DOCTORAL (PHD) DISSERTATION

THE EFFECTS OF LAND USE CHANGE ON AQUATIC COMMUNITIES

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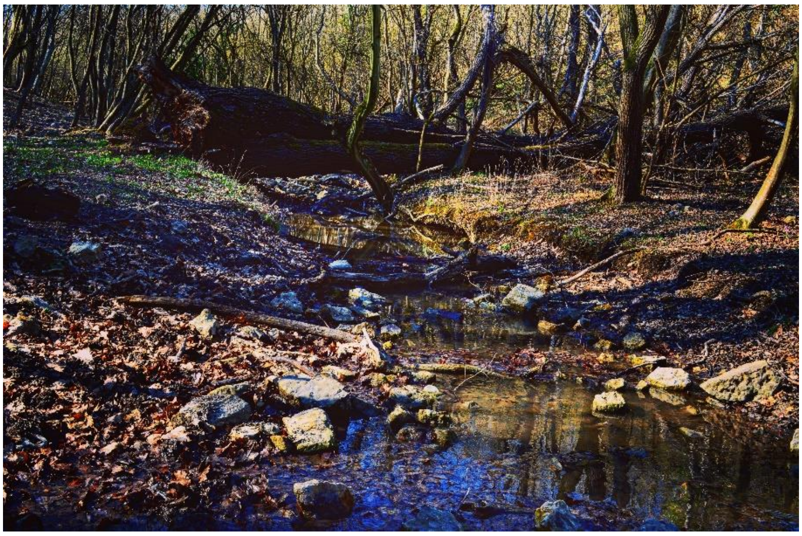

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The effects of land use change on aquatic communities

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Propose acceptance (yes / no)

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Content

ABSTRACT

Land use changes pose a huge threat to freshwater ecosystems all over the world. Effective management and conservation of freshwater ecosystems require a comprehensive understanding of the complex impacts of land use changes on the freshwater environment and ecology. The aim of this dissertation was to study the effects of land use changes in various freshwater ecosystems. Accordingly, the main objectives included:

i. Investigating the impact of an urban environment in the Balaton Uplands by comparing streams running through natural and urban areas, as well as the macroinvertebrate communities inhabiting them.
ii. Exploring the impacts of the transformation of natural reed-vegetated shorelines into recreational beaches on chironomid assemblages in Lake Balaton.
iii. Examining the consequences of linear infrastructures and landscape fragmentation on larval amphibian communities of ponds in Western Hungary.

The major conclusions of the thesis were as follows:

i. There were notable distinctions between the natural and urban stream environments. Urban sections were characterized by a high proportion of concrete, algae, plants and high current velocity, while a low proportion of particulate organic matter, wood and canopy coverage, and degraded condition of riparian vegetation. Urbanization had a negative impact on taxa richness and Shannon diversity of macroinvertebrates and altered their assemblage composition, however, these biotic attributes exhibited considerable variability across different streams. While under natural conditions the significance of microhabitat heterogeneity prevailed, in urban sections the relevance of site-level parameters became more prominent suggesting that under such conditions, not only microhabitat but broader-scale (site, landscape) factors may contribute to shaping the composition of macroinvertebrate assemblages.
ii. Environmental variables showed significant differences between natural reed, open and beach habitats in Lake Balaton. The reed habitat was characterized by low dissolved oxygen, high amount of macrophytes and algae, and a high organic matter content. The open habitat was characterized by deep water and high pH, while the beach habitat differed from the reed and open habitat as it had the highest proportion of sand substrate. The transformation from a natural reed shoreline to a recreational beach had an overall negative impact on the richness and abundance of chironomids causing 18% reduction in the taxon richness and 5.6% reduction in abundance, along with altered community

composition. However, biotic parameters showed a significant variation depending on the shoreline of Lake Balaton from which the samples were taken, i.e. whether it was the southern or northern shoreline. Chironomid assemblages in the northern shoreline appeared to be more susceptible to habitat transformation.

iii. Among landscape variables, distance to the nearest highway and the percentage cover of road surface within a 1000-m radius had the strongest and clearest effect on the mean community abundance of amphibian larvae. Relationships with accessible habitat and total habitat amount were uncertain, while there were no clear relationships with a major railway. Considering habitat variables, larval abundance increased with pond size, but there were mixed relationships with the presence of fish. Our findings imply that road effects had a stronger impact on amphibian abundance than the combined effects of roads and habitat amount in the study area. Highways appeared to be negatively impacting amphibian communities within a wide road-effect zone up to 1 km from ponds.

Land use changes induce degradation of the local environment and natural landscape. Richness and abundance of freshwater organisms, such as macroinvertebrates and amphibians, displayed significant declines on account of habitat transformations and urbanization. However, biotic responses showed considerable variations depending on the environment and the species composition. It indicates that to better understand the effects of these land use changes on freshwater ecosystems a holistic approach is required considering both comprehensive and individual aspects.

ZUSAMMENFASSUNG

DIE AUSWIRKUNGEN VON LANDNUTZUNGSÄNDERUNGEN AUF AQUATISCHE GEMEINSCHAFTEN

Landnutzungsänderungen stellen eine enorme Bedrohung für Süßwasserökosysteme weltweit dar. Eine effektive Bewirtschaftung und Erhaltung von Süßwasserökosystemen erfordert ein umfassendes Verständnis der komplexen Auswirkungen von Landnutzungsänderungen auf die Süßwasserumwelt und -ökologie. Das Ziel dieser Dissertation war es, die Auswirkungen von Veränderungen in der Landnutzung in verschiedenen Süßwassergewässern zu untersuchen. Entsprechend umfassten die Hauptziele:

i. Die Untersuchung der Auswirkungen der urbanen Umwelt im Balaton-Hochland durch den Vergleich von Bächen in natürlichen und städtischen Gebieten sowie der sie bewohnenden Makroinvertebraten- Gemeinschaften.
ii. Die Auswirkungen der Umwandlung natürlicher Schilf-Ufergebiete in Freizeitstrände auf Chironomiden-Gemeinschaften im Balaton-See erforschen.
iii. Untersuchung der Auswirkungen von linearen Infrastrukturen und der Fragmentierung der Landschaft auf Larven-Amphibiengemeinschaften in Teichen in Westungarn.

Die wichtigsten Schlussfolgerungen der Arbeit waren wie folgt:

i. Es gab bemerkenswerte Unterschiede zwischen den natürlichen und städtischen Fließgewässerumgebungen. Die städtischen Abschnitte zeichneten sich durch einen hohen Anteil an Beton, Algen, Pflanzen und höherer Strömungsgeschwindigkeit aus, während der Anteil an partikulärer organischer Substanz, Holz und Überdachung der Vegetation gering war und der Zustand der Ufervegetation degradiert war. Die Urbanisierung hatte einen negativen Einfluss auf die Artenvielfalt und Shannon-Diversität der Makroinvertebraten sowie auf deren Gemeinschaftszusammensetzung. Dennoch zeigten diese biotischen Merkmale erhebliche Variabilität zwischen verschiedenen Gewässern. Während unter natürlichen Bedingungen die Bedeutung der Mikrohabitat-Heterogenität überwog, wurde in städtischen Abschnitten die Relevanz von standortspezifischen Parametern stärker betont. Dies legt nahe, dass unter solchen Bedingungen sowohl Faktoren auf Mikrohabitat-Ebene als auch auf breiterer Skala (Standort, Landschaft) zur Gestaltung der Zusammensetzung von Makroinvertebratengemeinschaften beitragen können.

ii. Umweltvariablen zeigten signifikante Unterschiede zwischen natürlichen Schilf-, offenen und Strandhabitaten am Balaton. Das Schilfhabitat war durch einen niedrigen Sauerstoffgehalt, eine hohe Anzahl von Makrophyten und Algen sowie einen hohen Organikgehalt gekennzeichnet. Das offene Habitat zeichnete sich durch tiefe Gewässer und einen hohen pH-Wert aus, während sich das Strandhabitat vom Schilf- und offenen Habitat unterschied, da es den höchsten Anteil an Sandsubstrat aufwies. Die Umwandlung von natürlichen Schilfufern in Erholungsstrände hatte insgesamt einen negativen Einfluss auf die Artenvielfalt und Häufigkeit von Zuckmücken, wodurch die Artenvielfalt um 18% und die Häufigkeit um 5,6% reduziert wurden und sich die Gemeinschaftszusammensetzung veränderte. Jedoch zeigten biotische Parameter eine signifikante Variation abhängig davon, von welchem Ufer des Balaton-Sees die Proben genommen wurden, d.h. ob es sich um das südliche oder nördliche Ufer handelte. Chironomiden-Gemeinschaften am nördlichen Ufer schienen anfälliger für die Veränderung des Lebensraums zu sein.

iii. Unter den Landschaftsvariablen hatten die Entfernung zur nächsten Autobahn und der prozentuale Anteil der Straßenfläche im Umkreis von 1000 m den stärksten und deutlichsten Einfluss auf die durchschnittliche Gemeinschaftshäufigkeit von Amphibienlarven. Die Beziehungen zu zugänglichem Lebensraum und zur Gesamtanzahl des Lebensraums waren unsicher, während es keine klaren Beziehungen zu einer Hauptbahn gab. In Bezug auf die Habitatvariablen erhöhte sich die Larvenhäufigkeit mit der Teichgröße, aber es gab gemischte Beziehungen zur Anwesenheit von Fischen. Unsere Ergebnisse legen nahe, dass die Auswirkungen von Straßen einen stärkeren Einfluss auf die Amphibienhäufigkeit hatten als die kombinierten Effekte von Straßen und der Menge an Lebensraum in der Studienregion. Autobahnen scheinen Amphibienpopulationen in einem breiten Straßeneffekt-Bereich von bis zu 1 km Entfernung von den Teichen negativ zu beeinflussen.

Landnutzungsänderungen deuten auf eine Verschlechterung der lokalen Umwelt und der natürlichen Landschaft hin. Die Vielfalt und Häufigkeit von Süßwasserorganismen wie Wirbellosen und Amphibien nahmen aufgrund von Lebensraumveränderungen und Urbanisierung signifikant ab. Die biotischen Reaktionen zeigten jedoch erhebliche Variationen, abhängig von der Umwelt und der Artenzusammensetzung. Dies deutet darauf hin, dass zur besseren Erforschung der Auswirkungen dieser Landnutzungsänderungen auf

Süßwasserökosysteme ein ganzheitlicher Ansatz erforderlich ist, der sowohl umfassende als auch individuelle Aspekte berücksichtigt.

KIVONAT

A TÁJHASZNÁLATBAN BEKÖVETKEZŐ VÁLTOZÁSOK HATÁSA A VÍZI KÖZÖSSÉGEKRE

A tájhasználatban bekövetkező változások jelentős fenyegetést jelentenek a világ édesvízi ökoszisztémáira. Az édesvízi ökoszisztémák hatékony kezelése és megőrzése megköveteli a földhasználati változások édesvízi környezetre és ökológiára gyakorolt hatásainak átfogó megértését. Jelen disszertáció tudományos célkitűzése az volt, hogy tanulmányozza a tájhasználatban bekövetkező változások hatásait különböző édesvízi ökoszisztémákban. Ennek megfelelően a fő célkitűzések a következők voltak:

i. Felmérni a városi környezet átalakító hatását a Balaton-felvidéken a természetes és városi környezetben futó patakok, illetve az azokban élő makroszkopikus vízi gerinctelen együttesek összehasonlítása révén.
ii. Feltárni, hogy a Balaton természetes nádasainak rekreációs célú strandokká történő átalakítása milyen hatással van az ott élő árvaszúnyog együttesekre.
iii. Megvizsgálni, hogy milyen következményei vannak az utaknak és a tájszintű fragmentációnak a nyugat-magyarországi kistavak kétéltű közösségeire.

A disszertáció főbb következtetései a következők voltak:

i. Jelentős különbségeket lehetett megfigyelni a természetes és városi patak környezet között. A városi szakaszokat a betonozottság, az alga, a vízi növényzet magas aránya, nagy áramlási sebesség, alacsony szemcsés szervesanyag tartalom, a fásszárúak hiánya, alacsony lombkorona lefedettség, illetve leromlott állapotú parti vegetáció jellemezte. Az urbanizáció negatív hatással volt a makrogerinctelenek fajgazdagságára és Shannon-diverzitására, és megváltoztatta fajösszetételüket. Azonban ezek a biotikus jellemzők jelentős változékonyságot mutattak a különböző patakok között. Míg természetes körülmények között a mikrokörnyezet változatosságának jelentősége érvényesült, a városi szakaszokban az élőhelyszintű paraméterek relevanciája hangsúlyosabbá vált, ami arra utal, hogy ilyen körülmények között mind a mikrokörnyezeti tényezők, mind a tágabb térbeli skálájú faktorok (élőhely, táj) hozzájárulhatnak a makrogerinctelen együttesek szerveződéséhez.
ii. A környezeti változók szignifikáns különbségeket mutattak a természetes nádas, a nyíltvízi és a strandi élőhelyek között a Balatonban. A természetes nádast alacsony oldott oxigéntartalom, nagy mennyiségű makrofita és alga, valamint magas

szervesanyag tartalom jellemezte. A nyíltvizet nagy vízmélység és magas pH jellemezte, míg a strandok abban különböztek leginkább a nádastól és a nyíltvízi élőhelytől, hogy a domináns üledék a homok volt. A természetes nádas átalakítása rekreációs célú strandokká általánosságban negatív hatással volt az árvaszúnyogok fajgazdagságára és abundanciájára, 18%-os csökkenést okozva a fajszámban és 5,6%-os csökkenést az abundanciában, mindeközben megváltoztatta az árvaszúnyog közösség összetételét is. A biotikus paraméterek azonban jelentős eltérést mutattak attól függően, hogy a Balaton melyik partvonaláról vettük a mintákat, azaz hogy a déli vagy az északi partvonalról volt-e szó. Az északi partvonalon található árvaszúnyog együttesek érzékenyebbek voltak az élőhelyátalakításra.

iii. A kétéltű lárvák átlagos egyedszámára a tájszintű változók közül a legerőteljesebb hatást a tavak úttól mért távolsága és az útburkolat a tavak körül meghatározott 1 km sugarú körön belüli aránya gyakorolta. Az elérhető és az összes élőhely mennyisége és a lárvák abundanciája közötti kapcsolat bizonytalan volt, míg a vasút nem mutatott egyértelmű hatást. A lokális élőhelyi változókat tekintve a lárvaállomány növekedett a tó méretével, de vegyes hatások mutatkoztak a halak jelenlétével. Eredményeink azt mutatják, hogy az utak közvetlen hatása erőteljesebb a kétéltűekre, mint az utak és az élőhely mennyiségének kombinált hatása a vizsgált területen. Úgy tűnik azonban, hogy az utak akár 1 km távolság esetén is negatív hatással lehetnek a tavak kétéltű közösségeire.

A tájhasználatban bekövetkező változások a helyi környezet és a természeti táj leromlását okozzák. Az édesvízi élőlények, esetünkben a makrogerinctelenek és a kétéltűek fajszáma és abundanciája jelentős csökkenést mutatott az élőhelyek átalakulása és az urbanizáció következtében. A biotikus válaszok azonban jelentős eltéréseket mutattak a környezettől és a fajösszetételtől függően. Mindez azt mutatja, hogy ezen tájhasználati változások édesvízi ökoszisztémákra gyakorolt hatásainak jobb megértéséhez holisztikus megközelítésre van szükség, amely mind átfogó, mind egyedi szempontokat figyelembe vesz.

1. INTRODUCTION

Humans, as the most influential ecosystem engineer species on Earth, significantly transform their environment and directly or indirectly alter the availability of resources of other species (Jones et al., 1994). They generally modify their environment to satisfy their increasing needs. Land use refers to the human activities and practices that occur on a piece of land. It encompasses how the land is utilized, managed, and modified for various purposes, including residential, commercial, industrial, agricultural, recreational, and conservation purposes, for example: urban area, cropland, pasture, forest, grassland etc. Land use determines how land resources are allocated and distributed to meet the needs of human communities. It involves decisions regarding the location, design, and intensity of land development, as well as the allocation of land for different uses. Land use is influenced by social, economic, cultural, and environmental factors, and it plays a crucial role in shaping the physical, social, and ecological characteristics of a region. Land use change refers to the alteration or modification of the way land is utilized for various human activities. It involves transforming the purpose or characteristics of the land, typically from one land use type to another. The most important processes of land use changes include urbanization, agricultural expansion, deforestation, land reclamation, industrialisation, and infrastructure development. Urbanization refers to the conversion of natural, rural or undeveloped land into urban areas, including the construction of buildings, roads, and infrastructure to accommodate growing populations. Agricultural expansion includes the transformation of natural habitats, such as forests or grasslands, into agricultural land for crop cultivation or livestock farming to meet the increasing demand for food. Deforestation is the clearing of forests for various purposes, including timber extraction, urban land, agricultural expansion, or any infrastructure development. Land reclamation includes the process of converting bodies of water or wetlands into land for agricultural, residential, or industrial purposes, typically through drainage or filling. Industrialisation is a change of land for industrial purposes, such as the establishment of factories, power plants, or mining operations. Finally, infrastructure development is the construction of transportation networks, such as roads, highways, railways, airports and ports to improve connectivity and facilitate trade and transportation which processes are strictly associated with urbanization. These indicate that urbanization and agriculture are the main drivers of land use changes and other processes usually serve urban or agricultural purposes. In the ecological aspect, land use change includes any way in which humans modify natural landscapes. Human populations exploit natural resources and shape their environment since their emergence (Ellis, 2021), however, we consider land use and land use change in a strict sense with the appearance of agriculture and permanent settlements around 10,000 years ago (Stephens et al., 2019). Converting natural habitats into agricultural lands and human settlements initiated the complex ecosystem changing activity of humans which resulted in the most rapid degradation of natural systems in Earth’s history. Despite the growing attention towards the global environmental changes resulting from human activities, ranging from intensified agricultural practices through urbanization to human recreation, there is still limited understanding of the environmental impacts caused by human land use on Earth's transformation.

One of the most destructive land use changes is urbanization. Urbanization is the movement of people from rural to urban areas and the conversion of the rural environment to urban leading to increased population size in cities, the expansion of urban land area and a growing number of settlements (UN DESA, 2019). The growing human population, reaching now eight billion (UN DESA, 2022), drives urban development and *vice versa* to such an extent that it presents the greatest natural challenges we experienced so far. While around 55% of the world’s population lives in cities today, in 1950 it was only 30% and by 2050 it is expected to increase to 68% (UN DESA, 2019). Although the rate of urban growth is significantly lower in Europe and North America than in the developing regions, they are still the highest urbanized regions in the world with 74% of people living in cities today, which is projected to rise to 83% by 2050 (UN DESA, 2019). In Hungary, despite a significant decline in the population (Obádovics, 2019), a pronounced suburbanization process began in 1990, leading to a rapid urban sprawl and an extensive conversion of land into artificial surfaces (Kovács et al., 2019). On a local scale, urbanization means a complex environmental process including detrimental changes and effects, such as pollution, alteration of the local climate, removal of vegetation, drainage and extraction of freshwater, habitat loss and fragmentation which result in damaged and degraded ecosystems (Grimm et al., 2008). Urbanization is considered a major driving force of biodiversity and species loss (Savard et al., 2000; McKinney, 2002; Pauchard et al., 2006; Simkin et al., 2022) including some of the largest local extinctions among native species (Kowarik, 1995; McKinney, 2002). Road construction is a direct consequence of urbanization as it involves the planning, design, and development of roads within urban areas to facilitate movement and connectivity between different locations. The expansion of urban areas typically leads to the need for more extensive road networks, reflecting the interdependence between urbanization and road construction. Urbanization and road construction are responsible for the increase of impervious surfaces leading to intensive surface runoff and the disruption of the hydrological cycle. Instead of being absorbed into the ground, rainwater rapidly runs off these surfaces and collects in stormwater drains and channels. This contributes to changes in water quality as well, rainwater runoff collects pollutants such as oil, heavy metals, fertilizers, and pesticides, which contaminants are then transported into nearby waterbodies, degrading water quality and impacting aquatic organisms and ecosystems. A high proportion of impervious surfaces in urban areas also affects the temperature dynamics of the environment, known as the urban heat island effect. The accumulation and retention of heat by impervious surfaces lead to higher temperatures in cities compared to surrounding areas. This thermal modification can influence the physiology, behaviour, and distribution of freshwater organisms, including fish, invertebrates, macrophytes and algae.

Human recreation presents a relatively new chapter of human-induced land use changes. As people engage in recreational pursuits such as tourism, outdoor sports, and leisure activities, they require the development of infrastructure leading to the transformation of natural landscapes. It includes the conversion of the natural environment into built environments, such as the construction of resorts, hotels, recreational areas, bicycle roads and transportation infrastructure. Therefore, human recreation can directly lead to the degradation and destruction of natural habitats. Besides, intensive recreational use and its consequences, such as trampling, vehicle traffic and the removal of vegetation can accelerate soil erosion and degradation. Human recreation can also disturb wildlife by loud noises, light pollution, excessive presence or direct disturbance of nesting sites, causing stress and behavioural changes, which affect the feeding and breeding activities and, thus, the overall survival of animals. Increased human activity in recreational areas usually leads to elevated levels of pollution and increased littering due to the improper disposal of trash and chemicals. Finally, recreational activities can inadvertently introduce non-native or invasive species to natural ecosystems. Tourism and travel of people across different regions and countries often lead to the unintentional introduction of non-native species into new environments, disturbing the ecological balance and negatively affecting biodiversity (McNeill et al., 2011; Anderson et al., 2015; Robinson & McNeill, 2022). There is a close connection between environmental quality and recreational activities. The appeal of a location and its biodiversity are strong factors influencing the influx of visitors (Siikamäki et al., 2015; Habibullah et al., 2016), but this can also lead to conflicts between recreational interests and environmental protection objectives. For instance, conflicts may arise when popular tourist destinations coincide with habitats of endangered species (Siikamäki et al., 2015). Water-based recreation are particularly important for human well-being. Worldwide, nearly half of the global population resides within a proximity of less than 3 km from freshwater ecosystems (Kummu et al., 2011). Accordingly, impacts from water-based recreational activities are ranked as one of the most important threats to freshwaters in Europe (EEA, 2015).

Freshwater ecosystems are essential parts of the main lands' biodiversity. They can be divided into three main groups as lentic ecosystems, including lakes, ponds, reservoirs and other lentic (slow-moving water) waterbodies such as marshes, bogs, swamps, fens, pools etc.; lotic ecosystems, including rivers and streams and other lotic (faster-moving water) waterbodies such as brooks and springs etc.; and wetlands, which are transitions between aquatic and terrestrial systems (ecotones), they are distinct ecosystems flooded or saturated by water permanently (years, decades) or seasonally (weeks, months) and can be linked to lentic (lacustrine wetlands) or lotic (riverine or riparian wetlands) ecosystems or not connected to these (palustrine wetlands). Freshwaters are under higher pressure from anthropogenic impacts and suffering from declines in biodiversity far greater than terrestrial and marine ecosystems making them some of the most threatened systems in the world (Collen et al., 2014), and indicating that their conservation requires special attention (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Their area declined by 64% globally between 1997 and 2011 and by 50% between 1970 and 2008 in Europe (Costanza et al., 2014; Gozlan et al., 2019). This is rather unfortunate because they have key importance not just for biodiversity but in human survival and well-being, as well. Indeed, freshwaters are providing goods and services such as water supply (drinking water), food supply (fish, molluscs, crustaceans, and fertile soil for agriculture), water quality control, prevention of erosion, climate regulation, habitat provision, and recreation and tourism (water sports, angling, boating) (Vári et al., 2022). The connections between freshwater biodiversity and human livelihoods seem to be more direct and tangible compared to other ecosystems (Collen et al., 2014). Freshwater ecosystems also provide habitat for numerous species of fish, invertebrates, amphibians and birds. Although these systems occupy less than 1% of the surface of Earth, they support 10% of the known species, including one-third of all vertebrates (Strayer & Dudgeon, 2010). On the other hand, according to Collen et al. (2014), nearly one in three freshwater species is threatened with extinction on a global scale. Given their ecological, social, and economic significance, the protection, conservation, and sustainable management of freshwaters are essential for maintaining their health and the well-being of both human and natural systems.

2. AIMS

2.1. Motivation

As an environmental scientist, I have a keen interest in comprehensively exploring environmental issues and potential solutions. Throughout my academic journey, my diverse range of interests has led me to explore various research areas, spanning from environmental education and ecological farming to soil studies. However, my primary focus has been on ecology, particularly applied ecology. I have started to work with freshwater organisms in 2019 as an assistant research fellow and later as a Ph.D. student. My research primarily centered around aquatic macroinvertebrates, offering me the opportunity to conduct surveys and utilize innovative software, such as EUTAXA, for the identification of stream-living macrofauna – a novel effort in Hungary. My particular interest lies in understanding the impact of human activities on freshwater organisms. Consequently, my research focused on human-induced land use changes, notably urbanization, within one of Hungary's vital protected areas, the Balaton Uplands National Park. The dual nature of the Balaton Uplands, encompassing the shoreline of Lake Balaton with heightened human activity and the uplands maintaining close-to-natural conditions, provided an ideal background for my investigations. I specifically chose headwater streams as my study area due to their significance as primary freshwater habitats for macrofauna, housing endemic and highly sensitive species. These streams also embody the duality of the region, as Lake Balaton collects their water. Later, my research expanded, allowing me to collaborate with other researchers on various freshwater environments and organisms. Our studies delved into the impact of tourism and recreational activities on Lake Balaton, particularly focusing on the significant changes in natural reed-vegetated shorelines. We investigated how chironomids, a crucial animal group in the lake, respond to these disturbances. I was involved in the fieldwork, as well as in the meticulous process of larval sampling and sorting. Additionally, we explored ponds and amphibians, examining how this sensitive group reacts to linear infrastructures like roads and railways, serving as barriers and pollution sources intricately linked to urbanization. This study enhanced my knowledge in research planning in case of pond ecosystems, as well as in the sampling and identification of amphibian larvae.

The general aim of my thesis was to study the effects of land use changes and alterations on different freshwater ecosystems and organism groups. Particularly, the thesis was focused on three types of land use changes and three types of waterbodies: the conversion of natural forests into urban areas along low-order streams; the transformation of natural reed-vegetated shorelines into recreational beaches in a large, shallow lake; and the construction of linear infrastructures and fragmentation of ponds on landscape scale.

2.2. Urbanization and stream macroinvertebrates (Research topic 1)

The aim of this study was to investigate the impact of urbanization on low-order streams in the Pannon Biogeographic Region. We accomplished this by contrasting the abiotic and biotic parameters of streams originating from natural habitats and flowing through a moderately urbanized landscape. Additionally, we analysed how local environmental factors accounted for biotic variations. Our study aimed to answer the following questions in particular: (1) What are the environmental factors that differentiate urban streams from those in natural conditions? (2) Does urbanization have an impact on macroinvertebrate community attributes such as taxa richness, abundance, Shannon diversity, and assemblage composition? (3) Which environmental variables account for variations in community attributes? (4) Which group of environmental variables accounts for the most significant amount of community variation?

2.3. Recreational beaches and chironomid assemblages in Lake Balaton (Research topic 2)

The objective of this study was to reveal the effects of recreational beaches on habitat structure and associated chironomid communities of Lake Balaton. Particularly, we were interested in answering the following questions: (1) How habitat transformation influence environmental properties? (2) Do these changes result in distinct habitat types considering environmental properties? (3) How recreation beaches influence the richness, abundance and composition of chironomid communities? (4) How do environmental variables influence the richness, abundance and composition of chironomid communities? Considering the sensitivity of chironomids to the environment and the process of establishing beaches in Lake Balaton, we formulated the following hypotheses:

H1: The transformation of reed-covered shorelines to beaches has a significant impact on the richness, abundance and composition of chironomid communities because chironomids are sensitive to changes in habitat properties.

H2: The transformation of reed-covered shorelines to soft bottom area has significant effect on chironomid communities because chironomids are sensitive to the habitat alteration associated with the removal of reed.

H3: In the southern shoreline, the transformation of soft bottom area to beaches has significant effect on chironomid communities due to the effect of trampling.

H4: In the northern shoreline, the transformation of soft bottom area to beaches has an effect on chironomid communities because chironomids are sensitive to sand addition.

2.4. Linear infrastructures and pond ecology (Research topic 3)

Our aim was to study the relationships between road and rail infrastructure and the abundance of larval amphibian communities in a highly-fragmented landscape in Central Europe. We hypothesized that ponds with high larval abundance would likely produce more metamorphosing juveniles, assuming that they did not dry out. We predicted that accessible habitat is a better predictor of larval amphibian abundance than (1) the total amount of habitat surrounding ponds, (2) distance to a highway, or (3) road cover surrounding ponds. We investigated whether using a main railway line to calculate accessible habitats was a better predictor of amphibian abundance than using highways. We also examined the relative influence of local habitat variables on amphibian abundance. We predicted that: (1) amphibian abundance will increase with increased pond area, and (2) amphibian abundance will decrease with fish presence in ponds.

3. RESEARCH TOPIC ONE – Urbanization and stream macroinvertebrates

3.1. Introduction

Urbanization has grown into a major interest in stream ecology as many of the lotic waterbodies flowing through populated areas experience high pressures from anthropogenic sources. This process results in a state referred to as ‘urban stream syndrome’ (Meyer et al., 2005; Walsh et al., 2005), which presents a complex biological, physical and chemical impact system on urbanization-affected streams. Increased flow velocity, more frequent flash floods, elevated concentrations of nutrients and contaminants, altered channel morphology and stability are included as the main environmental symptoms. The urban stream syndrome has a strong impact on stream inhabitants, as well. It leads to a reduction in biotic richness and increased dominance of tolerant taxa, while accelerating biological invasions. Aquatic macroinvertebrate assemblages are among of the most impacted groups, while they are essential for stream functioning. They feed on a wide range of sources such as algae, coarse detritus, fine particulate organic matter or other aquatic organisms as predators (Cummins, 1974). They have a large role in ecosystem engineering (Mermillod-Blondin, 2011; Statzner, 2012) as bioturbators and filterers managing nutrient cycling and deposition, and cleaning the water. They provide food for animals at higher trophic levels, such as amphibians (Nery & Schmera, 2016) or fish

(Covich et al., 1999). The environmental changes generated by the urban stream syndrome cause general alterations in their species composition, mostly resulting in sensitive groups (e.g. Ephemeroptera, Plecoptera, Trichoptera) to be less abundant or absent in urbanized stream sections, while tolerant taxa, mainly Oligochaeta and Diptera become dominant (Walsh et al., 2005). Urbanization has an overall negative effect on the species diversity of freshwater macroinvertebrates (Gál et al., 2019).

There is a need to understand what level of urban degradation can generate detectable alterations in stream assemblages. For instance, fish communities showed fast degradation as catchment imperviousness exceeded 10-15% (Klein, 1979; Wang et al., 2000, 2001), but Utz et al. (2010) suggested that even the lowest levels of urban degradation may cause species loss in fish community and the sensitivity to urbanization may depend on the species and also on the biogeographic region. Regarding macroinvertebrates, Walsh et al. (2001) suggested a significant decrease in their diversity once impervious surface cover of the catchment was above 10%. Later, it was revealed that this limit should be as low as 5% (Schueler et al., 2009; Fitzgerald et al., 2012), while the study of Cuffney et al. (2010) indicated that any level of imperviousness can cause considerable degradation and limits of 10% or 5% do not provide a significant safeguard for the protection of macroinvertebrate communities. On the other hand, local scale characteristics have proven to be the most important determinants for macroinvertebrates over different spatial scales (Luo et al., 2018), and Gál et al. (2020) demonstrated that local human-made structures, such as road crossings or culverts cause rapid degradation of native macroinvertebrate communities. Relatively short generation times and presence in a wide range of trophic positions indicate fast responses of stream macroinvertebrates to environmental alterations and that even small changes in the local habitat properties can affect their diversity (Collier & Clements, 2011). Accordingly, urbanization involves not only landscape-scale alterations but also changes in local physical parameters. These changes include microhabitat-level (i.e. substrate-related) changes, as well as site-level changes in hydromorphology and riparian vegetation.

Microhabitat and its complexity is of vast importance for the structure and function of freshwater assemblages (Taniguchi & Tokeshi, 2004; Willis et al., 2005). Following the ‘habitat heterogeneity hypotheses’ a higher variety of habitats leads to higher species diversity (MacArthur & MacArthur, 1961). Indeed, individual species of benthic macroinvertebrates are generally associated with particular microhabitat types (Giller & Malmqvist, 1998; Leitner et al., 2015; Vilenica et al., 2018), and their selection is determined by the characteristics of the streambed substrate (Rempel et al., 2000; Vilenica et al., 2018; Doretto et al., 2022). The quality and heterogeneity of mineral and organic substrate define the number of microhabitats, therefore substrate is the primary physical variable affecting macroinvertebrate richness and abundance (Erman & Erman, 1984; Duan et al., 2008). Urban alterations often generate a major degradation of the streambed, which results in a poor substrate and, consequently microhabitat, heterogeneity.

On the site-level, urbanization means concrete channelization, including straightening and streambank fixation, increasing surface imperviousness (Paul & Meyer, 2001; Walsh et al., 2005). These concrete channels suffer from high flow extremes with faster ascending and descending phases (Walsh et al., 2005), with an increased chance of macroinvertebrates drifting downstream or causing their direct mortality (Konrad & Booth, 2005). Channelization of streams causes a general degradation of the hyporheic zone as the concrete bottom prevents the connection of surface water to groundwater. The hyporheic zone is important for its unique fauna (Williams & Hynes, 1974) as well as for other macroinvertebrates, which use the interstitial spaces of the hyporheic zone in their early development stages (Williams, 1984; Stubbington, 2012). These interstitial spaces are also crucial during high storm events or desiccation by providing refuge and aiding the recolonization process (Stubbington, 2012; Lewandowski et al., 2019). The zone has an important role in nutrient cycling and also in mitigating contamination (Hancock, 2002; Lewandowski et al., 2019). Streambank fixation includes the thinning or complete removal of riparian vegetation along urban streams (Paul & Meyer, 2001). Riparian vegetation forms an interface between stream and terrestrial ecosystems. It provides food and refuge for stream macro fauna, and buffers temperature, solar radiation and flow regimes (Pusey & Arthington, 2003; Sargac et al., 2021). Under natural conditions, riparian vegetation has an essential effect on microhabitat heterogeneity and hydromorphology. It decreases riparian erosion, determines the proportion of different grain-sizes by preventing fine sediment accumulation in the streambed, and regulates channel width and water depth. Conversely, it allows the accumulation of leaf litter and woody debris, thereby increasing microhabitat complexity and regulating current velocity.

The Pannon Biogeographic Region in Central Europe shows a dense network of riverine systems with a diverse stream invertebrate fauna including endemic species, while it has been experiencing rapid urban sprawl (Kovács et al., 2019; Lennert et al., 2020). On the other hand, ambiguous results were found in recent studies (Bozóki et al., 2018; Szita et al., 2019; Tóth et al., 2019; Czeglédi et al., 2020; Erős et al., 2020; Gál et al., 2020) regarding urban impacts on stream ecology in the region and thus further studies were recommended for better understanding.

