of far upstream WRV in one out of these three subdatasets (M.6). In the remaining two (LL.1, M.5) the significant positive effect was caused by near upstream WRV indicating that functions of WRV already were provided over a rather short distance of 500 m, which can substantially improve the ecological status of macroinvertebrate communities. This observation is in line with Kail et al. (2021), who observed that 400 m of shading by WRV results in a new thermal equilibrium of water temperature in lowlands. The sampling sites in subdataset M.6, where far upstream WRV had the significant effect, were highly morphologically degraded, suggesting that WRV at a larger spatial scale is necessary to compensate for instream habitat deficits.

In other rural but non-agricultural subdatasets, the effect of WRV on the ecological status was similar in lowland (LL.2, regression coefficient = 0.329) or somewhat lower in mountain streams (regression coefficient in M.1 = 0.255; M.2 = 0.149). Woodland cover in the catchment and locally around the sampling sites was much larger in these three subdatasets and correlated with WRV in two of them (LL.2, M.1). Therefore, the observed effects cannot be clearly attributed to WRV and might have been at least partly due to positive effects of large-scale forest cover. This would be consistent with other studies reporting strong positive effects of catchment woodland cover (Wahl et al., 2013).

4.2 Urbanized catchments

Other than expected, the effect of WRV on the ecological status was not clearly limited or superimposed by urban catchment landuse. Also, the percentage cover identified as the root split node well mirrored previously identified thresholds for urban cover with respect to the state of the macroinvertebrate community (Kail et al., 2012). Causes for the overall impact of urban areas are manifold (Walsh et al., 2005). For instance, increased runoff from impervious cover and flood prevention measures result in alterations to the hydrological regime. Furthermore, urban areas are sources for nutrients and hazardous substances, which eventually end up in streams. These impacts are evident in this study and reflected by generally lower multimetric (MMI) scores for subdatasets above the root split point (catchment urban cover) in both stream types.

However, within this limited range of low MMI scores, far upstream WRV still has a significant effect on the ecological status in urbanized catchments in lowland streams (LL.3). And even the by far largest effects are found in mountain streams in urbanized catchments (M.8, M.9, and M.10). Solely considering the regression coefficients one might expect that managing the woody riparian cover between 0 and 100% could improve the macroinvertebrate ecological status by as much as five status classes, i.e. from bad to high. This contradicts our expectations. However, given the lack of sites with high WRV cover and high ecological status such an extrapolation of the regression model over-interprets the results. Nevertheless, within the limited range of the data, results indicate that increasing WRV cover might be an appropriate restoration measure even in urban catchments. It seems that when there are virtually no adverse effects from agriculture to be buffered by near upstream WRV, the degree of naturalness in the far upstream riparian corridor, expressed by WRV cover, is a key determinant of macroinvertebrates' ecological status at urban sites.

While the presence of far upstream WRV could be a proxy for the lack of near-stream urban pressures, the effect might also be due to functions provided by far upstream WRV, like decreasing water temperature or aiding aerial dispersal. These functions might – while not necessarily mitigating stressors related to urbanization like point source pollution and stormwater runoff – still improve habitat conditions rendering WRV a worthwhile restoration tool. In contrast to rural, agricultural settings, where near upstream WRV was most important, longer segments of WRV seem to be necessary to substantially improve habitat conditions in urban settings. Only in streams affected by urbanization in concert with agriculture and hydromorphological degradation even the positive effects of far upstream WRV are limited or superimposed by this multiple pressure situation (M.11).

Subdataset M.10 is furthermore special due to the, at first counterintuitive, negative effect from near upstream WRV along with the positive effect from far upstream WRV. Further inspection revealed a spatial cluster of sites within M.10 (Fig. 5), characterized by near upstream WRV upwards of 50% that nevertheless maintains poor MMI scores. This spatial cluster is located in the vicinity of Frankfurt am Main, a major metropolitan area, in small stream tributaries to the Nidda, which discharges to the river Main, as well as other close-by smaller direct tributaries to the Main. We suspect some local effect not accounted for in the data to be responsible. Excluding these sites from the subdataset, a positive effect would exist for both scales of woody riparian vegetation.

5. Conclusion

Numerous small scale studies confirmed the beneficial effects of WRV on macroinvertebrates, while the results of recent large scale studies (Le Gall et al. 2021; Palt et al., 2022) question the effectiveness of woody riparian vegetation (WRV) to improve the ecological status. Our findings clearly reveal that effects of WRV on ecological status are large, but context specific as they differ in magnitude and scale according to catchment landuse, local landuse and hydromorphology. While the identification of context-specificity of the relationship between woody riparian vegetation and the macroinvertebrate community is hardly surprising, this analysis first succeeds in confirming underlying assumptions using a large dataset.

In streams mainly impacted by catchment urbanization, longer upstream reaches bordered by WRV seem to be necessary to substantially improve habitat conditions enhancing macroinvertebrates' ecological status in the range from bad to moderate conditions. Establishing WRV is potentially particularly relevant for river management in rural, agricultural settings, where an increase in WRV from 0 to 100% can improve ecological status by up to two classes. Thus developing WRV can be an effective measure to reach good ecological status. We conclude that establishment of WRV is a key measure in the management and restoration of small streams, which is effective and easily applicable.

6. Authors' contributions

MP, DH and JK conceived the ideas; MP designed the methodology and analysed the data; MP and JK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion

Our study relied on the assemblage of available data from the authors' own country and therefore no data collection was needed. The research was conducted in cooperation with local state authorities and agency stakeholders were involved in the greater study project.

7. Acknowledgements

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Tables

Table 1: Spearman's ρ rank correlation coefficient between near and far upstream woody riparian vegetation (WRV) and catchment woodland cover for subdatasets with a significant effect (bold) from WRV on the macroinvertebrate multimetric index.

	Spearman's ρ			
Subdataset	near upstream WRV		far upstream WRV	
LL.1	**-0,086**		0,115	
LL.2	**0,404**	***	0,547	***
LL.3	0,128		**0,291**	***
M.1	0,153		**0,614**	***
M.2	**-0,103**		0,354	***
M.5	**-0,144**		0,33	*
M.6	0,019		**0,3**	*
M.8	0,211		**-0,066**	
M.9	-0,449	*	**-0,182**	
M.10	**0,044**		**0,24**	*

Figures

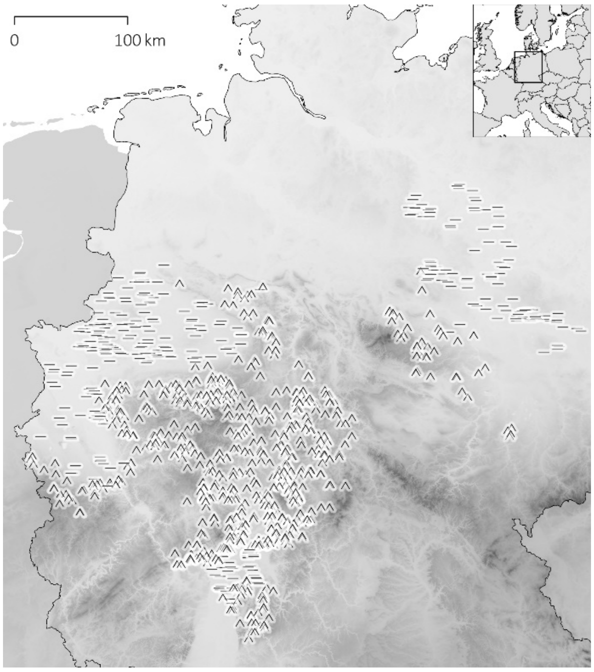

Fig. 1: Location of macroinvertebrate sampling sites in Germany: Bars show lowland and chevrons mountain streams.

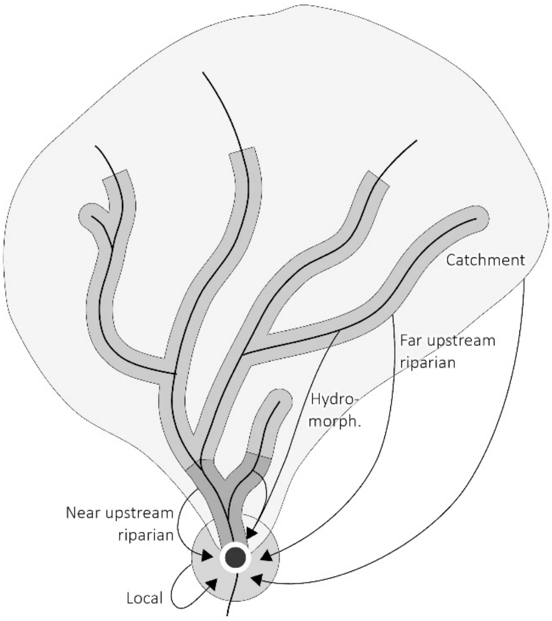

Fig. 2: Landuse was assessed in the catchment, locally in a 250 m circle around the sampling site and at two lengths in the riparian corridor upstream from the sampling site 30 m to either side of the stream: Near upstream extents for 500 m, and far upstream for 5,000 m respectively. Available hydromorphological assessments were aggregated for both upstream lengths. Not to scale.

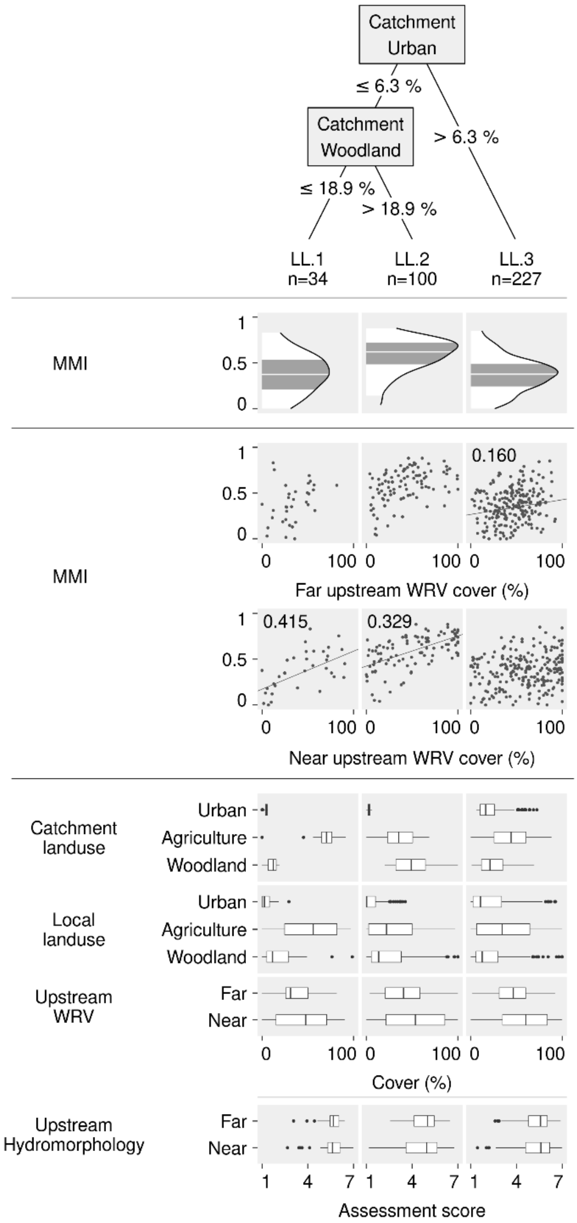

Fig. 3: Partitioning tree for lowland sites. Density distributions of the macroinvertebrate multimetric index (MM) for each final subdataset (columns) with boxplot-like coloration of quantiles. Relationship between the MMI and the near and far upstream woody riparian vegetation (WRV) shown in scatterplots with significant effects indicated by regression coefficient and line. Distribution of all candidate partitioning variables given as boxplots.

