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Table of contents

1. Abstract	1
2. Introduction.....	2
3. Methods.....	5
3.1 Study area.....	5
3.2 Study design	7
3.3 Field work.....	7
3.4 Laboratory work	9
3.5 Statistics.....	12
4. Results.....	14
4.1 Sample overview	14
4.2 Abiotic characteristics.....	15
4.3 Fauna analyses	20
4.4 eDNA metabarcoding	28
4.5 Vertebrate interactions with dendrotelmata	29
5. Discussion	31
5.1 Dendrotelmata as habitats	31
5.2 Types of dendrotelmata.....	32
5.3 Aquatic insect community in dendrotelmata	33
5.4 Faunal differences between different dendrotelmata types	34
5.5 Impact of urbanisation	36
5.6 Forest management practices.....	38
5.7 Microhabitat $\neq$ microhabitat	39
5.8 Aquatic insects detected by eDNA metabarcoding	41
5.9 Meiofauna detected by eDNA metabarcoding.....	42
6. Conclusions	43
7. Literature	44
8. Appendix.....	61
8.1 Voucher specimens and sequence records	61
8.2 Supplementary figures	61
8.3 Supplementary tables.....	66
9. Zusammenfassung (German abstract)	98

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Stayin' Alive – Aquatic Fauna in Terrestrial Plants

1. Abstract

Phytotelmata are aquatic microhabitats in and on plants, which are often overlooked but harbour specialised communities. Although they are found in Central Europe, the ecology of their associated taxa remains relatively unexplored. In this study I investigated the fauna of water-filled treeholes (dendrotelmata) in an urban park within the city of Vienna and in a rural floodplain forest outside the city to determine how urbanisation impacts water chemistry and aquatic fauna. For microhabitat comparison, plastic containers (ovitrap) were installed at the same locations. I recorded limnochemical parameters across three seasons, identified insect larvae morphologically, supplemented identifications with environmental DNA (eDNA) metabarcoding and analysed multivariate patterns.

Dendrotelmata were nutrient-rich and oxygen-poor, with environmental conditions and fauna impacted by urbanisation, leading to taxon-specific responses. Four taxa differed significantly: the marsh beetle *Prionocyphon serricornis* and the mosquito *Aedes geniculatus* were more frequent at the rural location, whilst the hoverfly *Myathropa florea* and biting midges of the genus *Dasyhelea* were associated with the urban setting. *Dasyhelea* also significantly preferred ovitraps, which differed fundamentally from natural dendrotelmata by exhibiting higher oxygen concentrations, lower nutrient loading, greater temperature fluctuations and a different community composition. Species-environment relationships were primarily structured by conductivity (nutrient load) and oxygen concentration. A comparison of methods showed that eDNA metabarcoding detected aquatic insect taxa less comprehensively than morphological identification, but additionally recorded Rotifera and Nematoda.

This study demonstrates that urbanisation affects microhabitats such as dendrotelmata. Furthermore, it is evident that ovitraps are ecological surrogates with limitations and altered biotic communities, yet they are suitable for targeted monitoring of non-native mosquitoes. To capture the biodiversity of these microhabitats, eDNA metabarcoding requires further methodological development. For nature conservation this means that the preservation of natural treehole structures is vital and that taxonomic expertise remains important.

Keywords: phytotelmata; microhabitat; urbanisation; metabarcoding; non-native mosquitoes

2. Introduction

In addition to rivers, lakes and oceans, there are also other small aquatic habitats. Even in areas with high anthropogenic impact, they can be found, such as rain barrels, flower pots and buckets. Although aquatic microhabitats are vital components of functioning ecosystems, they are largely neglected.

A unique habitat is small water bodies within and on plants, which were termed phytotelmata by Varga (1928). Besides the water-filled leaf axils of teasel plants (*Dipsacus* Linnaeus, 1758), the most common type in Europe consists of tree holes in various forms, so-called dendrotelmata (Kitching, 1971; Oboňa et al., 2024; Schmidl et al., 2008). Although these obscure small freshwater habitats are probably the most numerous astatic water bodies in temperate forests (cf. Carpenter, 1982; Petermann & Gossner, 2022), they are still barely examined (Devetter, 2004; Oboňa et al., 2021; Oboňa & Dominiak, 2014). The research focus on phytotelmata is primarily in the Neotropics, where water-bearing bromeliads (Poales: Bromeliaceae) have been extensively studied (Rogy & Srivastava, 2023; Teixeira et al., 2018). In both, the tropical and temperate regions, mainly insects were investigated (Devetter, 2004; Kitching, 1971; Mogi, 2004). These include the marsh beetles (Coleoptera: Scirtidae) and Diptera larvae, such as mosquitoes (Culicidae), biting midges (Ceratopogonidae), non-biting midges (Chironomidae), moth flies (Psychodidae), soldier flies (Stratiomyidae), dagger flies (Empididae), hoverflies (Syrphidae) and muscid flies (Muscidae) (Gossner et al., 2026; Schmidl et al., 2008; Verdonschot et al., 2008). Other invertebrates, such as Rotifera or Nematoda, were almost disregarded (Almeida & Souza, 2020; Koste et al., 1991; Mogi, 2004; Ptatscheck & Traunspurger, 2014; Walsh et al., 2014).