The Balaton Uplands area in Hungary, which is located in the ecoregion, is part of a National Park with a wide range of valuable aquatic ecosystems. Balaton Uplands is characterized by small settlements and an associated low level of urban development and impervious surfaces (e.g. roads). The settlements in the area are concentrated mostly along the shore of Lake Balaton, which is a major destination for tourism in Hungary. During tourist season an increased urban stress occurs on the influent streams. In addition to this, population growth (due to population reallocation) is projected in the near future for the Balaton Uplands area (Lennert, 2019). Consequently, it is crucial to understand the effects of urbanization in this area to estimate the changes on biodiversity due to increasing urban stress and to recommend actions to mitigate the impacts on stream ecosystems.

3.2. Materials and methods

3.2.1. Study area

The study area was located in Balaton Uplands, Hungary (**Appendix 1**). The area is characterized by a continental climate with a slight Mediterranean aspect causing the mean annual temperature is around 10 °C and the typical annual precipitation is between 600-700 mm. Balaton Uplands is featured with gentle hills between 250-300 m a.s.l. and covered mostly by natural deciduous forests, vineyards and agricultural areas. Small (wetted width < 5 m) low-order streams are flowing through small towns and villages towards Lake Balaton in the area. These streams are mostly short in length and characterized by a small catchment area and low level of catchment urbanization (urban land cover is under 10%). Five streams (Aszófői, Burnót, Cserkúti, Koloska, Örvényesi) were selected based on the criteria of having both natural and urban sections along their course (**Fig. 1**). Along streams, six sites were selected in natural sections and six sites in urban sections, respectively. The length of sampled sites varied between 20 and 50 metres (usually shorter in urban areas) and the distance between sites was at least 20 metres. The average spatial distance between urban and natural sampling sites within streams was 1.50 km (min. in Örvényesi: 0.57 km, max. in Koloska: 3.59 km). Based on this sampling design we used a total of 5 [streams] x 2 [land use type: natural and urban] x 6 [sites] = 60 samples.

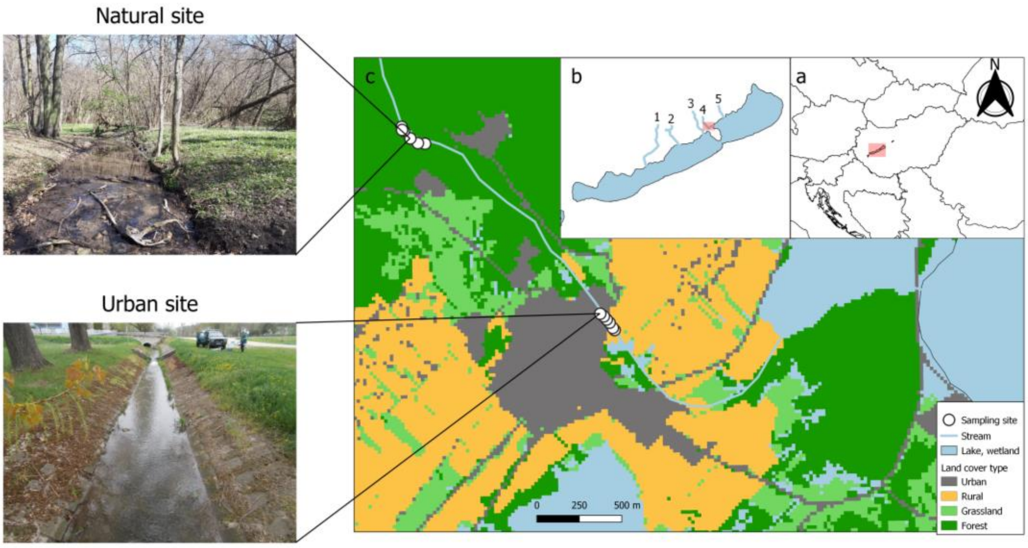

Fig. 1 a) Hungary in Central Europe with the position of Lake Balaton, b) Lake Balaton and the studied streams (1: Burnót, 2: Cserkúti, 3: Örvényesi, 4: Aszófői, 5: Koloska), c) Schematic representation of the study design showing Aszófői stream as an example. Land cover types based on the Ecosystem Base Map of Hungary (Ministry of Agriculture, 2019). Urban: any type of buildings, roads, railways, including green areas within human settlements; Rural: any tape of agricultural area, Grassland: all grassland, Forest: all forest type. Map was made using QGIS software with version 3.8.3 – Zanzibar (QGIS Development Team, 2019).

3.2.2. Environmental variables

To evaluate abiotic parameters at each site a Stream Visual Habitat Assessment (SVHA) protocol was used. We recorded wetted width at three cross-sections, while other physical habitat parameters, such as water depth and current velocity were measured at three randomly selected points. To measure current velocity a Valeport Model 801 (Flat) EM Flow Meter was used. Mineral streambed material (bedrock, boulder [> 25.6 cm], cobble [6.4 - 25.6 cm], pebble [1.6-6.4 cm], gravel [0.2-1.6 cm], sand [0.0125 - 0.2 cm], silt [<0.0125 cm] and concrete) and organic substrate composition (algae, particulate organic matter [POM], wood, macrophytes, terrestrial plants) was assessed as percentage. We recorded different components of riparian vegetation, such as the presence of trees, shrubs and grasses at both sides of the stream. Then, we summed the presence of the six riparian vegetation components into a riparian condition index (RCI, ranging between 0 and 6). We also assessed canopy coverage of the sites at the peak of the growing season in mid-summer, estimated as percentage of covering. To consider the human impact of the sites, we assessed the presence of stagnation, bank fixation (left, right, bed), litter, sedimentation, pollution, straightening and transverse concrete structures at each site. In order to quantify the human impact, we summed the nine human impact components into a human impact index (HII, ranging between 0 and 9). We divided the environmental variables into two groups according to microhabitat-level (mineral and organic substrate: proportion of bedrock, boulder, cobble, pebble, gravel, sand, silt, concrete, algae, POM, wood, macrophytes, terrestrial plants) and site-level including variables of hydromorphology (wetted width, water depth, current velocity), riparian vegetation (canopy cover and RCI), and human impact index (HII).

3.2.3. Sampling and identification of macroinvertebrates

We collected aquatic macroinvertebrates in April 2018. A multi-habitat sampling method and "kick and sweep" technique with a 500 μm mesh size hand-net were used for collection (AQEM Consortium, 2002). We took 10 subsamples at each site, by disturbing an area of 0.25 × 0.25 m. Subsamples were pooled in the field (**Fig. 2**). Collected animals were preserved in alcohol (70% ethanol and Patosolv©) and transported to the laboratory for identification (**Fig. 2**). Specimens were identified under stereomicroscope to the lowest possible taxonomic level (usually species) by experts using the EUTAXA software (Lechthaler & Car, 2005; Lechthaler & Stockinger, 2005; Lechthaler, 2009; Bauernfeind & Lechthaler, 2014) and relevant identification keys (Soós, 1963; Elliott, 1977; Hynes, 1977; Richnovszky & Pintér, 1979; Savage, 1989; Bass, 1998; Disney, 1999; Csabai, 2000; Bauernfeind & Humpesch, 2001; Csabai et al., 2002; Askew, 2004; Eiseler, 2005; Waringer & Graf, 2011; Ambrus et al., 2018). Protected taxa are listed in the valid 100/2012. (IX.28.) decree of Ministry of Rural Development, while species are classified as non-native based on DAISIE - Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2009).

Fig. 2 Processes of sampling, sorting and identification of macroinvertebrates. (Photos: Dénes Schmera, Attila Bohus)

3.2.4. Statistical analyses

We used Spearman's rank correlation tests to analyse the relationships between environmental variables. Standardized Principal Component Analysis (PCA) (Podani, 2000) and Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA or ADONIS in R, hereafter ADONIS) (Anderson, 2001) with Euclidean distance were used to assess differences in environmental variables between urban and natural sites.

Linear mixed-effects models (LME models) were used to test the effect of urbanization on the number of taxa (taxa richness), Shannon diversity and the number of individuals (abundance, log-transformed) for the whole macroinvertebrate and EPT (Ephemeroptera, Plecoptera and Trichoptera) communities. We used taxa richness, Shannon diversity and macroinvertebrate abundance as response variables, while stream section (natural, urban) was a fixed factor and stream identity (Aszófői, Burnót, Cserkúti, Koloska, Örvényesi) was a random factor. EPT abundances were dominated by a single taxon, thus we conducted the analysis of abundance of EPT without *Baetis rhodani* (Pictet, 1843). Therefore, the abundance of EPT was marked as Abu-EPT-$_{\mathrm{Br}}$ (-Br subindex refers to assemblage without *B. rhodani*). The percentage of EPT species from all macroinvertebrate species (relative richness, EPT%) was determined for each site and we used an LME model to test how urbanization affected the relative richness of EPT species. LME models were also used to test the effect of urbanization on each dominant taxon. Abundances of *B. rhodani*, *Electrogena ujhelyii* (Sowa, 1981) and Chironomidae spp. were log(x+1)-transformed, while abundances of *Gammarus roeselii* Gervais, 1835 and *G. fossarum* Koch, 1836 were square-root transformed to better meet the assumptions of normality. Similar to previous analyses, we used abundance as a response variable, while stream section (natural, urban) as a fixed factor and stream identity (Aszófői, Burnót, Cserkúti, Koloska, Örvényesi) as a random factor.

Non-metric Multidimensional Scaling (NMDS, Kruskal, 1964) and ADONIS (Anderson, 2001) with Bray-Curtis distance were used to test the community-based separation of natural and urban sections. All macroinvertebrate taxa, as well as only EPT taxa, were used in a separate analysis as dependent variables, while stream section and identity were independent variables. We used Spearman's rank correlation tests to evaluate relationships between environmental variables and macroinvertebrate taxa richness, abundance and Shannon diversity for the entire macroinvertebrate and separately for EPT assemblages. The response of the most abundant taxa was also analysed using Spearman's correlations.

Variance partitioning (VP; Borcard et al., 1992) with Redundancy Analysis (RDA) was used to examine how microhabitat-level as well as site-level parameters explained assemblage variation of the entire macroinvertebrate assemblage, and EPT separately. Natural and urban sections were tested separately. Negative variances were considered as zero variances (Legendre, 2008). We excluded some variables from variance partitioning analyses due to their zero variance: the proportion of terrestrial plants and concrete in natural sections, and the proportion of bedrock, boulder and wood in urban sections. Stepwise (both forward and backward) model selection methods were used to derive the best-fit model for both microhabitat-level and site-level (Blanchet et al., 2008). An ANOVA (Analysis of Variance) -like permutation test for Redundancy Analysis was used to test the significance of the different partitions such as the RDA models of microhabitat-level and site-level parameters. Statistical analyses were performed in R (version 4.0.2, R Development Core Team, 2020) using packages *vegan* (Oksanen et al., 2019), *lmerTest* (Kuznetsova et al., 2020) and *PerformanceAnalytics* (Peterson et al., 2020).

3.3. Results

3.3.1. Habitat properties

Spearman correlations of the environmental variables showed that the proportion of algae was highly ($\rho > 0.75$) correlated with the proportion of concrete, current velocity and the human impact index, while the proportion of concrete and the HII were also highly correlated. The HII index showed high negative correlations with the proportion of sand and canopy cover. (**Appendix 2**). Principal Component Analysis showed a marked separation of urban and natural sites (**Fig. 5**). Natural sites are positioned at the positive values of the first PCA axis while urban sites at the negative values of the first PCA axis. High proportion of concrete, algae, plants and higher current velocity characterized urban sites. Natural sites showed more considerable variability. Some sites showed high proportion of particulate organic matter and wood (negative values of the second PCA axis) while other natural sites were wider with cobble and boulder substrates (positive values of the second PCA axis). The higher proportion of canopy cover and better condition of riparian vegetation (higher RCI) also characterized natural sites. Individual streams offered unique habitats for macroinvertebrates. ADONIS showed a significant difference between natural and urban sites (df = 1, SS = 202389, $R^2 = 0.297$, F = 24.533, $p < 0.001$) and between streams (df = 4, SS = 195821, $R^2 = 0.288$, F = 5.551, $p < 0.001$). Section and stream identity explained very similar amounts of variation of environmental variables.

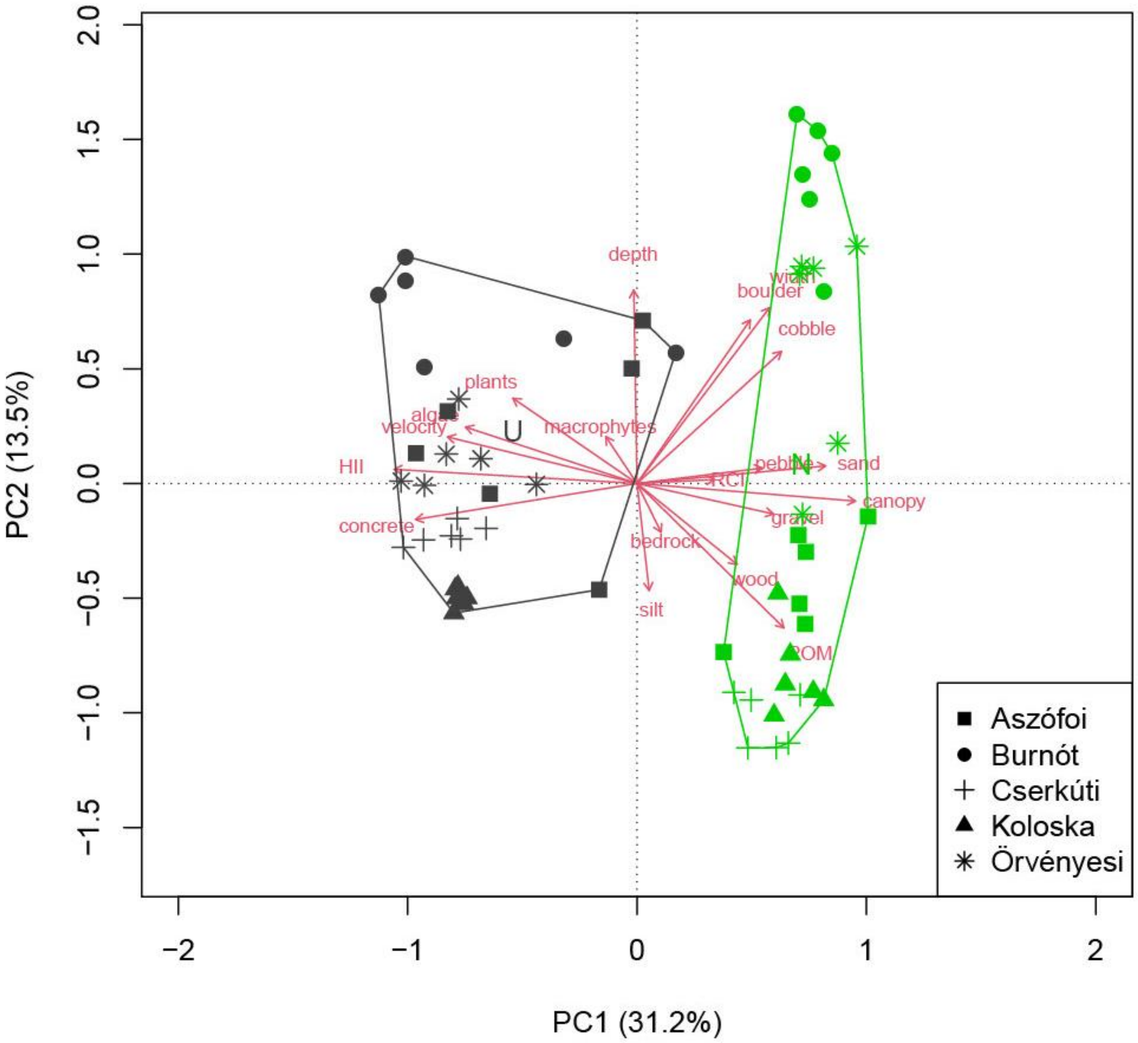

Fig. 5 Standardized PCA of the sites based on the environmental variables of the studied sections (natural: green symbols, urban: dark grey symbols; ordination hulls: N: natural, U: urban), showing the five examined streams.

3.3.2. General effect of urbanization

We identified 108 taxa from the collected 29,691 macroinvertebrate individuals (**Appendix 3**). The most abundant (>1000 individuals) taxa were *Gammarus roeselii* (11,267 individuals), *Baetis rhodani* (6,067 individuals), *Gammarus fossarum* (4,408 individuals), Chironomidae spp. (2,032 individuals) and *Electrogena ujhelyii* (1,136 individuals). Three protected *Astacus astacus* (Linnaeus, 1758), *Calopteryx virgo* Linnaeus, 1758, *Orthetrum brunneum* Fonscolombe, 1837 and one non-native, invasive [*Potamopyrgus antipodarum* (Gray, 1843)] taxa were identified. The invasive *P. antipodarum* was present only in one stream with negligible abundance (40 individuals). The highest number of taxa (33) was represented by Trichoptera (caddisflies), while there was only one species of Decapoda (*Astacus astacus*) and Megaloptera (*Sialis fuliginosa* Pictet, 1836).

Taxa richness of macroinvertebrates ranged between 6 and 28 taxa per site. Richness was higher for natural sites (natural: mean = 16.400, SD = 4.731; urban: mean = 12.733, SD = 4.394). The LME model for taxa richness showed that urbanization had a negative effect on the number of taxa (Welch-Satterthwaite t-test: urban section estimate = -3.667, SE = 1.039, df = 54, t = - 3.529, p < 0.001) and stream identity as a random factor explained 26% of the total variance. Streams showed considerable variability around the effect of urbanization (**Fig. 6**).

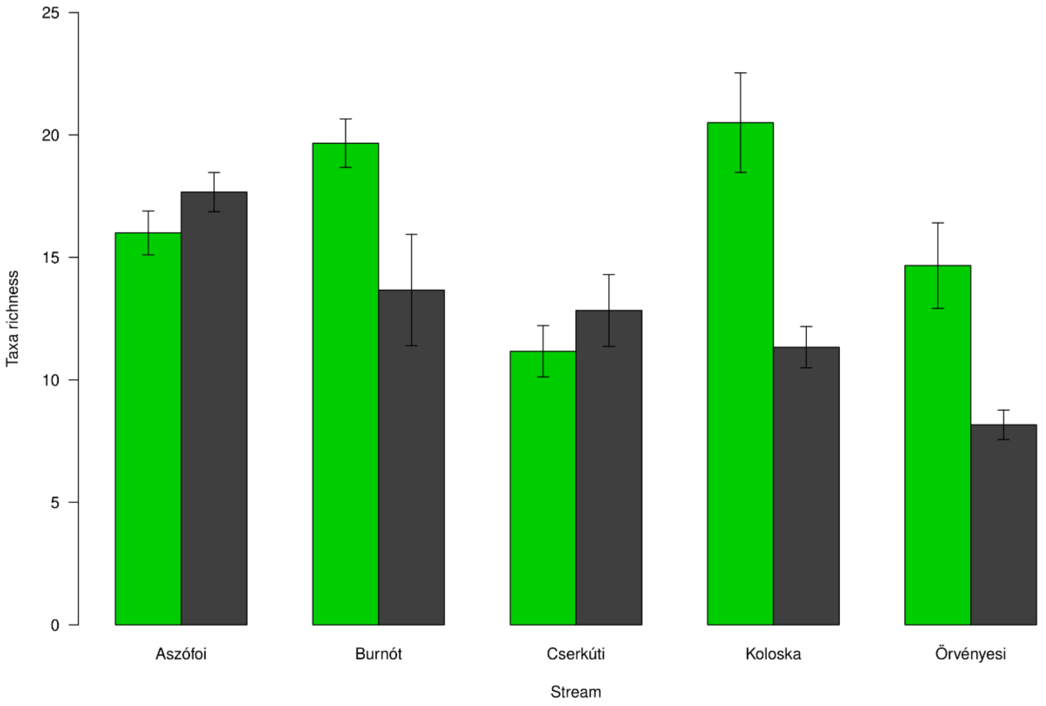

Fig. 6 The mean (bar) and standard error (whiskers) of the taxa richness of macroinvertebrate assemblage in natural (green) and urban (dark grey) sections of the studied streams.

Shannon diversity indices ranged between 0.666 and 2.289 (natural: mean = 1.499, SD = 0.350; urban: mean = 1.297, SD = 0.247). The LME model showed that urbanization had a negative effect on Shannon diversity (Welch-Satterthwaite t-test: urban section estimate = -0.203, SE = 0.062, df = 54, t = - 3.246, p = 0.002), while stream identity as a random factor explained 41% of the total variance. Similar to richness, Shannon diversity also showed substantial heterogeneity in different streams (**Fig. 7**).

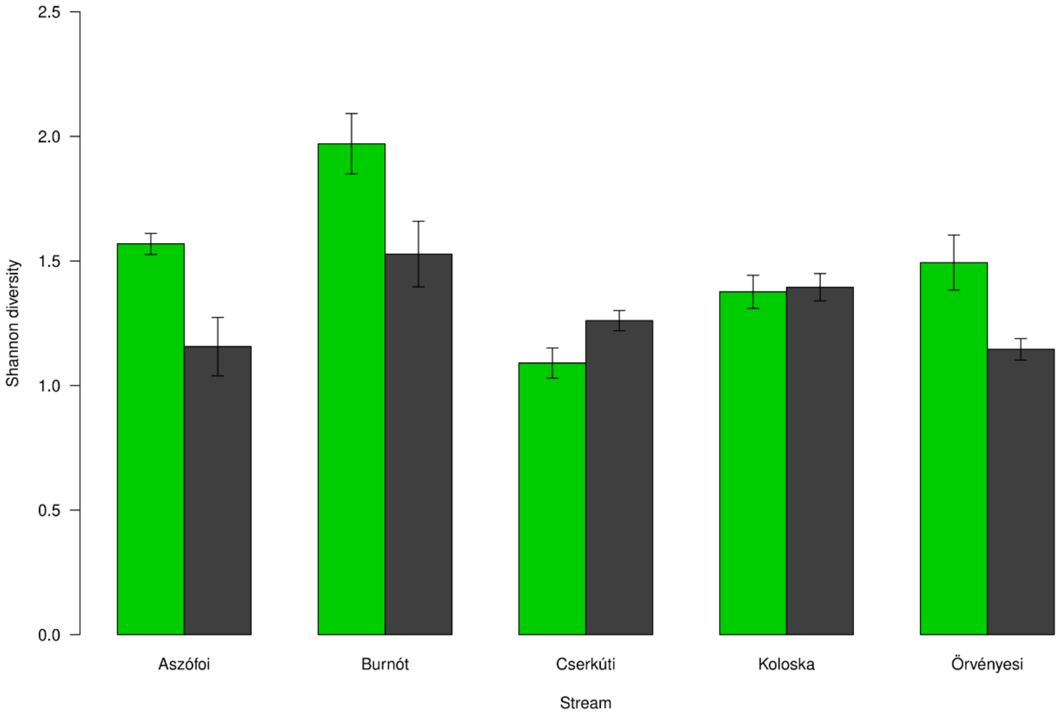

Fig. 7 The mean (bar) and standard error (whiskers) of the Shannon diversity of macroinvertebrate assemblages in natural (green) and urban (dark grey) sections of the studied streams.

The number of individuals showed high variance, ranged between 78 and 1818 per site and was higher in urban sites (natural: mean = 391.733, SD = 178.093; urban: mean = 597.967, SD = 425.908). The LME model for abundance data showed that urbanization had no effect on the number of individuals (Welch-Satterthwaite t-test: urban section estimate = 0.266, SE = 0.157, df = 54, t = 1.690, p = 0.097). Stream identity as a random factor explained 25% of the total variance. Abundances varied in different streams (**Fig. 8**).

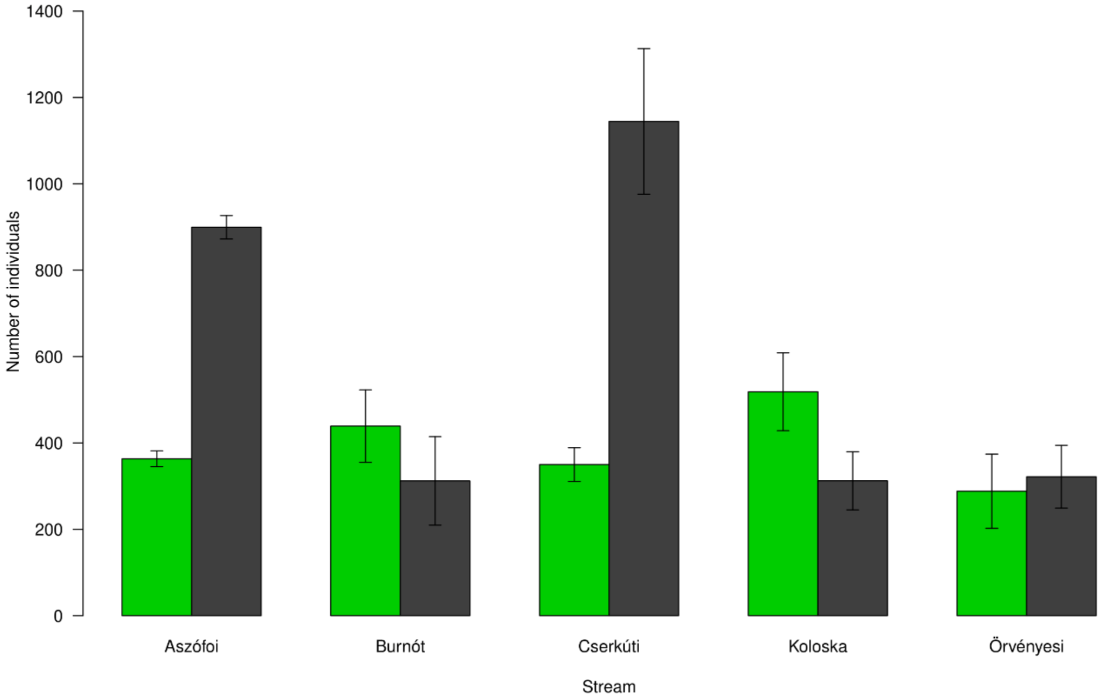

Fig. 8 The mean (bar) and standard error (whiskers) of the number of individuals of macroinvertebrate assemblages in natural (green) and urban (dark grey) sections of the studied streams.

EPT (Ephemeroptera, Plecoptera and Trichoptera) were present with 44 taxa and 9,562 individuals. EPT richness ranged between 1 and 13 species per site (natural: mean = 7.300, SD = 2.706; urban: mean = 5.100, SD = 2.496). The LME models showed that urbanization had a negative effect on EPT community attributes, such as richness (Rich-EPT), abundance (Abu-EPT$_{\text{-Br}}$) and Shannon diversity of EPT (Sha-EPT), while the relative richness of EPT (EPT%) showed no relationship with urbanization (**Table 1**). Regarding the dominant species, urbanization showed negative (*Electrogena ujhelyii*), neutral (*Gammarus fossarum*, Chironomidae spp.) and positive (*Baetis rhodani, Gammarus roeselii*) effects on the number of collected individuals (**Table 1**).

Table 1 The output of LME models explaining the effect of urbanization (Estimate) on the community attributes of EPT (Rich-EPT: taxa richness of EPT, Abu-EPT$_{\text{-Br}}$: abundance of EPT without *Baetis rhodani*, Sha-EPT: Shannon diversity of EPT, EPT%: relative richness of EPT) and on the dominant taxa.

Attribute/Taxa	Transformation	Estimate	SE	df	t	p
Rich-EPT	-	-2.233	0.583	54	-3.829	<0.001
Abu-EPT$_{\textit{-Br}}$	log	-0.804	0.198	54	-4.062	<0.001
Sha-EPT	-	-0.796	0.072	54	-11.08	<0.001
EPT%	-	-5.026	2.873	54	-1.749	0.086
Gammarus roeselii	square root	3.506	1.717	54	2.042	0.046
Baetis rhodani	log	1.639	0.258	54	6.340	<0.001
Gammarus fossarum	square root	-0.596	0.725	54	-0.821	0.415
Chironomidae spp.	log	0.148	0.242	54	0.614	0.542
Electrogena ujhelyii	log	-2.257	0.246	54	-9.193	<0.001

NMDS (**Fig. 9**) showed a clear separation of the samples among the macroinvertebrate assemblages collected at natural and urban sites. Natural sites mainly appeared at negative values of the second NMDS axis, while urban sites at positive values of the second NMDS axis.

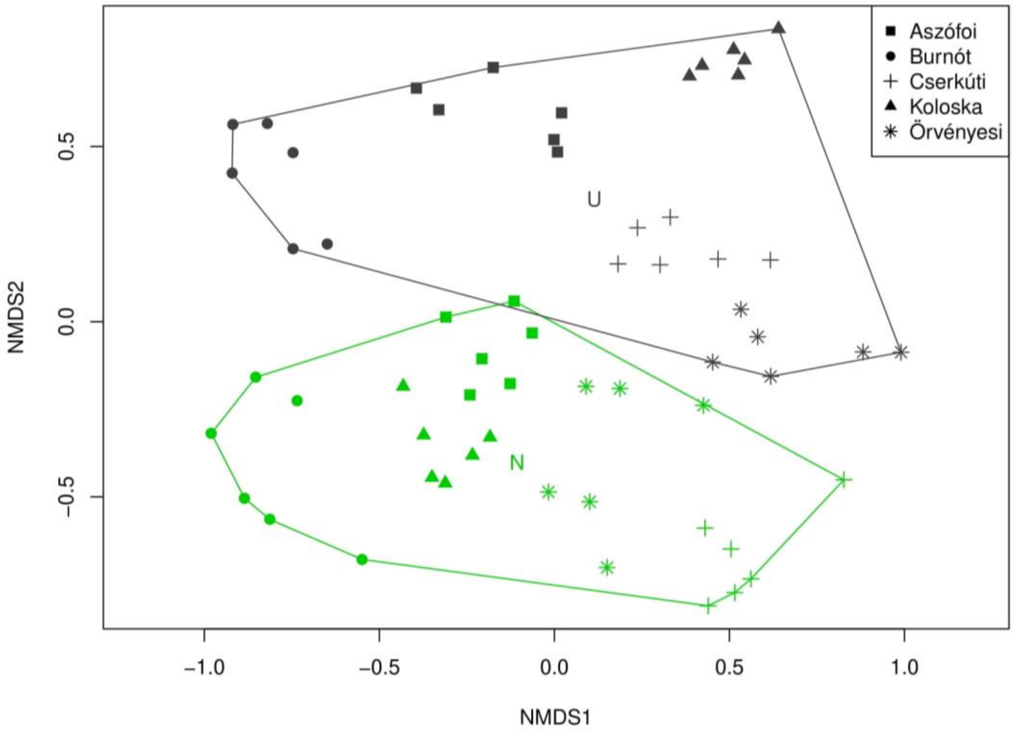

Fig. 9 NMDS plot of sites based on the identified taxa showing the separation according to section (green symbols: natural, dark grey symbols: urban; ordination hulls: N: natural, U: urban) and stream.

Although section based separation was evidently strong, ADONIS showed that stream identity had a greater ability to partition sites than stream section (**Table 2**).

Table 2 Summary of the PERMANOVA (ADONIS) testing the effect of section and stream identity on the identified taxa (number of permutations: 999).

Factor	df	SS	R^2	F	p
Section	1	1.542	0.098	11.268	0.001
Stream id.	4	6.736	0.430	12.303	0.001
Residuals	54	7.391	0.472		
Total	59	15.669	1.000		

Hence, streams possessed unique community members, present only in a given stream. According to NMDS, assemblages of certain streams were more similar; for example, Cserkúti and Örvényesi or Koloska and Aszófői stream, while Burnót stream was distinctly separated from the other sites. Interestingly, urban sites were more clustered within and more separated between streams, while natural sites were more scattered and less separated. The NMDS performed exclusively on EPT assemblages showed a somewhat different result (**Appendix 4, Appendix 5**). Natural and urban sites were separated mostly along the first NMDS axis. Contrary to the results of the entire macroinvertebrate assemblages, streams were not well separated.

3.3.3. Relationship between local environmental variables and biotic attributes of macroinvertebrate assemblages

Taxa richness of the entire macroinvertebrate assemblage (Rich-Ent) was negatively correlated with the proportion of concrete and algae (**Table 3**) at microhabitat-level, while it was positively correlated with wetted width at site-level. The abundance of the entire macroinvertebrate assemblage (Abu-Ent) did not correlate strongly with the any of environmental variables (**Table 3**). Shannon diversity (Sha-Ent) showed a strong positive correlation with wetted width (**Table 3**).

Considering only the EPT community, taxa richness (Rich-EPT) showed a positive correlation with POM, wood and canopy cover, and a negative correlation with the proportion of concrete, algae and current velocity (**Table 3**). The abundance of EPT without *Baetis rhodani* ($\text{Abu-EPT}_{\text{-Br}}$) was positively correlated with the proportion of gravel, wetted width and water depth, while negatively correlated with the proportion of concrete. Shannon diversity (Sha-EPT) showed a strong positive correlation with the proportion of cobble, gravel, sand, POM, wood, wetted width and canopy cover. Sha-EPT was negatively correlated with the proportion of concrete, the proportion of algae, current velocity and HII, while EPT% did not show strong correlations. (**Table 3**).

Among the most abundant species, the abundance of *Baetis rhodani* was strongly negatively correlated with the proportion of gravel, sand and wetted width, and strongly positively correlated with the proportion of concrete. It was positively correlated with the human impact index. The abundance of *Electrogena ujhelyii* was strongly positively correlated with the proportion of boulder, cobble, pebble, gravel, sand and the proportion of POM and canopy cover. It was strongly negatively correlated with the proportion of concrete, the proportion of algae, current velocity and HII. *E. ujhelyii* abundance was positively correlated with the proportion of wood and wetted width. The abundance of *Gammarus roeselii* was strongly negatively correlated with the riparian condition index and negatively correlated with the proportion of pebble and silt. It was positively correlated with the proportion of macrophytes and wood, and water depth. The abundance of *G. fossarum* showed a similar pattern but in the opposite direction: positively correlated with the proportion of pebble, while negatively correlated with the proportion of wood and water depth. The abundance of Chironomidae spp. was strongly negatively correlated with wetted width and water depth and showed a positive correlation with the proportion of silt and RCI (**Table 3**).

Table 3 Spearman's rho (ρ) correlation coefficients between environmental variables and biotic attributes of macroinvertebrate assemblages (Rich-Ent: taxa richness of the entire macroinvertebrate assemblage, Abu-Ent: abundance of the entire macroinvertebrate assemblage, Sha-Ent: Shannon diversity of the entire macroinvertebrate assemblage, Rich-EPT: taxa richness of EPT, Abu-EPT$_{\text{-Br}}$: abundance of EPT without *Baetis rhodani*, Sha-EPT: Shannon diversity of EPT, EPT%: proportion of EPT taxa in the entire macroinvertebrate assemblage), and most abundant taxa (*Gammarus roeselii*, *G. fossarum*, *Baetis rhodani*, *Electrogena ujhelyii*, Chironomidae spp.*)*. Statistically significant ($p < 0.05$) correlations are shown only. Bold indicates highly significant ($p < 0.001$) correlations.