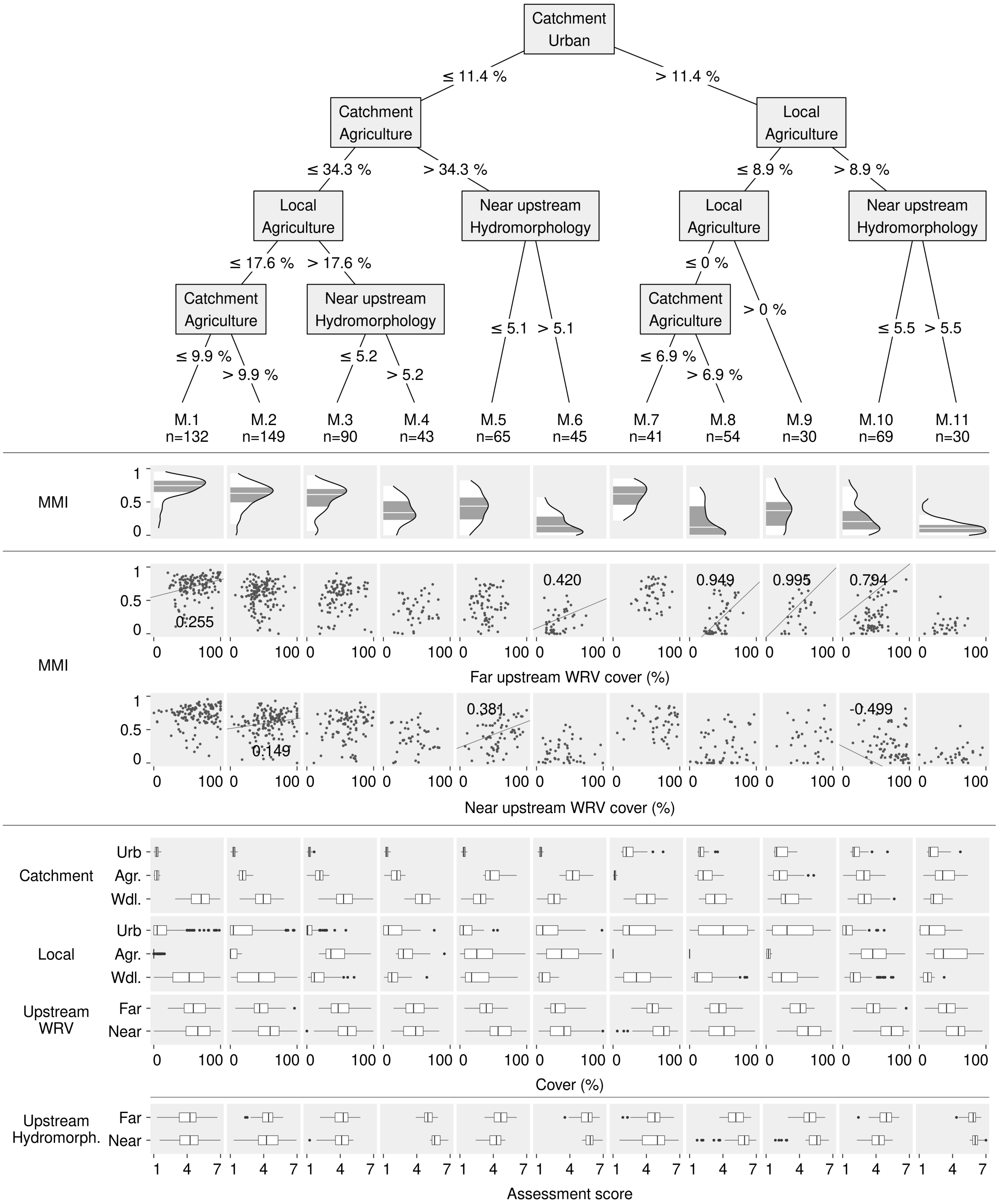

Fig. 4: Partitioning tree for mountain sites. Density distributions of the macroinvertebrate multimetric index (MM) for each final subdataset (columns) with the boxplot-like coloration of quantiles. Relationship between the MMI and the near and far upstream woody riparian vegetation (WRV) shown in scatterplots with significant effects indicated by regression coefficient and line. Distribution of all candidate partitioning variables given as boxplots (Abbreviations: "Urb." = urban, "Agr." = agriculture, "Wdl." = woodland).

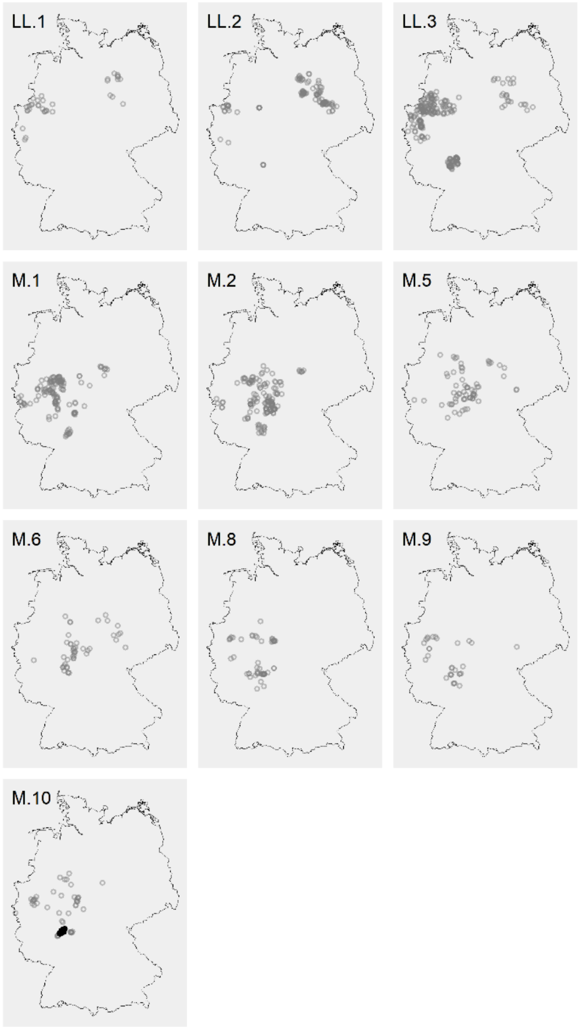

Fig. 5: Sites in subdatasets with significant effects of woody riparian vegetation (WRV). Lowland sites in the top row. Sites in subdataset M.10 contributing to a negative effect of WRV in black.

Beteiligung an Veröffentlichungen

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- Durchführung der Experimente (experimental work): nicht zutreffend
- Datenanalyse (data analysis): 100%
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- Statistische Analyse (statistical analysis): 100%
- Manuskripterstellung (writing the manuscript): 100%
- Überarbeitung des Manuskripts (revising the manuscript): 50%

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FRESHWATER ECOLOGY

The effect of riparian woodland cover on ecosystem service delivery by river floodplains: a scenario assessment

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Abstract. Sixteen ecosystem services were quantified for the riverine landscapes of the Nahe, Stever (Germany), Bresse plain, and Azergues (France), to assess the effects of riparian woodland cover. Future woodland cover in 2050 was modeled to reflect contrasting scenarios of river management aligned to the well-established shared socioeconomic pathways. The scenarios are labeled as current, pessimistic, best practice, and ambitious riparian management practices (RMPs). We linked services to floodplain land use and river morphology and quantified them separately for spatial segments (0.5–1 km in length, $n = 118$–3419, depending on river length), using an analytical framework, the "Mononen cascade." Conservative monetary value estimates were based on net producer income before tax and subsidy, a shadow market price for carbon, flood damage functions, or willingness to pay for recreation and non-use. Most services were linked to land use, some affected the value of other services through simple rules (woodland shade affected trout survival hence angling benefit, a minimum of woodland affected pest regulation, hence crop productivity). In the current landscape state, provisioning, regulating, and cultural services all showed optimum curves with woodland cover: Provisioning services and cultural services were maximal around 45%, whereas this was around 30% for regulating services. More woodland was present in steeper near-source segments. Averaged across rivers, mean total service provision was estimated at 1084 ± 4 €$\cdot$ha$^{-1}\cdot$yr^{-1}, with 40%, 36%, and 24% contributed by, respectively, provisioning, regulating, and cultural services. The three scenarios led to a limited change in total ecosystem service delivery, even if mean woodland cover was reduced from 27% to 17% in the pessimistic RMP and increased to 70% in the ambitious RMP for the most extreme case of the Stever. Provisioning services declined with increased woodland cover and cultural services increased. Regulating services did not change that much, because they are dominated by flood prevention in our assessment. The "best practice" scenario appeared to combine a modest increase in cultural services with a slight increase in provisioning service. An ambitious nature conservation objective as in the ambitious RMP appears possible without seriously compromising overall societal benefit.

Key words: ecosystem services cascade; riparian woodland; river restoration; shared socioeconomic pathways; Strahler river order; water quality.

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INTRODUCTION

The presence or absence of riparian woodland is thought to have a major influence on biodiversity and ecosystem functioning of streams and adjacent floodplains (Sweeney and Newbold 2014). Under natural conditions, most European rivers would be accompanied by woodland (Brown et al. 2018; a recent North American example in Whited et al. 2007). The establishment of woodland buffers is generally considered an effective restoration measure (Bernhardt et al. 2005, Stutter et al. 2012). The effect on flood buffering, however, is not straightforward (Leyer et al. 2012), and local conditions may determine a balance between biodiversity benefits and possibly adverse flooding effects upstream. Similar unforeseen trade-offs may occur among other functions as well, which calls for a comprehensive assessment of all possible effects of a measure, such as woodland restoration, across the whole extent of the current or historical floodplain of a river (Tockner et al. 2000).

The ecosystem services approach can be used as an integrating framework for such a comprehensive assessment, as it can link floodplain land use as well as river characteristics (together reflecting the ecosystem) to an exhaustive list of societal benefits (Burkhard et al. 2009, Bateman et al. 2013, Vermaat et al. 2020). A priori, it is important that critical methodological concerns are considered. This implies that the quantified services should be "final," hence directly contribute to human well-being (Boyd and Banzhaf 2007), that double counting is carefully checked, that different underlying assumptions for monetary value estimates or other rankings are understood (Wallace 2007, Bateman et al. 2011, Bouma and van Beukering 2015) and that its anthropocentricity is understood (i.e., "the benefits people obtain from ecosystems" or "nature's contribution to people"; MEA 2005; Braat 2018; Díaz et al. 2018; Kenter 2018).

Variation in woodland cover in the floodplain and the riparian area of rivers can thus be linked to variation in the provision of different services by the river and its floodplain. We used a modification of the ecosystem services "cascade" of Boerema et al. (2017) proposed by Vermaat et al. (2020) for this purpose. The view of ecosystem services as a cascade that flows from an ecosystem with structural components via intermediate functions to a final service that is of benefit to humans and thus can be valued economically is presented originally by Haines-Young and Potschin (2010). Mononen et al. (2016) and Boerema et al. (2017) summarize the debate on how the different elements of such a cascade can be understood. Variants of this "cascade" framework have been applied in decision support for the multiple use of landscapes (Dick et al. 2017), in regional and national assessments of the manifold of ways in which whole landscapes contribute to human well-being through ecosystem services (Martín-López et al. 2012, Mononen et al. 2016, Maseyk et al. 2018), and in integrated assessments of ecosystem restoration success (Vermaat et al. 2016).

In Europe, floodplain woodland cover varies substantially among and within river; it is often highest in the upper reaches, although this is under strong control of geomorphology and land-use patterns (Petts and Foster 1985). To explore the possible interactive effects of a future increase in woodland as a possible consequence of environmental policy or ongoing demographic processes such as the depopulation of the countryside, scenarios can be used. Scenarios are a common tool to systematically study the potential consequences of differences in policy focus and societal development (Lorenzoni et al. 2000; Berkhout et al. 2002, Busch 2006; O'Neill et al. 2017). We used the Shared Socioeconomic Pathway (SSP) scenarios of societal development developed by O'Neill et al. (2017) as they have become widely used benchmarks. The SSPs describe contrasting trajectories of societal change in terms of demography, economic development, technological advances, and national and global policy focus on issues of international cooperation, sustainability, and climate change. These SSPs have been used for projections of future land use, world energy markets, and climate modeling (O'Neill et al. 2017). We downscaled these SSP scenarios into a set of specific riparian management practices (RMPs) that describe measures taken by river management expressed as changes in floodplain land use and other river characteristics. Their effect was assessed with our ecosystem services assessment framework. Since the framework allows the tracing of separate services, identifying trade-offs among services (Martín-López et al. 2012) as a consequence of different scenarios is possible.

The underlying generic assumption would be that river restoration with increased woodland has an overall positive ecological effect, also measurable in ecosystem service provision, although the objective of a restoration effort is often implicit and inarticulate (Bernhardt et al. 2005, Jähnig et al. 2011). Gilvear et al. (2013) proposed that river restoration would generally lead to a decrease in provisioning services, whereas regulating and cultural services would increase. Increasing woodland cover can be seen as a form of restoration and then should lead to the same general pattern. However, different scenarios that involve substantial variation in the cover of riparian woodland may have opposing effects: More woodland will be negative for agricultural productivity in the floodplain but positive for in-stream water temperature mitigation and hence trout survival, as one trade-off (Broadmeadow et al. 2011). Since several such potential trade-offs may occur, phrasing a zero hypothesis is not straightforward, and we therefore chose to phrase more open questions:

1. What is the effect of riparian woodland cover on the suite of ecosystem services provided by rivers and their floodplains? Can we identify systematic patterns?
2. How do different riparian management practices (RMPs, linked to SSPs) perform in terms of ecosystem service delivery?
3. Can we generalize on trade-offs among different services that occur as a function of variable riparian woodland cover? Does the effect of increased woodland cover follow the prediction by Gilvear et al. (2013)?

MATERIALS AND METHODS

Case study rivers

We selected two lower-mountain and two lowland river systems in, respectively, Germany and France: The Nahe, Stever, Azergues, and the Bresse plain. The latter actually combines three smaller rivers in a homogeneous landscape, and its riparian network has been studied by Van Looy et al. (2017). These mid-sized rivers are part of the drainage network of, respectively, the Rhine and Rhone. They differ among others in slope, underlying geology, land cover pattern, human population density, and intensity of agricultural land use (Table 1) and thus are considered to reflect a variety of riverine landscapes in the Northwest of Central Europe, with the lowland Stever and Bresse being under the most intensive agriculture.

Ecosystem service assessment framework

We used the ecosystem services framework that Vermaat et al. (2020) adopted from Mononen et al. (2016) and Boerema et al. (2017) and labeled the “Mononen cascade.” Briefly, it is based on the ecosystem services classification CICES 5.1 and specifies the subsequent steps in the cascade for each service linking these to land cover and river morphology (Fig. 1). It uses the three MEA (2005) categories of provisioning, regulating, and cultural services to group the different final services. Each service is quantified in terms of biophysical units (benefit sensu Mononen et al. 2016; such as $kg \cdot ha^{-1} \cdot yr^{-1}$) and subsequent monetary units (societal benefit sensu Mononen et al. 2016, $€ \cdot ha^{-1} \cdot yr^{-1}$), which can be summed as an estimate of total economic value (TEV; 1 € ≈ 1.25 US$ median midmarket 2011–2021). The “Mononen cascade” originally consists of four elements: ecosystem structure, ecosystem function, societal benefit, and societal value. We use land-use cover as proxy for ecosystem structure. Then, we merge the two steps function and benefit into one element, the service in biophysical units since all underlying ecosystem functions that potentially contribute to a final service can be seen as intermediate and the final function is thus also the final service (as in Boerema et al. 2017 and Vermaat et al. 2020). Finally, we use a range of valuation methods from environmental economics (Brander et al. 2006, Bouma and van Beukering 2015) to arrive at a monetary estimate of societal “value,” the third element in our adapted cascade. We want to stress that we use such monetary value estimates for final services and an aggregation of these into an estimate of TEV (as a rate per area and year) as a tangible indicator for comparative use in scenario evaluations and in communication with policymakers. They should not be interpreted as directly convertible to market prices or absolute “values.”

Table 1. Characteristics of the four study rivers.

Characteristics	Nahe	Stever	Azergues (including Brevenne and Turdine)	Bresse (combines Chalaronne, Veyle, Reyssouze)
Drains into	Rhine	Lippe	Saone	Saone
Segment slope (%)†	3.66 ± 3.72 (0–35.83)	0.46 ± 0.59 (0–6.09)	4.84 ± 3.33 (0.25–15.03)	0.59 ± 0.53 (0.03–3.70)
(Sub-)segment width (m)‡	101.1 ± 79.0	90.1 ± 94.0	149.7 ± 142.7	112.8 ± 126.4
River length quantified (km)	3303	942	424	663
No. segments (sub-segments)	3499 (5638)	445 (1696)	119	171
Percentage woodland§ in floodplain (current)	39	27	36	19
Percentage agriculture in floodplain (pasture and cropland, current)	40	63	37	65
Percentage built-up in floodplain (current)	12	4	18	8
Nitrogen surplus (kg $N \cdot ha^{-1} \cdot yr^{-1}$, ~2000–2010)¶	30	120	30	40
Human population density in catchment (No./km^2 ~2010)#	170	194	131	147

† Values are expressed as mean ± standard deviation (SD) with range in parentheses.
‡ Values are expressed as mean ± SD.
§ Percentages land cover are averages across the (sub)segments.
¶ Based on Grizetti et al. (2007) and Poisvert et al. (2017).
\# From regional statistics.

For all 16 quantified services, the assumptions and data sources are summarized in Table 2. A worked-out spreadsheet including all steps in the cascade is available as Data S1.

Deriving riparian management practices from benchmark shared socioeconomic pathway scenarios of societal change

We use a set of scenarios of societal change that have been derived from the benchmark SSPs (O'Neill et al. 2017) and were articulated for our specific purpose to reflect plausible, contrasting trajectories of riparian management in Europe (our RMPs). This articulation is documented separately in Vermaat et al. (2018). We set the starting year or baseline at approximately 2015 and label it as "current." Our chosen horizon in the future is 2050, as a compromise between a relevant time span for current policymakers and the time needed for policy to be fully implemented in landscapes. Furthermore, it is likely that by that time the trajectories of geophysical climate change grasped with the different Representative Concentration Pathways will not yet be markedly different beyond the projected uncertainty bands (IPCC 2014). This allows us to focus on the societal aspects of plausible futures described in the SSPs which simplifies the number of alternatives to be compared. It also excludes the possibly confounding uncertainty in, for example, the future hydrology of our study streams. As a consequence, our estimate of flood damage prevention is based on current flow regimes, which may well be a conservative underestimate.