Environmental variable	Rich-Ent	Abu-Ent	Sha-Ent	Rich-EPT	Abu-EPT$_{\text{-Br}}$	Sha-EPT	EPT%	*G. roeselii*	*G. fossarum*	*B. rhodani*	*E. ujhelyii*	Chironomidae spp.
Microhabitat-level												
bedrock (%)												
boulder (%)	0.389		0.399	0.255	0.380	0.378				-0.355	**0.518**	-0.289
cobble (%)	0.378		0.374		0.265	**0.419**				-0.404	**0.511**	
pebble (%)						0.316		-0.347	0.383	-0.336	**0.508**	
gravel (%)	0.328		0.406	0.295	**0.433**	**0.536**				**-0.475**	**0.543**	
sand (%)	0.367		0.334	0.346	0.351	**0.712**				**-0.418**	**0.682**	
silt (%)								-0.299				0.408
concrete (%)	**-0.436**		-0.280	**-0.505**	**-0.522**	**-0.799**	-0.313			**0.554**	**-0.705**	
algae (%)	**-0.464**		-0.263	**-0.435**	-0.382	**-0.690**					**-0.623**	
terrestrial plants (%)						-0.342					-0.332	
macrophytes (%)		0.285						0.328				-0.309
POM (%)	0.369			**0.466**	0.277	**0.692**	0.274				**0.532**	
wood (%)	0.376		0.294	**0.482**	0.329	**0.557**	0.278	0.319	-0.388		0.408	
Site-level												
current velocity (cm/s)	-0.374			**-0.422**	-0.305	**-0.664**					**-0.578**	
width (cm)	**0.479**		**0.480**	0.356	**0.495**	**0.494**			-0.413	**-0.504**	0.277	**-0.428**
depth (cm)	0.283		0.268	0.257	**0.509**			0.407	-0.349			**-0.608**
canopy cover (%)	0.371			**0.464**	0.359	**0.716**	0.307			-0.298	**0.656**	
RCI		-0.397	0.265					**-0.470**		-0.318		0.338
HII	-0.346			-0.406	-0.324	**-0.752**				0.341	**-0.729**	

3.3.4. Community variation

Regarding the entire macroinvertebrate assemblage of natural sections, variance partitioning showed that microhabitat-level explained the highest pure variation (21%), while site-level parameters had limited pure explanation power (1%, **Table 4**). The shared effect of microhabitat and site-level parameters explained 17% of total variance. The total explained variance was 39%. Regarding the analysis of urban sections, variance partitioning showed that both microhabitat and site-level parameters explained a large pure variation (35% and 26%, respectively), followed by their shared effect (9%, **Table 4**). The total explained variance was 70%, resulting in remarkably less residual variance than in natural section. All RDA models were significant.

Microhabitat-level variables explained the highest variation (27%) within the EPT assemblages of natural sections, followed by a shared effect of microhabitat and site-level parameters (3%) and a pure effect of site-level parameters (2%, **Table 4**). The total explained variance was 32%. When the assemblages of urban sections were analysed, site-level parameters explained the largest amount of community variation (25%). The shared effect of microhabitat and site-level variables explained 36%, while microhabitat-level variables had a limited explanatory power (4%, **Table 4**). The total explained variance was 65%. All RDA models proved to be significant.

Table 4 Results of the variance partitioning (explained variance in %) of the entire macroinvertebrate assemblage and the EPT assemblage collected from natural and urban stream sections separately. Micro: microhabitat-level variables, site: site-level variables. Explained variables proved to be significant by RDA.

All macroinvertebrates				
Section	Micro	Site	Micro + Site	Residuals
Natural	21	1	17	61
Urban	35	26	9	30
EPT				
Section	Micro	Site	Micro + Site	Residuals
Natural	27	2	3	68
Urban	4	25	36	35

3.4. Discussion

The complete impact of urban development on the freshwater environment is not fully comprehended. Research findings indicate that the diversity and composition of stream organisms may be adversely influenced even by moderate levels of urbanization (Cuffney et al., 2010; Collier & Clements, 2011; Richardson, 2019). There is a lack of clarity regarding whether and how the urbanization-related alterations driven by the degradation of the local physical habitat affect stream biota. Our findings indicate that low-order streams undergo significant local degradation as they move from natural forested areas to moderately-urbanized landscapes. Both microhabitat and site-level parameters varied between the natural and urban stream sections. These differences in habitat parameters contributed to a decrease in macroinvertebrate richness and a shift in their composition. Through our analyses, we discovered that stream identity accounts for a significant portion of community variation. This highlights the need for greater consideration of the unique responses of individual streams to urbanization.

Throughout our study, we observed differences between the urban and natural sections in terms of their local environmental variables. Notably, substrate heterogeneity shifted in response to urbanization, with urban sites featuring a straight stream channel, less variation in mineral substrate, and a preponderance of concrete surfaces. Additionally, the streams in urban sites were observed to be narrower, shallower, and flowing at a faster pace. This is a common characteristic of urban streams, resulting from channelization and the use of concrete lining on the streambed (Paul & Meyer, 2001; Walsh et al., 2005). In the urban sites, riparian vegetation was typically diminished, leading to the proliferation of herbaceous plants and algae, as there was no longer any canopy limitation on light availability (Taylor et al., 2004; Sargac et al., 2021). This growth may also indicate that the natural sites were nutrient-limited, whereas the urban sites received a greater nutrient load (Taylor et al., 2004; Walsh et al., 2005). Our study found that, consistent with the findings of Sargac et al. (2021), the input of leaf litter and other allochthonous organic matter was restricted in the urban sites. We observed that urbanization had a similar impact on each local stream environment, indicating a clear association with habitat degradation. This is in contrast to the results of Czeglédi et al. (2020) who found no connection between urbanization-related variables and local stream environmental variables within the same ecoregion.

While there was a significant difference in macroinvertebrate communities between the urban and natural sites, each stream, even in the urban sections, had its own unique community. It appears that the impact of local species pools, specific to each stream, cannot be superseded by the influence of urbanization. This was already demonstrated in fish assemblages (Stoll et al., 2014; Czeglédi et al., 2020) and in tropical macroinvertebrate communities (Al-Shami et al., 2014). The well-documented adverse impacts of urbanization, such as biotic homogenisation, were not as noticeable in our study. Likewise, Utz et al. (2010) reported significant variations in the effects of urbanization depending on the geographic region, regional species pool, and even the local species composition. We hypothesise that the lack of a consistent reaction from the local species pools may be attributed to the comparatively lower level of urbanization observed in our study area. In cases where urban degradation is more severe (i.e. there is a greater amount of artificial surface cover, higher levels of pollution, and a more pronounced alteration of hydromorphology), the influence of urbanization on the communities may exceed that of the stream identity. Under such conditions, the communities could be less resistant, and the role of the original species pool would be diminished. Szita et al. (2019), however, did not observe any significant differentiation in the assemblage structure between urban and reference sites within the same region, even though their research encompassed a larger city. This could be attributed to the possibility that the communities examined in their study were already more degraded compared to those in our research. Alternatively, this could be because they compared sites located upstream and downstream of the city, suggesting that the community might have undergone regeneration after being impacted by urbanization. For instance, the study of Gál et al. (2020) found that macroinvertebrates could recover relatively quickly following disturbance. On the other hand, we observed a less pronounced reaction of EPT (Ephemeroptera, Plecoptera, and Trichoptera) assemblages to urbanization when compared to the entire macroinvertebrate assemblage. Additionally, the compositions of EPT were relatively uniform across various streams. Various taxonomic groups within EPT exhibit distinct responses to human modifications, and even individual species' responses could significantly influence the findings. The level of urban degradation in our sites could potentially promote the presence of tolerant taxa, but it may not have surpassed the threshold to filter out more sensitive taxa.

The number of taxa and the Shannon diversity index were notably lower in urban sites compared to natural sites. This finding is consistent with other studies that have demonstrated a negative association of richness and diversity with urbanization (Walsh et al., 2005; Stepenuck et al., 2008; Cuffney et al., 2010; Wang et al., 2012; Gál et al., 2019; Gao et al., 2022), It should be noted, however, a different study conducted also in the Pannon Biogeographic Region identified a positive correlation between Shannon diversity and urbanization level at the landscape scale (Bozóki et al., 2018). Similar to the findings of Gál et al. (2019), we observed that stream identity accounted for a significant proportion of the variance, indicating substantial heterogeneity in the impact of urbanization on macroinvertebrate diversity across streams.

Despite observing a decline in richness and diversity caused by urbanization, we did not find a significant decrease in the abundance of macroinvertebrates between natural and urban sites. Previous studies have demonstrated that macroinvertebrate abundance can rise significantly downstream as the urban gradient intensifies due to elevated pollution levels (Álvarez-Cabria et al., 2011). This trend is particularly noticeable in tropical regions where the primary carbon sources are autochthonous (Lau et al., 2009; Wiederkehr et al., 2020; Gao et al., 2022). Conversely, in temperate climates, abundance is more likely to decline downstream (Paul & Meyer, 2001). In studies that involve high levels of urbanization, greater abundance has been attributed to high numbers of Chironomidae and Oligochaeta (Paul & Meyer, 2001; Walsh et al., 2005). Nevertheless, our findings indicated that Chironomidae abundance did not differ significantly between natural and urban sites, and the abundance of Oligochaeta was negligible at all sites. *Gammarus roeselii* and *Baetis rhodani* were the species that accounted for the high number of individuals in urban sites. Despite being generalists in European streams with a broad dietary range, they are less tolerant than Oligochaeta or Chironomidae, which are known to be highly resilient (Gabriels et al., 2010). Again, this leads to the conclusion that there is a weak level of urbanization that does not yet support extremely tolerant species.

Urbanization often results in an increase in the abundance of macroinvertebrates that are more tolerant, whereas EPT taxa are usually more sensitive to changes. As a result, EPT taxa are often used as indicators of well-oxygenated, pollution-free water in water quality assessments (Lenat, 1988; Hamid & Rawi, 2017). Thus, our results, indicating a significant reduction in species richness, Shannon diversity, and abundance in urbanized sites, are consistent with earlier research (Walsh et al., 2007; Cuffney et al., 2010; Álvarez-Cabria et al., 2011; Collier & Clements, 2011; Wang et al., 2012; Luo et al., 2018). The relative richness of EPT remained stable at around 40% in both urban and natural sites, suggesting that some of the EPT taxa that are more tolerant to urbanization were able to persist in the community, while other non-EPT taxa showed a decline in richness in the urban sites.

Our analysis of individual taxa revealed variations in their abundances between the natural and urban sites. For instance, mayflies such as *Baetis rhodani* and *Electrogena ujhelyii*, which are both part of the scraper functional feeding group and primarily feed on periphytic algae (Cummins & Klug, 1979; Schmedtje & Colling, 1996; Tachet et al., 2000), exhibited differences in their distribution. *Baetis rhodani* was found to be more abundant in urban sections, while *Electrogena ujhelyii* was more prevalent in natural sections. This suggests that one species might replace the other depending on the level of urbanization. For example, *Baetis rhodani* has a higher tolerance to potential urban effects, such as heavy metal pollution (Rehfeldt & Söchtig, 1991). In the study on the impact of road crossings on macroinvertebrate diversity, Gál et al. (2020) also discovered that *B. rhodani* is a tolerant species, and similarly, Vilenica et al. (2018) observed that *B. rhodani* can thrive on various substrates and favours high water velocity, which is frequently present in urban streams. During our study, *B. rhodani* exhibited an adverse correlation with the natural mineral substrate but a positive correlation with the concrete cover. Conversely, the heptageniidaean *Electrogena ujhelyii* displayed a preference for natural substrate and its abundance was negatively correlated with concrete cover and current velocity. The body size of the final instar larvae of *Baetis* is smaller than those of *Electrogena* and small size may be advantageous in urban stream sites (Edegbene et al., 2020). While *Baetis rhodani* was observed in most streams, it was noticeably absent in Burnót stream. Furthermore, other *Baetis* species such as *B. vernus* Curtis, 1834, *B. muticus* (Linnaeus, 1758), and *B. pentaphlebodes* Ujhelyi, 1966 were present in other streams but absent in Burnót stream. It is noteworthy that the New Zealand mudsnail (*Potamopyrgus antipodarum*), an invasive species, was exclusively found in Burnót stream. Even though we observed the snail in low numbers, previous studies have shown that the population of *P. antipodarum* can vary considerably over different seasons and years in freshwaters across Europe and North America (Extence, 1981; Moffitt & James, 2012; Moore et al., 2012; Gérard et al., 2018). As both *Potamopyrgus antipodarum* and *Baetis* species graze on periphyton [although the diet of *P. antipodarum* includes organic detritus and macrophytes as well (Alonso & Castro-Díez, 2008)], there could be interspecific competition. Previous studies have shown a negative effect of *P. antipodarum* on native grazer taxa (Moore et al., 2012). Additionally, Burnót is the largest of our studied streams and may support the presence of fish, which can exert predatory pressure, potentially explaining the unique macroinvertebrate community and absence of some *Baetis* species.

Two gammarid species (*G. roeselii* and *G. fossarum*) with known niche segregation (Mauchart et al., 2014) showed opposite correlations with some environmental variables in our study. *G. roeselii* prefers urban sites and is known to adapt to degraded conditions, while *G. fossarum* prefers natural sites and is known as a superior competitor which favours close-to-natural conditions (Mauchart et al., 2014; Krasznai et al., 2016).

Natural environmental conditions positively influenced macroinvertebrate richness and diversity at both microhabitat and site-level, whereas urbanization-related factors like concrete proportion and high current velocity had a negative impact. The human impact index (HII) was a reliable predictor of local habitat degradation, and microhabitat-level degradation indicators were closely linked to it. Regarding the riparian parameters, canopy coverage was a better indicator of natural conditions than the riparian condition index (RCI), as trees have a direct impact on stream fauna by providing organic matter and shading, while RCI assessed also shrubs and grasses. Riparian tree cover was negatively associated with the presence of shrubs and mainly grasses, which were often absent on natural stream sites, while deforested urban sites provided unshaded opportunities for these plants. Canopy cover was also a significant indicator of EPT assemblage attributes, while *Baetis rhodani* was negatively correlated with both riparian canopy cover and RCI, consistent with the findings of Forio et al. (2020).

According to the variance partitioning analysis, under natural conditions, microhabitat-level environmental variables had a greater impact on the structure of macroinvertebrate assemblages than site-level parameters. The importance of site-level parameters increased in urban sections, especially for sensitive taxa such as EPT, suggesting that under such conditions, both microhabitat heterogeneity and broader-scale effects may play a role in determining the macroinvertebrate assemblage composition. The role of environmental factors in shaping community variation was greater in urban sections compared to natural ones. The larger amount of unexplained variance in natural sections may be attributed to biotic interactions or natural stochasticity. According to Turrini et al. (2016), urbanization can decrease trophic interactions, including top-down control by predators. This suggests that in urban streams environmental conditions may play a more important, while biological interactions a less prevalent role in shaping local compositions. Nonetheless, the urban-related environmental deterioration was comparable across all streams, whereas the biotic characteristics displayed notably divergent patterns among them. This finding may underscore the significance of the local (stream) species pool in shaping the biological reaction to urbanization. Another possibility is that macroinvertebrates exhibit distinct responses to moderate variations in local habitat degradation or to larger scale differences (e.g. different settlement sizes, closeness to Lake Balaton).

We demonstrated a notable impact of environmental parameters at both the microhabitat and site levels on macroinvertebrate assemblages. This observation supports the notion that restoring microhabitat heterogeneity alone, without considering site-level or broader-scale approaches, may not suffice for the successful restoration of macroinvertebrate communities in streams affected by urbanization (Palmer et al., 2010; Verdonschot et al., 2016; Zerega et al., 2021). Nevertheless, macroinvertebrate community variation was significantly influenced by stream identity, indicating that the degradation of assemblages in the urban sections is strongly dependent on the unique compositions of individual streams. The distinct responses of individual streams to urban stress imply the necessity of the consideration of stream-specific aspects in the efforts to prevent, mitigate, and recover from urbanization impacts. This also suggests that there might not be universal treatments applicable to reduce the effects of urbanization in streams (Zerega et al., 2021). However, regarding our study, the concrete substrate material proved to be the most significant variable reducing macroinvertebrate richness and diversity, indicating that actions need to focus on decreasing the proportion of the concrete material on the streambed in urban stream sites. The ideal restoration process may would be to remove the concrete channels and restore riparian vegetation. However, this might not be possible in most cases, as roads and buildings are built close to concrete channels, and the biological consequences are unpredictable. Efforts to increase the proportion of natural substrate material in the streambed and the modification of flow conditions are likely to be effective, but the biological responses are not guaranteed (Palmer et al., 2010). Nevertheless, forthcoming actions in stream management should carefully consider not only functional but also conservation aspects when establishing urban streams. The emphasis should be on stream construction and management strategies that prefer nature-based solutions and avoid the use of concrete materials.

4. RESEARCH TOPIC TWO – Recreational beaches and chironomid assemblages in Lake Balaton

4.1. Introduction

Human-made changes in the environment resulted in extensive consequences in the global distribution of organisms (Vitousek et al., 1997). Lakes and ponds have been used for agricultural and aquacultural purposes for a long time now, they have been polluted and they are going through drastic changes due to climate warming (Johnson et al., 2018). Although some of these pressures have been mitigated or even eliminated in recent decades as a result of different action plans such as the Clean Water Act in the USA or the Water Framework Directive in Europe, the recreational use of lentic waterbodies has increased. Activities, such as fishing, sailing, water sports, bird watching, and bathing present a form of new challenges and pressures for lake ecosystems. Although the importance of recreation for human well-being and local economies is well-appreciated and considered a major ecosystem service of lakes (Vári et al., 2022), unfortunately, less attention has been paid to the effects of tourism on these ecosystems (Monz et al., 2013; Venohr et al., 2018). Therefore, we have only limited information on how recreational beaches influence the habitat and the biodiversity of lake shorelines (but see Brauns et al., 2007). To get a better understanding, here we focused on how the establishment and the use of recreational beaches influence a lake's biodiversity.

As the shoreline of a lake is not primarily adequate for recreational use, because - among other features – natural vegetation (including emergent, floating, and submerged vegetation) is a physical obstacle for many activities (e.g. swimming), the removal of shoreline vegetation is an essential step for establishing beaches. Shoreline vegetation is important for lake fauna and is considered a hot spot of biodiversity (Strayer & Findlay, 2010). Submerged macrophytes and reeds present unique systems with well-defined habitat structures and associated ecological communities (Cheruvelil et al., 2000; Varga, 2001). The removal of this vegetation can cause drastic changes in the habitat structure and might eliminate or replace organisms which depend on this habitat complexity. Besides vegetation removal, tourists can cause significant disturbance to bottom-dwelling communities by treading. Trampling experiments, performed in headwater streams, demonstrated both negative (Escarpinati et al., 2014) and neutral effects (Bossley & Smiley, 2018), however, recreational beaches are assumed to have a generally negative effect on sediment-living macroinvertebrate communities because the selective force of treading (see filtering hypothesis in Poff, 1997). For example, a comparative study of Brauns et al. (2007) performed in German lowland lakes found that macroinvertebrate diversity is significantly lower in recreational beaches than in natural shorelines. This was explained by the reduced habitat heterogeneity (missing roots, coarse woody debris, reed and stones) in recreational beaches compared to that in natural shorelines. On the other hand, we have still no clear idea of how recreational beaches influence bottom-dwelling organisms.

Chironomids are important members of the littoral, shore, and benthic macroinvertebrate communities. Their activity is important in the sediment, they act as bioturbators by reworking the top-sediment layers – oxygenating and cycling nutrients and organic matter (Armitage et al., 1995). Larval chironomids provide food for fish, while adults for amphibians and terrestrial predators such as birds, bats and insects. Chironomid larvae present diverse environmental optima and tolerance, indicating that they are ideal model organisms for freshwater biomonitoring (Rosenberg, 1992).

With its 593 km^2 surface area, Lake Balaton is the largest shallow lake in Central Europe, and one of the foremost touristic destinations in the region. Due to its shape (approximately 77.9 km in length in an east–west direction and on average 7.2 km in width), Lake Balaton has an indeed long (240 km) shoreline, indicating a great proportion and importance of shoreline processes. The bottom of the lake is covered by soft sediments (Tóth, 2016) and its macrofauna is dominated by chironomid communities with 60 to 95% of the total biomass (Specziár & Bíró, 1998). On the natural shoreline, the dominant vegetation is reed (Tóth, 2016). Contrasting shoreline types are produced by the prevailing northern winds: the northern shoreline is wind-protected and covered by silty substrate, while the southern shoreline is exposed to wind, wave activity is more intensive, and covered mostly by sand. Increasing tourism requires clearing the natural reed-vegetated shorelines resulting in open soft-bottom areas. These areas are then filled with sand on the northern shoreline, while this action is not necessary on the southern shoreline as the dominant substrate is sand. These cleared, sand-filled shorelines are used as recreational beaches. All in all, this means a human-induced transformation of natural reed-vegetated shorelines into recreational beaches, which process is rather similar in other tourist lakes all over the world.

4.2. Materials and methods

4.2.1. Study area

The study area was Lake Balaton, the largest lake in Central Europe (surface area: 593 km^2), a multi-purpose freshwater waterbody used to source drinking water for nearby settlements and for a wide range of recreational activities, such as bathing, sport fishing and sailing. Extended sections of the shoreline of Lake Balaton were turned into beaches by removing natural vegetation and stabilizing the shore with concrete and riprap structures to accommodate increasing tourism. There are differences between the northern and southern shoreline and in order to account for these differences we selected 5-5 sampling sites in each shoreline. Within each site three habitats were sampled: (1) natural reed-vegetated shoreline, hereafter reed habitat, (2) open area, which is not used as beach, (3) recreational beach, which is used by beach goers or impacted by beach goers i.e. > 1.5 m depth (**Fig. 3, Appendix 6**). Five sampling points (1 m^2 area) were randomly selected within each habitat. Therefore, our sampling design consisted of 2 [shorelines] x 5 [sampling sites] x 3 [habitats] x 5 [sampling points] = 150 samples.

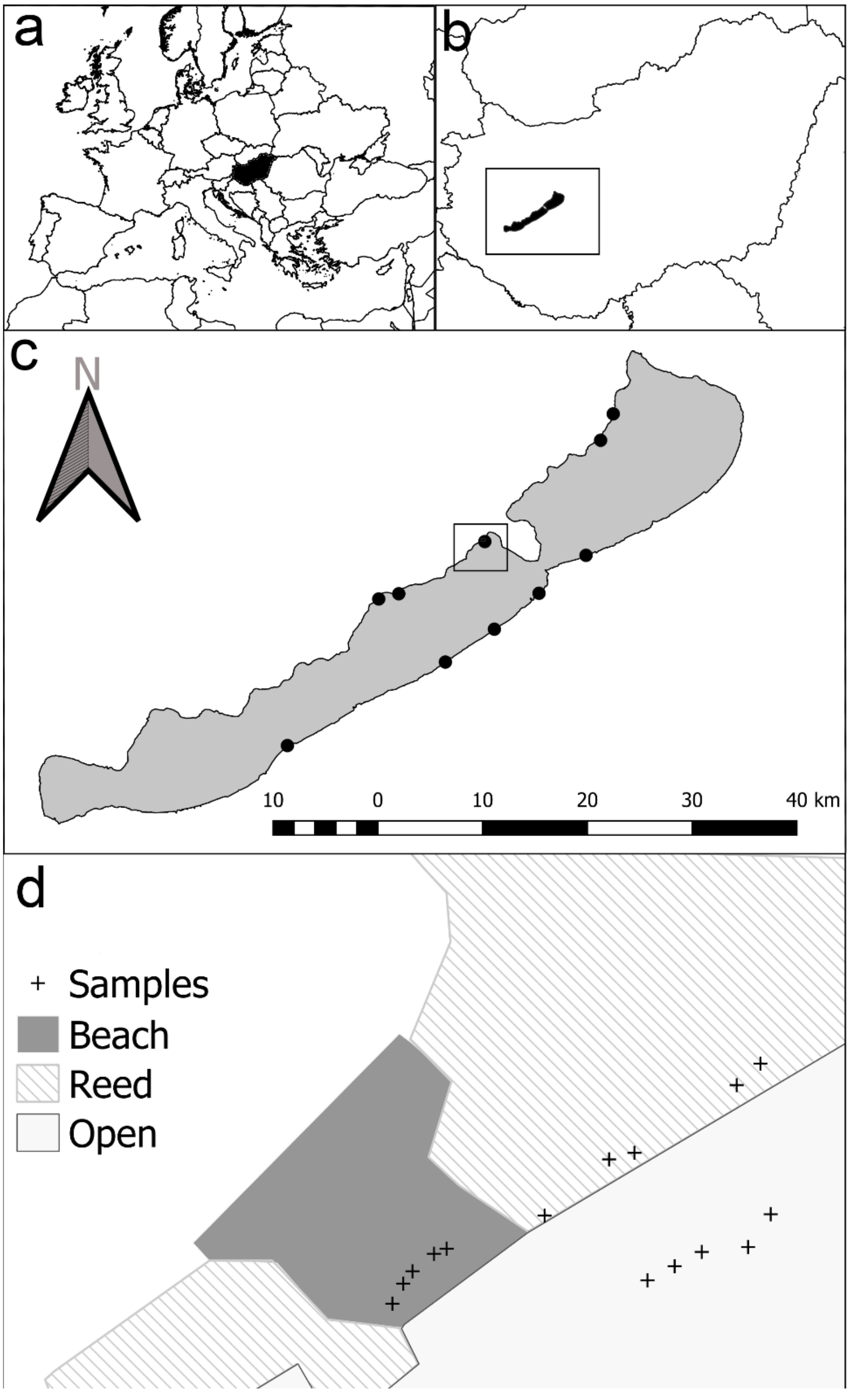

Fig. 3 Map of the study area: (a) Hungary in Europe, (b) the position of Lake Balaton in Hungary, (c) Lake Balaton with study sites (full dots), and (d) the schematic representation of the study design in reed, open and beach habitats.

4.2.2. Environmental variables

GPS position of each sampling point was recorded with a GPS receiver, while we documented parameters on site, such as shoreline position (north or south), habitat (reed, open or beach), water depth (m), water temperature (°C), pH and dissolved oxygen (DO, mgL^{-1}) just above the bottom. We estimated vegetation cover within a circle of 3 m diameter around the sampling point visually as percentage of emergent (reed), submerged and floating-leaved macrophytes, and filamentous algae (mostly *Cladophora* sp., hereafter algae). Substrate composition of samples was also visually estimated as percentage of silt (grain size < 0.06 mm), sand (0.06-2 mm) and mollusc shell (mainly *Dreissena polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897)). We assessed organic matter content (fine particulate organic matter [FPOM], coarse particulate organic matter excluding reed leaves [CPOM] and reed leaves) using a score varying between 0 (not present) to 5 (extremely abundant). These visual assessment methods are widely used in freshwater ecology (Hughes et al., 2010). Relative organic matter content was also assessed in the upper 2 cm of the sediment layer according to loss-on-ignition method at 550 °C for 1 hour (LOI550, Heiri et al., 2001). In six samples, the relative organic matter content could not be quantified due to the low amount of collectable sediment in some reed habitat sampling points. Our environmental variables were selected based on the experienced and known sensitivity of chironomids (Árva et al., 2015b, 2017).

4.2.3. Sampling and identification of chironomids

We sampled benthic chironomid larvae between 8 and 26 July 2019 with an Ekman grab sampler (sampling area: 0.022 m^2). Three sampling units were taken at each sampling point to increase the representativeness of samples and to support comparability to other studies (Árva et al., 2015a; Specziár et al., 2018). Then, we merged the three sampling units and considered them as one sample (therefore the total area per sample: 0.065 m^2). Samples were washed through a 0.25 mm mesh sieve and transported laboratory in a cooling box. We separated the chironomid specimens from the sediment alive by the sugar flotation method (Anderson, 1959) and preserved them in 70% ethanol. Larvae were slide-mounted and identified to species or lowest possible taxonomic level (details in Árva et al., 2015b).

4.2.4. Statistical analyses

Based on our visual assessment, the majority of the samples contained no or a limited amount of reed leaves, CPOM and FPOM (scores 0 or 1, **Appendix 7**). A centred Principal Component Analysis (PCA) showed that the first principal component explained the majority (75%) of among-sample variation, therefore, we used it only as an indicator of organic matter. Akaike Information Criterion corrected for the number of cases and parameters estimated (AICc) (Garamszegi & Mundry, 2014) was used to select the best-fit linear model explaining the effects of habitat, shoreline position and their interaction on environmental variables. In case of a significant habitat effect, a Tukey test was used for multiple comparisons. We used Variation

Inflation Factors (VIFs) to check for collinearity of environmental variables. Based on VIF, the percent cover of silt and sand showed collinearity (Pearson r = 0.868, $p < 0.001$) indicating that the substrate composition of a sample was dominated by sand or silt, but the two components rarely co-occurred in high proportions. To avoid collinearity, we did not use silt in the further analyses. We used Linear Discriminant Analysis (LDA) to examine the separation of the three habitats based on environmental variables.

Linear models (LMs) were used to test the individual and joint effects of habitat and shoreline position on the richness and abundance of chironomid communities. Taxon richness (number of taxa) and log-transformed abundance were used separately as response variables (both modelled by Gaussian distribution). LMs were also used to examine which environmental variables influenced the richness and abundance of chironomids. Relative organic matter as a predictor was omitted from these analyses due to missing data. The best-fit models were selected using AICc and Akaike weights (Garamszegi & Mundry, 2014). Delta AICc indicates the difference in the fit between a particular model considered and that of the best-fit model. The AIC weight represents the probability of the model that was calculated among all possible pairs.

ADONIS (Anderson, 2001) with Bray-Curtis distance (Podani, 2000) was used to test how habitat type, shoreline position and their interaction influenced community composition. We used indicator species analysis (Dufrêne & Legendre, 1997) to determine indicator species for the different habitats in different shoreline positions. Because a detrended correspondence analysis (DCA) indicated a relatively long gradient length (4.254 in standard deviation units on the first axis) in our community data, canonical correspondence analysis (CCA) was chosen. CCA showed that the first eight canonical axes explained 35.2% of community variation. We used the *envfit* function of the vegan package to select environmental variables with significant effects. Statistical analyses were performed in R (R Development Core Team, 2020) using the *faraway* (Faraway, 2016), *multcomp* (Hothorn et al., 2008), *MuMIn* (Barton, 2020) and *vegan* (Oksanen et al., 2019) packages.

4.3. Results

4.3.1. Habitat properties and differences

LDA showed overall differences in environmental variables between the studied habitats (**Fig. 10**). The first axis explained 94.4% of the variance between habitats and clearly separated reed habitat from open and beach habitats, sampling points of reed habitat positioned at the negative values of the first LDA axis, while sampling points of open and beach habitats at the positive values of the first axis. The second LDA axis explained 5.6% of the between-habitat variance and separated open and beach habitats, sampling points of open habitat positioned mostly at the negative values of the second axis, while points of beach habitat at the positive values of the same axis. According to the LDA, reed habitat was the most heterogeneous as sampling points occupied a wide range of the first axis compared to the points of open and beach habitats.

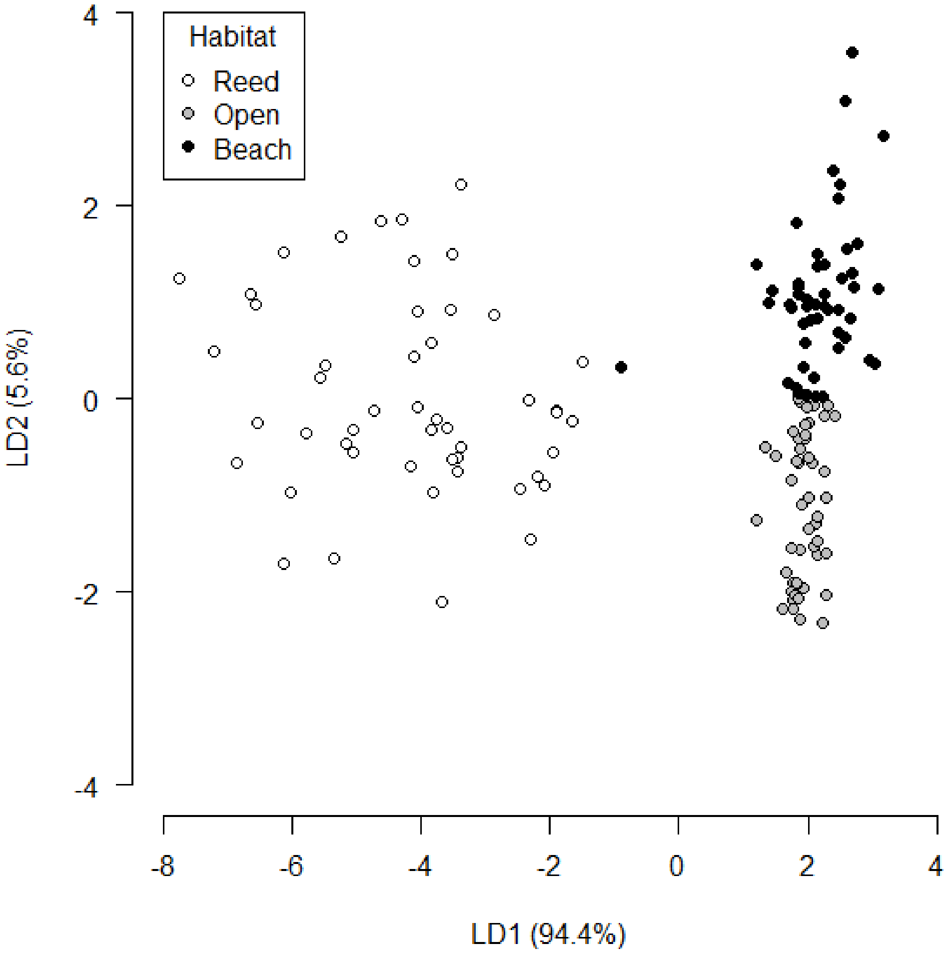

Fig. 10 Ordination plot of linear discriminant analysis (LDA) showing the separation of habitats based on environmental variables.

Environmental variables showed significant differences between habitats (**Table 5**). The reed habitat was characterized by low level of dissolved oxygen and high proportion of mollusc shells, the open habitat was characterized by high water depth and pH, while the beach habitat differed from the others by high proportion of sand substrate. Besides reed, other macrophytes and also algae have the highest coverage in reed habitat. Organic matter and relative organic matter content were the highest in reed habitat, followed by open and beach habitats, presenting significant differences between habitats. Water temperature and silt content was the highest in open habitat, followed by reed and beach habitats. According to best-fit models in most cases not only habitat but also shoreline position, as well as their interaction explained environmental variables (**Table 5**). The inclusion of the interaction in the best-fit model suggests that differences in variables between habitats strongly depended on shoreline position. While the proportion of sand was generally high (around 80%) and the same in the three habitats in the southern shoreline, in the northern shoreline we observed high values only in beach habitat (**Appendix 8**).

Table 5 Comparison of environmental variables of reed, open and beach habitats. Variables given as mean (±SE). Values not sharing an index letter proved to be different at $p < 0.05$ in pairwise comparisons based on Tukey test. The best-fit model considering the predictors habitat, shoreline position and their interactions were selected based on AICc.