We selected three out of the five SSPs (respectively SSP1, SSP2, and SSP3, also labeled "sustainability," "middle of the road," and "regional rivalry" in the literature; O'Neill et al. 2017; Popp et al. 2017). We downscaled these to reflect three different, contrasting overall pathways of change in society which then led us to three corresponding plausible ways in which European riparian management would develop: either with a stronger focus on environmental sustainability, or continuing along current lines, or moving away from and ignoring environmental concerns (Riparian Management Practices or RMPs labeled as "ambitious," "best practice," or "pessimistic"; Vermaat et al. 2018; characteristics in Table 3). Current inland water management in

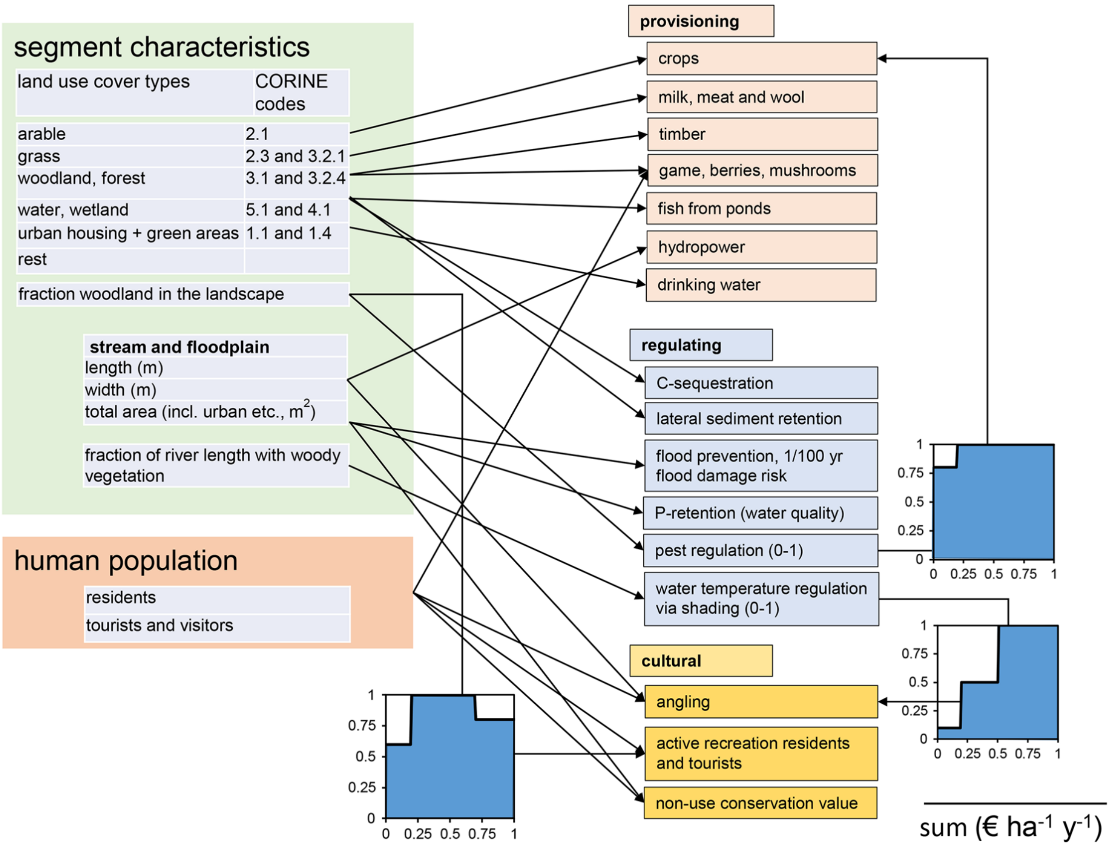

Fig. 1. Flow of 16 different ecosystem services from ecosystem structure (expressed as different types of land use, floodplain, and river metrics in the green box) to annual service flow in biophysical benefit and monetary value estimates. The elements benefit and value in the "Mononen cascade" are pooled here for simplicity. The box "riparian human population" provides population estimates from riparian municipalities through which the valley runs, used for the estimation of a number of services. Provisioning, regulating, and cultural services are indicated with different colors. Three small "knowledge rule" step diagrams indicate the effect of intermediate services, respectively, that of woodland cover on pest regulation expressed in crop revenue, that of riparian woodland cover on stream temperature, brown trout survival and hence value for angling, and that of landscape heterogeneity as the percentage woodland on attractiveness for recreation. Axis units of these diagrams are dimensionless fractions. Further explanation in Table 2.

the European Union is governed by the Water Framework Directive (WFD), and we aligned our RMPs with the currently known policy cycle and measures of this WFD (White and Howe 2003). Our first draft RMPs have been discussed with panels of institutional stakeholders for each of the four study river systems and adjusted when necessary. For the Nahe, we met on 20 November 2017 at the office of the federal state government of Rhineland-Palatinate in Mainz with eight participants; for the Stever, we met on 2 June 2018 in the office of the district government in Münster with 10 participants; and for the Bresse and Azergues, this occurred at IRSTEA in Lyon on 5 July 2018, with 13 participants from both rivers. In each workshop, at least two of the authors were present. An additional purpose of the workshops was to be informed of possible local sources of information for the quantification of the 16 ecosystem services.

Table 2. Relevant ecosystem services selected and aggregated when necessary from CICES 5.1 and quantified in the four river systems.

Service (CICES 5.1 codes)	Description	Explanation, sources
Provisioning		
Crops (1.1.1.1)	Net farm gate revenue arable farms (154–1152 €·ha^{-1} [cropland]·yr^{-1})	Income of farmer minus costs, but before taxes and subsidy, a benchmark statistic that is not market consumer price of a product, hence excludes any increases along the value chain. Data are from Mueller and Mueller (2017) from a standard set of representative and intensively monitored farms in Rheinland-Pfalz, Germany; from Boerman et al. (2015) for the Stever and from Agreste (2017) for the two French systems. In the Nahe, vineyards have not been included as they are outside the floodplain
Dairy, meat, hides, wool fleeces (1.1.3.1 and 1.1.3.2)	Net farm gate revenue dairy farms (201–1054 €·ha^{-1} [grassland]·yr^{-1})	Based on the same sources as crops. We have assumed dairy products to be the final service, and not cattle fodder. Sheep stocks reportedly are limited in the study areas and the value is based on a world market estimate per fleece of 19.5 €
Fish from ponds, mainly trout (1.1.4.1)	Gross income minus costs per km stream length (0–14 €·ha^{-1}·yr^{-1})	Several fish farms occur along the Stever and in the Bresse; productivity and net revenue estimated from Hiller and Wichmann (2010); values normalized per area floodplain
Timber (1.1.5.2)	Conservative annualized net present value estimate based on annual beech or fir productivity for Northern and Central Europe (138–218 €·ha^{-1} [forest]·yr^{-1})	We use a conservative low-end value for Germany based on Duncker et al (2012, different scenarios with different rates of interest, range of 0–800 €·ha^{-1}·yr^{-1}), Hastreiter (2017, 130 €·ha^{-1}·yr^{-1}, net revenue small scale forestry) and Boesch et al. (2018, 300 €·ha^{-1}·yr^{-1}). For France, the values were adjusted from Societe Forestiere (2018)
Berries and mushrooms, game (1.1.5.1 and 1.1.6.1)	Conservative estimate from a comparative European review, mainly Germany and France (12–24 €·ha^{-1} [woodland]·yr^{-1}, 90% due to game)	French and German data adopted from Schulp et al. (2014), which has a similar estimate as Boesch et al. (2018) for Germany
Hydropower (4.2.1.3)	Reported current locally generated hydropower (0–11 €·ha^{-1} [floodplain]·yr^{-1})	Values are normalized from length of 3rd-order streams to floodplain area. Consumer price is halved to reduce the benefits accumulating in the value chain and remain comparable with net farm gate revenues as for crops and dairy. Based on Anderer et al (2009) for the Nahe, on LANUV (2017) for the Stever, and stakeholder reporting on the Bresse. The Azergues currently has no hydropower generation
Drinking water (4.2.1.1)	Reported local extraction and use of surface water (0–5 €·ha^{-1} [floodplain]·yr^{-1})	This can be river water infiltrated into aquifers and then extracted again, or direct use. Market price is halved to reduce the benefits accumulated in the value chain and remain comparable to net farm gate revenue. Values are normalized to floodplain area. In the Nahe and the Bresse drinking water is mainly extracted from deep aquifers and no river water is used. A substantial fraction (crude estimate 40%) of the Stever flow is infiltrated at Haltern into a sandy aquifer, together with water from the Muehlenbach and natural groundwater recharge, at to produce drinking water for parts of the Ruhrgebiet region (data drinking water company Gelsenwasser AG and information service of Nordrhein-Westfalen www.elwasweb.nrw.de)
Regulating		
Greenhouse gas reduction (2.2.6.1)	Carbon sequestration in coniferous, deciduous woodland and riparian bushes at, respectively, 6, 5 and 4 ton C·ha^{-1}·yr^{-1} (based on Paul et al. 2009); we assume that mixed woodland is similar to deciduous	For the "current" state of riparian management, a low price of 5 euro per ton C is used (Elsasser et al. 2010, Loeschel et al. 2013), For the ambitious RMP, we assume a moderate increase due to the further development of a carbon credit market to 20 euro (Vermaat et al. 2016, Boesch et al. 2018). For "best practice," we use 10, and for "pessimistic," we use 1 euro per ton C

(Table 2. Continued.)

Service (CICES 5.1 codes)	Description	Explanation, sources
Erosion control: lateral sediment retention (2.2.1.1 and 2.2.1.2)	Expressed as riparian woodland P-loss prevention for erosion-derived material from the lateral zone adjacent to the stream (kg P·ha^{-1} [floodplain]·yr^{-1})	P is used as simple proxy for top-soil to avoid any possible double counting. Median low-end potential P loads for grassland and arable land (from Venohr et al. 2017) are reduced relative to the proportion of the river length that has riparian woodland. If this proportion is 1, all the potential load is retained. Grassland has 1 kg P·ha^{-1}·yr^{-1} available for erosion, cropland 2 kg P·ha^{-1}·yr^{-1}. A low-end conservative value estimate for P is derived from an artificial fertilizer market price of 1.1322 €/kg P from a 2010 median market price at www.indexmundi.com
Flood prevention (2.2.1.3)	Damage function based on the risk of a 1/100 yr flood and a median distribution of different land-use types over the river corridor (0–7 €·ha^{-1} [floodplain]·yr^{-1})	Assumption is that one flooded upstream reach prevents the damage of flooding a median downstream reach of equivalent area, hence with the median distribution of land use across the whole river. Value of built-up land is particularly high (252 €/m^2, agricultural land has 7, and woodland has 1). This is conservatively down-adjusted to the height of the flood wave relative to property or crop (we use 0.2), normalized to an annual value with a factor 1/100. Based on De Moel and Aerts (2011) and then normalized to floodplain area. Duration and height of the 1/100 flood was estimated from locally available water authority data repositories and reports: for the Nahe from: http://www.gda-wasser.rlp.de, for the Stever from: www.elwasweb.nrw.de and www.luadb.it.nrw.de; for the Bresse from https://www.vigicrues.gouv.fr/niv2-bassin.php?CdEntVigiCru=18; and for the Azergues from the same website and the Plans Prevention des Risques d'Inondation at www.rhone.gouv.fr. A median flood duration of 7 d was used for all rivers except for the Azergues where we reduced it based on expert judgment of JP
Pest regulation (2.2.3.1 and 2.2.3.2)	Expressed as a modulation of crop productivity (provisioning service 1.1.1.1 above) linked to the presence of woodland and hedges as source of pest control. Modulation is a simple knowledge rule: if woodland cover <25%, then crop productivity reduced to 80%	Based on Tscharntke et al. (2012), who present a rule of thumb on a minimum woodland and hedge cover for central European landscapes
Water quality improvement: nutrient retention (2.2.5.1)	Waterborne phosphorus retention in stream and in riparian floodplain during a flood	Only phosphorus is used to conservatively prevent double counting. Different forms of nitrogen, BOD, or toxic substances are not addressed separately, and hence, this is likely a conservative underestimate. From load reduction per stream km as well as P sedimentation during a flood event and combined with a conservative low market price for P of 1.1322 €/kg P derived from artificial fertilizers in the same way as for erosion control. Load reduction per km of stream length is derived from De Klein and Koelmans (2011), and Olde Venterink et al. (2003) at around 200 kg P/km river length for low land rivers and conservatively reduced to 10 kg P/km river length for the steep Nahe and to 100 kg P/km for the other three rivers, because of a higher slope and flow in the current systems, and in accordance with unpublished MONERIS model estimates by Gericke and Venohr for the Nahe. Load reduction during flood is estimated at 0.14 kg P·ha^{-1}·yr^{-1} for the Nahe, 0.05 for the Stever, 0.50 for the Azergues and 0.01 for the Bresse from local reported flood events and concentrations. The two retention mechanisms are normalized to floodplain area. Concentrations and loads for the Nahe from Ittel and Saelzer (2015), for the Stever from the ELWAS database (www.elwasweb.nrw.de), for the Azergues from Barry and Faure (2011), and for the Bresse from Gay Environnement (2016)

(Table 2. Continued.)

Service (CICES 5.1 codes)	Description	Explanation, sources
Water temperature regulation through riparian shading (2.2.6.2)	Shading affects the probability of trout survival and is expressed as a modulating effect on the cultural service angling. Knowledge rule: if 50% of the main river length is shaded by woodland, then 100% survival, else a stepwise decline in survival to a residual survival of 10%	The fish survival knowledge rule is directly linked to the value estimate for the cultural service recreative angling (Fig. 1), because trout is the most favored species for angling (Arlinghaus 2004). The trout survival knowledge rule is based on Broadmeadow et al (2011) who showed that in a stream in S England periods with water temperature over 25°C were effectively prevented if woodland cover of the stream exceeded 50% of its length. This temperature is the "incipient lethal water temperature" which, if maintained over 7 d, will cause 50% mortality
Cultural		
Recreative angling (taken separate from hunting, 1.1.6.1)	Angling days per km of stream	This is based on the proportion of households with one angler and the number of households in a catchment, and a low-end conservative estimate of their reported willingness to pay for angling per year from Arlinghaus (2004:275) and Federation Nationale de la Peche en France (2014) and Le Goffe and Salanie (2004; 130 €/yr per angler); value is normalized to river length and then floodplain area. Household numbers are derived from regional population statistics
Active recreation in the river and its floodplain corridor (all in CICES category 3.1 pooled)	Separate local estimates for the number of local and residents and tourist visitors that use and appreciate the area per year from local statistics. Multiplied with their willingness to pay for this and modulated by a knowledge rule on the appreciation of a scenic landscape: if forest cover declines below 20% tourist appreciation drops to 60%, if it is above 70% then appreciation drops to 80% (95–138 €·ha^{-1} [non-urban floodplain]·yr^{-1})	Knowledge rule on scenic landscape is based on Frank et al. (2013); willingness to pay of residents and visitors based on Elsasser et al. (2010) and Boesch et al (2018). Resident population and tourism data for the Nahe have been obtained from the public statistics of Rheinland-Pfalz: https://www.statistik.rlp.de/, those for the Stever from Wittkampf (2016), and those for Bresse and Azergues from Barry and Faure (2011)
Nature conservation non-use (all in CICES category 3.2 pooled)	Willingness to pay per valley household (5–162 €·ha^{-1} [non-urban floodplain]·yr^{-1})	Based on nationwide studies in Germany on household willingness to pay for nature conservation (Wuestemann et al. 2014; Boesch et al. 2018; 231 €·yr^{-1}·household^{-1}; 27% of households willing to pay, estimated household size 2 persons) and for France on Garcia et al. (2011), 50 €·yr^{-1}·household^{-1}; 58% of households willing to pay, household size 3 persons). Estimates adjusted to local population sizes from municipality national statistics and then normalized to floodplain area

Notes: Value estimates are expressed as euro per ha catchment per year, and monetary values can be considered approximately 2010–2015 values. An estimated biophysical service flow (e.g., kg·ha^{-1}·yr^{-1}), or a range for the monetary value estimate (€·ha^{-1}·yr^{-1}) is reported wherever it is a simple link to land use. A fully worked-out example of our data spreadsheet is provided as Data S1. In the Descriptions, the values in parentheses are ranges of monetary value estimates across the four catchments for the "current" state; or biophysical flow. RMP, riparian management practice.

Land use in floodplain segments

The four river networks were divided into river segments. These are homogenous with respect to national river types, Strahler order, and valley slope (based on the official river networks of the federal states in Germany and from the SYRAH CE network of Valette et al. 2012 in France). This resulted in river segments of different lengths up to several kilometers. To ensure comparability between segments, all segments with a length larger 1 km were subdivided into sub-segments with a length of 0.5–1.0 km and segments with a length less than 0.5 km were excluded from the analysis. The riparian area along the river sub-segments was demarcated using information on the river corridor or alluvial floodplain from local agencies or assuming it to be 12 times bank-full channel width, but at least 30 m on each side of the river. This corresponds to the functional definition of riparian

Table 3. Articulation of four Riparian Management Practices (RMPs) derived from the respective Shared Socioeconomic Pathways (SSPs, O'Neill et al. 2017; full downscaling of SSPs for the four study rivers in Vermaat et al. 2018).

Riparian management practice	Corresponding SSP label (from O'Neill et al. 2017)	In brief	Details: choices for implementation
Current, baseline	—	–	Current, the present situation in the four river systems, which approximately reflects the situation in 2015
Pessimistic	SSP3: "regional rivalry—a rocky road"	WFD no longer pursued, intensity of non-ecological agriculture is increased	• No additional WFD measures implemented, maintenance of structural measures stopped. • Woody vegetation along cropland removed
Best practice	SSP2: "middle of the road"	River management is continued in the period toward 2050 according to the current WFD regulations	• All woody buffer measures as planned in the first and second River Basin Management Plan† cycle are implemented. • In addition, similar measures were assumed to be implemented after the end of the WFD in 2027 to 2050: In the Nahe, 10 m wide woody buffers are developed along each side of all river segments that are classified as priority (Schwerpunktgewaesser) in the Nahe catchment. This is feasible for "best practice" since already between 2000 and 2015, about 1000 of the 8000 river km in Rhineland-Palatinate have been restored. In the Stever, all measures presently considered necessary to reach good ecological status are implemented. For French catchments, all the restoration programs involving riparian buffer management planned by the local stakeholders have been implemented. Furthermore, a sub-basin of Azergues and a sub-basin of Bresse had a dedicated management program for the riparian corridor, which also served as a basis for this scenario
Ambitious	SSP1: "sustainability—taking the green road"	A further development of the WFD toward a more sustainable water use	• Woody vegetation is developed in the whole riparian area, approximately corresponding to the meander belt width or active floodplain, at least a buffer of 30 m on each side of the river. • Except for the following areas: urban areas, transport lines (e.g., roads, railroads), electricity transmission corridors, open, non-forested nature reserves

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† RMBP cycle is the policy cycle of the Water Framework Directive (WFD), water quality legislation across the European Union (White and Howe 2003).

areas of Ilhardt et al. (2000) and Verry et al. (2004). Since riparian woodlands provide ecosystem services such as nutrient retention and recreation in a larger landscape context, the whole floodplain was considered in addition, which was technically implemented by demarcating the official 100-yr flooding area, covering large parts of the valley floor, but at least including the riparian area. Land use in the riparian area and floodplain was described by quantifying the area covered by the following land cover classes: urban, urban green spaces, open mining, arable land, grassland, non-woody natural vegetation, woodland-shrubs, woodland-coniferous, woodland-mixed, woodland-deciduous, lakes, wetlands, rivers, and transport lines (roads, railroads). For the two German catchments, the most detailed official land-use data set ATKIS (covering woody vegetation up from a minimum size of 0.1 ha) was complemented by woody vegetation in the riparian area down to single lines of trees along rivers identified on orthophotos using remote sensing. For the two French catchments, a land-use data set with an even higher spatial resolution was already available (0.004 ha; Decherf et al. 2014).

In addition, land-use data were changed according to the RMPs (Table 3) and the area covered by the land-use classes was recalculated.

RESULTS

In the current situation, the mean percentage of woodland in a floodplain segment was found to vary between 25% and 50%, but differences among individual rivers as well as river segments are substantial (Figs. 2, 3; Appendix S1: Fig. S1). Pooled across rivers, the three groups of services each show an "optimum curve" pattern with the available woodland in the floodplain (Fig. 2). River type, expressed as Strahler order, corresponds with the percentage woodland in the floodplain, with more woodland in lower order segments (Fig. 2). Visually estimated optima in woodland cover appears to be somewhat different for the three service groups (Fig. 2): Regulating services are maximal around 30% woodland cover (Strahler orders 4 and 5), provisioning, and cultural services around 45% (the mean woodland cover for Strahler order 2). In an overall analysis of variance (Table 4), segment area was the covariate explaining least, whereas the percentage woodland was more important than Strahler order for provisioning and cultural services, but not for regulating services. Here, Strahler order was more important, likely through the predominance of flood risk prevention. Also, both Strahler order and percentage woodland were independently significant, suggesting that they affect service delivery differently, despite the apparent underlying parallel trend in Fig. 2. Total explained variance of the model was particularly high for cultural services (48%), and this is likely due to the underlying optimum curve in the knowledge rule for the relation between recreation and woodland cover, which is supported when the individual segment estimates are inspected (Fig. 3).