Environmental variable	Reed	Open	Beach	Predictors of the best-fit model based on AICc
Water depth (m)	0.86 (±0.07) a	1.39 (±0.07) b	0.95 (±0.04) a	Habitat + Shoreline position + Interaction
Water temperature (C°)	22.80 (±0.18) ab	23.26 (±0.17) a	22.55 (±0.19) b	Habitat
pH	8.47 (±0.02) a	8.68 (±0.01) b	8.54 (±0.02) a	Habitat + Shoreline position
Dissolved oxygen (mg/L)	6.36 (±0.02) a	7.20 (±0.01) b	6.95 (±0.02) b	Habitat + Shoreline position
Sand (%)	42.2 (±6.93) a	45.7 (±6.22) a	84.6 (±3.88) b	Habitat + Shoreline position + Interaction
Silt (%)	34.2 (±4.54) a	51.8 (±6.05) b	13.3 (±3.91) c	Habitat + Shoreline position + Interactions
Mollusc shells (%)	7.5 (±4.47) a	2.5 (±0.70) b	2.1 (±0.94) b	Habitat + Shoreline position + Interactions
Organic matter (PCA axis value, log(x+1) transformed)	0.13 (±0.06) a	-0.08 (±0.03) b	-0.24 (±0.03) c	Habitat + Shoreline position + Interactions
Relative organic matter (%)	10.33 (±0.06) a	6.19 (±0.03) b	1.85 (±0.03) c	Habitat + Shoreline position + Interactions
Cover of reed (%)	52.4 (±2.26) a	0.0 (±0.00) b	0.00 (±0.00) b	Habitat
Cover of macrophytes (%)	20.2 (±3.99) a	8.5 (±2.07) b	5.8 (±1.39) b	Habitat + Shoreline position + Interactions
Cover of algae (%)	3.6 (±1.68) a	0.0 (0.00) b	0.6 (±0.06) b	Habitat + Shoreline position

4.3.2. Richness and abundance of chironomids

We found 37 taxa among the identified 20,168 individuals (**Appendix 9**). The most dominant taxa were *Cladotanytarsus mancus gr* (Walker, 1856) (5,967 individuals), *Polypedilum nubeculosum* (Meigen, 1804) (3,915 individuals), *Cladopelma virescens* (Meigen, 1818) (1,747 individuals) and *Procladius choreus* (Meigen, 1818) (1,529 individuals).

Recreational beaches had an overall negative impact on chironomid taxon richness and abundance (**Fig. 11**, **Table 6**). Generally, beaches caused 18% reduction in richness compared to the natural reed habitats. The mean richness of chironomid taxa were 8.36 for reed and 6.81 for beach habitat. Taxon richness of chironomids depended on the shoreline position, the northern shoreline showed higher richness than the southern. In addition to this, the effect of the habitat types on richness was also shoreline-specific, as indicated by the significant interaction term in our linear model (**Table 6**). While taxon richness decreased in the northern shoreline, it did not change in the southern (**Fig. 11**). Regarding abundance, beaches caused a 5.6% reduction from 120 individuals in reed habitat to 113 individuals in the beach habitat. Similar to richness, abundance also showed shoreline dependence. We observed less individuals in the southern shoreline, and the effect of the habitat type on the abundance was also shoreline-specific. In the northern shoreline reed habitat showed the highest abundance of chironomids, followed by open and beach habitat. In contrast, in the southern shoreline, open habitat had the most individuals and the reed habitat had the least (**Fig. 11**, **Table 6**). On the other hand, there was no difference in richness of chironomids between reed habitat and open habitat and there was no difference in abundance between reed and open habitats. We found also no evidence that transformation from open to beach habitat would decrease the richness and abundance of chironomids, either in the northern or the southern shoreline (**Fig. 11**, **Table 6**).

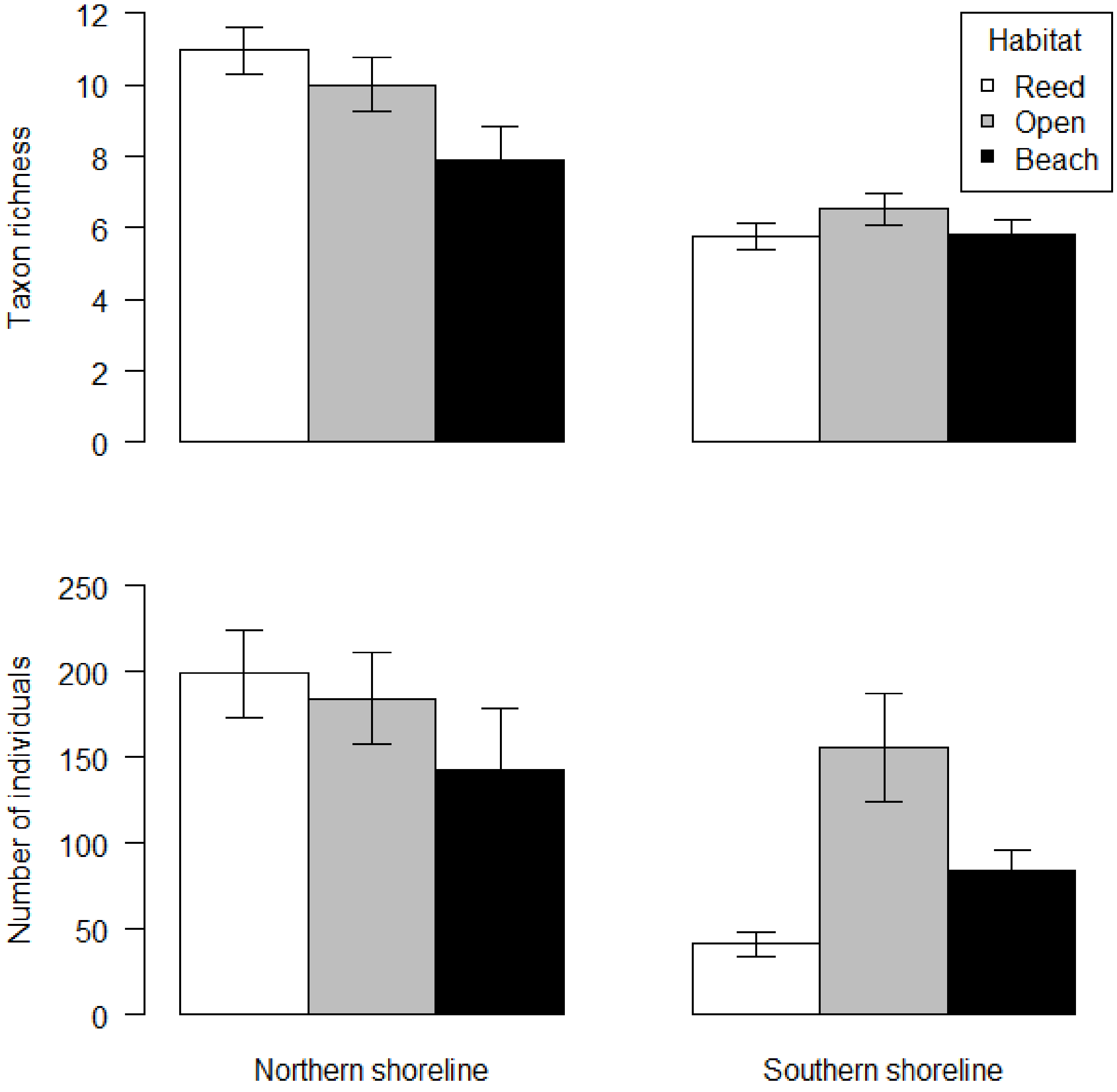

Fig. 11 Response of taxon richness (top) and number of individuals (bottom) on the transformation of the reed-covered shoreline (reed) to open habitat (open) and to recreational beaches (beach) in the northern (left) and southern (right) shorelines of Lake Balaton. Bars show mean values and whiskers standard errors.

Table 6 Output of linear models (LMs) testing our hypotheses regarding taxon richness and number of individuals.

Hypothesis number	Compared habitats	Response variable	Predictor	Estimate	SE	t	p
1	Reed vs. Beach	Taxon richness	Beach	-3.080	0.918	-3.354	**0.001**
			South	-5.200	0.918	-5.662	<**0.001**
			Interaction	3.120	1.299	2.402	**0.018**
		Number of individuals (log-transformed)	Beach	-0.907	0.291	-3.122	**0.002**
			South	-1.744	0.291	-6.002	<**0.001**
			Interaction	1.631	0.411	3.971	<**0.001**
2	Reed vs. Open	Taxon richness	Open	-0.960	0.817	-1.174	0.243
			South	-5.200	0.817	-6.362	<**0.001**
			Interaction	1.720	1.156	1.488	0.140
		Number of individuals (log-transformed)	Open	-0.301	0.278	-1.083	0.282
			South	-1.744	0.277	-6.275	<**0.001**
			Interaction	1.393	0.393	3.544	<**0.001**
3	Open vs. Beach	Taxon richness	Beach	-0.720	0.619	-1.162	0.251
	(southern shoreline)	Number of individuals (log-transformed)	Beach	-0.368	0.317	-1.159	0.252
4	Open vs. Beach	Taxon Richness	Beach	-0.368	0.317	-1.159	0.252
	(northern shoreline)	Number of individuals (log-transformed)	Beach	-0.368	0.317	-1.159	0.252

The best-fit linear model with the lowest AICc and with the highest probability of fit revealed that the taxon richness of chironomids was influenced by several environmental variables (**Table 7**). This model showed a strong positive effect (slope > 1) for organic matter, and a strong negative effect (slope < -1) for water depth and pH, as well as negative effects of algae and sand, and positive effects of macrophytes and temperature (**Table 7**). Alternative and still plausible statistical models included these strong positive and negative effects, and other effects, as well (**Table 7**). Regarding abundance, the weights of the best-fit models are extremely low (2.2, 1.8 and 1.8% for the first three) suggesting that the explanation of chironomid abundance is not straightforward and several alternative statistical models are plausible. The best-fit model showed only a weak impact of some environmental variables (**Table 7**) including the negative effect of water depth, dissolved oxygen, reed cover and sand, while the positive effect of organic matter content and water temperature. Alternative and still plausible statistical models suggest the importance of several environmental variables mostly with weak effects, too (**Table 7**).

Table 7 The three best-fit linear models explaining the effects of environmental variables on the taxon richness and abundance of chironomids.

Response variable	Predictors (slope)	df	AICc	Delta AICc	Weight
Taxon richness	algae (-0.06), water depth (-2.93), organic matter (2.47), pH (-5.27), reed (-0.04), sand (-0.04), macrophytes (0.04), temperature (0.51)	10	743.1	0.00	0.316
	water depth (-3.17), organic matter (2.55), pH (-5.25), reed (-0.05), sand (-0.04), macrophytes (0.04), temperature (0.46)	9	744.7	1.52	0.148
	algae (-0.06), water depth (-2.96), organic matter (2.46), pH (-5.26), reed (-0.04), sand (-0.05), macrophytes (0.04), shells (-0.01), temperature (0.52)	11	745.4	2.31	0.100
Number of individuals	water depth (-0.61), organic matter (0.48), oxygen (-0.39), reed (-0.02), sand (-0.01), temperature (0.21)	8	458.1	0.00	0.022
	organic matter (0.56), pH (-1.32), reed (-0.01), sand (-0.01), temperature (0.19)	7	458.5	0.42	0.018
	organic matter (0.68), oxygen (-0.41), reed (-0.01), temperature (0.23)	6	458.6	0.43	0.018

4.3.3. Composition of chironomids

ADONIS revealed that the community composition of chironomids was significantly different between the reed and beach habitats and between the northern and the southern shoreline (**Table 8**). Interaction between habitat and shoreline position indicated that compositional differences between reed and beach habitat were strongly shoreline dependent. Chironomid composition was also different between reed and open habitats, and between the northern and southern shorelines, while habitat-shoreline interaction also indicated strong shoreline dependence (**Table 8**). Considering compositions of open and beach habitats, a significant difference was found on the northern shoreline and marginally significant on the southern shoreline (**Table 8**). Our findings indicated that chironomid compositions showed high sensitivity to habitat differences and shoreline position.

Table 8 Output of ADONIS testing the effect of habitat and shoreline position on chironomid community composition.

Hypothesis	Compared habitats	Predictor	df	SS	MS	F	R^2	p
1	Reed vs. Beach	Habitat	1	2.709	2.709	12.349	0.091	**0.001**
		Shoreline	1	4.379	4.379	19.958	0.146	**0.001**
		Interaction	1	1.758	1.758	8.012	0.058	**0.001**
		Residuals	96	21.065	0.219		0.704	
		Total	96	29.913			1.000	
2	Reed vs. Open	Habitat	1	2.386	2.386	10.222	0.073	**0.001**
		Shoreline	1	5.455	5.455	23.368	0.166	**0.001**
		Interaction	1	2.639	2.639	11.306	0.080	**0.001**
		Residuals	96	22.409	0.233		0.681	
		Total	96	32.89			1.000	
3	Open vs. Beach	Habitat	1	0.487	0.487	2.293	0.045	0.054
	(southern shoreline)	Residuals	48	10.200	0.213		0.954	
		Total	49	10.688			1.000	
4	Open vs. Beach	Habitat	1	1.668	1.668	6.079	0.112	**0.001**
	(northern shoreline)	Residuals	48	13.170	0.275		0.888	
		Total	49	14.838			1.000	

Indicator species analysis revealed ten indicator taxa for reed habitat (*Polypedium nubeculosum*, *Cladopelma virescens*, *Chironomus balatonicus* Dévai, Wülker & Scholl 1983, *Microtendipes chloris* agg., *Cladopelma viridulum* [Linnaeus, 1767], *Ablabesmyia longistyla* Fittkau, 1962, *Paratanytarsus* sp., *Tanytarsus* sp., *Zavreliella marmorata* [van der Wulp, 1859], *Psectrocladius sordidellus* gr.), six for open habitat (*Procladius choreus*, *Tanypus kraatzi* [Kieffer, 1912], *Tanypus punctipennis* Meigen, 1818, *Fleuria lacustris* Kieffer, 1924, *Microchironomus tener* [Kieffer, 1918] and *Parachironomus varus* [Goetghebuer, 1921]), and a single taxon for beach habitat (*Dicrotendipes nervosus* [Staeger, 1839]) on the northern shoreline. On the southern shoreline we found four indicator taxa for open habitat (*Lipiniella moderata* Kalugina, 1970, *Cladotanytarsus mancus* gr., *Cryptochironomus defectus* [Kieffer, 1913] and *Cricotopus sylvestris* gr.), and there was no indicator species for reed and beach habitats. Canonical correspondence analysis showed significant impact of environmental variables on the community structure of chironomids (**Fig. 12**). The first CCA axis explained 17.1% of the variance of chironomid community and represented a gradient of decreasing proportion of sand and increasing organic matter content. The second axis explained 10.7% of the variance, representing a gradient of increasing reed cover, mollusc shells and decreasing dissolved oxygen and pH. Samples of the northern reed habitat positioned mostly at the positive values of the first and the second axis, indicating a community preferring high level of reed coverage, mollusc shell content, organic matter content and submerged macrophyte coverage. Samples of the northern open habitat were present mostly at the positive values of the first axis and negative values of the second axis, northern open habitat community preferred deeper water. Samples of the northern beach habitat positioned mostly in the middle of the CCA plot, indicated more similarity with the southern chironomid communities compared to other northern communities. Samples of the habitats on the southern shoreline were present at the negative values of the first axis, clustered closely. It seems southern communities were determined by high sand content and higher oxygen and pH levels. The distribution of samples indicated substantially higher heterogeneity in the northern than in the southern habitats.

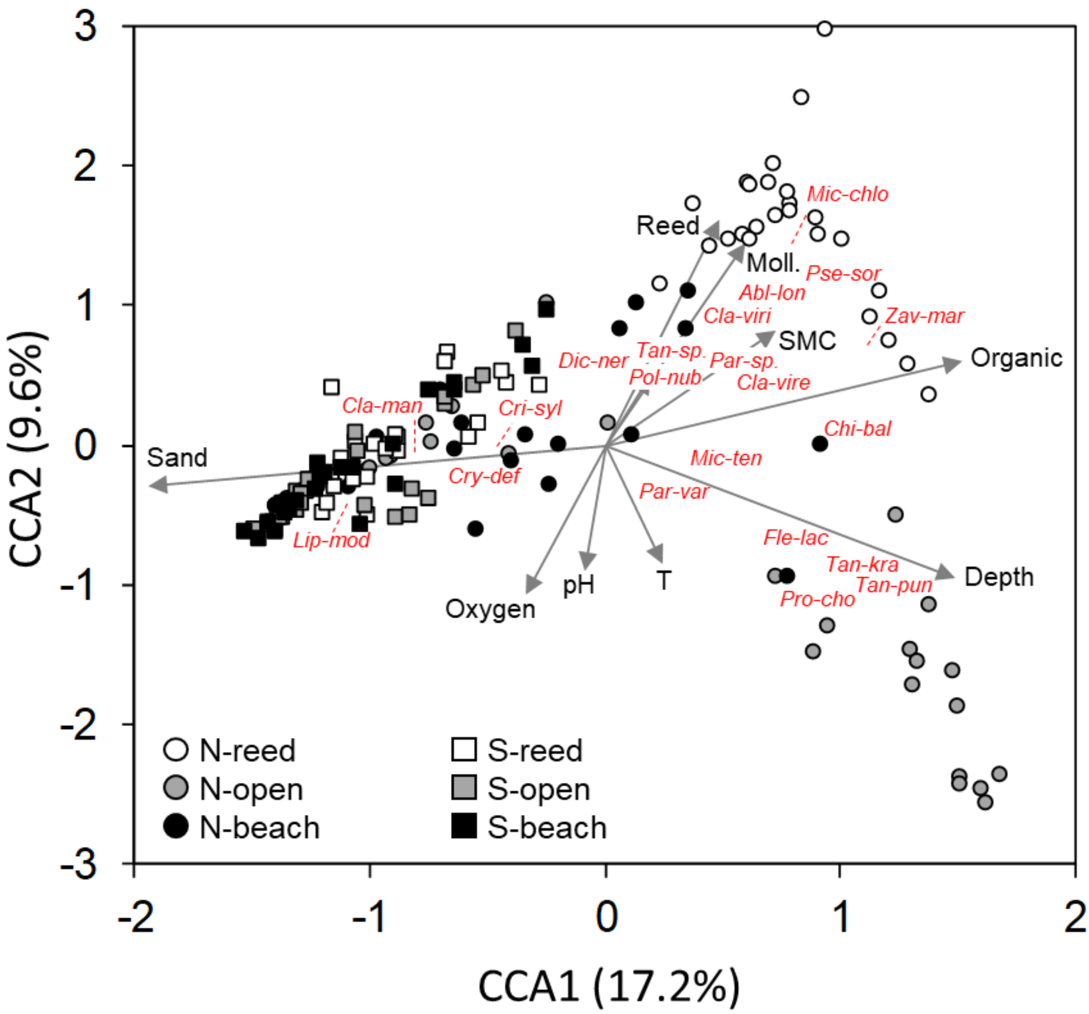

Fig. 12 Ordination plot of canonical correspondence analysis. White circles show reed, grey circles open while black circles beach habitats, circles show sites at the northern shoreline while squares sites at the southern shoreline. Red text displays indicator taxa (*Abl-lon*: *Ablabesmyia longistyla*, *Chi-bal*: *Chironomus balatonicus*, *Cla-man*: *Cladotanytarsus mancus* gr., *Cla-vire*: *Cladopelma virescens*, *Cla-viri*: *Cladopelma viridulum*, *Cri-syl*: *Cricotopus sylvestris* gr.*Cry-def*: *Cryptochironomus defectus Dic-ner*: *Dicrotendipes nervosus*, *Fle-lac*: *Fleuria lacustris*, *Lip-mod: Lipiniella moderata*, *Mic-chl*: *Microtendipes chloris* agg., *Mic-ten*: *Microchironomus tener*, *Par-sp.*: *Paratanytarsus* sp., Par-var: *Parachironomus varus*, *Pol-nub*: *Polypedium nubeculosum*, *Pro-cho: Procladius choreus*, *Pse-sor*: *Psectrocladius sordidellus* gr., *Tan-kra: Tanypus kraatzi*, *Tan-Pun: Tanypus punctipennis*, *Tan-sp.*: *Tanytarsus* sp., *Zav-mar*: *Zavreliella marmorata*), grey arrows and text show environmental variables (scale factor =2 for plotting) proved to be significant by *envfit* test (Moll: mollusc shells, T: temperature, SCM: submerged macrophyte coverage).

4.4. Discussion

The impact of recreational beaches on the biodiversity of lake shorelines is not well understood. To address this gap in knowledge, we collected chironomid assemblages from three different shoreline habitats (natural reed-vegetated shorelines, open areas, and beaches) and compared their diversity. Our results indicate that the conversion of reed habitats to beaches had adverse effects on the abundance and taxonomic richness of chironomids. Moreover, this habitat transformation also affected the composition of chironomid assemblages. These findings suggest that the creation and utilization of recreational beaches could have detrimental consequences for local biodiversity.

One of the major anthropogenic impacts affecting freshwater biodiversity is habitat alteration (Chapin et al., 2000). Our study revealed that the removal of reeds, i.e. the transformation of the reed habitat to an open one, resulted in an increase in water depth and a decrease in reed cover, which both can be linked to the habitat transformation. Additionally, we observed less obvious changes, such as a reduction in the presence of mollusc shells, macrophytes, algae, and organic matter (**Table 5**). The decline in organic matter (**Table 5**) could be attributed to the absence of *Phragmites australis* (Cav.) Trin. ex Steud. This could be explained by the fact that this plant is highly productive and only a small proportion of its production is consumed by herbivores (Newman, 1991). Therefore, reeds not only contribute to the aesthetic value of the landscape but form the basis of a detritus-based ecosystem. These ecosystems accumulate detritus in the form of shed leaves and dead stems at the bottom (Bedford & Powell, 2005), which serve as both substrate and food for organisms (Karádi-Kovács et al., 2015). The presence of this food source, combined with the unique habitat structure (**Fig. 10**), creates an appropriate environment for algae, macrophytes, and molluscs. Additionally, the shells of molluscs can remain intact for an extended period even after the organisms have died, potentially providing a habitat for other organisms (Schmidlin et al., 2012). Collectively, these results imply that the transformation of reed habitats can result in numerous alterations to the structure of the environment (**Fig. 10**), which could potentially trigger changes in the composition of local assemblages.

We observed changes in the habitat parameters associated with the transformation of open habitats to beaches, too (**Table 5**). For instance, we found that the water depth decreased and the proportion of sand increased on beaches. However, these parameters varied depending on the shoreline position and the interaction between these two factors (**Table 5**). Significant interactions indicate that there were differences in the construction of beaches between the northern and southern shorelines: our habitat assessment evidently identified the sand addition at the northern shoreline. Our findings also revealed that although reed habitats offer a diverse habitat, this heterogeneity was reduced in beaches (**Fig. 10**). Overall, our observations indicate that the conversion of reed habitats to beaches caused changes in habitat parameters and a decrease in habitat heterogeneity.

We found that the transformation of reed habitats into beaches led to a reduction in both taxon richness and abundance (**Table 6**). This outcome is consistent with a previous case study conducted in German lowland lakes (Brauns et al., 2007) and aligns with the overall impact of urbanization on freshwater macroinvertebrate diversity (Gál et al., 2019; de Vries et al., 2020), as well as with the well-established negative influence of human disturbance on macroinvertebrates in coastal sandy beaches (Costa et al., 2020). Brauns et al. (2007) identified five habitat types within natural shorelines, including roots, coarse woody debris, reed, sand, and stones, and attributed the biodiversity of natural sites to the existence of these five habitat types. In contrast, our study focused solely on reed habitat and attributed changes in biodiversity to alterations in habitat parameters and the within-reed habitat heterogeneity. Although the explanations for these case studies are not mutually exclusive and both relate to the presumed positive effect of habitat heterogeneity on biodiversity (Palmer et al., 2010), our findings complement those of Brauns et al. (2007) and support the general consensus that human-induced habitat alteration has a negative impact on shoreline biodiversity.

We did not observe any significant effects on the local taxon richness of chironomids due to the removal of reed (hypothesis 2), trampling (hypothesis 3), or sand addition (hypothesis 4), as evidenced in **Table 6**. However, the negative estimate values suggest a non-significant reduction of richness. Although these intermediate steps (hypotheses 2, 3, and 4) did not have a significant impact on diversity, we believe that they must have influenced diversity to some extent, given the overall negative effect of habitat transformation from reed to beach on both richness and abundance (hypothesis 1, which includes all the above-mentioned hypotheses). Despite the potential influence of the intermediate steps, we were unable to find any significant effect, most likely due to our sample sizes combined with the variability of chironomid communities in Lake Balaton (Árva et al., 2015b). Linear models explaining the potential effect of environmental variables suggested that the amount of organic matter in the sample, in line with the productivity-biodiversity relationship (Chase & Leibold, 2002), could support a higher level of chironomid richness (**Table 7**). Additionally, the linear models indicated that water depth had a negative impact on the taxon richness and abundance of chironomids (**Table 7**). This finding supports our previous studies on the chironomid assemblages of Lake Balaton, where shoreline habitats were rich and abundant in chironomids, while offshore locations were poor in taxa and abundance (Árva et al., 2015a, 2015b). Furthermore, recent studies provide comprehensive evidence regarding the dominant significance of gradients in substratum composition (i.e. the proportion of sand versus silt), water depth, and macrophyte coverage, in terms of chironomid beta and gamma diversity in Lake Balaton (Árva et al., 2015b; Specziár et al., 2018).

Chironomid taxa exhibit various environmental optima and tolerance levels (Rosenberg, 1992). Consistent with this, our study revealed that the chironomid community composition was sensitive to the conversion of reed to beach habitat (Hypothesis 1), conversion of reed to open habitat (Hypothesis 2), and sand addition (Hypothesis 4), all of which led to significant changes in habitat parameters due to human activity. Moreover, our observations revealed variations in the chironomid communities between the northern and southern shorelines, indicating that the within-lake natural differences also played a significant role in shaping their composition. (Árva et al., 2015a) categorized four primary habitats in Lake Balaton based on the chironomid assemblages' response to their environment: reed habitat, riprap habitat (not relevant in this study), macrophyte-free open water habitat with silt substrate, and southern littoral habitat (which includes both reed and open habitats) with sand substrate. In our study, reed habitat, open habitat, and southern open water habitat corresponded to this habitat classification, and this was further supported by highly-consistent indicator taxa. Indicator taxa of reed habitat are generally associated with the presence of macrophytes and macroscopic algae (*Cladopelma virescens*, *C. viridulum*, *Microtendipes chloris* agg., *Paratanytarsus* sp., *Polypedilum nubeculosum*, *Psectrocladius sordidellus* gr., *Tanytarsus* sp., *Zavreliella marmorata*), prefer moderate to high amount of decomposing organic matter (*Chironomus balatonicus*, *Paratanytarsus* sp., *Tanytarsus* sp.) and tolerate low concentrations of dissolved oxygen (*Cladopelma virescens*, *C. viridulum*, *Paratanytarsus* sp., *Tanytarsus* sp.) (Cañedo-Argüelles & Rieradevall, 2011; Árva et al., 2015a, 2017). Indicator taxa of open habitat generally associate with deeper water, silt sediment with low to moderate amount of decomposing organic matter (*Procladius choreus*, *Tanypus punctipennis*, *Fleuria lacustris*, *Microchironomus tener*), but also include elements that indicate the presence or proximity of macrophytes, high amount of decomposing organic matter and occasional oxygen deficit (*Tanypus kraatzi*, *Parachironomus varus*) (Wolfram, 1996; Árva et al., 2015a, 2017); namely, that we sampled open habitat within the littoral zone. Indicator taxa of the southern littoral zone were commonly found on substrates with sandy composition (*Lipiniella moderata*, *Cladotanytarsus mancus* gr., and *Cryptochironomus defectus*) and on sandy or other hard substrates that had an algal coating (*Cricotopus sylvestris* gr.) (Wolfram, 1996; Moller Pillot, 2009; Árva et al., 2015a, 2017). The construction of beaches in the southern shoreline appears to have caused changes in chironomid communities within the natural range of the southern littoral habitat described by Árva et al. (2015a). On the other hand, in the northern shoreline, it is evident that beaches constitute a distinct, new artificial habitat type. The characteristic presence of *Dicrotendipes nervosus* on northern beaches, together with the notable abundance of *Cladotanytarsus mancus* gr., may be linked to several environmental factors, such as relatively shallow water with good oxygenation, reduced levels of silt, moderate levels of decomposing organic matter in the sediment, and a moderate density of macrophytes and macroscopic algae, particularly when compared to adjacent reed and open habitats (Árva et al., 2015a, 2017). Therefore, consistent with earlier research, our findings corroborate the significance of environmental factors in structuring macroinvertebrate communities in the littoral zone (Heino, 2013; Heino & Tolonen, 2018).

There is mounting evidence that the development of residential shorelines and catchments by humans poses a significant threat to biodiversity in lake ecosystems (Miler et al., 2013; Twardochleb & Olden, 2016). Such development is often linked to an increase in recreational and tourist activities. While the benefits of tourism for human well-being and the local economy are widely recognized, the impact of tourism on lake ecosystems has received less attention (Monz et al., 2013; Venohr et al., 2018). In a study by Cao et al. (2016), a negative correlation was found between a tourism-stress index of lakes and the richness of their littoral macroinvertebrate communities, indicating that tourism generally has a detrimental effect on lake biodiversity. Our findings support this conclusion and highlight the negative impact of artificial beaches on local biodiversity.

There are several implications for decision-making from our findings. To preserve the biodiversity of natural reed habitats, it is important to evaluate their distribution and quality along the lake shoreline. Remote sensing is a useful tool for this purpose, as it can assess the size of reed vegetated areas, their quality, and temporal dynamics (Tóth, 2018; Jing et al., 2020). Additionally, different modelling and forecasting techniques can be utilized to predict future changes (Tiyasha & Yaseen, 2020; Zhou, 2020). Based on these predictions, and considering the needs of tourism and protective laws, it is possible to maintain the future of natural reed areas and their diversity.

From a conservation perspective, our study have important suggestions for decision-making. Specifically, we recommend that natural reed habitats should not be converted into beaches in the future, especially along the northern shoreline. The formerly extensive reed areas of Lake Balaton have been fragmented, and only cover a total area of 11 km^2 (Tóth & Szabó, 2012), while most of the shoreline has been transformed into rip-rap habitat. Therefore, instead of natural reeds, artificial rip-rap habitats should be considered as the primary candidates for creating recreational beaches. This approach would allow for the satisfaction of touristic and economic needs without eliminating habitats of high conservation importance.

While the impact of shoreline alterations is currently observed only at a local scale, our study offers a foundation to identify potential long-term effects on the biodiversity of the entire lake caused by human activities. Our findings might be extrapolated to other lakes and ecosystems, emphasizing that the provision of diversified economic and societal benefits by beaches must be balanced with conservation efforts to prevent biodiversity loss. Therefore, future action plans must weigh both economic and conservation aspects to maintain and establish recreational beaches sustainably.

5. RESEARCH TOPIC THREE – Linear infrastructures and pond ecology

5.1. Introduction

Urbanization will likely have more profound impacts on biodiversity in both rural and urban areas as the exponential growth of linear infrastructures continues to fragment the landscape (Pullin et al., 2009). Roads are one of the most common and inescapable forms of urbanization, presenting a great service of urban spreading (van der Ree et al., 2015). Globally, 25 million kilometres of new roads are projected to be built by 2050, which means a 60% increase in the total length of roads compared to the data in 2010 (Laurance et al., 2014). In Europe, almost a quarter of all land area (22.4%) is located within 500 m of the nearest transport infrastructure and 50% is located within 1.5 km, leading to declining populations of birds and mammals (Torres et al., 2016). Undeniably, Europe is probably the most highly fragmented by transport infrastructures of all continents (Selva et al., 2011). It seems, that Central European countries also fit in this trend (Selva et al., 2011). In Hungary 500 km of new highways have been built since 2010 (MTI, 2020).

The local and regional biodiversity is likely to be significantly impacted by road construction. Wildlife is affected by roads and road traffic in various ways, from direct mortality to changes in the biophysical environment within a road-effect zone (Forman, 2000; van der Ree et al., 2015). There are numerous and wide-ranging ecological effects of roads on aquatic and terrestrial habitats (Findlay & Bourdages, 2000; Trombulak & Frissell, 2000), such as destruction, fragmentation and degradation of habitats that many wetland-dependent species rely on, which often occur during road construction (Forman & Alexander, 1998; Trombulak & Frissell, 2000). Similarly, rail infrastructure can lead to the separation of animal populations and cause mortality (Barrientos et al., 2019). As a result, roads and railways are posing a threat to numerous animal species that rely on the link between aquatic and terrestrial habitats (Trombulak & Frissell, 2000; Hamer & McDonnell, 2008; Dorsey et al., 2015). Amphibians are among the most vulnerable animal groups, with one-third of their species facing the risk of extinction due to urbanization (Hamer & McDonnell, 2008). The lifecycle of pond-breeding amphibians is highly complex and depends on inter-connected networks of freshwater ponds (Semlitsch, 2000), making them especially sensitive to the loss, fragmentation, and degradation of wetlands (Cushman, 2006; Hamer & McDonnell, 2008), and susceptible to the effects of road construction and traffic (Hels & Buchwald, 2001; Beebee, 2013; Hamer et al., 2015). In addition, amphibians are especially susceptible to being killed on roads because they are slower and smaller compared to other types of vertebrates (Rytwinski & Fahrig, 2012). Species that are highly mobile are at an even greater risk of mortality on roads because they tend to encounter roads more frequently (Gibbs, 1998; Carr & Fahrig, 2001). When there are obstacles that prevent dispersal between aquatic breeding habitats and terrestrial areas, it can hinder the metapopulation dynamics and result in a decrease in the size of regional populations (Semlitsch, 2002; Becker et al., 2007). In fragmented landscapes supporting heavy traffic, there is typically a reduction in the presence and abundance of amphibian species (Hartel et al., 2010; Cayuela et al., 2015). This is often due to the negative relation between forest cover and the density of roads and traffic (Eigenbrod et al., 2008a). In Central European countries like Hungary, the decline of amphibians has been linked to the building of roads, which, together with other types of changes to the landscape, have led to the destruction of 97% of wetlands (Vörös et al., 2015). Since 2004, road construction in Hungary has resulted in a net loss of habitat, degradation, and a decline in biodiversity (Mihók et al., 2017). In many regions, road building has disrupted populations of amphibians and disconnected their breeding and hibernation sites (Vörös et al., 2015). Consequently, we need more research in Hungary to comprehend the impact of roads on amphibians and to establish effective conservation programs that are sustainable in the long term (Vörös et al., 2015). Our research will provide additional information to address the lack of understanding of how amphibians react to linear infrastructure in Central and Eastern Europe on a landscape scale. To quantify the effects of roads on amphibian populations, we used accessible habitat as a separate metric from habitat loss (Eigenbrod et al., 2008b; Hamer, 2016, 2018). We defined accessible habitat as the amount of terrestrial habitat (e.g. forest patch) that can be reached from a focal patch of habitat (e.g. breeding pond) without crossing a road or railway (Eigenbrod et al., 2008b). Habitats that are not fragmented are more conducive to the richness and abundance of the community compared to habitats on the opposite side of a road since they allow for essential life-history processes such as dispersal between the hibernation and breeding sites. The impact of a major road such as a 4-lane highway that needs to be crossed to access other habitat patches is much more detrimental to the population compared to a smaller road, for example a 2-lane secondary road, that does not impede access to habitat.