For clarity, we have grouped the 16 services in the three MEA classes. Among the provisioning services, agricultural production and timber were generally most important in the current situation; among the regulating services, this was flood prevention; and among cultural services, recreation was predominant (Table 5). An exception was the Stever, where drinking water production was an important provisioning service, and non-use for biodiversity conservation was in the same order of magnitude as active recreation. The Stever was also distinctly higher in estimated agricultural value per ha than the other three rivers, likely reflecting the more intensive agricultural practice of lowland farming in Northwestern Europe (cf. Table 1).

The RMPs we outlined as plausible alternative future states of river management led to substantial differences in woodland cover in the river floodplain (Fig. 4). In all, we implemented the largest increases in woodland for the ambitious RMP. The overall effect for each river, however, was quite variable. Whereas for the Stever total ecosystem provision declined in the ambitious RMP, it increased for the other three rivers. However, within each river these differences in TEV among the RMPs are modest (maximal effect ratio ambitious/current = 1.15 for the Bresse). The effect ratio was often higher for cultural services, but this could coincide with a decline for provisioning services (e.g., 1.57 and 0.60 for the Stever, but 1.55 and 1.05 for the Bresse, see also Fig. 4). Overall, the absolute patterns were strongest for the Stever (Fig. 4), revealing a trade-off between provisioning and cultural services underlying the apparent flat response in TEV. Regulating services did not change very much across the different RMPs, particularly because they are dominated by our flood prevention estimate. Slight increases with the ambitious RMP (Fig. 4) are due to the increase in carbon sequestration with increasing woodland, and an assumed higher carbon price, and also due to a higher lateral sediment retention with increased woodland (Table 2).

DISCUSSION

Our analysis suggests that in the current landscape configuration, all three service categories showed optimum curves with increasing woodland cover: Provisioning services and cultural services were maximal around 45%, whereas this was around 30% for regulating services. This apparent systematic pattern is more variable in the individual rivers (Appendix S1: Fig. S1). The river management scenarios (RMPs) we implemented led to major differences in riparian woodland cover, but the overall effect on total ecosystem service provision (TEV) was limited.

In three of the four rivers, an increase in cultural services was accompanied with a decrease in provisioning services. Among the predictions made by Gilvear et al. (2013), only the trade-off between cultural and provisioning services was supported by our findings, which we take as an argument for caution in generalizations.

When addressing the potential effect of woodland cover on ecosystem service provision, we must keep in mind that woodland cover in the studied river systems is not low (Table 1: 19–39%), compared to the riverine landscapes such as the one studied by Vermaat et al. (2016; average 25%, range 0–81%) or Maseyk et al. (2018). The latter authors found that an increase in wooded riparian buffers from zero to 7% led to only marginal changes in dairy production, landscape amenity, and three water quality variables. Actually, a substantial proportion of the segments of the lowland rivers Stever and Bresse have woodland cover below 25% (Fig. 3), but the large spatial variability in woodland cover along the stream becomes invisible in our aggregate means (compare Figs. 2, 3). Strahler order and woodland cover covaried, so that lower order upland stream segments have more woodland.

The estimated optimum in total ecosystem service provision at intermediate woodland cover (around 45%) and intermediate Strahler order (2–3) is comfortably close to the advice of 50% from an earlier qualitative review of multiple benefits of riparian woodland (Broadmeadow and Nisbett 2004). Overall patterns in regulating, provisioning, and cultural services suggest an increase in regulating services with increasing stream order, and a decrease in provisioning services and cultural services. This is likely the consequence of the geomorphological landscape configuration in these river networks, where floodplains become larger with higher stream order, and thus have more space for flood retention, but also for competing land-use forms other than agriculture. Steeper, first-order parts of the network often have more woodland due to the combination of suitability and demand for land, as in Tomscha et al. (2017). These are also the landscapes preferred for recreation and nature conservation. We interpret this as an overall, systematic pattern, which of course is subject to substantial local variation (Fig. 3). It must be noted that we did include first-order streams, contrary to Tomscha et al. (2017), because even though a floodplain may not be apparent in the landscape, these small upland streams do flood and the riparian woodland does provide all services we considered here. Our pattern in TEV does not correspond with the findings of Felipe-Lucia et al. (2014) for a Spanish river-and-floodplain system, who report a maximum in the diversity of services provided by the floodplain with a full riparian woodland coverage, but very different approaches make a direct comparison difficult.

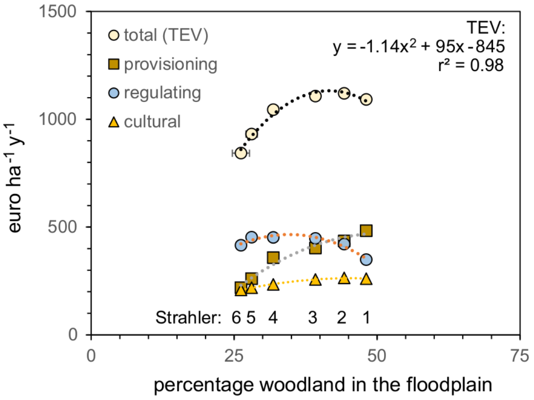

Fig. 2. Effect of the current percentage of woodland in the river corridor on ecosystem service delivery aggregated over all segments in the four river systems. The 16 services are pooled into the three MEA categories provisioning, regulating, and cultural. Strahler order is used as an ordering indicator of river type, with headwater streams having order 1. All polynomial fits are significant ($r^2 > 0.93$, $P < 0.01$), but only the one for total services is displayed. Note that vertical and horizontal standard errors are included but these are generally too small to be depicted due to the high number of segments included. Percentage woodland declined significantly with Strahler order but a regression explained a limited proportion of the variance ($y = -5x + 53$, $r^2 = 0.05$, $P < 0.001$, $n = 7622$). A similar figure broken down for the most important services and the four individual rivers is given in Appendix S1: Fig. S1.

The major change in woodland cover we realized in the ambitious RMP, which is based on the sustainability-oriented SSP1, did not lead to equally major shifts in total ecosystem service

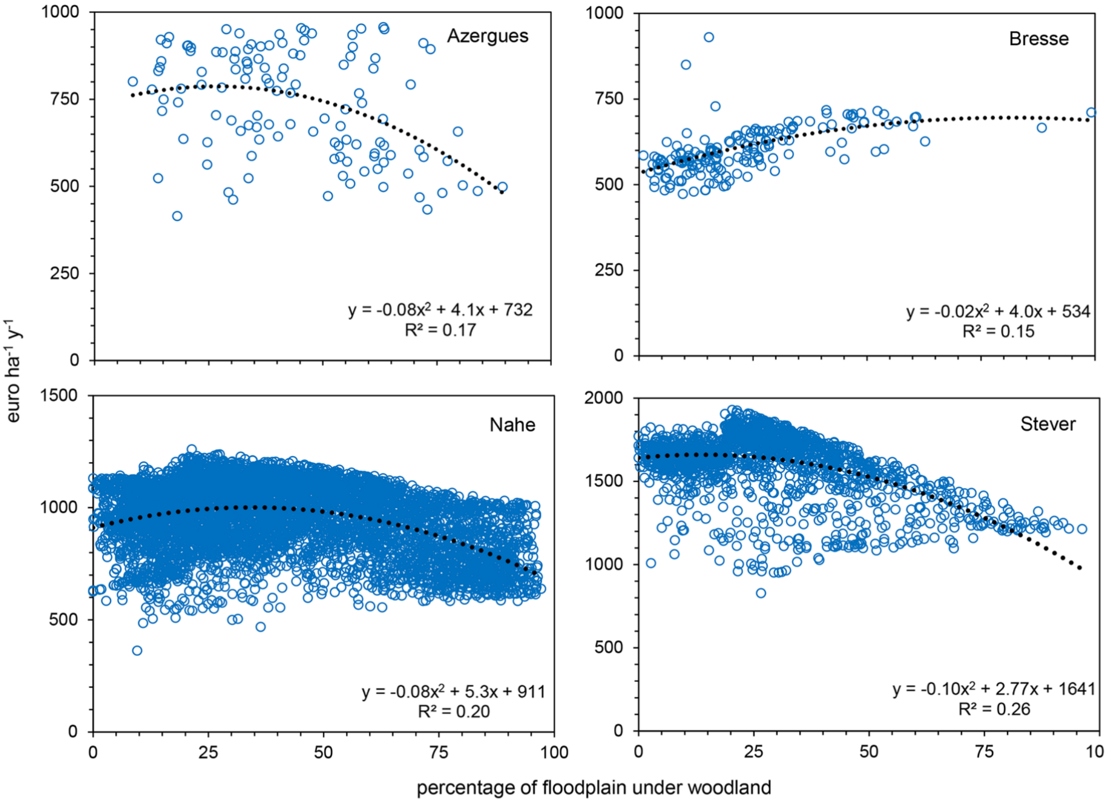

Fig. 3. Individual segment estimates of total economic value as sum of all provisioning, regulating, and cultural services quantified for all four rivers vs. current woodland cover.

delivery, but it led to an increase in cultural services at the expense of provisioning services (Fig. 4). For the Stever, it led to a decline in our value estimate of total ecosystem services, due to the replacement of intensively used agricultural land by woodland that has lower net returns and the predominance of these two provisioning services in the total value estimate (cf. Table 5). However, for the other three rivers total ecosystem service provision increased with woodland cover, particularly due to cultural services. The overall higher value of regulating services for the Nahe and the Bresse is due to a combination of absolute floodplain area (largest in the Nahe, Table 1) and the higher proportion of built-up areas (largest in the Bresse), as these contribute most to the value estimate of flood prevention (Table 2). The second most conspicuous pattern in our scenario outcomes is the limited difference between the remaining three RMPs. Both the pessimistic and the best practice RMP led to only slight changes in woodland cover with similar effects on the patterns in ecosystem service delivery. Notably in the Stever, the best practice RMP would already lead to an increase in cultural services without negatively affecting provisioning services, that is, farming output and drinking water production. It must be noted that the value estimate for nature conservation is derived from an overall appreciation of German citizens for nature protection, rather than a local appraisal of such a landscape change derived from choice experiment surveys as in, for example, Vermaat et al. (2016). Hence, this most likely is a low, conservative estimate, since local valuation studies for charismatic species, such as trout, may well elicit higher value estimates (cf. Martín-López et al. 2007). A third issue is the limited response in regulating services (Fig. 4c), which are dominated by our flood prevention estimate. This is

Table 4. Analysis of variance of the effect of Strahler order (1–6) with segment area and area woodland in the segment as covariates on total, provisioning, regulating, and cultural services value estimates.

Factor in the model	Total services	Provisioning	Regulating	Cultural
Intercept	42	9	55	20
Segment area	3	2	1	3
Area woodland in the segment	42	64	10	75
Strahler order	13	25	34	2
Total variance explained by the model (%)	19	21	23	48

Notes: Data pooled over the four river systems. Total degrees of freedom 7624. Presented are the percentage in the model sums of squares attributed to each factor and the total variance explained by the corrected model. All three factors included explained a highly significant part of the variance ($P < 0.001$).

Table 5. Most important (contributing >5 €·ha^{-1}·yr^{-1}) ecosystem services for each of the four study rivers under the current situation.

	Provisioning (€·ha^{-1}·yr^{-1})			Regulating (€·ha^{-1}·yr^{-1})			Cultural (€·ha^{-1}·yr^{-1})		
River (TEV)	Service	Mean	%	Service	Mean	%	Service	Mean	%
Nahe (935)	Dairy	140	53	Flood prevention	412	97	Recreation	115	46
	Timber	63	24	Carbon sequestration	10	2	Angling	70	28
	Crops	42	16				Conservation non-use	63	25
	Subtotal	264			423			248	
Stever (1590)	Crops	464	44	Flood prevention	299	91	Recreation	78	37
	Drinking water	353	34	Water quality: P-retention	13	3	Conservation non-use	73	35
	Dairy	168	16	Carbon sequestration	7	4	Angling	59	28
	Subtotal	1062			319			210	
Bresse (538)	Dairy	52	36	Flood prevention	279	96	Recreation	72	70
	Crops	51	35	Water quality: P-retention	6	2	Conservation non-use	17	17
	Timber	25	18	Carbon sequestration	5	2	Angling	13	13
	Fish culture	14	9						
	Subtotal	146			290			102	
Azergues (787)	Dairy	50	33	Flood prevention	487	97	Recreation	85	65
	Crops	48	31	Carbon sequestration	9	2	Angling	33	25
	Timber	42	28	Water quality: P-retention	8	2	Conservation non-use	13	10
	Subtotal	152			504			131	

Note: Presented ares mean estimated monetary value per ha, percentage contributed to its MEA class, as well as subtotals and grand totals, the latter an estimate of total economic value (TEV).

likely due to the fact that we have not varied population density, settlement policy or land and house pricing, or the location of settlements in our RMPs because we chose these RMPs to be limited to measures within the remit of European water management institutions. Thus, our estimate of flood damage value is likely both a conservative low-end value and unrealistically stable, but we think it is justified to limit the number of assumptions in our scenario articulations. Finally, Fig. 4 suggests a trade-off between provisioning and cultural services, in contrast to what we deduce from the pattern in the current situation in Fig. 2. So, if the current situation is pushed toward the occupation of agricultural land with woodland (ambitious RMP), this leads to a decline in overall value—an obvious "trade-off." Martín-López et al. (2012) also found a trade-off between provisioning and cultural services in an extensive study of societal preferences in eight areas across Spain. The apparent contradiction in our data is due to the fact that in the "current" situation we see a changing pattern along the length of the four rivers pooled, whereas when the comparison with the ambitious RMP is made, we see a change over time, and the separate pattern for each river is not equally intense.

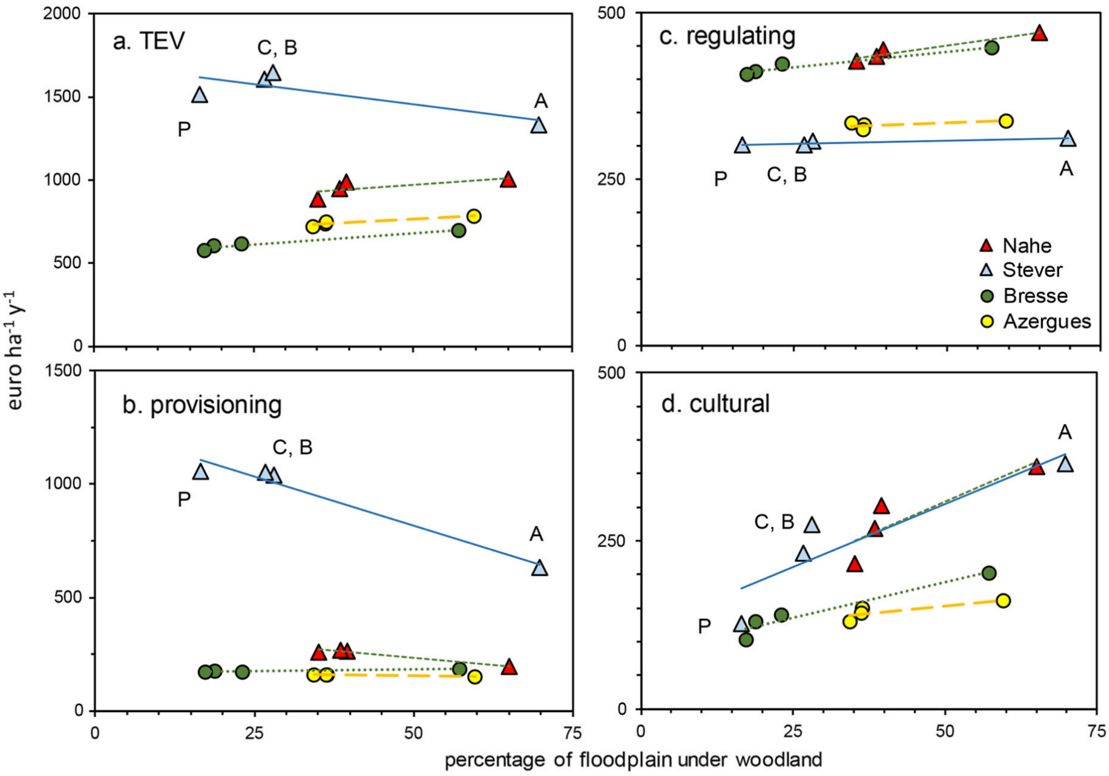

Fig. 4. Effect of the different Riparian Management Practices (RMPs) on (a) total ecosystem service delivery expressed as total economic value, (b) regulating, (c) provisioning, and (d) cultural services, all plotted against the percentage of woodland for each RMP. P, pessimistic; C, current; B, best practice and A, ambitious. The order of woodland cover of these four RMPs is the same for each river, from low to high: P, C, B, A. Different symbols indicate the four different rivers (see legend).

The "Mononen cascade" framework applied here was developed from the cascade model proposed by Mononen et al. (2016), which again has its roots in the cascade presented by among others Haines-Young and Potschin (2010). We will not reiterate the discussion whether "nature can be valued at all" (Gómez-Baggethun et al. 2010, Hermelingmeier and Nicholas 2017), but important premises of our approach are that one can attribute final services to land-use cover types and that monetary estimates of these services are consistent and "valid," though not necessarily "accurate" or "precise." Our compilation of different value estimates each with its underlying approaches and assumptions is a seriously disputed aspect of TEV estimates (among others Schröter et al. 2014). We think it allows comparison across scenarios or policy alternatives and services, if only framed carefully in a consistent study design (Boerema et al. 2017, Hanna et al. 2018), and thus can be used to inform policy. The valuation step, in principle, is not different from using a ranking scale which is summed, as applied in, for example, Burkhard et al. (2009) or Newton et al. (2012), but the monetary valuation causes a weighing of the different services, rather than treating all individual services as equal. Our weighing with a monetary ruler is equally traceable as using ranks or scores (Table 2), but it is based on expressed societal preferences, which indeed may lead to lower value estimates for nature conservation non-use than for active recreation (Table 5), although in three of our four rivers these are remarkably close. Vermaat et al. (2020) discuss the methodological strengths and weaknesses of the current framework in more detail.

Briefly, we see two important limitations of our current study. First, our approach would have benefited from a spatial linking of stream segments in the river network, so that we could have estimated flood prevention, but also nutrient and sediment retention in a more realistic way. We are not aware of a study that has succeeded in combining such hydrological realism with an assessment of the full suite of ecosystem services. Second, we have not done a formal uncertainty or sensitivity analysis, because estimating uncertainties without empirical basis would be mere guesswork. For example, a sensitivity analysis on the effect of our flood prevention estimate in the sum of regulating services and also that of our knowledge rule on the effect of woodland cover on recreational appreciation would have been useful. Vermaat et al. (2016) assessed changes in ecosystem service provision due to restoration of European rivers and their floodplains with a similar though less formalized approach. Our current TEV estimates are similar in order of magnitude (their median unrestored TEV 1000 €·ha^{-1}·yr^{-1}; ours 843 €·ha^{-1}·yr^{-1}). A final methodological point is our consistent choice for the most conservative low-end estimate, wherever we had the choice. Our justification is that we want to remain far from optimistic advocacy (Bouma and van Beukering 2015) and that we combine estimates based on highly different underlying approaches, but the consequence is that some of our estimates indeed are low. An obvious example is carbon sequestration: Other work, such as the natural capital accounting exercise for the UK (Trenbirth and Dutton 2020), uses 20 €/t C for non-traded carbon equivalents as a mid-level for 2010 which increases in the subsequent years, compared to our baseline of 5 €/t (Table 2). Overall, this implies that our value estimates best can be seen as indicative, but internally consistent, and then for an approximate time window of 2010–2015 for the baseline scenario.

If we equate our ambitious RMP to a major restoration effort, we can test the hypothesis of Gilvear et al. (2013). Increased woodland cover, however, only led to a substantial decrease in provisioning services in one of the four rivers, regulating services increased in two, whereas cultural services indeed increased in all cases. Hence, we cannot simply generalize along the lines of Gilvear et al. (2013) but must revert to more service- or landscape-specific hypotheses. For example, the market value of woodland linked to timber and an increasing demand for biomass to replace fossil fuel (Trømborg et al. 2020) should not be ignored, but also the intensity of adjacent land use, and hence, the land rent (cf. the Stever and Vermaat et al. 2016) is relevant when monetary value estimates of all possible services are of interest. At the landscape scale of a river and its floodplain, we see that greatly increasing the percentage covered with woodland, as in the ambitious RMP, may well lead to an increase in cultural services, hence appreciation by recreation including anglers, at the expense of provisioning services, here particularly agriculture.

Compared to previous assessments of ecosystem services provision along rivers, our study combines high spatial detail, a comprehensive and well-defined set of ecosystem services that includes a final monetary value estimate, and a verification stage with stakeholder representatives, rather than a limited selection of services or a rank-based scoring system. This largely corresponds with the five recommendations made by Hanna et al. (2018): assess multiple services, use reproducible data and methods, include service interactions, select extent study area relevant to question, and engage with stakeholders. The latter has been important in the verification of our scenario's, without these reflective workshops, our scenario articulations as RMPs would have been less realistic to river managers and land-use planners. At the same time, we experienced that we had to maintain a balance with our basis in the benchmark SSPs to ensure comparability with other scientific work on scenarios.