On the other hand, it is likely that roads and railways differ in their impact on habitat fragmentation (Selva et al., 2011), however, there is yet no empirical data to confirm this. In Western Europe, an increase in accessible habitat such as forest cover within barrier-based buffers, that extend up to 2500 m around ponds, has been found to result in a higher presence of amphibians (Zanini et al., 2008), and it is true conversely, sealed roads and urban cover surrounding ponds in Eastern European landscapes have been found to decrease anuran occupancy and abundance (Hartel et al., 2009b, 2010). The application of the accessible habitat concept to evaluate the impact of roads and railways on amphibian communities in fragmented landscapes of Central or Eastern Europe has not been investigated yet. To address this gap, we conducted a study to examine the relationship between road and rail infrastructure and the abundance of larval amphibians in a highly fragmented landscape located in Central Europe. Our focus was on the abundance of amphibians during the larval stage due to the well-established relationship between habitat quality and species demography (Van Horne, 1983), nonetheless, we recognize that comprehending juvenile demography may be more crucial in determining the impact of roads on amphibian populations (Petrovan & Schmidt, 2019). A variety of factors, for example hydroperiod, can lead to significant year-to-year fluctuations in the size of larval populations, which can ultimately impact the community structure due to fluctuating recruitment of juveniles (Semlitsch et al., 1996). Because of this, our study offers a glimpse of larval community abundance during a single breeding season.

5.2. Materials and methods

5.2.1. Study area

The study area was between Lake Balaton and Budapest, Hungary approximately 50 km South-West of Budapest along several highways (M7 motorway, no. 7, no. 8, no 801 roads, all ≥ 4-lanes) and the main railway line from Budapest to Veszprém. The study area was comprised predominantly of agricultural land but also included small towns, floodplains and nature conservation areas (**Fig. 4**), accordingly, it was a mixed peri-urban/agricultural landscape, highly fragmented by transportation infrastructure making an ideal system to examine the response of amphibian communities to roads and railways. Initially, 50 ponds (lentic waterbodies) were selected using Google Earth Pro images (Google Inc., 2020) and the

Ecosystem Base Map of Hungary (Ministry of Agriculture, 2019). Constraints on property access and water availability at some sites resulted in a final set of 30 ponds being selected. We selected sites to ensure sufficient variation in pond area, distance to highways and the extent of natural and urban features in the surrounding landscape. Sites included various types of ponds, such as highway stormwater retention ponds, recreational fishing ponds, farm dams, ditches and canals, and floodplain ponds. We grouped sites into 12 spatial clusters comprised of 1-5 sites, with sites in the same cluster being <1000 m apart, to approximate the mean dispersal distances of adult amphibians expected to occur in the study area (Smith & Green, 2005). Sites within clusters were typically separated by vegetated areas (e.g. grassland) with no intervening urban infrastructure, highways, the main railway or other obvious barriers. The mean distance to the nearest surveyed site was 411 m (SD = 838; range: 14 – 3977 m).

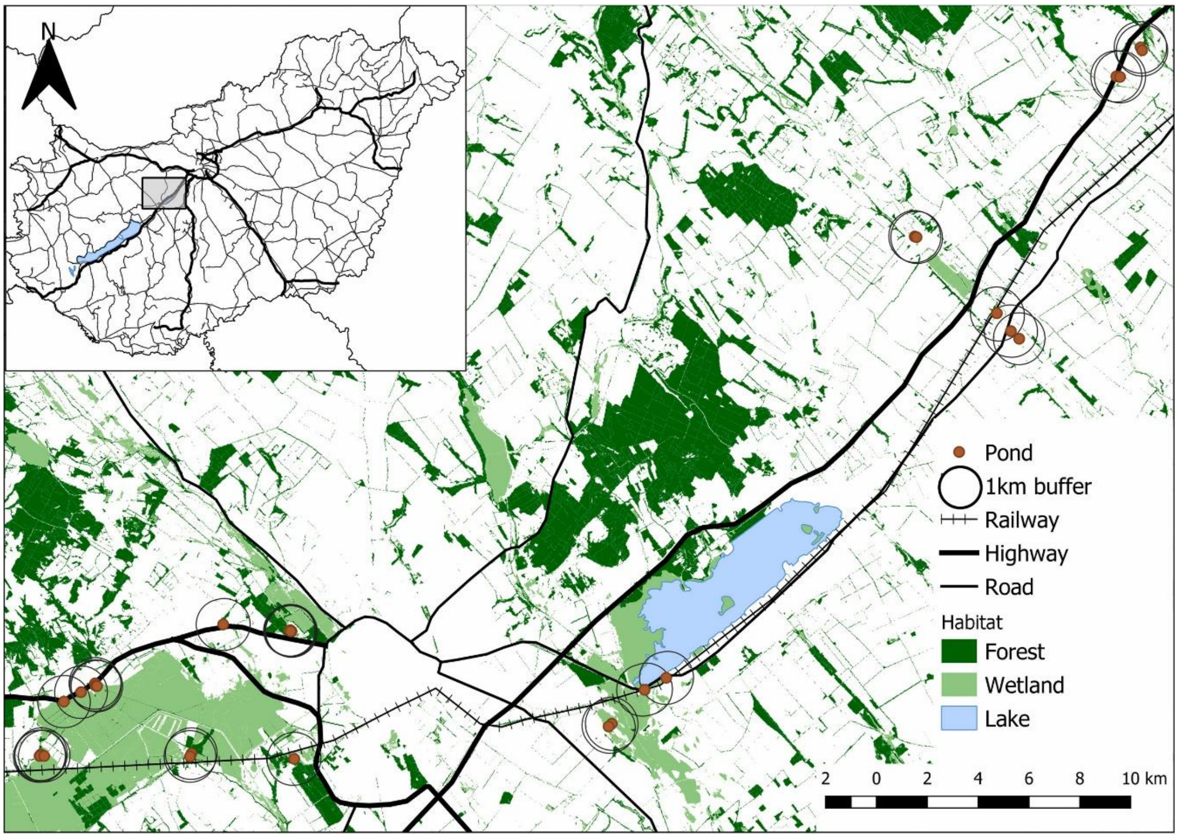

Fig. 4 Map of the study area in Western Hungary. Highways = sealed roads, ≥4 lanes; Roads = sealed roads, 2 lanes. Habitat classed as "Lake" was included under wetland habitat in the analysis.

5.2.2. Environmental variables

Landscape-scale variables

We defined accessible habitat (%) as the total area of forest and wetland habitat within a 1000-m radius of a pond edge that could be assessed without crossing only highways (**Access_hwy**) or highways and the main railway (**Access_hwy_rail**). Forest habitat included forests, woodland and woody/ herbaceous vegetation, whereas wetland habitat included permanent and temporary marshes and lakes. We selected a 1000-m radius as the landscape buffer to cover the dispersal distances of most amphibian species expected to occur in the study area (Vos & Stumpel, 1995; Smith & Green, 2005), which was smaller than the maximum dispersal distance recorded for some species (Smith & Green, 2005). We assumed that highways represented the greatest barrier to amphibian movement in the study area, and that sealed 2-lane roads with a smaller physical footprint and presumably lower traffic volumes were having a weaker barrier effect (Eigenbrod et al., 2008b). We also predicted that the railway would have a smaller barrier effect than highways for similar reasons. Therefore, highways and the railways were used to delineate accessible habitats. The total area of forest and wetland habitat within a 1000-m radius of a pond (**Habitat%**), ignoring the presence of highways and the railway within the buffer, was included as a separate variable to assess habitat area in predicting the effect of habitat loss on amphibian abundance, separately from road effects. Road cover (%) within a 1000-m radius around a pond (**Roads**) was calculated using mapped road surfaces and used to assess the effect of the total area (length and width) of all sealed roads on amphibian abundance in the study area, separately from habitat loss. As road cover is often correlated with the density of urban infrastructure (Parris, 2006; Hamer & McDonnell, 2008) it was also a surrogate variable for the degree of urbanization around a site. To assess road and rail effects separately, and to determine if a road-effect zone was affecting amphibian abundance in ponds close to highways and the railway, we measured the distance from a pond margin to the nearest highway (**Dist_hwy**) or to a highway or the railway (**Dist_hwy_rail**). QGIS v.3.10 was used to measure distances and for all area calculations (QGIS Development Team, 2020).

Local-scale variables

As hydroperiod and the presence of predatory fish species are often important determinants of amphibian community structure (Wellborn et al., 1996) we recorded the presence of fish (**Fish**) at sites during the aquatic surveys (fish presence = 1; non-detection = 0) and scored hydroperiod according to the percentage of the full water-holding capacity of each pond during field surveys. Three types of ponds were classified according to hydroperiod: ephemeral ponds (1) were completely dry on at least one survey; semi-permanent ponds (2) dried down to ≤ 20% of full water levels; permanent ponds (3) retained > 20% of full capacity throughout the study. Increased pond area and hydroperiod have been shown to reduce turnover in metacommunities of larval amphibians, while fish presence decreases population densities (Werner et al., 2007). Larger habitat patches can also support higher population sizes within metapopulations

(Hanski, 1994). Consequently, pond area (**Area**) was included and calculated from digitised polygons using Google Earth Pro. At the shoreline of ponds water temperature was also recorded.

5.2.3. Larval amphibian surveys

We conducted three aquatic surveys in the 30 ponds over one breeding season in the spring and summer of 2020 (survey 1: April/May 2020; survey 2: June 2020; survey 3: July 2020), considering the breeding season of amphibian species recorded in the region previously (Berninghausen & Berninghausen, 2001). We undertook repeated surveys to reduce uncertainties that may arise from high variability in larval abundance within a single season. Ponds with sufficient water levels (water depth >5 cm) were dip-netted during the day using a net designed for safe capture of amphibians (300-mm wide frame, 350 mm deep, 1 mm mesh size). We calculated the number of net sweeps beforehand regarding to pond area - one net sweep for every 25 m^2 of pond surface area (Shulse et al., 2010) resulting in 2-281 sweeps per pond (mean = 45, SD = 56). The number of net sweeps was modified in ponds with reduced water levels but still scaled to the inundated area. Dip-net sweeps were approximately 1.5 m in length and were performed in all microhabitat types (e.g. open water, emergent/submerged vegetation) to target the preferences of amphibian larvae (Shaffer et al., 1994). We surveyed ponds within the same spatial cluster generally on the same day, and to minimise bias, survey timing of each cluster was randomised. In small (<1000 m^2) and some larger ponds amphibian larvae caught during dip-netting were held temporarily in a plastic bucket and then we identified, counted and released them unmarked. In larger ponds, larvae were processed upon capture and then released. To avoid double-counting of individuals the distance between the point of release and the next dip-net sweep was >5 m. Presence of fish at sites was confirmed visually and we recorded the count of fish captured in dip-nets. We identified amphibian larvae to species level using Berninghausen & Berninghausen (2001), while taxonomy follows Speybroeck et al. (2020). Larvae of green frogs [*Pelophylax lessonae* (Camerano, 1882), *P. kl. esculenta* and *P. ridibunda* (Pallas, 1771)] were consolidated under the *Pelophylax* spp. complex. Frog and toad larvae were defined as individuals within Gosner development stages 25 (small tadpoles large enough to be reliably identified) through stages 42–44 (metamorphosing tadpoles with front and hind limbs; Gosner, 1960); newt larvae were identified using similar morphological parameters (stages 39–55; Gallien & Bidaud, 1959). We followed standard hygiene protocols to minimise the risk of spreading the amphibian chytrid fungal diseases *Batrachochytrium dendrobatidis* Longcore, Pessier et. Nichols, (1999) and *B.*

salamandrivorans Martel, Blooi, Bossuyt and Pasmans (2013) during fieldwork (Phillott et al., 2010). As fieldwork was conducted at the peak of the human coronavirus (COVID-19), we worked under strict protocols to minimise the risk of its transmission.

5.2.4. Statistical analyses

In contrast to the previous studies, in this study, we used Bayesian statistics. We developed multi-species abundance models (MSAMs) to assess relationships between larval amphibian abundance and landscape- and local scale variables. MSAMs are hierarchical (community) N-mixture models that allow abundance to be estimated from repeated count surveys while adjusting for imperfect detection of individuals (Royle, 2004; Royle et al., 2005, 2007). Models for individual species are linked together into a hierarchical model and they collectively represent community-level responses to environmental covariates, increasing the precision of parameter estimates for species observed at a few sites by considering each within the context of the broader community and borrowing strength from more abundant species (Dorazio et al., 2006; Kéry & Royle, 2008; Zipkin et al., 2009). Hence, these models account for interspecific variation in egg clutch size and other reproductive parameters by estimating the mean larval abundance across all species in the community and then relating mean community abundance to covariates.

MSAMs were built from a series of individual N-mixture models utilizing the original formulation of Royle (2004) and Royle et al. (2005) and using the count data from larval surveys. The first level of the model is a sub-model which assumed true but imperfectly observed abundance, where the abundance of species i at site j, N_{ij}, is a Poisson random variable: $N_{ij} \sim \text{Poisson}(\lambda_{ij})$, where λ_{ij} is the expected or mean abundance (Royle et al., 2005). We added a random effects term to models for spatial autocorrelation (Cluster) because breeding dispersal of adult amphibians may be occurring between closely-spaced wetlands (e.g. <100 m apart), resulting in spatially-aggregated patterns of larval abundance in breeding ponds. The spatial aggregation of sites in the study area also resulted in overlapping and therefore non-independent landscape buffers. Failing to account for spatial autocorrelation can lead to biased parameter estimates (Wintle & Bardos, 2006), whereas overlapping landscape buffers can result in lower variation in predictor variables (Eigenbrod et al., 2011); however, there was sufficient variation in the covariates we examined. As overdispersion is a common phenomenon in count data and can bias parameter and abundance estimates in N-mixture models (Knape et al., 2018; Link et al., 2018), a random effects term for overdispersion and unexplained variation in abundance (ε)

was included in each model (Kéry et al., 2009). Mean abundance was expressed as a log-linear function of site-level covariates in six separate models:

$$\log(\lambda_{ij}) = \beta_{0\mathrm{i}} + \beta_{1i}(\mathrm{Area}_j) + \beta_{2i}(\mathrm{X}_j) + \beta_{3i}(\mathrm{Fish}_j) + \mathrm{Cluster}_\mathrm{j} + \varepsilon_i$$

where X_j is one of the six landscape scale covariates calculated at site *j* (**Access_hwy, Access_hwy_rail, Habitat, Roads, Dist_hwy, Dist_hwy_rail**). Covariates **Dist_hwy**, **Dist_hwy_rail** and **Area** were log10(x)-transformed prior to analysis. We put **Area** to all models to account for variation in pond size, therefore, sampling area. Each sub-model had a maximum of three covariates given the recommendation of a minimum *n*/*k* of 10 where *n* is the number of sites and *k* is the number of estimated parameters (Harrison et al., 2018). **Fish** was selected for inclusion over **Hydroperiod** because fish predators can eliminate amphibian larvae from ponds and can colonise ephemeral ponds during floods (Semlitsch, 2002). There was no strong correlation between **Hydroperiod** and **Fish** (rs = 0.445), or among the covariates included in each model (|r| or |rs| <0.6; **Appendix 11**).

The probability of detection was modelled using the proportion of full water-holding capacity of a site (**Water**); water temperature (**Temp**); and the number of days since 1 February 2020 (**Days**). Reduced water levels at a site may increase larval densities and hence affect detectability; conversely, increased water levels may encourage breeding activity and spawning (Hartel et al., 2011). Larval activity likely increases with higher water temperatures (Wells, 1977). The covariate **Days** accounts for variation in detection since the beginning of the breeding season, as species differ in spawning time (Berninghausen & Berninghausen, 2001); detection of species with a prolonged reproductive strategy is likely to increase over the season, whereas detection of early breeding species will decrease with **Days** (Wells, 1977). Detection was modelled as a binomial process: C_{ijk} ~Binomial (p_{ijk}, N_{ij}), where C_{ijk} is the number of detected individuals (i.e. count) of species *i* at site *j* on survey *k*, while p_{ijk} is the probability of detecting each individual of species i at site j on survey k (Royle et al., 2005). Following this, detection probability was expressed as a logit-link function of the three survey-specific covariates in each model:

$$\mathrm{logit}(p_{ijk}) = \beta_{0\mathrm{i}} + \beta_{1i}(\mathrm{Water}_{jk}) + \beta_{2i}(\mathrm{Temp}_{jk}) + \beta_{3i}(\mathrm{Days}_{jk})$$

Continuous covariates in abundance and detection sub-models were standardised (mean = 0, SD = 1), this allowed direct comparison of model coefficients, therefore, the relative importance of each covariate could be determined according to the magnitude of the coefficient (Schielzeth, 2010). Missing values of water temperature (e.g. dry ponds) were replaced by the mean.

An additional component of the hierarchical model called community-level hyper-parameters (μ) was added to govern species-level parameters which were treated as random effects (Zipkin et al., 2009). Community summaries and model parameters in each sub-model were estimated using Bayesian inference with priors for the hyper-parameters drawn from a normal distribution; $N(-1, 5)$ for intercept terms (β_{0i}), $N(1, 5)$ for β_{1i}, β_{2i}, β_{3i}. Hyper-parameters for precision (σ) were drawn from a uniform distribution ($U [0.01, 0.5]$); while cluster and overdispersion terms were also modelled using uniform priors ($U [0, 1]$). We assumed that species would show broadly similar responses to road effects and landscape fragmentation; i.e. species responses in the metacommunities were drawn from a common distribution where species have similar ecological requirements (Pacifici et al., 2014). We calculated the mean and standard deviation of the model coefficients, and the 2.5th and 97.5th percentiles of the posterior distribution, which represents a 95% Bayesian credible (or confidence) interval (BCI). Parameter estimates of covariates with a BCI that did not overlap zero were considered to be clearly important, whereas estimates with a BCI overlapping zero had greater uncertainty and were considered to be less important. However, some minor overlap of the BCI with zero was tolerated in inferring relationships (see Cumming & Finch, 2005). Covariates with smaller variance (standard deviation: σ) on hyper-parameters were considered to have similar effects across all amphibian species; larger σ indicated dissimilar effects.

Modelling was performed in JAGS (version 4.3.0, Plummer, 2013) via package *R2jags* (Su & Yajima, 2015) from R (version 3.6.1, R Development Core Team, 2019). Each model was run using three replicate Markov chain Monte Carlo (MCMC) iterations to generate 700 000 samples from the posterior distribution of each model after discarding a ‘burn-in’ of 50 000 samples, with a thinning rate of 3. Convergence of the Markov chains was checked by visual inspection of trace plots and the Brooks-Gelman-Rubin statistic ($\hat{R}$); acceptable convergence was achieved when $\hat{R} < 1.05$ (Gelman & Rubin, 1992; Brooks & Gelman, 1998).

Model selection using Bayesian hierarchical models is still contentious and there is no consensus on optimal model selection criterion for Bayesian models (Broms et al., 2016). Accordingly, we adopted a three-tier approach to select the best-supported model for prediction among the six abundance models. Firstly, we used the strength (magnitude) and clarity of parameter estimates to determine which covariates were most influential, consequently, which model could provide the clearest inferences on abundance. Secondly, we used Bayesian p-values to assess the model fit by calculating the Freeman-Tukey fit statistic (see Stolen et al., 2019). Poorly-fitting and overdispersed N-mixture models provide misleading estimates of abundance, detection and effects of covariates with high probability (Knape et al., 2018). Values close to 0.5 indicate acceptable model fit while p-values ≤ 0.1 indicate a potential lack-of-fit (Gelman et al., 1996). Finally, we used the Deviance Information Criterion (DIC; Spiegelhalter et al., 2002) for model selection, with the better-supported models having low DIC values. The use of DIC for ranking hierarchical Bayesian models is not considered ideal because of the models' latent parameters (Hooten & Hobbs, 2015; Broms et al., 2016), although DIC has been widely used to rank hierarchical models based on their anticipated predictive performance (Stevens & Conway, 2019).

5.3. Results

5.3.1. Larval amphibian surveys

We detected seven amphibian species from six families, with at least one species detected at 25 of the 30 sites. Most frequent species were smooth newt (*Lissotriton vulgaris* [Linnaeus, 1758]) and agile frog (*Rana dalmatina* Fitzinger, 1838) both with a naïve occupancy rate of 0.43, while the least frequent species was European tree frog (*Hyla arborea* [Linnaeus, 1758]) which larvae were detected at only five sites (naïve occupancy rate = 0.17). The other four species, such as fire-bellied toad (*Bombina bombina* [Linnaeus, 1761]), common toad (*Bufo bufo* [Linnaeus, 1758]), *Pelophylax* spp. complex and common Eurasian spadefoot toad (*Pelobates fuscus* [Laurenti, 1768]) were detected at 7-12 sites (naïve occupancy rates: 0.23 – 0.40). The number of species at a site ranged between 0 and 6 with a mean of 2.3 (SD = 1.9). We caught altogether 2,580 amphibian larvae during the three surveys, ranging from 40 (*H. arborea*) to 1178 (*Bufo bufo*) individuals (mean = 86.0, SD = 119.4, **Appendix 12**) per species.

We detected fish at 15 sites, native species, for example, common rudd/pearl roach (*Scardinius erythrophthalmus* [Linnaeus, 1758]), and non-native species, e.g. Prussian carp (*Carassius gibelio* [Bloch, 1782]) or pumpkinseed (*Lepomis gibbosus* [Linnaeus, 1758]), were also found. Four sites dried out during the study (ephemeral ponds), and two sites dried out in survey 2 but refilled to ~ 25% of full water-holding capacity in survey 3, presumably after heavy rain caused localised flooding of an adjacent waterway and were colonised by Prussian carp. Water levels were substantially reduced (≤5% of capacity) at a further six sites during surveys 2 and 3. A summary of the landscape and local covariates is in **Appendix 10.**

5.3.2. Model performance

Among the four MSAMs that assessed relationships with roads the **Dist_hwy** and **Roads** models showed the strongest and clearest relationships between mean community abundance of amphibian larvae and distance to the nearest highway and the percentage cover of road surface within a 1000-m radius ($\mu_{\text{Dist\_hwy}} = 2.451$, 95% BCI: 1.872– 3.034; $\mu_{\text{Roads}} = –2.490$, BCI: –3.044 to –1.953; **Table 9**). From the two models **Dist_hwy** model had a better fit with the data (**Dist_hwy**: $p = 0.248$; **Roads**: $p = 0.196$) and had the lowest DIC (**Table 9**). Parameter estimates between mean community abundance and the landscape-scale covariates in the **Access_hwy** and **Habitat** models were considerably smaller than estimates in the **Dist_hwy** and **Roads** models, and the 95% BCIs overlapped zero slightly ($\mu_{\text{Access\_hwy}} = 0.593$, BCI: –0.035 – 1.214; $\mu_{\text{Habitat}} = 0.559$, BCI: –0.067 – 1.166; **Table 9**). Both the **Access_hwy** model and **Habitat** model had an acceptable model fit (**Access_hwy**: $p = 0.179$; **Habitat**: $p = 0.189$), but less than **Dist_hwy** and **Roads** models, and had a higher DIC (**Table 9**). According to DIC values **Access_hwy** model is a better-supported model than **Habitat** model. Among the four MSAMs **Dist_hwy** model proved to be the best-supported model indicating that direct road effects had a higher relative influence on amphibian abundance than accessible habitat. Parameter estimates for local-scale covariates and detection covariates derived from the **Dist_hwy** model are reported (**Table 9**).

MSAMs with the inclusion of the distance to the main railway did not improve performance. **Dist_hwy_rail** model had minor non-convergence, with estimates of three parameters having $\hat{R} = 1.1$ (see **Table 9** and **Appendix 13**). Estimates of mean community abundance were similar in **Dist_hwy_rail** model as in **Dist_hwy** model ($\mu_{\text{Dist\_hwy\_rail}} = 2.210$; 95% BCI: 1.666–2.757), but the DIC was considerably higher (**Table 9**), suggesting that distance to the railway had no apparent effect on amphibian abundance at ponds. **Access_hwy_rail** model showed a small positive, but highly ambiguous relationship between mean community abundance and accessible habitat delineated by either the highway or the railway ($\mu_{\text{Access\_hwy\_rail}} = 0.199$; 95% BCI: –0.461 – 0.875), and the DIC was higher than in the **Access_hwy** model (**Table 9**) indicating no apparent relationship between the main railway line and accessible habitat. On the other hand, both railway models fit the data with acceptable accuracy (**Dist_hwy_rail**: $p = 0.256$, **Access_hwy_rail** model: $p = 0.201$).

The **Dist_hwy** model showed clear relationships with the individual species abundances of all seven amphibian species (**Table 10**), while there was an uncertain relationship for one species in the **Roads** model, with the 95% BCI for the *Pelophylax* spp. complex overlapping zero widely (**Appendix 13**).

Table 9 Summary of community-level hyper-parameters for abundance (λ) and detection (β) for the larvae of seven amphibian species. Estimates include 95% Bayesian credible intervals (BCI). Clear relationships for hyper-parameters of the covariates are where the 95% BCI does not overlap zero (highlighted in bold, except intercept coefficients). μ = mean community response; σ = standard deviation in the response to the covariate across species; sd = standard deviation; DIC = Deviance Information Criterion (models with lower DIC have greater support).

Model	Covariates	Mean	SD	95% BCI		DIC
Dist_hwy						6765.7
$\mu_{\lambda 0}$	Intercept	0.981	0.347	0.298	1.654	
$\sigma_{\lambda 0}$	Intercept	0.380	0.115	0.067	0.497	
$\mu_{\lambda 1}$	**Area**	**1.803**	**0.216**	**1.379**	**2.226**	
$\sigma_{\lambda 1}$	Area	0.482	0.017	0.438	0.499	
$\mu_{\lambda 2}$	**Dist_hwy**	**2.451**	**0.296**	**1.872**	**3.034**	
$\sigma_{\lambda 2}$	Dist_hwy	0.486	0.013	0.451	0.500	
$\mu_{\lambda 3}$	Fish	0.154	0.219	–0.273	0.584	
$\sigma_{\lambda 3}$	Fish	0.493	0.007	0.475	0.500	
$\mu_{\beta 0}$	Intercept	–4.108	0.246	–4.593	–3.629	
$\sigma_{\beta 0}$	Intercept	0.477	0.023	0.416	0.499	
$\mu_{\beta 1}$	**Water**	**1.109**	**0.179**	**0.758**	**1.459**	
$\sigma_{\beta 1}$	Water	0.477	0.020	0.424	0.499	
$\mu_{\beta 2}$	**Temp**	**0.357**	**0.168**	**0.029**	**0.688**	
$\sigma_{\beta 2}$	Temp	0.462	0.031	0.384	0.499	
$\mu_{\beta 3}$	**Days**	**0.571**	**0.175**	**0.229**	**0.915**	
$\sigma_{\beta 3}$	Days	0.467	0.029	0.394	0.499	
Dist_hwy_rail						7130.5
$\mu_{\lambda 0}$	Intercept	0.999	0.368	0.298	1.733	
*$\sigma_{\lambda 0}$	Intercept	0.402	0.104	0.095	0.498	
$\mu_{\lambda 2}$	**Dist_hwy_rail**	**2.210**	**0.278**	**1.666**	**2.757**	
$\sigma_{\lambda 2}$	Dist_hwy_rail	0.479	0.019	0.428	0.499	
Roads						6953.6
$\mu_{\lambda 0}$	Intercept	0.861	0.349	0.160	1.529	
$\sigma_{\lambda 0}$	Intercept	0.362	0.127	0.048	0.497	
$\mu_{\lambda 2}$	**Roads**	**–2.490**	**0.278**	**–3.044**	**–1.953**	
$\sigma_{\lambda 2}$	Roads	0.493	0.006	0.476	0.500	
Habitat						8176.9
$\mu_{\lambda 0}$	Intercept	0.766	0.344	0.102	1.444	
$\sigma_{\lambda 0}$	Intercept	0.387	0.112	0.075	0.497	
$\mu_{\lambda 2}$	Habitat	0.559	0.314	–0.067	1.166	
$\sigma_{\lambda 2}$	Habitat	0.492	0.008	0.469	0.500	
Access_hwy						7631.3
$\mu_{\lambda 0}$	Intercept	0.720	0.352	0.015	1.383	
$\sigma_{\lambda 0}$	Intercept	0.388	0.112	0.073	0.497	
$\mu_{\lambda 2}$	Access_hwy	0.593	0.319	–0.035	1.214	
$\sigma_{\lambda 2}$	Access_hwy	0.493	0.007	0.474	0.500	
Access_hwy_rail						8058.4
$\mu_{\lambda 0}$	Intercept	0.739	0.350	0.062	1.439	
$\sigma_{\lambda 0}$	Intercept	0.378	0.117	0.060	0.497	
$\mu_{\lambda 2}$	Access_hwy_rail	0.199	0.342	–0.461	0.875	
$\sigma_{\lambda 2}$	Access_hwy_rail	0.493	0.007	0.476	0.500	

Notes: Hyper-parameter estimates are presented for each model that assessed the relative importance of the landscape-scale covariates, however, estimates for local-scale covariates (Area, Fish) and detection covariates were extracted from the Dist_hwy model as it was the best-supported model (note the magnitude and certainty of the coefficients for the landscape-scale covariates). Dist_hwy = distance to nearest highway; Dist_hwy_rail = distance to nearest highway or the railway; Roads = % cover of road surface within a 1000 m radius of a site; Habitat = % forest + wetland habitat within a 1000 m radius of a site; Access_hwy = % forest + wetland habitat within a 1000 m radius of a site that can be accessed without crossing a highway (i.e., accessible habitat); Access_hwy_rail = % forest + wetland habitat within a 1000-m radius of a site that can be accessed without crossing a highway or the main railway (i.e., accessible habitat); Area = pond area; Fish = presence (1) or absence (0) of fish at a site; Water = % of full water-holding capacity at a site; Temp = water temperature; Days = number of days since 1 February 2020. * parameter estimate did not converge ($\hat{R}$ = 1.1)

Table 10 Summary of species-specific estimates for abundance (λ) and detection (β) covariates for the larvae of seven amphibian species. Parameter estimates were extracted from the Dist_hwy model. Estimates include 95% Bayesian credible intervals (BCI). Clear relationships are where the 95% BCI does not overlap zero (highlighted in bold, except intercept coefficients). SD = standard deviation.

Species	Species-specific parameter		Mean	SD	95% BCI	
Bombina bombina	λ_0	Intercept	1.389	0.487	0.463	2.349
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.249**	**0.220**	**1.821**	**2.684**
	λ_2	**Dist_hwy**	**1.644**	**0.321**	**1.017**	**2.280**
	λ_3	**Fish**	**–2.129**	**0.248**	**–2.623**	**–1.650**
	β_0	Intercept	–4.288	0.370	–5.044	–3.580
	β_1	**Water**	**1.148**	**0.100**	**0.956**	**1.348**
	β_2	**Temp**	**–0.187**	**0.069**	**–0.322**	**–0.051**
	β_3	**Days**	**0.697**	**0.111**	**0.483**	**0.918**
Bufo bufo	λ_0	Intercept	1.576	0.529	0.600	2.647
(Family: Bufonidae)	**λ_1**	**Area**	**3.872**	**0.178**	**3.527**	**4.226**
	λ_2	**Dist_hwy**	**4.375**	**0.333**	**3.728**	**5.049**
	λ_3	Fish	–0.149	0.159	–0.458	0.162
	β_0	Intercept	–5.411	0.286	–6.014	–4.884
	β_1	**Water**	**1.006**	**0.065**	**0.879**	**1.134**
	β_2	**Temp**	**–0.093**	**0.042**	**–0.175**	**–0.011**
	β_3	**Days**	**0.484**	**0.043**	**0.400**	**0.569**
Hyla arborea	λ_0	Intercept	0.933	0.495	–0.077	1.888
(Family: Hylidae)	**λ_1**	**Area**	**1.889**	**0.417**	**1.069**	**2.704**
	λ_2	**Dist_hwy**	**3.546**	**0.489**	**2.598**	**4.511**
	λ_3	Fish	–0.328	0.373	–1.072	0.387
	β_0	Intercept	–4.181	0.461	–5.107	–3.299
	β_1	Water	–0.001	0.181	–0.354	0.356
	β_2	**Temp**	**0.657**	**0.195**	**0.286**	**1.051**
	β_3	**Days**	**1.641**	**0.264**	**1.145**	**2.180**
Lissotriton vulgaris	λ_0	Intercept	1.078	0.483	0.103	2.033
(Family: Salamandridae)	**λ_1**	**Area**	**1.452**	**0.334**	**0.798**	**2.106**
	λ_2	**Dist_hwy**	**2.147**	**0.389**	**1.391**	**2.920**
	λ_3	Fish	–0.069	0.293	–0.649	0.497
	β_0	Intercept	–3.869	0.452	–4.770	–3.008
	β_1	**Water**	**0.910**	**0.167**	**0.591**	**1.247**
	β_2	**Temp**	**0.393**	**0.137**	**0.128**	**0.663**
	β_3	**Days**	**0.921**	**0.169**	**0.595**	**1.257**

Species	Species-specific parameter		Mean	SD	95% BCI	
Pelobates fuscus (Family: Pelobatidae)	λ_0	Intercept	1.013	0.489	0.029	1.981
	λ_1	**Area**	**2.207**	**0.406**	**1.409**	**3.002**
	λ_2	**Dist_hwy**	**3.223**	**0.474**	**2.302**	**4.165**
	λ_3	**Fish**	**–1.012**	**0.344**	**–1.697**	**–0.347**
	β_0	Intercept	–4.107	0.466	–5.029	–3.203
	β_1	**Water**	**1.603**	**0.280**	**1.078**	**2.177**
	β_2	**Temp**	**–0.488**	**0.161**	**–0.812**	**–0.177**
	β_3	Days	–0.203	0.222	–0.651	0.222
Pelophylax spp. complex (Family: Ranidae)	λ_0	Intercept	1.060	0.480	0.098	1.995
	λ_1	**Area**	**1.323**	**0.262**	**0.818**	**1.843**
	λ_2	**Dist_hwy**	**0.955**	**0.304**	**0.363**	**1.556**
	λ_3	**Fish**	**3.490**	**0.281**	**2.950**	**4.057**
	β_0	Intercept	–5.878	0.323	–6.529	–5.257
	β_1	**Water**	**2.913**	**0.186**	**2.552**	**3.280**
	β_2	**Temp**	**1.665**	**0.110**	**1.454**	**1.887**
	β_3	**Days**	**0.758**	**0.089**	**0.588**	**0.935**
Rana dalmatina (Family: Ranidae)	λ_0	Intercept	1.370	0.519	0.426	2.464
	λ_1	**Area**	**0.562**	**0.189**	**0.192**	**0.932**
	λ_2	**Dist_hwy**	**2.979**	**0.297**	**2.407**	**3.575**
	λ_3	Fish	0.242	0.192	–0.135	0.621
	β_0	Intercept	–4.560	0.353	–5.256	–3.871
	β_1	**Water**	**0.306**	**0.058**	**0.194**	**0.421**
	β_2	**Temp**	**–0.134**	**0.035**	**–0.202**	**–0.067**
	β_3	**Days**	**–0.766**	**0.093**	**–0.952**	**–0.586**

Notes: Area = pond area; Dist_hwy = distance to nearest highway; Fish = presence (1) or absence (0) of fish at a site; Water = % of full water-holding capacity at a site; Temp = water temperature; Days = number of days since 1 February 2020.