In conclusion, we have shown that our set of seven provisioning, six regulating, and three cultural services, as quantified with the "Mononen cascade" for four central European river systems, currently all show optimum curves with increasing woodland cover: Provisioning services and cultural services were maximal around 45%, whereas this was around 30% for regulating services. On average, river type, expressed as Strahler order, was found to correspond quite closely with the percentage woodland in the floodplain, with more woodland in steeper lower order segments.

Geomorphological and land cover variation among and within individual river systems is pooled into this average, but can be substantial (Table 1, Fig. 3; Appendix S1: Fig. S1). The three different modeled woodland cover scenarios led to a remarkably limited change in total ecosystem service delivery, even if mean woodland cover was reduced from 27% to 17% in the pessimistic RMP and increased to 70% in the ambitious RMP for the most extreme case of the Stever. We did, however, see a clear decline of provisioning service with increased woodland cover and an increase in cultural services. Regulating services did not change that much, because they are dominated by flood prevention in our assessment. It appears that the "best practice" scenario combines a modest increase in cultural services with a slight increase in provisioning services. Also, the outcome suggests that very ambitious nature conservation objectives can be met with a limited decrease in total societal benefit (TEV) only, and despite the low-end monetary value estimates for nature conservation non-use.

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3 General Discussion

The research assembled in this thesis supports the conjecture that woody riparian vegetation is a natural control on aquatic systems on various levels as expected from the overwhelming collection of evidence in literature. First, Kail et al. (2021) assess the effect of a singular function of woody cover in effective temperature control. Second, while initially falling short of demonstrating effects on the higher level of the macroinvertebrate ecological status assessment, in Le Gall et al. (2022) and Palt et al. (2022), Palt et al. (submitted) reconciles the underlying literature with empirical evidence by demonstrating strong context-specific relationships. Third, Vermaat et al. (2021) show that management of floodplain woody cover even while following highly ambitious standards does not have to come at a high cost on the socioeconomic level.

Regarding the effect on water temperature regulation, the findings in Kail et al. (2021) are encouraging for river managers given that a 10 m wide continuous strip of woody cover already can successfully mitigate lack of shading in an upstream section after few hundred meters to great extent. The magnitude of the effects is in the realm of other studies on this topic (e.g. Rutherford et al., 2004), which suggests a fair degree of transferability and generalization.
From the perspective of management, 10 m wide buffers are entirely realistic, albeit not manageable everywhere given current circumstances. Nevertheless, since heating in small streams due to widespread lacks of shading accumulates in tributaries across drainage basins, the effect becomes practically irreversible in the larger more downstream stretches. Excess thermal energy there no longer can be mitigated by managing shade. Crucially with increasing stream size human uses might in turn become impaired (e.g. use of cooling in thermal power plants), linking this function of woody riparian vegetation to quite prominent provisioning ecosystem services. Emotively phrased, every watt of energy intercepted from penetrating small streams by a canopy cover within a catchment does not straightforwardly factor into water temperatures at its outlet.
Coincidentally, the small tributaries lacking shade for long stretches, which would benefit from riparian management for the purposes of temperature regulation, typically can be found in agricultural landscapes, where they literally are channel past arable lands. This is also where the strongest effects on macroinvertebrates are found by Palt et al. (submitted) and where woody riparian vegetation is required for maintaining or achieving a good ecological status. These synergies need to be considered when restoration measures are planned. For instance, while planting a theoretical dense strip of non-native deciduous plants might serve the purposes of

temperature regulation from a purely technical point of view, sacrificing diversity and not allowing a native and adapted biocenosis constitutes a wasted opportunity of achieving multiple goals simultaneously. Given the magnitude of effects achieved by woody cover on temperature regulation as well as the potentially feasible amount of woody riparian cover needed, there should be strong motivation for further concerted efforts protecting streams and making them more resilient facing climate changes.

Thanks to the year round water temperature measurements it is possible to distinguish between conditions in early spring and summer. It is encouraging to see that effects are very strong in spring when many aquatic organisms are actually in crucial phases of their development. Providing stable habitat conditions by maintaining moderate diurnal water temperature amplitudes should be highly beneficial. Also by encompassing different meteorological conditions over the long period of data collection, more general effect sizes are quantified next to the already well established, albeit important, strongest effects on sunny, hot days. This allows for the development of simple tools, that practitioners can rely on in order to simulate possible effects in stream reaches they know. An example for such a tool has been derived from this study within the OSCAR Biodiversa project (https://mars-project-sat.shinyapps.io/oscar_temperature_empirical/). Thanks to the large dataset it is also possible to communicate expected variability based on these results.

Large datasets initially prove to be a challenge with regards to assessing the effect of woody riparian vegetation on macroinvertebrate communities (Le Gall et al., 2022; Palt et al., 2022). As riparian areas are located on the edge of terrestrial and aquatic systems it is not surprising, that catchment landuse pressures would be of great importance (Dahm et al., 2013). Additionally, there exist some mechanisms that circumvent riparian buffers altogether so a decoupling of catchment stressors from freshwater ecosystems is not possible (e.g. drainage of arable land, waste water effluents; Section 1.1). Due to the high diversity of functional links and context variables, weighing functions and their effects is still illusive.

Despite using very high resolution data on woody cover within the riparian corridor, the gap between the thoroughly documented individual functional links between woody riparian vegetation and macroinvertebrates as an instream biotic quality element, is not closed. Relying on woody cover derived from orthoimages specifically for Palt et al. (2022) does not facilitate more insight than more pragmatic previous approaches (e.g. Death & Collier, 2010). Only by disentangling the context of functioning of woody riparian vegetation are the actual effects successfully embedded in the landscape that they occur in (Palt et al., submitted). In this case, the differentiation between subdatasets is data-driven, as opposed to Tolkkinen et al. (2021)

who otherwise found very similar effect sizes. This shows that goals set by the Water Framework Directive can be indeed achieved by management on the spatial scales available to river managers. Nevertheless, by describing subdatasets with limited albeit significant (e.g. some degrees of urban landuse) or with no effects form wood riparian vegetation at all (e.g. mixture of urban landuse and strongly impaired hydromorphology), clearly there exist limitations. While this might potentially even play a role in explaining the ongoing lack of success despite widespread restoration and conservation activities in freshwater ecosystems (Jähnig et al., 2010) it more importantly calls for some prioritisation of measures as well as realistic management of context-dependent expectations. In continuation to Feld et al. (2018) scale dependencies of the effects of woody riparian vegetation do not only exist within the riparian corridor but also on the level of catchment landuse and pressures.

Despite the additional encouragement derived from e.g. Kail et al. (2021) and Palt et al. (2022) that positive outcomes form riparian restoration are rightfully expected, it does not seem likely that planers would start allocating the amounts of landcover required to fulfil potential functionalities (ca. 30 m wide buffers, Section 1.1) for establishing meaningful woody riparian vegetation, given constraints regarding ownership of land and competing interests with agriculture as well as e.g. flood protection.

However, Vermaat et al. (2021) show that ambitious management of woody riparian vegetation including converting agricultural areas is socioeconomically viable as a whole. While there exists an optimum curve in monetizing nature's contribution to people with respect to woodland cover in the floodplain, even woody cover excessive of that maximum is not overly costly on an economical level. However there is nuance to this, since this is mostly due to a shift from provisioning to cultural ecosystem services.

Consequently, riverine restoration needs to be addressed at a social and societal level as well. For one, a fair and appropriate economical compensation for the loss of immediate productivity needs to be put in place, where it is not so already. Otherwise, existing resistance from landowners towards any changes to agricultural practices or even property will likely not waver. Sustainable solutions need not only to be so ecologically speaking, but also socially as well as economically. Therefore participatory processes driven by dialog between stakeholders remain highly integral.

Given the importance of social benefits to balance losses of provisioning services, it is furthermore necessary to partly reconsider goals of restoration and conservation of freshwater ecosystems anew. Without sacrificing on ecological goals it seems possible to attract societal revenue, either through monetized goods and services (e.g. recreational angling, commercial canoeing) but also much more generally through other contributions to people by nature, such as landscape aesthetics, sense of identity or merely providing a backdrop for social relations (Hanna et al; 2018; Kaiser et al., 2021). As sweeping ecological scuesses of restoration activities continue to linger, by incorporating synergies between biological and societal goals, acceptance for further and even more ambitious efforts can be generated in order to keep momentum on the way to more ecologically health freshwater ecosystems.

4 Conclusion

This theses is concerned with woody riparian vegetation as a standalone landscape feature on various levels: individual effects on the physical aquatic environment, effects on aquatic communities as a whole, as well as human benefits from floodplain landcover.

Notwithstanding, the straightforward and therefore highly helpful messages to practitioners in river management regarding water temperature control (Kail et al., 2021) and ecosystem services (Vermaat et al., 2021), contextualizing effects on riverine biota is probably where this thesis is most important. By demonstrating both the initial limitations (Le Gall et al., 2022; Palt et al., 2022) but also the ability to then successfully disentangle relevant effects from their larger-scale contexts (Palt et al., submitted), old lessons can be learned again for future research and management. Firstly, responses, processes and predictors are predictably non-linear. Persistence in developing sound analytical frameworks is key. Secondly, and more significantly, established knowledge from vast numbers of studies is translated into dimensions meaningful to practitioners, i.e. the ecological status. This quantifies what is at stake for riparian management and as a whole this thesis hopefully encourages effective restoration planning.

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Formal Declarations

Declaration:

In accordance with § 6 (para. 2, clause g) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I represent the field to which the topic "Impact of woody riparian vegetation along streams on aquatic biodiversity" is assigned in research and teaching and that I support the application of Martin Palt.

Essen, _____________ ____

Name and signature of the
scientific supervisor/member of the member of the
University of Duisburg-Essen

Declaration:

In accordance with § 7 (para. 2, clause d and f) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I have written the herewith submitted dissertation independently using only the materials listed, and have cited all sources taken over verbatim or in content as such.

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Signature of the doctoral candidate

Declaration:

In accordance with § 7 (para. 2, clause e and g) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I have undertaken no previous attempts to attain a doctoral degree, that the current work has not been rejected by any other faculty, and that I am submitting the dissertation only in this procedure.

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Signature of the doctoral candidate