5.3.3. Larval community abundance

Mean number of amphibian larvae (i.e. mean community abundance) was predicted to increase from 0.77 at the site located nearest to a highway (18 m), to 28.22 at the site located furthest to a highway (3869 m, **Fig. 13**a). However, we experienced only a small increase in abundance at sites located 0 – 1000 m from a highway. It suggests that road-effect zones extended for up to 1 km. Similar responses were found to **Dist_hwy** across all species in the community ($\sigma_{\lambda 2}$ = 0.486; **Table 9**). Mean abundance was predicted to decrease from 24.92 at the site with the lowest road cover (0.04%) to 0.18 with the highest percentage cover of road surface within a 1000-m radius (7.03%, **Fig. 13**b). Regarding accessible habitat, mean community abundance was predicted to increase from 1.37 at the site with the lowest percentage of accessible habitat within a 1000-m radius to 4.04 at the site with the highest coverage (**Fig. 13**c). Similar predictions made for total habitat, mean abundance was predicted to increase from 1.44 at the site with the lowest percentage of surrounding total habitat to 4.05 at the site with the highest coverage of total habitat (**Fig. 13**d). These changes were notably smaller compared to the changes of mean larval abundance regarding the effects of distance from highway (**Dist_hwy**) and percentage of road surface within 1000 m radius (**Roads**).

A strong positive relationship was found between mean community abundance and pond area (μ_{Area} = 1.803, 95% BCI: 1.379 – 2.226; **Table 9**), which was also evident in the other five models (**Appendix 14**). The mean larval abundance was predicted to increase from 1.43 at the smallest to 67.33 at the largest pond (**Fig. 13**e). Mean abundance increased only slightly at ponds with an area of 0 – 2000 m^2 (1.43 – 3.91), while showing a sharper steep from 2000 m^2 pond area, suggesting that small ponds had low suitability as breeding sites in the study area. Responses to pond area were rather similar across all species as indicated by the small estimate for the variance parameter ($\sigma_{\lambda 1}$ = 0.482; **Table 9**).

Fish presence showed a positive, but negligible, relationship with mean larval abundance, the 95% BCI overlapped zero widely (μ_{Fish} = 0.154, 95% BCI: –0.273 – 0.584; **Table 9**). Mean larval abundance at sites with fish presence was 3.36 (ranged between 1.42 and 6.72) and 2.83 (ranged from 1.35 to 5.23) at sites with no fish detected (**Appendix 15**). Species showed high variability in response to fish presence ($\sigma_{\lambda 3}$ = 0.493; **Table 9**).

There was positive and negative spatial autocorrelation in larval abundance at sites within nine of the 12 clusters (95% BCIs not overlapping zero), indicating that the spatial position of ponds relative to other ponds affected larval community abundance (**Appendix 16**).

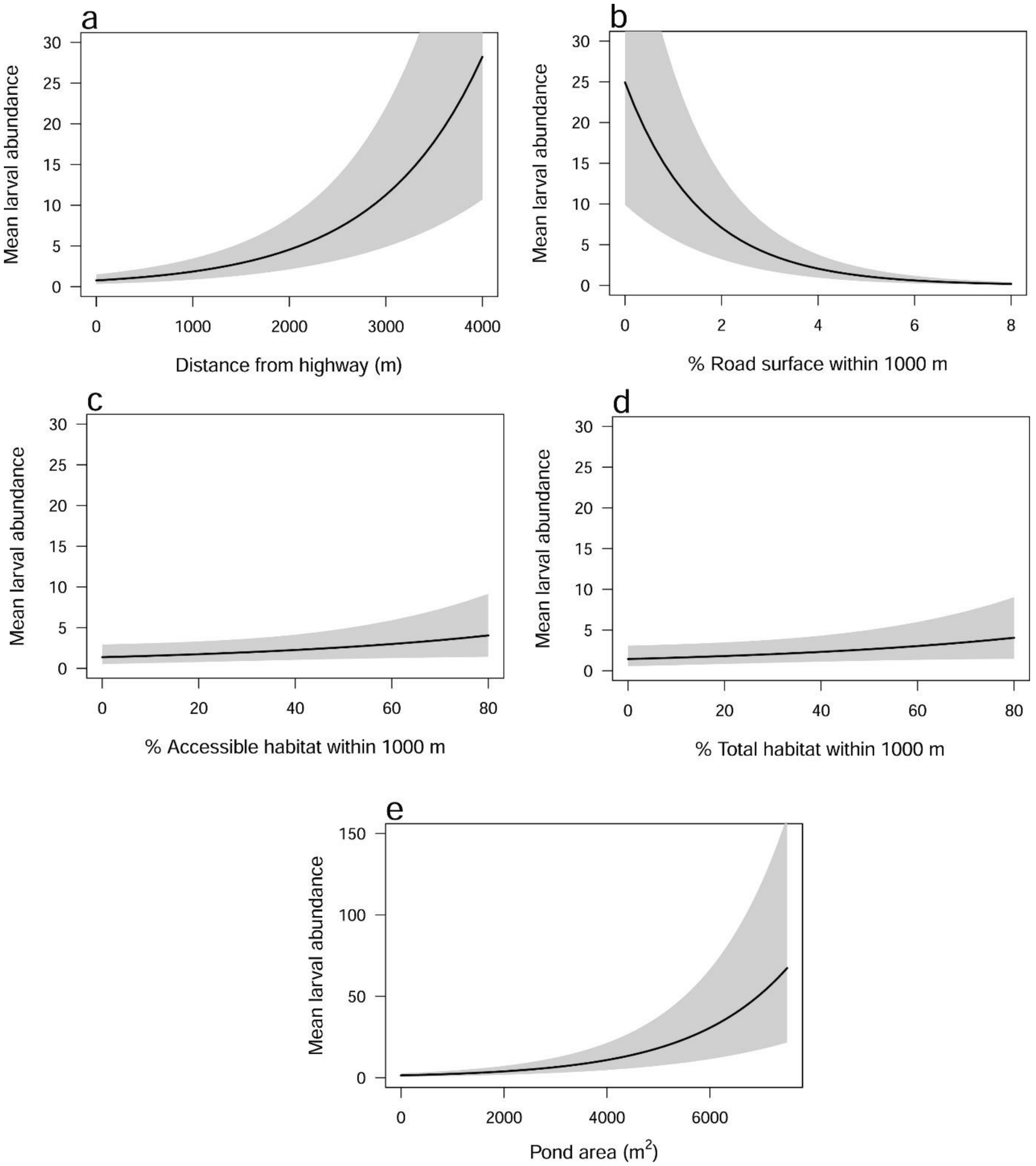

Fig. 13 Mean estimates of larval abundance (shaded areas are 95% Bayesian credible intervals) across the amphibian community versus five habitat covariates: (a) distance from highway; (b) % road surface within a 1000-m radius; (c) % accessible habitat within a 1000-m radius; (d) % total habitat within a 1000-m radius; and (e) pond area.

5.3.4. Larval species abundance

All seven species' mean abundance showed a clear positive relationship with distance to a highway (**Fig. 14**a). *Bufo bufo* showed the strongest ($\lambda_{\text{Dist\_hwy}}$ = 4.375, 95% BCI: 3.728–5.049), while the *Pelophylax* spp. complex the weakest ($\lambda_{\text{Dist\_hwy}}$ = 0.955; 0.363–1.556; **Table 10**) relation. Similarly strong effects of distance were found for *Rana dalmatina*, *Hyla arborea* and *Pelobates fuscus*, while the responses of *Bombina bombina* and *Lissotriton vulgaris* were also relatively similar. Roads had an evidently strong negative effect on larval abundance of all species between 0 – 1000 m distance. A clear negative relationship was found between the percentage of road cover surface within a 1000-m radius and the mean abundance of six from the seven species (**Fig. 14**b). Similar to **Dist_hwy**, *Bufo bufo* showed the strongest relationship with road cover (λ_{Roads} = –5.616; BCI: from –6.282 to –5.008; Table S4), while the *Pelophylax* spp. complex showed a weak, ambiguous relation (λ_{Roads} = –0.087; BCI: –0.555 – 0.368; **Appendix 13**). Larval abundance of six species showed really low values over 4% of road coverage within a 1000 m radius. There were mixed relationships between mean species abundance and percentage of accessible habitat within a 1000-m radius. *Bufo bufo*, *Hyla arborea*, *Lissotriton vulgaris* and *Pelobates fuscus* showed a positive, whereas *Bombina bombina*, *Rana dalmatina* and the *Pelophylax* spp. complex a negative relationship (**Fig. 14**c, **Appendix 13**). Again, *Bufo bufo* had the strongest relation to accessible habitat, similar to the case of **Dist_hwy** and **Roads**. Regarding the percentage of total habitat similar relationships were found as for accessible habitat (**Fig. 14**d, **Appendix 13**).

The pond area had a clear positive relationship with mean larval abundance for all species (**Fig. 14**e, **Table 10**). Similar to previous results, *Bufo bufo* showed the strongest relation (λ_{Area} = 3.872; BCI: 3.527 – 4.226), on the other hand, *Rana dalmatina* showed the weakest (λ_{Area} = 0.562; BCI: 0.192 – 0.932; **Fig. 14**e; **Table 10**). There was also a positive relationship in the other five models (**Appendix 13**).

Mixed relationships were found between mean species abundance and the presence of fish. Larvae of *Bombina bombina* and *Pelobates fuscus* showed a negative, while the *Pelophylax* spp. complex showed a strong positive relation to fish presence (**Table 10**, **Appendix 15**). Similar trends were evident in the other models, however, in the **Roads** model there was a clear positive relationship between *Bufo bufo* larval abundance and fish presence, while a clear negative relationship with *Lissotriton vulgaris* (**Appendix 13**).

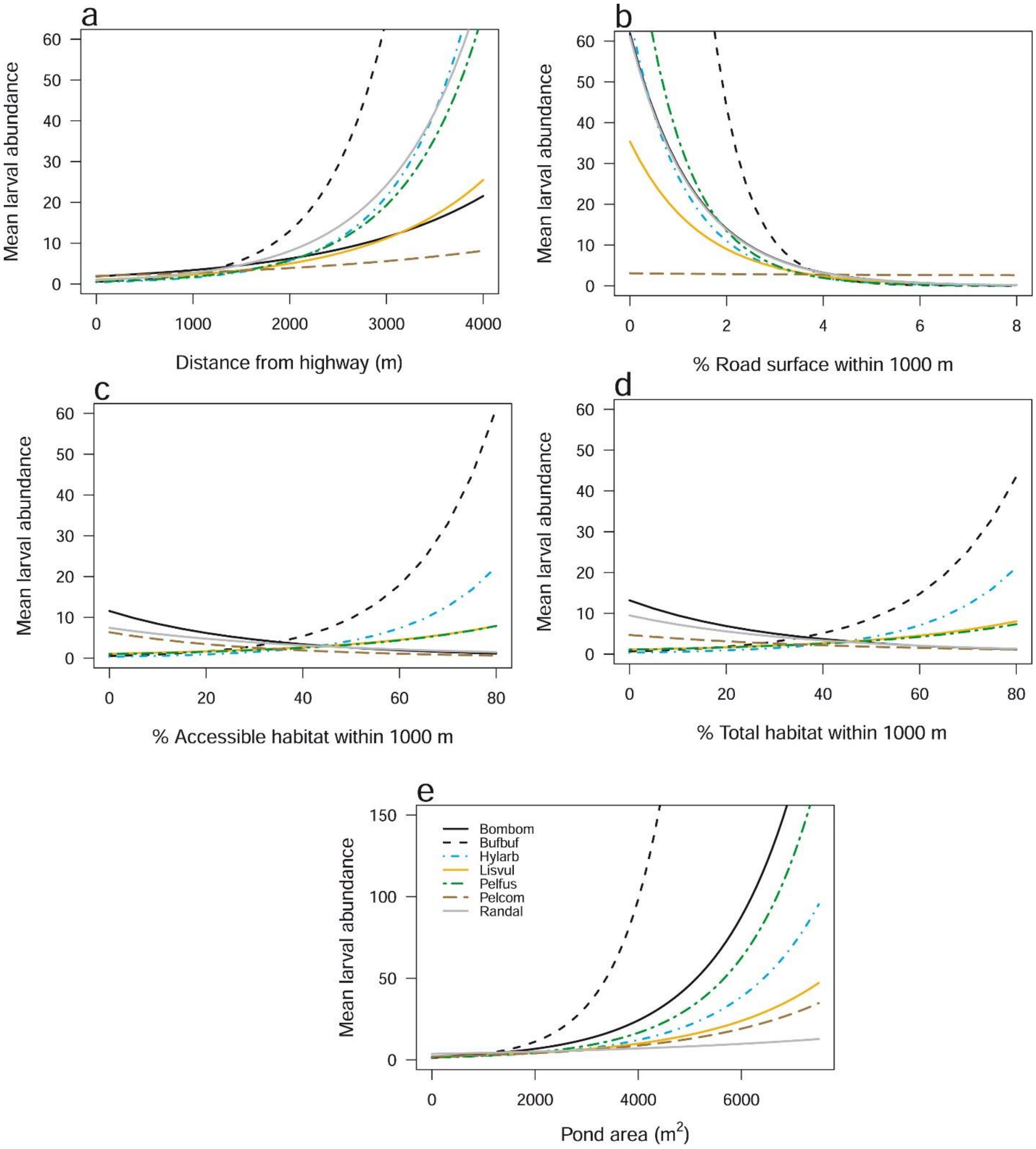

Fig. 14 Mean species-specific estimates of the abundance of seven amphibian species versus five habitat covariates: (a) distance from highway; (b) % road surface within a 1000-m radius; (c) % accessible habitat within a 1000-m radius; (d) % total habitat within a 1000-m radius; and (e) pond area. Credible intervals are omitted for clarity. Species codes: Bombom = *Bombina bombina*; Bufbuf = *Bufo bufo*; Hylarb = *Hyla arborea*; Lisvul = *Lissotriton vulgaris*; Pelfus = *Pelobates fuscus*; Pelcom = *Pelophylax* spp. complex; Randal = *Rana dalmatina*.

5.3.5. Detection probability

Clear positive relationships were found between the community means for the probability of detection and site water levels, water temperature and the number of days since 1 February 2020 (**Table 9**, **Appendix 14**). There were positive relationships between species detection probabilities and water levels for six species, the strongest relationship was found for the *Pelophylax* spp. complex (**Table 10**), while *Hyla arborea* showed a negative, but negligible, relation. Mixed relationships were found between detection probability and water temperature, *Bombina bombina*, *Bufo bufo*, *Pelobates fuscus* and *Rana dalmatina* had clearly negative relationships, whereas *Hyla arborea*, *Lissotriton vulgaris* and the *Pelophylax* spp. complex had positive relationships, with the strongest relationship for the *Pelophylax* spp. complex (**Table 10**). Positive relationships were found between detection probability and the number of days since 1 February for five species (prolonged breeding species), such as *Bombina bombina*, *Bufo bufo*, *Hyla arborea*, *Lissotriton vulgaris* and the *Pelophylax* spp. complex, while there was a negative relationship with *Rana dalmatina* (explosive breeding species), and *Pelobates fuscus* also showed a negative, but weak, relation (**Table 10**).

5.4. Discussion

The effects of roads on amphibian populations can be severe and potentially wide-ranging (Beebee, 2013; Hamer et al., 2015). We provide evidence that roads are having a negative impact on amphibian breeding communities in a landscape fragmented by agriculture and urbanization. The mean abundance of larval amphibian communities showed robust associations with the distance to a highway and the amount of road coverage within a 1000-m radius around the ponds. These relationships were stronger compared to the responses of the community to the accessible habitat proportion and the total habitat amount within a 1000-m radius. While our study was limited to a single breeding season, the findings indicate that the direct negative effects of roads have a stronger impact on amphibian abundance than the combined impact of roads and habitat amount in the study area. Our findings are consistent with a previous study carried out in an Eastern European rural landscape, which found that sealed roads with high traffic volumes (e.g., highways) had the greatest impact on pond occupancy by amphibians, surpassing the influence of landscape composition, such as forest cover (Hartel et al., 2010). However, unlike the study of Hartel et al. (2010), which was conducted in a semi-natural rural landscape, our study was conducted in an intensively-managed agricultural and peri-urban landscape. Therefore, our study represents the first attempt to investigate the effects of habitat fragmentation and roads on amphibians at a landscape scale in highly-modified landscapes in Central and Eastern Europe.

Wildlife is often impacted by roads within road-effect zones, of which significant ecological effect can extend outward from a road for kilometres in some instances (Forman & Alexander, 1998; Forman, 2000; Forman & Deblinger, 2000). We present evidence of a road-effect zone that extends up to 1 km from highways, resulting in significantly lower abundance of amphibian larvae in the ponds located within this zone. According to the study of Beebee (2013), the effects of roads on amphibian communities were observed up to a distance of 2 km from the roads. Highways can have adverse effects on amphibian reproduction in nearby ponds, leading to reduced population sizes of pond-breeding species due to road mortality (Gibbs & Shriver, 2005; Karraker & Gibbs, 2011; Beebee, 2013). In this way, highways could be compromising the population viability of amphibians in the study area through a range of direct, such as road mortality, and indirect impacts, such as traffic noise, altered hydrological patterns, and contaminated runoff (Trombulak & Frissell, 2000; Tennessen et al., 2014). We observed variations in the abundance of larvae occurring at distances >1 km from highways among different species. Among species, *Bufo bufo* showed the strongest reaction, displaying a significant negative relationship with road coverage within a 1000-m radius of ponds. Although this species is capable of traveling long distances, it tends to move relatively slowly during breeding migrations (Hels & Buchwald, 2001; Smith & Green, 2005). Due to their breeding migrations being frequently interrupted by roads, *Bufo bufo* has the highest percentage of amphibian road mortality in many parts of Europe (Hels & Buchwald, 2001; Hartel et al., 2009a; Brzeziński et al., 2012). In a study conducted by Eigenbrod et al. (2009), they observed road-effect zones extending up to 1 km from a highway in a rural landscape, with a decrease in the abundance of four anuran species, but the impact varied among species. In our study, we noticed significant impacts of roads on *Hyla arborea*, which displayed negative responses to roads and urbanization at broad spatial scales (up to 1 km) in other fragmented landscapes in Europe (Pellet et al., 2004a, 2004b). Roads had a negative impact on *Rana dalmatina*, which is susceptible to high rates of road mortality and showed reduced reproductive success in ponds surrounded by increasing urban land cover and high traffic roads (Hartel et al., 2009a, 2009b). In contrast, the abundance of *Pelophylax* spp. complex larvae did not show any negative association with highways and roads. While adult *Pelophylax* spp. are known to be highly vagile (Smith & Green, 2005), they are often found in urban ponds and highway stormwater ponds (Ficetola & De Bernardi, 2004; Herczeg et al., 2012; Le Viol et al., 2012), and tend to remain at ponds throughout the breeding season, making them less susceptible to road traffic

(Elzanowski et al., 2009). There was no observable impact of the main railway line on amphibian larval abundance, although there was some uncertainty in the parameter estimates, and so more field testing is required to confirm this prediction. Initially, we expected the effect of the railway on amphibian abundance to be less pronounced than that of roads, owing to the lower traffic flow on railways, characterized by long traffic-free periods, and narrower railway corridors compared to highway corridors (Barrientos et al., 2019). However, significant mortality rates can occur during the spring migration period near railway lines, particularly for species such as *Bufo bufo* (Budzik & Budzik, 2014). Because many aspects of railway ecology are still inadequately understood, additional empirical data on the effects of railways on animal populations are necessary (Dorsey et al., 2015; Barrientos et al., 2019).

The model assessing the relationship between amphibian abundance and accessible habitat delineated by highways received less support. Nevertheless, it outperformed the model that only included the total area of habitat surrounding the ponds. It seems plausible that highways are contributing to landscape fragmentation in the study area most likely by being barriers to breeding migrations, but the there is some uncertainty in the magnitude of the effect. Similar to this, Hartel et al. (2010) found that the presence of high-traffic roads at distances up to 800 m in Romanian ponds had a greater impact on amphibian occurrence compared to the effect of landscape composition. The larval abundance of *Bufo bufo* showed the strongest association with accessible habitat and total habitat within a 1000-m radius around a pond in our study. Previous research has shown that landscape composition surrounding ponds can affect breeding occupancy of *Bufo bufo* (Zanini et al., 2008) and connectivity with areas of high forest cover can increase pond occupancy (Hartel et al., 2010). The reason for the smaller impact of accessible habitat on the mean community abundance compared with distance to a highway may be that certain characteristics of the agricultural landscape surrounding the ponds, such as hedgerows that provide terrestrial habitat for amphibians (Boissinot et al., 2019), were not considered in the calculation of accessible habitat. Our study was conducted in an intensively-managed agricultural/peri-urban landscape, which may impede amphibian dispersal (Joly, 2019). As a result, the effects of highways on amphibian abundance may have been obscured by existing disturbances and habitat modifications surrounding ponds (e.g. agriculture; Lenhardt et al., 2013). Previous studies examining accessible habitat as a predictor of amphibian occupancy were conducted in landscapes that were less urbanized (Eigenbrod et al., 2008b; Hamer, 2016). Future studies that examine the impacts of roads using accessible habitat as a predictor variable, a greater effect of accessible habitat may be revealed if they are restricted to more rural areas. Our method of measuring accessible habitat had a limitation in that the area of habitat on the opposite side of the highway was often negligible (see **Fig. 4)**, resulting in only a slight difference between the mean area of total habitat and accessible habitat in the study area (**Appendix 10**), which could make it potentially challenging to distinguish the effect of the highways from the effect of total habitat area on amphibian abundance. The measure of habitat used in our study included both forest and wetland, and different species may use these habitats differently; for instance, *Bufo bufo* and *Rana dalmatina* are more likely to inhabit forests during the non-breeding period, whereas *Bombina bombina* and members of the *Pelophylax* spp. complex often remain in the pond vicinity throughout the breeding season (Elzanowski et al., 2009). To determine the relative contribution of forests and wetlands to landscape permeability for amphibians around ponds, future studies may need to implement further delineation of accessible habitat into different habitat types. For example, the amount of forest in a landscape may be more important than the amount of wetland (Quesnelle et al., 2015).

The relationship between the larval amphibian abundance and pond area was strong, with a consistent pattern observed across all species. This finding is in line with the metapopulation theory suggesting that larger patches of habitat can support more individuals (Hanski, 1994). Larger ponds offer greater habitat heterogeneity and more resources for aquatic species (Zedler & Kercher, 2005). Furthermore, larger ponds in the study area had a more extended hydroperiod, which might enhance the likelihood of individuals reaching metamorphosis (**Appendix 11**). The abundance of larvae showed mixed relationships with the presence of fish, likely due to the variety of species' life histories and their adaptations to coexist with fish (Wellborn et al., 1996). The negative relationships between fish presence and the abundance of *Bombina bombina* and *Pelobates fuscus* larvae were clear, as these species may lack adaptations to avoid fish predation. For instance, *Bombina bombina* larvae are mostly found in fishless ponds (Kloskowski et al., 2020), and *Pelobates fuscus* larvae abundance was negatively correlated with fish presence in other agricultural landscapes (Rannap et al., 2015). In contrast, there was a strong positive association between the larvae of the *Pelophylax* spp. complex and fish presence, as they can coexist successfully with fish by displaying morphological and behavioural responses to fish predators (Teplitsky et al., 2003; Hartel et al., 2007; Kloskowski et al., 2020). Although our study is limited by the single season sampling, our findings suggest that amphibian abundance in waterbodies is being reduced by highways and high-road densities in modified landscapes. To address the loss of waterbodies during road construction or to retain stormwater runoff, new ponds are frequently established adjacent to highways (Hamer et al., 2015; Clevenot et al., 2018), and these waterbodies may serve as breeding habitat for amphibians (Simon et al., 2009; Lesbarrères et al., 2010; Le Viol et al., 2012). During our study, we collected samples from three stormwater retention ponds located near a highway, and we observed that these ponds were mostly populated by a high number of larvae from the *Pelophylax* spp. complex. This species complex is known to thrive in ponds near highways due to its high tolerance to various environmental conditions, including the presence of fish and eutrophication (Scher & Thièry, 2005; Le Viol et al., 2012). Despite that highway stormwater ponds have the potential to serve as habitats for amphibians and other wetland-dependent organisms (Scher & Thièry, 2005; Le Viol et al., 2009), they may act as ecological traps (Battin, 2004; Clevenot et al., 2018), particularly if they are located within road-effect zones and are exposed to roadkill and pollutants, or are inhabited by fish (Snodgrass et al., 2008; Shulse et al., 2010; Le Viol et al., 2012). Along with this, except the *Pelophylax* spp. complex, we recorded much lower abundances of amphibian larvae in these ponds. Our recommendation for road mitigation projects aimed at preserving amphibians is to construct large ponds that are free of fish, in areas with low road density and no highways, as this can increase the persistence of metapopulations (Semlitsch, 2000, 2002; Shulse et al., 2012; Magnus & Rannap, 2019). Due to the notable spatial autocorrelation found in the community-level abundance (**Appendix 16**), ponds created in spatial clusters would likely promote inter-pond movements and thereby improve long-term persistence (Petranka et al., 2007; Rannap et al., 2009). Despite efforts to mitigate the impact of roads on amphibians, options are often limited to road reserves within the road-effect zone (Hamer et al., 2015). While mitigation measures aiming to overcome the barrier effect of roads, such as under-road toad tunnels (Helldin & Petrovan, 2019), can improve amphibian movement and increase landscape permeability, it may be more effective to locate compensatory habitat in roadless and low-traffic areas, as they represent undisturbed ecosystems with greater landscape connectivity compared to more-developed areas (Selva et al., 2015). From a landscape perspective, our results indicate that the construction of new ponds in non-urban areas over 1 km from highways and with less than 4% road surface within 1 km is more likely to support viable amphibian metacommunities.

6. CONCLUSIONS

As indicated by all three case studies, human-induced changes ultimately lead to the degradation of the local environment and cause structural changes in the landscape. The local alterations included the removal of natural vegetation, modification of bottom material, changes in water depth and quality, and pollution. In the stream environment, we observed concrete lining of the bed and embankment, straight channels with high current flow, lack of riparian vegetation, and intensive growth of nutrient-limited flora, such as algae.

The establishment of recreational beaches on the shorelines of Lake Balaton led to the removal of the natural reed vegetation and the replacement of the soft-bottom sediment. This destroyed entire ecosystems that previously functioned as biological hotspots of the lake. The remaining natural reed ecosystems in the lake are now the last refuges for native taxa in an extremely modified shoreline (Karádi-Kovács et al., 2023).

Road constructions in Western Hungary resulted in a highly fragmented landscape due to linear infrastructures, causing the loss of important habitats and inter-habitat connectivity, including the destruction of pond networks. Roads emerged as the main source of pollution in the landscape and created insurmountable obstacles for many animals. The road-effect zones extended up to 1 km, generating a wide range of direct and indirect effects.

These environmental changes had significant impacts on the biological communities. All three case studies reported a decrease in taxa richness and/or abundance of freshwater organisms, as well as a change in the community structure. Human-induced alterations tended to select more tolerant species within the community, but the degree of selection depended on the magnitude of the alteration and the natural species composition.

Our first study - stream macroinvertebrates - indicated that even moderate land use changes could lead to a reduction in the richness and diversity of freshwater fauna. The sensitivity to disturbance varied depending on unique local environments and biotic compositions. Supporting this, in our second study - shoreline chironomids - we observed that the transformation of natural reed vegetated habitats into beaches in the northern shoreline of Lake Balaton had a significant negative effect on chironomid richness and abundance, indicating that the magnitude of this transition might have reached a threshold for the northern assemblages. For instance, in the northern shoreline, besides the removal of the reed vegetation, the natural silt substrate material was replaced by sand. In contrast, assemblages in the southern shoreline, where the natural substrate material is sand, showed no significant response to beach establishment, as the community inherently consisted of more tolerant members.

Regarding amphibian abundance, pond distance from the road and road coverage were the most important predictors. Surprisingly, the amount of accessible habitat and total habitat had a minor impact, as road effects seemed to override habitat characteristics. Most species of amphibians showed a preference for ponds located further from roads, while road-affected ponds were dominated by highly tolerant species. To safeguard pond biodiversity constructing roads as far away as possible from these ecosystems is the most effective approach.

7. SUMMARY

The effects of land use changes on freshwater organisms are a growing concern worldwide. As human activities continue to alter landscapes and modify natural habitats, the impacts on freshwater ecosystems and the organisms that inhabit them are becoming increasingly evident. In this dissertation, I examined the effects of human-induced land use changes on freshwater ecosystems. The particular studies included both lotic and lentic waterbodies, as well as local and landscape scale environmental elements, while macroinvertebrates and amphibians as model organisms with a focus on urbanization, road construction, and the recreational use of freshwaters.

The research encompassed various waterbodies, each serving unique purposes. Lake Balaton, a significant tourist attraction, holds immense importance both for tourism and ecological reasons, and low-order streams and ponds, which are often overlooked but hold comparable significance to larger waterbodies.

Land use changes have had detrimental effects on both local and landscape elements of the natural environment. Local environments have undergone significant transformations, with urban areas witnessing the straightening of streams and the introduction of concrete linings, while the natural reed shoreline in Lake Balaton has been completely removed from recreational beaches. Moreover, changes in substrate composition have been observed, including decreased grain size in streams and the replacement of natural silt sediment with sand on recreational beaches. These local alterations have resulted in the loss of habitat heterogeneity. Additionally, roads have played a role in modifying the natural landscape, leading to fragmented landscape elements and a disruption in the connectivity between interconnected ponds, but the direct local effects of roads have been the most notable for larval amphibian communities. To fully understand the effects of land use changes on freshwater ecology, it is essential to consider both local parameters and landscape elements. This comprehensive understanding is crucial for managing and preserving the intricate dynamics of these ecosystems.

Land use changes have been found to have detrimental consequences on freshwater organisms, specifically impacting macroinvertebrate richness, abundance, and community composition. Urbanization and human-induced habitat transformation effects implied that local characteristics and species composition are essential determinants of macroinvertebrate reactions. Streams showed such unique responses suggesting that individual waterbodies might need distinct approaches to study human-induced alterations. Additionally, roads have caused a significant decline in larval amphibian abundance. Although accessible habitat was predicted to be the most important predictor for amphibian communities, direct road effects proved to be most crucial for larval abundance. It appears that to mitigate these negative effects a comprehensive approach is necessary, encompassing conservation and restoration initiatives, sustainable land-use practices, and effective environmental policies. It is crucial to protect and restore these freshwater habitats, implement strategies to reduce urban spreading, road construction and pollution, encourage sustainable resource utilization and human recreation, and address the spread of invasive species. By undertaking these measures, the health and biodiversity of freshwater ecosystems may be preserved for future generations.

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10. RESULTS IN THESIS POINTS

10.1. Urbanization and stream macroinvertebrates

Taxa richness and Shannon diversity were significantly lower in urban stream sections, but they showed considerable variability between different streams, stream identity as a random factor explained a notable amount of variance. Macroinvertebrate abundance showed no decrease in the urban sections, the mean abundance was higher in urban sites, but not significantly. EPT taxa was negatively affected by urbanization for all biotic attributes (richness, Shannon diversity and abundance), but the relative richness of EPT (EPT%) did not change in urban sections and remained high (around 40% of all species). Macroinvertebrate assemblage composition showed significant differences between natural and urban sections. Streams showed strong unique characteristics and distinct macrofauna. EPT compositions also differed between natural and urban sites, however, they were not well separated according to stream identity. Concrete coverage and current velocity were negatively associated with macroinvertebrate richness and Shannon diversity, while wetted width and canopy coverage had a positive effect. Macroinvertebrate abundance showed only a few negligible correlations with our predictors (except for EPT). The total variance of macroinvertebrate assemblage explained mostly by microhabitat-level environmental variables and site-level variables had minor importance in the natural sections. The total explained variance was relatively low. In the urban sections, both microhabitat and site-level variables explained a notable amount of the total variation and the total explained variance was substantially higher than in the natural sections. For the EPT assemblage, site-level variables were more important than microhabitat-level variables in the urban sections.

10.2. Recreational beaches and chironomid assemblages in Lake Balaton

The transformation from a natural reed shoreline to a recreational beach had an overall negative impact on the richness and abundance of chironomids causing an 18% reduction in the taxon richness and a 5.6% reduction in abundance. The richness of chironomids depended on the shoreline position with the northern shoreline having higher species richness. The effect of habitat transformation on taxon richness was also shoreline-specific and while it significantly decreased on the northern shoreline, it did not change on the southern shoreline. The abundance was also shoreline dependent, on the southern shoreline less individuals were found overall, and the beach habitat was more abundant in chironomids than reed. Chironomid taxon richness was positively associated with organic matter, and negative effects were found for water depth and pH. Community composition of chironomids was highly sensitive both to shoreline position and habitat differences. Composition of chironomids was different between the reed and beach habitats, between reed and open habitats, and between the northern and southern shorelines. Ten indicator taxa were observed for natural reed habitat, six for open and a single taxon for beach habitat in the northern shoreline, while four indicator taxa for open habitat in the southern shoreline. Environmental variables had a significant impact on the community structure of chironomids and indicator taxa was influenced by the most decisive parameters for each habitat, such as high amount of reed and organic matter in reed habitat, high water depth in open habitat and high proportion of sand in beach habitat.

10.3. Linear infrastructures and pond ecology

Among road models distance to the nearest highway and the percentage cover of road surface within a 1000-m radius had the strongest and clearest effect on the mean community abundance of amphibian larvae. Distance to the nearest highway model had the best fit with the mean community abundance data and showed clear effects on individual species abundance for all seven species observed and therefore considered to be the best-supported model. Accessible habitat and total habitat models showed considerably weaker effects on mean community abundance than the first two models. Railway models showed highly ambiguous effects on mean community abundance suggesting only a little impact of the railway on amphibians. There was only a small increase in abundance at sites located 0 – 1000 m from a highway suggesting that the road-effect zone extended for up to 1 km and further. Distance to the nearest highway was the most decisive for the mean amphibian species abundance showing a clear positive relationship with all seven species, with the strongest effect for *Bufo bufo* and the weakest for the *Pelophylax* spp. complex. Similarly, the percentage cover of road surface within a 1000-m radius clearly negatively influenced amphibian abundance with *Bufo bufo* as the most, while the *Pelophylax* spp. complex as the least sensitive species. The percentage of accessible habitat and total habitat within a 1000-m radius had notably smaller effects on amphibian abundance and showed mixed relationships with different species, but similar to the others, *Bufo bufo* showed the strongest relationship and was positively influenced by the amount of both accessible and total habitat. The pond area had a strong, clear positive effect on mean community abundance and on mean species abundance. The strongest relationship was found for *Bufo bufo*, whereas the weakest relationship was for *Rana dalmatina*. A positive, but ambiguous, relationship was observed between mean community abundance and fish presence with high variability in species responses. *Bombina bombina* and *Pelobates fuscus* larvae were negatively influenced by fish, whereas there was a strong positive effect of fish presence on the *Pelophylax* spp. complex.

11. LIST OF PUBLICATIONS

11.1. Papers related to the dissertation

Bohus, A., B. Gál, B. Barta, I. Szivák, K. Karádi-Kovács, P. Boda, J. Padisák, & D. Schmera, 2023. Effects of urbanization-induced local alterations on the diversity and assemblage structure of macroinvertebrates in low-order streams. Hydrobiologia 850: 881–899, https://doi.org/10.1007/s10750-022-05130-1, **IF: 2.822, SJR: Q1**

Árva, D., A. Mozsár, B. Barta, A. Specziár, M. Tóth, **A. Bohus**, B. Gál, & D. Schmera, 2021. Effects of recreational beaches on chironomid assemblages in a large, shallow lake. Ecological Indicators 125: 107469, http://doi.org/10.1016/j.ecolind.2021.107469, **IF: 4.958, SJR: D1**

Hamer, A. J., B. Barta, **A. Bohus**, B. Gál, & D. Schmera, 2021. Roads reduce amphibian abundance in ponds across a fragmented landscape. Global Ecology and Conservation 28:e01663, https://doi.org/10.1016/j.gecco.2021.e01663, **IF: 3.38, SJR: Q1**

11.2. Congress attendances related to the dissertation

Bohus, A.; Gál, B.; Schmera, D. (2021). Az urbanizáció hatása a makrogerinctelenek diverzitására kisvízfolyásokban. LXII. Hidrobiológus Napok, 6-8 October 2021, Tihany, Hungary, ***oral presentation***

Bohus, A.; Gál, B.; Barta, B.; Szivák, I.; Karádi-Kovács, K.; Boda, P.; Padisák, J.; Schmera, D. (2022). Effects of urbanization-induced local alterations on the diversity and assemblage structure of macroinvertebrates in low-order streams. XXV. Tavaszi Szél Konferencia, 6-8 May 2022, Pécs, Hungary, ***oral presentation***

Bohus, A.; Gál, B.; Barta, B; Szivák, I; Karádi-Kovács, K.; Boda, P.; Padisák, J.; Schmera, D. (2022). Effects of urbanization-induced local alterations on the diversity and assemblage structure of macroinvertebrates in low-order streams. 36th Congress of the International Society of Limnology (SIL 100), 7-10 August 2022, Berlin, Germany, ***oral video presentation***

11.3. Other publications

Mészáros, B., J. Bürgés, M. Tamás, B. Gál, **A. Bohus**, & D. Schmera, 2023. Effects of the urban environment on the developmental stability, size and body condition of dice snakes (*Natrix tessellata*) living in artificial lakeside habitats. Ecological Indicators 156: 111117, https://doi.org/10.1016/j.ecolind.2023.111117, **IF: 6.9, SJR: D1**

11.4. Other congress attendances

Barta, B.; Vad, Cs. F.; Márton, Zs.; Kratina, P.; Petermann, J. S.; Dobosy, P., **Bohus, A.**; Zezula, D.; Nash, L.; Duanyai, P.; Horváth, Zs. (2022). The effect of forest management and connectivity loss on water-filled tree hole communities. 36th Congress of the International Society of Limnology (SIL 100), 7-10 August 2022, Berlin, Germany, ***oral presentation***

Mészáros, B.; Bürgés, J. G.; Tamás, M.; Gál, B.; **Bohus, A.**; Schmera, D. (2023). A városi tájhasználat mértékének hatása a balatoni kockás siklók (*Natrix tessellata*) fluktuáló aszimmetriájára. 8. Szünzoológiai Szimpózium (SZÜSZI), 31 March – 01 April 2023, Tihany, Hungary, ***oral presentation***

APPENDIX

Appendix 1 GPS coordinates of the sites in the study area.

Stream	Land use	Code	N	E	Stream	Land use	Code	N	E
Aszófői	Natural	ASZ_N1	46°56'23,7"	17°49'16,6"	Cserkúti	Urban	CSER_U1	46°54'51,2"	17°40'19,6"
Aszófői	Natural	ASZ_N2	46°56'23,8"	17°49'14,6"	Cserkúti	Urban	CSER_U2	46°54'52,1"	17°40'19,3"
Aszófői	Natural	ASZ_N3	46°56'24,7"	17°49'12,5"	Cserkúti	Urban	CSER_U3	46°54'53,5"	17°40'18,3"
Aszófői	Natural	ASZ_N4	46°56'26,1"	17°49'10,7"	Cserkúti	Urban	CSER_U4	46°54'55,2"	17°40'16,8"
Aszófői	Natural	ASZ_N5	46°56'26,9"	17°49'10,1"	Cserkúti	Urban	CSER_U5	46°54'55,8"	17°40'16,2"
Aszófői	Natural	ASZ_N6	46°56'26,3"	17°49'10,2"	Cserkúti	Urban	CSER_U6	46°54'56,4"	17°40'16,0"
Aszófői	Urban	ASZ_U1	46°55'48,3"	17°50'9,4"	Koloska	Natural	KOL_N1	46°59'21,3"	17°53'11,3"
Aszófői	Urban	ASZ_U2	46°55'48,7"	17°50'8,9"	Koloska	Natural	KOL_N2	46°59'22,5"	17°53'11,6"
Aszófői	Urban	ASZ_U3	46°55'49,7"	17°50'8,0"	Koloska	Natural	KOL_N3	46°59'22,4"	17°53'11,7"
Aszófői	Urban	ASZ_U4	46°55'50,3"	17°50'7,2"	Koloska	Natural	KOL_N4	46°59'23,3"	17°53'11,8"
Aszófői	Urban	ASZ_U5	46°55'50,9"	17°50'6,4"	Koloska	Natural	KOL_N5	46°59'24,1"	17°53'12,1"
Aszófői	Urban	ASZ_U6	46°55'51,4"	17°50'5,4"	Koloska	Natural	KOL_N6	46°59'24,6"	17°53'11,9"
Burnót	Natural	BUR_N1	46°49'31,1"	17°33'45,0"	Koloska	Urban	KOL_U1	46°57'31,1"	17°54'30,8"
Burnót	Natural	BUR_N2	46°49'31,5"	17°33'44,3"	Koloska	Urban	KOL_U2	46°57'32,0"	17°54'30,0"
Burnót	Natural	BUR_N3	46°49'32,7"	17°33'43,6"	Koloska	Urban	KOL_U3	46°57'33,3"	17°54'28,7"
Burnót	Natural	BUR_N4	46°49'33,9"	17°33'43,2"	Koloska	Urban	KOL_U4	46°57'34,9"	17°54'27,3"
Burnót	Natural	BUR_N5	46°49'34,8"	17°33'42,9"	Koloska	Urban	KOL_U5	46°57'35,9"	17°54'26,2"
Burnót	Natural	BUR_N6	46°49'36,3"	17°33'43,1"	Koloska	Urban	KOL_U6	46°57'36,6"	17°54'25,3"
Burnót	Urban	BUR_U1	46°57'31,1"	17°34'5,0"	Örvényesi	Natural	ÖRV_N1	46°55'16,3"	17°48'46,3"
Burnót	Urban	BUR_U2	46°48'31,1"	17°34'2,7"	Örvényesi	Natural	ÖRV_N2	46°55'12,7"	17°48'46,2"
Burnót	Urban	BUR_U3	46°48'54,1"	17°34'0,2"	Örvényesi	Natural	ÖRV_N3	46°55'13,5"	17°48'44,8"
Burnót	Urban	BUR_U4	46°48'55,4"	17°33'58,6"	Örvényesi	Natural	ÖRV_N4	46°55'14,9"	17°48'43,3"
Burnót	Urban	BUR_U5	46°48'57,0"	17°33'56,8"	Örvényesi	Natural	ÖRV_N5	46°55'15,6"	17°48'41,4"
Burnót	Urban	BUR_U6	46°48'58,8"	17°33'54,6"	Örvényesi	Natural	ÖRV_N6	46°55'15,1"	17°48'38,9"
Cserkúti	Natural	CSER_N1	46°55'14,9"	17°39'42,7"	Örvényesi	Urban	ÖRV_U1	46°54'45,9"	17°49'2,1"
Cserkúti	Natural	CSER_N2	46°55'16,1"	17°39'38,6"	Örvényesi	Urban	ÖRV_U2	46°54'46,8"	17°49'3,9"
Cserkúti	Natural	CSER_N3	46°55'16,4"	17°39'37,5"	Örvényesi	Urban	ÖRV_U3	46°54'47,6"	17°49'4,4"
Cserkúti	Natural	CSER_N4	46°55'16,3"	17°39'35,0"	Örvényesi	Urban	ÖRV_U4	46°54'49,8"	17°49'0,2"
Cserkúti	Natural	CSER_N5	46°55'15,9"	17°39'33,9"	Örvényesi	Urban	ÖRV_U5	46°54'50,7"	17°49'0,6"
Cserkúti	Natural	CSER_N6	46°55'16,5"	17°39'31,0"	Örvényesi	Urban	ÖRV_U6	46°54'57,0"	17°49'0,6"

Appendix 2 Spearman correlation of environmental variables (*: significant at p = 0.05, **: significant at p = 0.01, ***: significant at p = 0.001).

Bedrock	0.09	0.03	0.15	-0.17	0.18	0.12	-0.16	-0.15	-0.02	0.12	-0.09	-0.09	-0.22	-0.18	0.03	0.11	0.08	-0.18
	Boulder	0.67***	0.38**	0.14	0.53***	-0.28*	-0.44***	-0.38**	0.11	0.10	-0.16	-0.25*	0.49***	0.24*	-0.09	0.32*	0.36**	-0.42***
		Cobble	0.57***	0.29*	0.60***	-0.2	-0.50***	-0.44	0.20	0.07	-0.26*	-0.31	0.41**	0.06	-0.31*	0.18	0.44***	-0.55**
			Pebble	0.50***	0.49***	-0.01	-0.57***	-0.52***	0-33*	-0.08	-0.26*	-0.24	0.16	-0.15	-0.46	0.25*	0.49***	-0.56***
				Gravel	0.56***	0.05	-0.64***	-0.62***	0.61***	0.46***	-0.31*	-0.23*	0.37**	0.04	-0.63***	0.19	0.52***	-0.61***
					Sand	0.09	-0.71***	-0.68***	0.55***	0.43***	-0.38**	-0.40**	0.36**	-0.07	-0.60***	0.29*	0.63***	-0.80***
						Silt	0.02	-0.18	0.21*	0.01	-0.25*	-0.24*	-0.18	-0.42***	-0.28*	0.18	0.05	0.01
							Concrete	0.80***	-0.66***	-0.42	0.13	0.20	-0.51***	-0.01	0.71***	-0.17	-0.74***	0.84***
								Algae	-0.69***	-0.41**	0.12	0.46***	-0.39**	0.09	0.76***	-0.03	-0.70***	0.79***
									POM	0.53***	-0.28*	-0.28*	0.10	-0.26	-0.64***	0.08	0.68***	-0.71***
										Wood	-0.17	-0.23*	0.23*	0.02	-0.36**	0.02	0.43***	-0.45**
											Macrophytes	0.38**	0.01	0.31*	0.26	-0.49***	-0.31*	0.34*
												Plants	-0.01	0.38**	0.51***	-0.10	-0.37**	0.40**
													Width	0.54***	-0.38**	-0.01	0.33**	-0.28*
														Depth	0.12	-0.15	-0.10	0.19
															Velocity	-0.02	-0.70***	0.67***
																RCI	0.11	-0.27*
																	Canopy	-0.78**
																		HII

Appendix 3 List of taxa in the examined streams.

Group	Family	Taxon	Protected[1]	Non-native[2]
Amphipoda	Gammaridae	*Gammarus fossarum* Koch, 1836		
		Gammarus roeselii Gervais, 1835		
Coleoptera	Dytiscidae	*Colymbetinae* sp.		
		Laccophilus sp.		
		Platambus maculatus (Linnaeus, 1758)		
	Elmidae	Elmidae sp.		
		Elmis maugetii Latreille, 1802		
		Elmis sp.		
		Limnius sp.		
		Limnius volckmari (Panzer, 1793)		
		Riolus cupreus (Müller, 1806)		
		Riolus sp.		
	Haliplidae	*Peltodytes caesus* (Duftschmid, 1805)		
	Hydraenidae	*Hydraena* sp.		
	Hydrophilidae	*Cymbiodyta marginella* (Fabricius, 1792)		
		Anacaena limbata (Fabricius, 1792)		
	Scirtidae	Scirtidae sp.		
Decapoda	Astacidae	*Astacus astacus* (Linnaeus, 1758)	X	
Diptera	Cecidomyiidae	Cecidomyiidae sp.		
	Ceratopogonidae	Ceratopogonidae sp.		
	Chironomidae	Chironomidae spp.		
	Culicidae	Culicidae sp.		
	Dixidae	*Dixa submaculata* Edwards, 1920		
	Dolichhopodidae	Dolichopodidae sp.		
	Empididae	Empididae sp.		
	Limoniidae	Limoniidae sp.		
	Muscidae	Muscidae sp.		

Group	Family	Taxon	Protected[1]	Non-native[2]
	Pediciidae	Pediciidae sp.		
	Psychodidae	Psychodidae sp.		
	Ptychopteridae	Ptychopteridae sp.		
	Rhagionidae	Rhagionidae sp.		
	Simuliidae	*Simulium costatum* Friederichs, 1920		
		Simulium lundstromi (Enderlein, 1921)		
		Simulium trifasciatum Curtis, 1839		
		Simulium vernum sp. (Macquart, 1826)		
	Stratiomydae	Stratiomyidae sp.		
	Tabanidae	Tabanidae sp.		
	Tipulidae	Tipulidae sp.		
Ephemeroptera	Baetidae	*Baetis muticus* (Linnaeus, 1758)		
		Baetis pentaphlebodes Ujhelyi, 1966		
		Baetis rhodani (Pictet, 1843)		
		Baetis sp.		
		Baetis vernus Curtis, 1834		
	Ephemeridae	*Ephemera danica* Müller, 1764		
	Heptageniidae	*Electrogena ujhelyii* (Sowa, 1981)		
	Leptophlebiidae	*Paraleptophlebia submarginata* (Stephens, 1835)		
	Siphlonuridae	*Siphlonurus* sp.		
Gastropoda	Lymnaeidae	*Lymnaea peregra* (Müller, 1774)		
	Tateidae	*Potamopyrgus antipodarum* (Gray, 1843)		X
Heteroptera	Corixidae	*Hesperocorixa linnaei* (Fieber, 1848)		
	Gerridae	*Gerris lacustris* (Linnaeus, 1758)		
	Nepidae	*Nepa cinerea* Linnaeus, 1758		
	Veliidae	*Velia caprai caprai* Tamanini, 1947		
		Velia saulii Tamanini, 1947		
Hirudinea	Erpobdellidae	Erpobdellidae sp.		
	Glossiphoniidae	*Glossiphonia* sp.		

Group	Family	Taxon	Protected[1]	Non-native[2]
		Helobdella sp.		
	Haemopidae	Haemopidae sp.		
Isopoda	Asellidae	*Asellus aquaticus* (Linnaeus, 1758)		
Megaloptera	Sialidae	*Sialis fuliginosa* Pictet, 1836		
Odonata	Calopterygidae	*Calopteryx virgo* Linnaeus, 1758	X	
	Libellulidae	*Orthetrum brunneum* Fonscolombe, 1837	X	
Oligochaeta		Oligochaeta sp.		
Plecoptera	Nemouridae	*Nemoura cinerea* (Retzius, 1783)		
		Nemurella picetii (Klapálek, 1900)		
Trichoptera	Goeridae	*Goera pilosa* (Fabricius, 1775)		
		Lithax obscurus (Hagen, 1859)		
		Silo pallipes (Fabricius, 1781)		
	Hydropsychidae	*Hydropsyche angustipennis* (Curtis, 1834)		
		Hydropsyche contubernalis McLachlan, 1865		
		Hydropsyche fulvipes (Curtis, 1834)		
		Hydropsyche saxonica McLachlan, 1884		
		Hydropsyche sp.		
	Hydroptilidae	*Hydroptila* sp.		
	Limnephilidae	*Anabolia furcata* Brauer, 1857		
		Annitella obscurata (McLachlan, 1876)		
		Chaetopteryx fusca Brauer, 1857		
		Chaetopteryx major McLachlan, 1876		
		Halesus digitatus (Schrank, 1781)		
		Halesus tesselatus (Rambur, 1842)		
		Limnephilidae sp.		
		Limnephilus auricula Curtis, 1834		
		Limnephilus binotatus Curtis, 1834		
		Limnephilus lunatus Curtis, 1834		
		Limnephilus rhombicus (Linnaeus, 1758)		

Group	Family	Taxon	Protected[1]	Non-native[2]
		Micropterna lateralis (Stephens, 1837)		
		Micropterna nycterobia McLachlan, 1875		
		Potamophylax cingulatus (Stephens, 1837)		
		Potamophylax nigricornis (Pictet, 1834)		
		Potamophylax rotundipennis (Brauer, 1857)		
	Polycentropodidae	*Plectrocnemia conspersa* (Curtis, 1834)		
	Psychomyiidae	*Lype reducta* (Hagen, 1868)		
		Tinodes pallidulus McLachlan, 1878		
		Tinodes unicolor (Pictet, 1834)		
	Rhyacophilidae	*Rhyacophila dorsalis* group		
		Rhyacophila fasciata Hagen, 1859		
		Rhyacophila obliterata McLachlan, 1863		
	Sericostomatidae	*Sericostoma personatum* (Kirby & Spence, 1826)		
Turbellaria		Turbellaria sp.		
Unionida	Unionidae	*Unio tumidus* Philipsson, 1788		
Veneroida	Sphaeriidae	*Sphaerium corneum* (Linnaeus, 1758)		
		Pisidium casertanum (Poli, 1791)		
		Pisidium henslowanum (Sheppard, 1825)		
		Pisidium milium Favre, 1927		
		Pisidium personatum Malm, 1855		
		Pisidium sp.		
		Pisidium subtruncatum Malm, 1855		
		Pisidium tenuilineatum Stelfox, 1918		

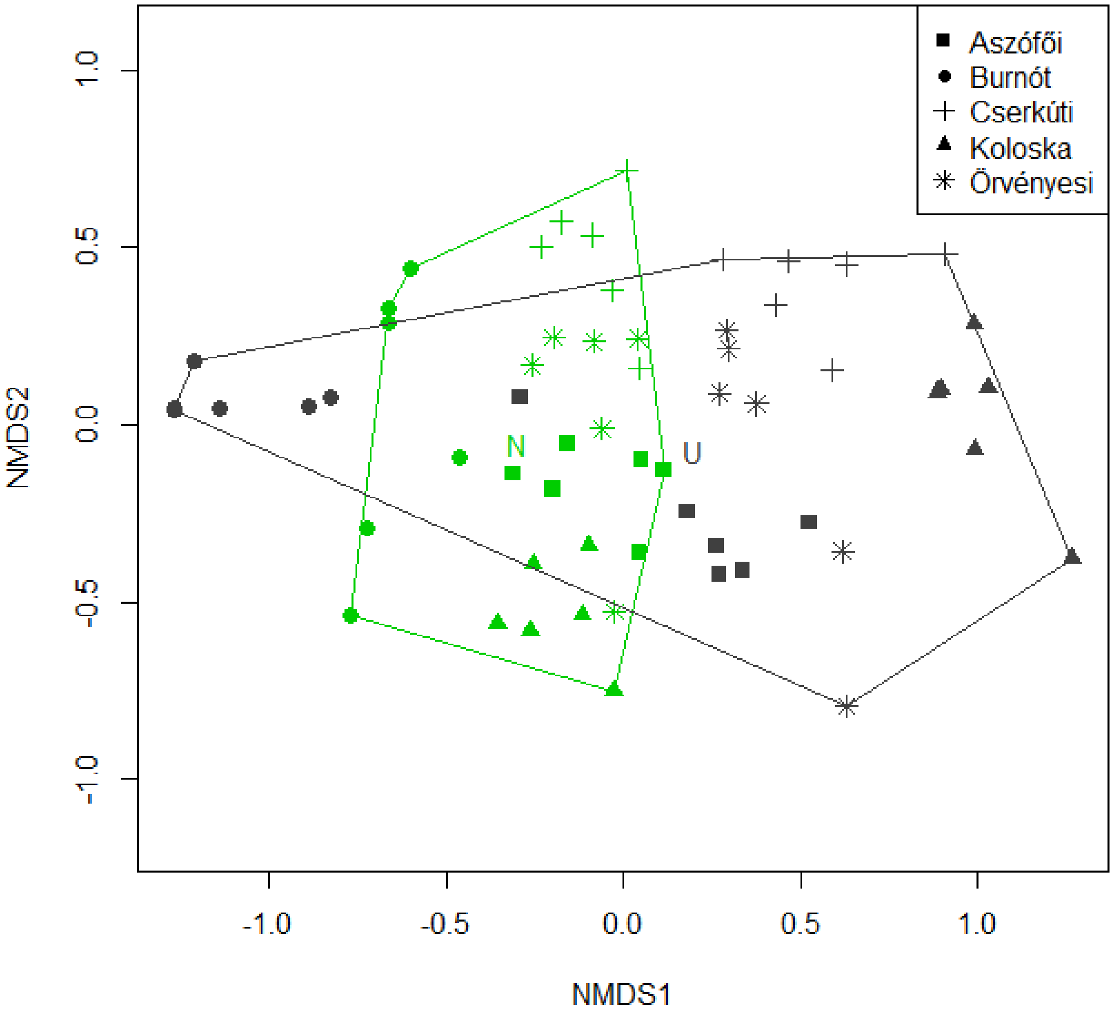
[1] 100/2012. (IX.28.) decree of Ministry of Rural Development

[2] Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2009)

Appendix 4 Summary of the PERMANOVA (ADONIS) testing the effect of section and stream identity on the identified EPT taxa (number of permutations: 999).

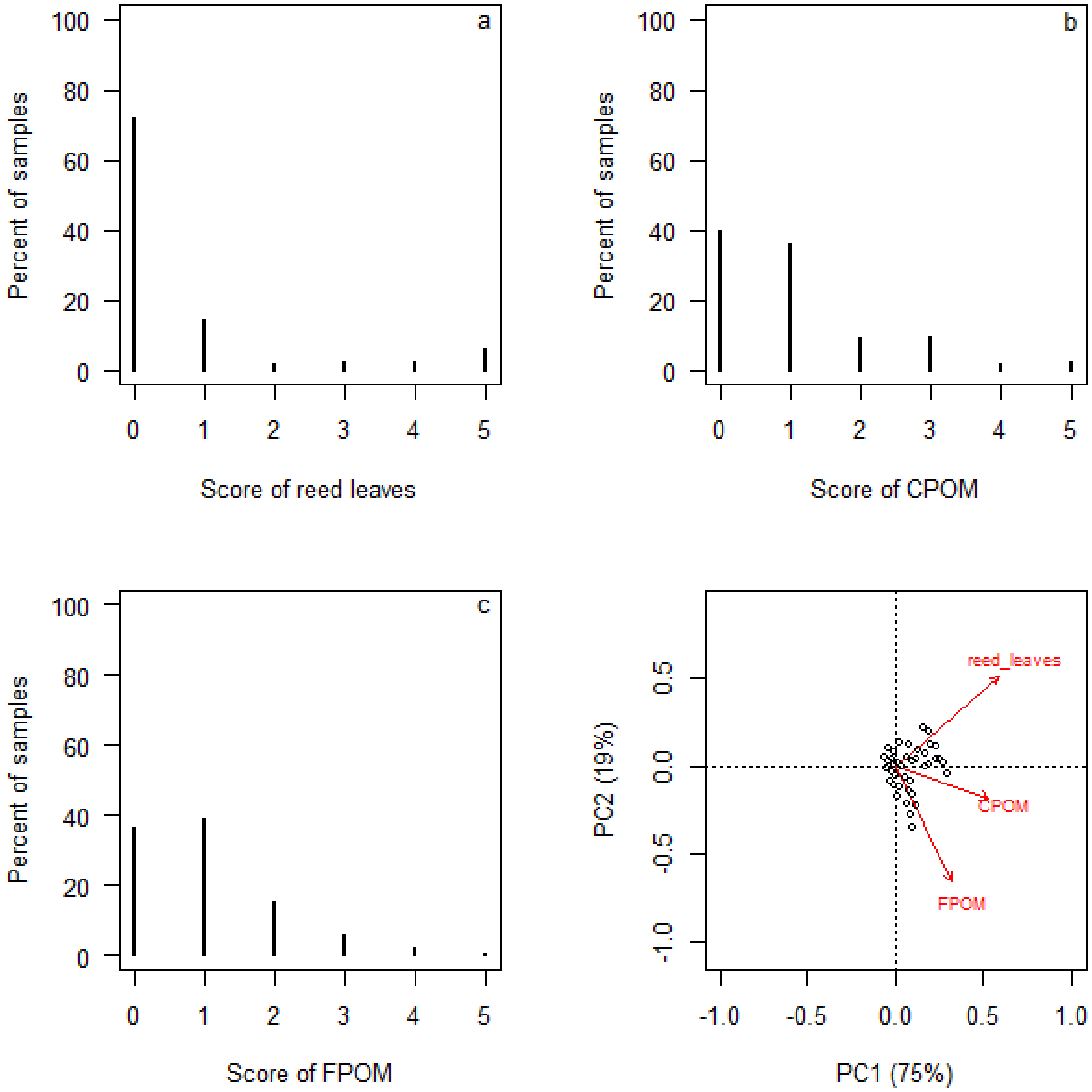
Factor	df	SS	R^2	F	p
Section	1	3.813	0.207	22.824	0.001
Stream id.	4	5.593	0.304	8.370	0.001
Residuals	50	9.021	0.490		
Total	59	18.426	1.000		

Appendix 5 NMDS plot of sites based on the identified EPT taxa showing the separation according to section (green: natural, dark grey: urban; ordination ellipses: N: natural, U: urban) and stream.

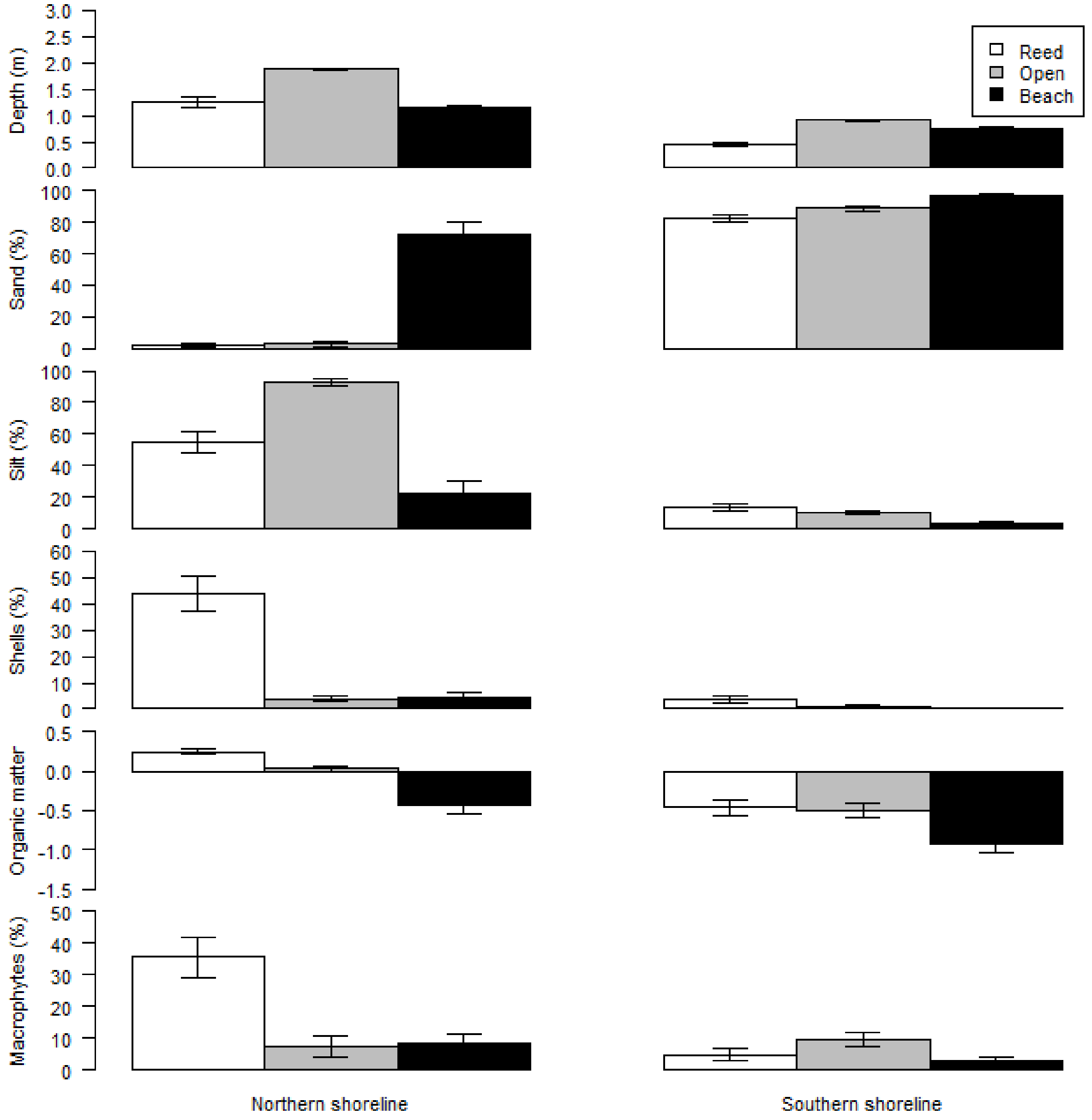


Appendix 6 The reed (top), open (middle) and beach (bottom) habitats at Káptalanfüred, Lake Balaton, Hungary.

Appendix 7 The frequency distribution of the scores of (a) reed leaves, (b) CPOM and (c) FPOM in the samples as well as (d) a biplot of centered Principal Component Analysis (PCA) of the samples.



Appendix 8 Effects of habitat and shoreline on selected environmental parameters. Bars show mean values and whiskers are standard errors.



Appendix 9 List of taxa identified in the present study.

Subfamily	Taxon
Tanypodinae	
	Ablabesmyia longistyla Fittkau, 1962
	Guttipelopia guttipennis (van der Wulp, 1861)
	Procladius (Holotanypus) choreus (Meigen, 1804)
	Tanypus (Tanypus) kraatzi (Kieffer, 1912)
	Tanypus (Tanypus) punctipennis Meigen, 1818
Orthocladiinae	
	Cricotopus (Cricotopus) bicinctus (Meigen, 1818)
	Cricotopus (Isocladius) sylvestris gr.
	Cricotopus (Cricotopus) tremulus (Linnaeus, 1758)
	Orthocladius (Orthocladius) oblidens (Walker, 1856)
	Psectrocladius sordidellus gr.
Chironominae	
	Chironomus (Chironomus) balatonicus Devai, Wülker & Scholl 1983
	Chironomus (Lobochironomus) dorsalis Meigen, 1818
	Chironomus (Chironomus) riparius Meigen, 1804
	Chironomus (Chironomus) salinarius Kieffer, 1916
	Chironomus sp.
	Cladopelma virecens (Meigen, 1818)
	Cladopelma viridulum (Linnaeus, 1767)
	Cladotanytarsus mancus gr.
	Cryptochironomus (Cryptochironomus) defectus (Kieffer, 1913)
	Dicrotendipes lobiger (Kieffer, 1921)
	Dicrotendipes nervosus (Staeger, 1839)
	Dicrotendipes tritomus (Kieffer, 1916)
	Endochironomus tendens (Fabricius, 1775)
	Fleuria lacustris Kieffer, 1924
	Glyptotendipes (Glyptotendipes) pallens (Meigen, 1804)
	Harnischia sp.
	Lipiniella moderata Kalugina, 1970
	Microchironomus tener (Kieffer, 1918)
	Microtendipes chloris agg.
	Parachironomus varus (Goetghebuer, 1921)
	Paratanytarsus sp.
	Phaenopsectra flavipes (Meigen, 1818)
	Polypedilum (Polypedilum) nubeculosum (Meigen, 1804)
	Polypedilum (Pentapedilum) sordens (van der Wulp, 1875)
	Stictochironomus sp.
	Tanytarsus sp.
	Zavreliella marmorata (van der Wulp, 1859)

Appendix 10 Descriptive statistics for (a) seven continuous variables, and (b) for the presence of fish and hydroperiod recorded at 30 ponds in western Hungary.

(a)

Covariate	Mean	SD	Min.	Max.
Habitat (%)	38.8	21.9	2.9	73.9
Access_hwy (%)	37.4	22.3	2.6	73.9
Access_hwy_rail (%)	33.1	20.2	2.6	58.3
Dist_hwy (m)	1472	1369	18	3869
Dist_hwy_rail (m)	446	463	18	1646
Roads (%)	3.67	2.02	0.04	7.03
Area (m^2)	1363	1786	46	7029

Habitat = % forest + wetland habitat within a 1000-m radius of a site; Access_hwy = % forest + wetland habitat within a 1000-m radius of a site that can be accessed without crossing a highway (i.e. accessible habitat); Access_hwy_rail = % forest + wetland habitat within a 1000-m radius of a site that can be accessed without crossing a highway or the main railway (i.e. accessible habitat); Dist_hwy = distance to nearest highway; Dist_hwy_rail = distance to nearest highway or the railway; Roads = % cover of road surface within a 1000-m radius of a site; Area = pond area.

(b)

	Number of sites	Proportion of sites
Fish present	15	0.50
Fish absent	15	0.50
Ephemeral wetlands	4	0.13
Semi-permanent wetlands	10	0.33
Permanent wetlands	16	0.53

Appendix 11 Correlation coefficients among nine habitat variables recorded at 30 ponds in western Hungary. Continuous variables were correlated using Pearson correlations (*r*) whereas categorical variables (Fish, Hydroperiod) were assessed using Spearman rank correlations (r_s).

	Habitat	Access_hwy	Access_hwy_rail	Dist_hwy	Dist_hwy_rail	Roads	Area	Fish
Habitat	-	-	-	-	-	-	-	-
Access_hwy	**0.995**	-	-	-	-	-	-	-
Access_hwy_rail	**0.951**	**0.945**	-	-	-	-	-	-
Dist_hwy	0.038	0.115	–0.050	-	-	-	-	-
Dist_hwy_rail	–0.264	–0.203	–0.213	**0.689**	-	-	-	-
Roads	–0.351	–0.384	–0.192	–0.459	–0.251	-	-	-
Area	0.189	0.207	0.103	0.232	–0.194	–0.080	-	-
Fish	0.112	0.158	0.089	0.304	0.119	0.204	0.528	-
Hydroperiod	0.326	0.339	0.351	0.064	–0.111	0.343	0.440	0.445

Habitat = % forest + wetland habitat within a 1000-m radius of a site; Access_hwy = % forest + wetland habitat within a 1000-m radius of a site that can be accessed without crossing a highway (i.e. accessible habitat); Access_hwy_rail = % forest + wetland habitat within a 1000-m radius of a site that can be accessed without crossing a highway or the main railway (i.e. accessible habitat); Dist_hwy = distance to nearest highway; Dist_hwy_rail = distance to nearest highway or the railway; Roads = % cover of road surface within a 1000-m radius of a site; Area = pond area; Fish = presence (1) or absence (0) of fish; Hydroperiod = ephemeral pond (1), semi-permanent pond (2) or permanent pond (3).

Dist_hwy, Dist_hwy_rail and Area were $\log_{10}(x)$-transformed prior to correlation analysis.

Coefficient in bold denotes a strong correlation ($r \geq 0.6$).

Appendix 12 Counts of amphibian larvae captured in dip-nets during standardised surveys at 30 ponds in Western Hungary. Mean counts are mean number of larvae captured per site over three surveys. SD = standard deviation.

Species	Total count	Mean count	SD
BOMBINATORIDAE			
Bombina bombina	294	9.8	31.1
BUFONIDAE			
Bufo bufo	1178	39.3	84.2
HYLIDAE			
Hyla arborea	40	1.3	4.2
SALAMANDRIDAE			
Lissotriton vulgaris	71	2.4	4.8
PELOBATIDAE			
Pelobates fuscus	44	1.5	3.8
RANIDAE			
Pelophylax spp. complex	368	12.3	33.2
Rana dalmatina	585	19.5	44.9
TOTAL SPECIES	2580	86.0	119.4

Appendix 13 Summary of species-specific estimates for abundance (λ) and detection (β) covariates for the larvae of seven amphibian species in five multi-species abundance models. See **Table 10** for parameter estimates in the Dist_hwy model. Estimates include 95% Bayesian credible intervals (BCI). Clear relationships are where the 95% BCI does not overlap zero (highlighted in bold, except intercept coefficients). SD = standard deviation.

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
Dist_hwy_rail						
Bombina bombina	λ_0	Intercept	1.490	0.533	0.488	2.600
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.286**	**0.218**	**1.860**	**2.715**
	λ_2	**Dist_hwy_rail**	**1.167**	**0.303**	**0.578**	**1.766**
	λ_3	**Fish**	**–2.054**	**0.254**	**-2.559**	**-1.563**
	β_0	Intercept	–4.401	0.364	-5.140	-3.713
	β_1	**Water**	**1.133**	**0.096**	**0.947**	**1.324**
	β_2	**Temp**	**–0.203**	**0.069**	**-0.338**	**-0.067**
	β_3	**Days**	**0.656**	**0.109**	**0.443**	**0.871**
Bufo bufo	*λ_0	Intercept	1.734	0.647	0.593	3.046
(Family: Bufonidae)	**λ_1**	**Area**	**3.487**	**0.167**	**3.165**	**3.820**
	λ_2	**Dist_hwy_rail**	**3.318**	**0.279**	**2.770**	**3.867**
	λ_3	**Fish**	**0.325**	**0.153**	**0.025**	**0.623**
	β_0	Intercept	–5.493	0.264	-6.016	-4.997
	β_1	**Water**	**1.111**	**0.067**	**0.980**	**1.244**
	β_2	**Temp**	**–0.110**	**0.043**	**-0.195**	**-0.026**
	β_3	**Days**	**0.529**	**0.044**	**0.443**	**0.616**

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
Hyla arborea	λ_0	Intercept	0.944	0.508	-0.060	1.938
(Family: Hylidae)	**λ_1**	**Area**	**1.900**	**0.400**	**1.116**	**2.684**
	λ_2	**Dist_hwy_rail**	**2.275**	**0.456**	**1.394**	**3.182**
	λ_3	Fish	–0.082	0.378	-0.838	0.647
	β_0	Intercept	–4.236	0.458	-5.149	-3.359
	β_1	Water	0.116	0.173	-0.220	0.460
	β_2	**Temp**	**0.780**	**0.208**	**0.385**	**1.201**
	β_3	**Days**	**1.768**	**0.266**	**1.268**	**2.313**
Lissotriton vulgaris	λ_0	Intercept	1.072	0.514	0.078	2.103
(Family: Salamandridae)	**λ_1**	**Area**	**1.487**	**0.337**	**0.824**	**2.147**
	λ_2	**Dist_hwy_rail**	**2.366**	**0.399**	**1.595**	**3.157**
	λ_3	Fish	0.255	0.294	-0.329	0.822
	β_0	Intercept	–3.910	0.476	-4.868	-3.018
	β_1	**Water**	**0.825**	**0.164**	**0.513**	**1.157**
	β_2	**Temp**	**0.397**	**0.139**	**0.128**	**0.672**
	β_3	**Days**	**0.832**	**0.167**	**0.508**	**1.165**
Pelobates fuscus	λ_0	Intercept	1.008	0.510	0.009	2.014
(Family: Pelobatidae)	**λ_1**	**Area**	**2.185**	**0.401**	**1.399**	**2.975**
	λ_2	**Dist_hwy_rail**	**2.932**	**0.453**	**2.050**	**3.830**
	λ_3	**Fish**	**–0.692**	**0.345**	**–1.380**	**–0.029**
	β_0	Intercept	–4.177	0.471	–5.108	–3.269

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_1	**Water**	**1.628**	**0.272**	**1.119**	**2.187**
	β_2	**Temp**	**–0.516**	**0.162**	**–0.840**	**–0.204**
	β_3	Days	–0.214	0.225	–0.667	0.215
Pelophylax spp. complex	λ_0	Intercept	0.994	0.503	0.003	1.983
(Family: Ranidae)	**λ_1**	**Area**	**1.395**	**0.289**	**0.887**	**1.978**
	λ_2	**Dist_hwy_rail**	**1.248**	**0.280**	**0.693**	**1.792**
	λ_3	**Fish**	**4.019**	**0.275**	**3.484**	**4.565**
	β_0	Intercept	–5.988	0.355	–6.664	–5.267
	β_1	**Water**	**2.980**	**0.199**	**2.579**	**3.357**
	***β_2**	**Temp**	**1.913**	**0.202**	**1.677**	**2.173**
	β_3	**Days**	**0.789**	**0.115**	**0.608**	**0.998**
Rana dalmatina	λ_0	Intercept	1.467	0.571	0.433	2.646
(Family: Ranidae)	**λ_1**	**Area**	**0.756**	**0.196**	**0.371**	**1.138**
	λ_2	**Dist_hwy_rail**	**3.556**	**0.297**	**2.988**	**4.146**
	λ_3	Fish	0.293	0.202	–0.109	0.682
	β_0	Intercept	–4.728	0.363	–5.475	–4.052
	β_1	**Water**	**0.218**	**0.057**	**0.106**	**0.329**
	β_2	**Temp**	**–0.142**	**0.034**	**–0.210**	**–0.075**
	β_3	**Days**	**–0.830**	**0.096**	**–1.023**	**–0.646**
Roads						
Bombina bombina	λ_0	Intercept	1.272	0.515	0.297	2.318

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.526**	**0.221**	**2.096**	**2.962**
	λ_2	**Roads**	**–2.944**	**0.298**	**–3.544**	**–2.378**
	λ_3	**Fish**	**–2.529**	**0.246**	**–3.019**	**–2.054**
	β_0	Intercept	–4.049	0.338	–4.738	–3.413
	β_1	**Water**	**1.009**	**0.095**	**0.827**	**1.198**
	β_2	**Temp**	**–0.196**	**0.069**	**–0.330**	**–0.062**
	β_3	**Days**	**0.554**	**0.102**	**0.356**	**0.756**
Bufo bufo	λ_0	Intercept	1.307	0.521	0.418	2.357
(Family: Bufonidae)	**λ_1**	**Area**	**3.463**	**0.178**	**3.120**	**3.813**
	λ_2	**Roads**	**–5.616**	**0.325**	**–6.282**	**–5.008**
	λ_3	**Fish**	**0.646**	**0.179**	**0.296**	**1.002**
	β_0	Intercept	–5.199	0.271	–5.771	–4.695
	β_1	**Water**	**0.897**	**0.066**	**0.770**	**1.028**
	β_2	**Temp**	**–0.102**	**0.042**	**–0.184**	**–0.021**
	β_3	**Days**	**0.378**	**0.043**	**0.294**	**0.463**
Hyla arborea	λ_0	Intercept	0.822	0.482	–0.159	1.746
(Family: Hylidae)	**λ_1**	**Area**	**2.128**	**0.398**	**1.349**	**2.907**
	λ_2	**Roads**	**–3.503**	**0.432**	**–4.364**	**–2.672**
	λ_3	Fish	–0.716	0.389	–1.488	0.036
	β_0	Intercept	–3.837	0.416	–4.666	–3.036
	β_1	Water	0.057	0.191	–0.314	0.435

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_2	**Temp**	**0.725**	**0.203**	**0.336**	**1.134**
	β_3	**Days**	**1.776**	**0.273**	**1.260**	**2.332**
Lissotriton vulgaris	λ_0	Intercept	0.961	0.484	0.009	1.920
(Family: Salamandridae)	**λ_1**	**Area**	**1.743**	**0.333**	**1.089**	**2.396**
	λ_2	**Roads**	**–2.682**	**0.369**	**–3.422**	**–1.976**
	λ_3	**Fish**	**–0.712**	**0.305**	**–1.312**	**–0.116**
	β_0	Intercept	–3.419	0.401	–4.229	–2.665
	β_1	**Water**	**0.963**	**0.172**	**0.636**	**1.308**
	β_2	**Temp**	**0.369**	**0.138**	**0.101**	**0.642**
	β_3	**Days**	**1.017**	**0.174**	**0.682**	**1.365**
Pelobates fuscus	λ_0	Intercept	0.866	0.477	–0.094	1.794
(Family: Pelobatidae)	**λ_1**	**Area**	**2.389**	**0.403**	**1.597**	**3.180**
	λ_2	**Roads**	**–3.892**	**0.422**	**–4.734**	**–3.082**
	λ_3	**Fish**	**–1.219**	**0.361**	**–1.934**	**–0.514**
	β_0	Intercept	–3.771	0.435	–4.635	–2.932
	β_1	**Water**	**1.576**	**0.278**	**1.053**	**2.143**
	β_2	**Temp**	**–0.537**	**0.167**	**–0.874**	**–0.218**
	β_3	Days	–0.218	0.228	–0.678	0.217
Pelophylax spp. complex	λ_0	Intercept	0.908	0.471	–0.034	1.828
(Family: Ranidae)	**λ_1**	**Area**	**2.671**	**0.283**	**2.121**	**3.235**
	λ_2	Roads	–0.087	0.235	–0.555	0.368

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	λ_3	**Fish**	**2.154**	**0.293**	**1.592**	**2.742**
	β_0	Intercept	–4.368	0.278	–4.956	–3.860
	β_1	**Water**	**2.474**	**0.198**	**2.092**	**2.866**
	β_2	**Temp**	**1.408**	**0.110**	**1.200**	**1.630**
	β_3	**Days**	**1.183**	**0.133**	**0.930**	**1.448**
Rana dalmatina	λ_0	Intercept	1.249	0.530	0.246	2.338
(Family: Ranidae)	**λ_1**	**Area**	**0.855**	**0.181**	**0.504**	**1.209**
	λ_2	**Roads**	**–2.954**	**0.292**	**–3.540**	**–2.395**
	λ_3	Fish	–0.121	0.195	–0.502	0.261
	β_0	Intercept	–3.897	0.365	–4.645	–3.206
	β_1	**Water**	**0.498**	**0.063**	**0.376**	**0.623**
	β_2	**Temp**	**–0.164**	**0.036**	**–0.236**	**–0.093**
	β_3	**Days**	**–0.548**	**0.094**	**–0.736**	**–0.366**
Habitat						
Bombina bombina	λ_0	Intercept	1.205	0.517	0.264	2.232
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.645**	**0.218**	**2.216**	**3.076**
	λ_2	**Habitat**	**–1.346**	**0.390**	**–2.135**	**–0.604**
	λ_3	**Fish**	**–1.983**	**0.245**	**–2.472**	**–1.508**
	β_0	Intercept	–4.196	0.328	–4.863	–3.577
	β_1	**Water**	**1.170**	**0.110**	**0.959**	**1.389**
	β_2	**Temp**	**–0.244**	**0.069**	**–0.380**	**–0.108**

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_3	**Days**	**0.829**	**0.124**	**0.590**	**1.077**
Bufo bufo	λ_0	Intercept	1.433	0.528	0.428	2.477
(Family: Bufonidae)	**λ_1**	**Area**	**3.650**	**0.180**	**3.296**	**4.001**
	λ_2	**Habitat**	**2.290**	**0.336**	**1.625**	**2.941**
	λ_3	Fish	–0.170	0.153	–0.467	0.125
	β_0	Intercept	–5.157	0.270	–5.719	–4.654
	β_1	**Water**	**0.818**	**0.067**	**0.687**	**0.951**
	β_2	**Temp**	**–0.154**	**0.043**	**–0.239**	**–0.069**
	β_3	**Days**	**0.352**	**0.044**	**0.266**	**0.439**
Hyla arborea	λ_0	Intercept	0.723	0.492	–0.253	1.693
(Family: Hylidae)	**λ_1**	**Area**	**2.061**	**0.409**	**1.258**	**2.862**
	λ_2	**Habitat**	**2.225**	**0.518**	**1.209**	**3.238**
	λ_3	Fish	–0.210	0.380	–0.968	0.524
	β_0	Intercept	–3.790	0.454	–4.696	–2.919
	β_1	Water	–0.369	0.227	–0.835	0.063
	β_2	**Temp**	**0.655**	**0.208**	**0.263**	**1.081**
	β_3	**Days**	**1.280**	**0.281**	**0.751**	**1.851**
Lissotriton vulgaris	λ_0	Intercept	0.842	0.488	–0.117	1.815
(Family: Salamandridae)	**λ_1**	**Area**	**1.673**	**0.348**	**0.989**	**2.352**
	λ_2	**Habitat**	**1.086**	**0.477**	**0.148**	**2.017**
	λ_3	Fish	0.001	0.293	–0.582	0.569

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_0	Intercept	–3.485	0.443	–4.376	–2.643
	β_1	**Water**	**0.629**	**0.181**	**0.281**	**0.991**
	β_2	**Temp**	**0.317**	**0.134**	**0.057**	**0.582**
	β_3	**Days**	**0.701**	**0.184**	**0.345**	**1.067**
Pelobates fuscus	λ_0	Intercept	0.798	0.491	–0.173	1.769
(Family: Pelobatidae)	**λ_1**	**Area**	**2.363**	**0.403**	**1.571**	**3.152**
	λ_2	**Habitat**	**1.027**	**0.496**	**0.050**	**1.998**
	λ_3	**Fish**	**–0.910**	**0.345**	**–1.601**	**–0.245**
	β_0	Intercept	–3.722	0.455	–4.627	–2.847
	β_1	**Water**	**1.457**	**0.291**	**0.910**	**2.051**
	β_2	**Temp**	**–0.536**	**0.167**	**–0.874**	**–0.216**
	β_3	Days	–0.283	0.237	–0.760	0.171
Pelophylax spp. complex	λ_0	Intercept	0.676	0.486	–0.327	1.610
(Family: Ranidae)	**λ_1**	**Area**	**1.929**	**0.260**	**1.427**	**2.444**
	λ_2	**Habitat**	**–0.800**	**0.360**	**–1.514**	**–0.100**
	λ_3	**Fish**	**3.876**	**0.267**	**3.360**	**4.418**
	β_0	Intercept	–5.150	0.227	–5.616	–4.727
	β_1	**Water**	**3.630**	**0.215**	**3.213**	**4.055**
	β_2	**Temp**	**1.595**	**0.105**	**1.396**	**1.807**
	β_3	**Days**	**1.182**	**0.155**	**0.878**	**1.482**
Rana dalmatina	λ_0	Intercept	1.108	0.501	0.180	2.153

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
(Family: Ranidae)	**λ_1**	**Area**	**1.227**	**0.184**	**0.866**	**1.587**
	λ_2	**Habitat**	**–1.107**	**0.351**	**–1.810**	**–0.438**
	λ_3	Fish	0.184	0.200	–0.212	0.576
	β_0	Intercept	–3.664	0.369	–4.424	–2.978
	β_1	**Water**	**0.563**	**0.066**	**0.436**	**0.694**
	β_2	**Temp**	**–0.161**	**0.036**	**–0.233**	**–0.091**
	β_3	**Days**	**–0.298**	**0.108**	**–0.511**	**–0.089**
Access_hwy						
Bombina bombina	λ_0	Intercept	1.167	0.513	0.159	2.152
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.615**	**0.217**	**2.194**	**3.041**
	λ_2	**Access_hwy**	**–1.308**	**0.393**	**–2.081**	**–0.556**
	λ_3	**Fish**	**–1.957**	**0.246**	**–2.450**	**–1.483**
	β_0	Intercept	–4.153	0.331	–4.848	–3.546
	β_1	**Water**	**1.243**	**0.116**	**1.022**	**1.475**
	β_2	**Temp**	**–0.240**	**0.070**	**–0.377**	**–0.103**
	β_3	**Days**	**0.894**	**0.129**	**0.646**	**1.153**
Bufo bufo	λ_0	Intercept	1.379	0.551	0.250	2.417
(Family: Bufonidae)	**λ_1**	**Area**	**3.724**	**0.178**	**3.371**	**4.071**
	λ_2	**Access_hwy**	**2.651**	**0.345**	**1.977**	**3.318**
	λ_3	Fish	–0.203	0.156	–0.508	0.102
	β_0	Intercept	–5.115	0.260	–5.636	–4.619

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_1	**Water**	**0.771**	**0.067**	**0.641**	**0.903**
	β_2	**Temp**	**–0.162**	**0.043**	**–0.246**	**–0.077**
	β_3	**Days**	**0.319**	**0.044**	**0.233**	**0.404**
Hyla arborea	λ_0	Intercept	0.669	0.500	–0.336	1.623
(Family: Hylidae)	**λ_1**	**Area**	**2.073**	**0.412**	**1.267**	**2.879**
	λ_2	**Access_hwy**	**2.298**	**0.520**	**1.276**	**3.317**
	λ_3	Fish	–0.216	0.381	–0.975	0.520
	β_0	Intercept	–3.785	0.453	–4.690	–2.917
	β_1	Water	–0.366	0.228	–0.830	0.067
	β_2	**Temp**	**0.648**	**0.208**	**0.255**	**1.071**
	β_3	**Days**	**1.294**	**0.282**	**0.761**	**1.868**
Lissotriton vulgaris	λ_0	Intercept	0.797	0.494	–0.176	1.766
(Family: Salamandridae)	**λ_1**	**Area**	**1.697**	**0.349**	**1.009**	**2.379**
	λ_2	**Access_hwy**	**1.092**	**0.483**	**0.140**	**2.036**
	λ_3	Fish	–0.014	0.295	–0.599	0.558
	β_0	Intercept	–3.479	0.440	–4.375	–2.645
	β_1	**Water**	**0.649**	**0.183**	**0.297**	**1.014**
	β_2	**Temp**	**0.308**	**0.133**	**0.048**	**0.571**
	β_3	**Days**	**0.728**	**0.186**	**0.368**	**1.097**
Pelobates fuscus	λ_0	Intercept	0.742	0.499	–0.250	1.704
(Family: Pelobatidae)	**λ_1**	**Area**	**2.389**	**0.405**	**1.595**	**3.182**

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	λ_2	**Access_hwy**	**1.140**	**0.498**	**0.170**	**2.120**
	λ_3	**Fish**	**–0.921**	**0.344**	**–1.610**	**–0.257**
	β_0	Intercept	–3.711	0.450	–4.600	–2.842
	β_1	**Water**	**1.458**	**0.293**	**0.908**	**2.058**
	β_2	**Temp**	**–0.539**	**0.168**	**–0.877**	**–0.219**
	β_3	Days	–0.281	0.237	–0.759	0.173
Pelophylax spp. complex	λ_0	Intercept	0.592	0.504	–0.431	1.536
(Family: Ranidae)	**λ_1**	**Area**	**1.964**	**0.257**	**1.467**	**2.471**
	λ_2	**Access_hwy**	**–1.305**	**0.367**	**–2.030**	**–0.576**
	λ_3	**Fish**	**3.837**	**0.275**	**3.326**	**4.399**
	β_0	Intercept	–5.049	0.206	–5.458	–4.650
	β_1	**Water**	**3.711**	**0.207**	**3.306**	**4.120**
	β_2	**Temp**	**1.550**	**0.102**	**1.355**	**1.755**
	β_3	**Days**	**1.377**	**0.140**	**1.097**	**1.648**
Rana dalmatina	λ_0	Intercept	1.076	0.490	0.142	2.048
(Family: Ranidae)	**λ_1**	**Area**	**1.211**	**0.186**	**0.848**	**1.576**
	λ_2	**Access_hwy**	**–0.915**	**0.358**	**–1.624**	**–0.213**
	λ_3	Fish	0.257	0.201	–0.142	0.650
	β_0	Intercept	–3.677	0.391	–4.488	–2.952
	β_1	**Water**	**0.578**	**0.067**	**0.448**	**0.712**
	β_2	**Temp**	**–0.163**	**0.036**	**–0.235**	**–0.092**

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	β_3	**Days**	**–0.300**	**0.107**	**–0.510**	**–0.091**
Access_hwy_rail						
Bombina bombina	λ_0	Intercept	1.109	0.491	0.192	2.154
(Family: Bombinatoridae)	**λ_1**	**Area**	**2.757**	**0.220**	**2.328**	**3.185**
	λ_2	**Access_hwy_rail**	**–2.925**	**0.465**	**–3.833**	**–2.027**
	λ_3	**Fish**	**–1.546**	**0.250**	**–2.047**	**–1.063**
	β_0	Intercept	–4.497	0.334	–5.198	–3.865
	β_1	**Water**	**1.361**	**0.111**	**1.146**	**1.580**
	β_2	**Temp**	**–0.268**	**0.070**	**–0.405**	**–0.130**
	β_3	**Days**	**1.091**	**0.131**	**0.837**	**1.350**
Bufo bufo	λ_0	Intercept	1.392	0.563	0.332	2.598
(Family: Bufonidae)	**λ_1**	**Area**	**3.577**	**0.182**	**3.223**	**3.939**
	λ_2	**Access_hwy_rail**	**1.760**	**0.374**	**1.052**	**2.482**
	λ_3	**Fish**	**–0.353**	**0.153**	**–0.650**	**–0.051**
	β_0	Intercept	–5.197	0.271	–5.725	–4.664
	β_1	**Water**	**0.871**	**0.067**	**0.742**	**1.003**
	β_2	**Temp**	**–0.169**	**0.044**	**–0.256**	**–0.082**
	β_3	**Days**	**0.370**	**0.044**	**0.283**	**0.456**
Hyla arborea	λ_0	Intercept	0.732	0.495	–0.253	1.711
(Family: Hylidae)	**λ_1**	**Area**	**2.025**	**0.407**	**1.225**	**2.822**
	λ_2	**Access_hwy_rail**	**1.965**	**0.525**	**0.935**	**2.993**

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
	λ_3	Fish	–0.326	0.371	–1.064	0.392
	β_0	Intercept	–3.929	0.458	–4.847	–3.054
	β_1	Water	–0.343	0.222	–0.796	0.078
	β_2	**Temp**	**0.702**	**0.207**	**0.310**	**1.123**
	β_3	**Days**	**1.352**	**0.273**	**0.839**	**1.908**
Lissotriton vulgaris	λ_0	Intercept	0.825	0.487	–0.143	1.782
(Family: Salamandridae)	**λ_1**	**Area**	**1.614**	**0.349**	**0.927**	**2.296**
	λ_2	Access_hwy_rail	0.813	0.507	–0.182	1.804
	λ_3	Fish	0.006	0.295	–0.575	0.580
	β_0	Intercept	–3.594	0.451	–4.499	–2.741
	β_1	**Water**	**0.655**	**0.180**	**0.311**	**1.015**
	β_2	**Temp**	**0.329**	**0.134**	**0.069**	**0.595**
	β_3	**Days**	**0.720**	**0.183**	**0.368**	**1.084**
Pelobates fuscus	λ_0	Intercept	0.776	0.490	–0.190	1.747
(Family: Pelobatidae)	**λ_1**	**Area**	**2.312**	**0.401**	**1.527**	**3.099**
	λ_2	Access_hwy_rail	0.581	0.522	–0.437	1.603
	λ_3	**Fish**	**–0.871**	**0.347**	**–1.564**	**–0.203**
	β_0	Intercept	–3.863	0.458	–4.771	–2.982
	β_1	**Water**	**1.513**	**0.287**	**0.977**	**2.101**
	β_2	**Temp**	**–0.539**	**0.166**	**–0.874**	**–0.220**
	β_3	Days	–0.254	0.234	–0.724	0.196

Model/ Species	Species-specific parameter		Mean	SD	95% BCI	
Pelophylax spp. complex	λ_0	Intercept	0.641	0.495	–0.335	1.606
(Family: Ranidae)	**λ_1**	**Area**	**1.762**	**0.257**	**1.264**	**2.269**
	λ_2	Access_hwy_rail	–0.585	0.384	–1.316	0.173
	λ_3	**Fish**	**4.220**	**0.267**	**3.714**	**4.763**
	β_0	Intercept	–5.566	0.258	–6.111	–5.092
	β_1	**Water**	**3.643**	**0.211**	**3.241**	**4.066**
	β_2	**Temp**	**1.670**	**0.106**	**1.467**	**1.884**
	β_3	**Days**	**1.003**	**0.140**	**0.744**	**1.289**
Rana dalmatina	λ_0	Intercept	1.053	0.492	0.107	2.045
(Family: Ranidae)	**λ_1**	**Area**	**1.192**	**0.185**	**0.829**	**1.551**
	λ_2	**Access_hwy_rail**	**–1.191**	**0.400**	**–1.958**	**–0.398**
	λ_3	**Fish**	**0.466**	**0.194**	**0.090**	**0.850**
	β_0	Intercept	–3.894	0.388	–4.658	–3.154
	β_1	**Water**	**0.466**	**0.064**	**0.341**	**0.593**
	β_2	**Temp**	**–0.158**	**0.036**	**–0.229**	**–0.088**
	β_3	**Days**	**–0.460**	**0.108**	**–0.673**	**–0.248**

Dist_hwy_rail = distance to nearest highway or the railway; Roads = % cover of road surface within a 1000–m radius of a site; Habitat = % forest + wetland habitat within a 1000–m radius of a site; Access_hwy = % forest + wetland habitat within a 1000–m radius of a site that can be accessed without crossing a highway (i.e. accessible habitat); Access_hwy_rail = % forest + wetland habitat within a 1000–m radius of a site that can be accessed without crossing a highway or the main railway (i.e. accessible habitat); Area = pond area; Fish = presence (1) or absence (0) of fish at a site; Water = % of full water–holding capacity at a site; Temp = water temperature; Days = number of days since 1 February 2020.

* parameter estimate did not converge ($\hat{R}$ = 1.1).

Appendix 14 Summary of community-level hyper-parameters for abundance (λ) (Area and Fish only) and detection (β) for the larvae of seven amphibian species in five multi-species abundance models. See **Table 9** for parameter estimates of landscape-scale covariates, abundance sub-model intercepts and estimates in the Dist_hwy model. Estimates include 95% Bayesian credible intervals (BCI). Clear relationships for hyper-parameters of the covariates are where the 95% BCI does not overlap zero (highlighted in bold, except intercept coefficients). μ = mean community response; σ = standard deviation in the response to the covariate across species; SD = standard deviation.

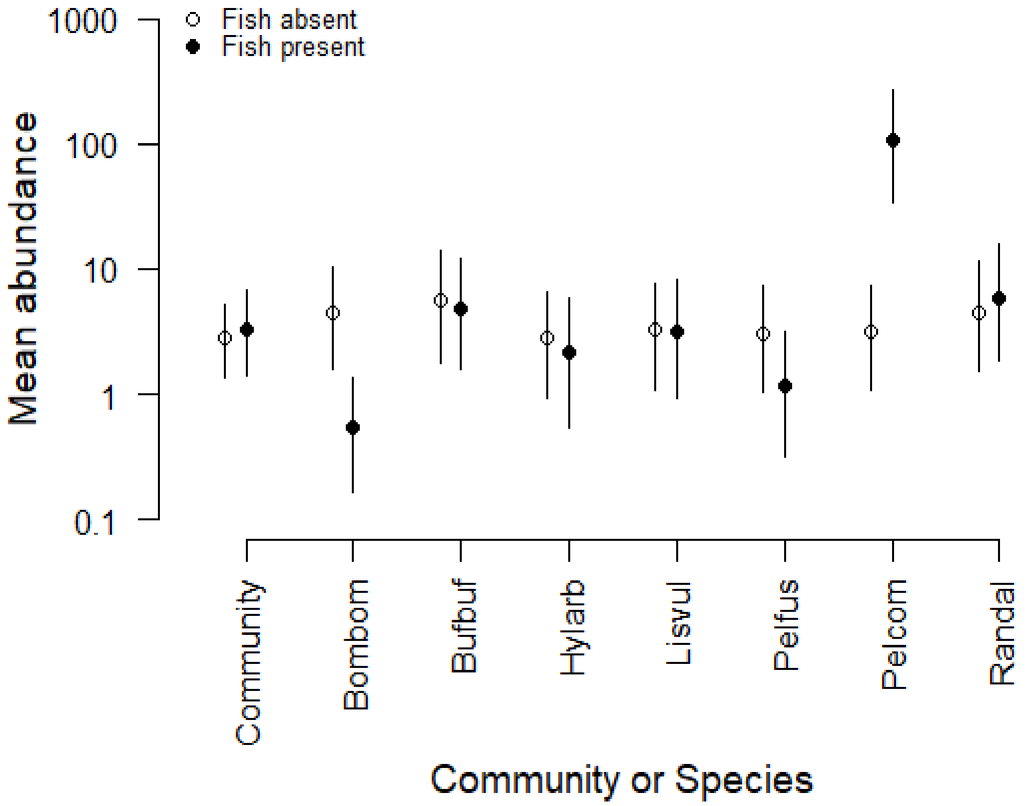
Model	Covariates	Mean	SD	95% BCI	
Dist_hwy_rail					
$\mu_{\lambda 1}$	**Area**	**1.799**	**0.214**	**1.380**	**2.219**
$\sigma_{\lambda 1}$	Area	0.475	0.022	0.417	0.499
$\mu_{\lambda 3}$	Fish	0.399	0.220	–0.031	0.830
$\sigma_{\lambda 3}$	Fish	0.494	0.006	0.478	0.500
$\mu_{\beta 0}$	Intercept	–4.185	0.249	–4.680	–3.705
$\sigma_{\beta 0}$	Intercept	0.478	0.022	0.420	0.499
$\mu_{\beta 1}$	**Water**	**1.124**	**0.179**	**0.773**	**1.476**
$\sigma_{\beta 1}$	Water	0.478	0.020	0.426	0.499
$\mu_{\beta 2}$	**Temp**	**0.398**	**0.173**	**0.062**	**0.740**
$\sigma_{\beta 2}$	Temp	0.470	0.026	0.405	0.499
$\mu_{\beta 3}$	**Days**	**0.572**	**0.176**	**0.229**	**0.918**
$\sigma_{\beta 3}$	Days	0.470	0.026	0.403	0.499
Roads					
$\mu_{\lambda 1}$	**Area**	**2.081**	**0.213**	**1.663**	**2.500**
$\sigma_{\lambda 1}$	Area	0.472	0.024	0.409	0.499
$\mu_{\lambda 3}$	Fish	–0.157	0.220	–0.588	0.275
$\sigma_{\lambda 3}$	Fish	0.491	0.009	0.467	0.500
$\mu_{\beta 0}$	Intercept	–3.667	0.234	–4.128	–3.211
$\sigma_{\beta 0}$	Intercept	0.463	0.035	0.372	0.499
$\mu_{\beta 1}$	**Water**	**1.058**	**0.176**	**0.713**	**1.403**
$\sigma_{\beta 1}$	Water	0.466	0.029	0.392	0.499
$\mu_{\beta 2}$	Temp	0.316	0.167	–0.009	0.647
$\sigma_{\beta 2}$	Temp	0.456	0.036	0.369	0.499
$\mu_{\beta 3}$	**Days**	**0.647**	**0.176**	**0.303**	**0.995**

Model	Covariates	Mean	SD	95% BCI	
$\sigma_{\beta3}$	Days	0.469	0.027	0.399	0.499
Habitat					
$\mu_{\lambda1}$	**Area**	**2.055**	**0.215**	**1.632**	**2.475**
$\sigma_{\lambda1}$	Area	0.470	0.026	0.403	0.499
$\mu_{\lambda3}$	Fish	0.244	0.219	–0.187	0.674
$\sigma_{\lambda3}$	Fish	0.494	0.006	0.478	0.500
$\mu_{\beta0}$	Intercept	–3.730	0.238	–4.203	–3.269
$\sigma_{\beta0}$	Intercept	0.473	0.026	0.404	0.499
$\mu_{\beta1}$	**Water**	**1.110**	**0.183**	**0.751**	**1.470**
$\sigma_{\beta1}$	Water	0.487	0.013	0.453	0.500
$\mu_{\beta2}$	Temp	0.315	0.169	–0.014	0.648
$\sigma_{\beta2}$	Temp	0.462	0.031	0.384	0.499
$\mu_{\beta3}$	**Days**	**0.597**	**0.174**	**0.258**	**0.940**
$\sigma_{\beta3}$	Days	0.452	0.039	0.356	0.498
Access_hwy					
$\mu_{\lambda1}$	**Area**	**2.069**	**0.214**	**1.648**	**2.486**
$\sigma_{\lambda1}$	Area	0.472	0.025	0.407	0.499
$\mu_{\lambda3}$	Fish	0.244	0.221	–0.189	0.676
$\sigma_{\lambda3}$	Fish	0.494	0.006	0.477	0.500
$\mu_{\beta0}$	Intercept	–3.709	0.239	–4.182	–3.246
$\sigma_{\beta0}$	Intercept	0.471	0.028	0.397	0.499
$\mu_{\beta1}$	**Water**	**1.127**	**0.183**	**0.768**	**1.486**
$\sigma_{\beta1}$	Water	0.487	0.012	0.455	0.500
$\mu_{\beta2}$	Temp	0.306	0.168	–0.022	0.638
$\sigma_{\beta2}$	Temp	0.461	0.032	0.381	0.499
$\mu_{\beta3}$	**Days**	**0.631**	**0.175**	**0.291**	**0.976**
$\sigma_{\beta3}$	Days	0.458	0.035	0.371	0.499
Access_hwy_rail					
$\mu_{\lambda1}$	**Area**	**2.016**	**0.216**	**1.590**	**2.438**
$\sigma_{\lambda1}$	Area	0.471	0.025	0.406	0.499

Model	Covariates	Mean	SD	95% BCI	
$\mu_{\lambda 3}$	Fish	0.343	0.218	–0.082	0.772
$\sigma_{\lambda 3}$	Fish	0.494	0.006	0.479	0.500
$\mu_{\beta 0}$	Intercept	–3.894	0.241	–4.372	–3.428
$\sigma_{\beta 0}$	Intercept	0.476	0.023	0.414	0.499
$\boldsymbol{\mu_{\beta 1}}$	**Water**	**1.143**	**0.183**	**0.784**	**1.502**
$\sigma_{\beta 1}$	Water	0.487	0.012	0.454	0.500
$\mu_{\beta 2}$	Temp	0.328	0.169	–0.002	0.662
$\sigma_{\beta 2}$	Temp	0.465	0.029	0.392	0.499
$\boldsymbol{\mu_{\beta 3}}$	**Days**	**0.605**	**0.175**	**0.265**	**0.950**
$\sigma_{\beta 3}$	Days	0.458	0.035	0.371	0.499

Area = pond area; Fish = presence (1) or absence (0) of fish at a site; Water = % of full water-holding capacity at a site; Temp = water temperature; Days = number of days since 1 February 2020.

Appendix 15 Mean estimates (log-transformed; vertical bars are 95% Bayesian credible intervals) of community abundance and species-specific abundance of the larvae of seven amphibian species versus the presence or absence of fish at ponds. Species codes: Bombom = *Bombina bombina*; Bufbuf = *Bufo bufo*; Hylarb = *Hyla arborea*; Lisvul = *Lissotriton vulgaris*; Pelfus = *Pelobates fuscus*; Pelcom = *Pelophylax* spp. complex; Randal = *Rana dalmatina*.



Appendix 16 Model coefficients (posterior means and 95% Bayesian credible intervals) of random effects for spatial autocorrelation on larval abundance in ponds at 12 clusters in the study area. Parameter estimates were extracted from the Dist_hwy model. Spatial autocorrelation within clusters is evident where credible intervals do not overlap zero.