The number of studies on limnochemistry also remains modest. Some surveys only recorded key physicochemical parameters such as temperature, oxygen, pH and conductivity (Devetter, 2004; Oboňa et al., 2024), whilst others additionally considered nutrient concentrations such as ammonium, nitrate, phosphorus and sulfate (Carpenter, 1982; Gossner et al., 2016; Schmidl et al., 2008; Zittra & Waringer, 2014). Only a few studies, such as those of Paradise & Dunson (1998) and Verdonschot et al. (2008), included dissolved organic carbon (DOC) in the water column. In general, conditions in phytotelmata are described as nutrient-rich and oxygen-poor (Rogy & Srivastava, 2023; Schmidl et al., 2008; Walker et al., 1991), mainly due to allochthonous input and heterotrophic processes (Verdonschot et al., 2008). Carpenter (1982) demonstrated in laboratory experiments that the chemical composition of phytotelmata depend on the nutrient supply provided by the respective plant species. However, as Devetter (2004) and Verdonschot et al. (2008) emphasise, these microhabitats are also characterised by small volume and are primarily fed by rainwater, resulting in major fluctuations and

variability. Drying out with drought, frost in winter and dilution/overflow during heavy rainfall highlight the extreme dynamics that can prevail (Moore & Lee, 1991; E. L. Rotheray, 2013; Verdonschot et al., 2008; Walker et al., 1991).

Hemeroby, the degree of anthropogenic impacts on ecosystems (Falko et al., 2025; Kowarik, 2004; Walz & Stein, 2014), also has consequences for phytotelmata. Studies on the impact of forest management revealed that insect communities in water-filled treeholes are adversely affected by increasing intensity of forestry activities. This is attributed to alterations in tree species composition, reductions in the availability as well as diversity of microhabitats and declines in microhabitat properties such as the quantity of detrital resources (Bartel et al., 2025; Gossner et al., 2016; Petermann et al., 2020). An aspect which has been largely overlooked in this context is urbanisation. Phytotelmata are found primarily in old natural forests beyond human settlements (Blakely et al., 2012), but they also occur in urban parks (Oboňa et al., 2021), gardens (Smolák et al., 2022) and greenhouses (Kolicka et al., 2016). A citizen science project by Sommer & Petermann (2026) used plastic buckets filled with leaf litter to investigate the effects of urban structures on their aquatic insect communities. Surprisingly, the results showed no influence neither on the number of individuals nor on species richness, but the community composition changed. The common house mosquito, *Culex pipiens* s.l. Linnaeus, 1758, was linked to increasing urbanisation, whereas the Asian bush mosquito, *Aedes japonicus* (Theobald, 1901), followed a reverse pattern.

Mosquitoes are among the most prominent representatives of phytotelmata, some of which are even specialised for this habitat (Mogi et al., 2024; Yates, 1979; Zित्रa & Waringer, 2014). Treehole dwelling species of the genus *Aedes* repeatedly received media attention (Giardullo, 2018), since they act as potential vectors of various pathogens, such as the Chikungunya or Dengue virus (Li et al., 2014; Prudhomme et al., 2019). The mosquito species found in European phytotelmata include *Aedes geniculatus* (Olivier, 1791), *Anopheles plumbeus* Stephens, 1828, and the common house mosquito complex *Culex pipiens* s.l. / *Cx. torrentium* (Becker et al., 2020; Schmidl et al., 2008; Zित्रa & Waringer, 2014). Additionally, non-native species are known to dwell in phytotelmata or similar microhabitats, such as rock pools, within their natural area of distribution. These are the previously mentioned Asian bush mosquito, *Aedes japonicus* (Bakran-Lebl et al., 2021; Kaufman & Fonseca, 2014), the Korean bush mosquito, *Aedes koreicus* (Edwards, 1917) (Fuehrer et al., 2020; Montarsi et al., 2014), and the famous Asian tiger mosquito, *Aedes albopictus* (Skuse, 1884) (Bakran-Lebl et al., 2021; Li et al., 2014). However, much remains unclear about their larval ecology, and in recently settled areas they have so far been found mainly in artificial containers (Mogi et al., 2020, 2024).

The abundance and diversity of mosquito communities generally decline under conditions of intense landscape anthropisation. This is primarily attributed to the reduced diversity and size of wetlands (Ferraguti et al., 2016; Perrin et al., 2022), although the specific host utilisation by adult females may also be a contributing factor (Takken & Verhulst, 2013; Yan et al., 2021). An exception are opportunistic and anthropophilic mosquito species, which also use artificial elements such as rain barrels or plant saucers as breeding habitats and humans as hosts for their feeding (Ferraguti et al., 2016; Perrin et al., 2022). In addition, urban landscapes facilitate the biological invasions of non-native species because highly frequented infrastructure and reduced predation provide ideal conditions for their spread (Carlon & Dominoni, 2024; Francis & Chadwick, 2015; Pabst et al., 2025). The composition of a mosquito community is thus changing as a consequence of urbanisation, and this appears to be the case in phytotelmata as well. Mogi et al. (2020, 2024) investigated mosquito larvae in treeholes and artificial containers. They showed that *Aedes japonicus* tends to occur in rural forests, whereas *Aedes albopictus*, classified as anthropophilic, dominates in urban landscapes. These findings regarding the urban-rural gradient in mosquitoes inhabiting phytotelmata are therefore consistent with other studies that collected larvae using artificial containers (Kolimenakis et al., 2021; Sommer & Petermann, 2026) or imagos captured using traps (Garrido et al., 2025; Li et al., 2014).

The national monitoring program in Austria relies primarily on plastic buckets called ovitraps, in which the oviposition by females is regularly checked and the eggs are identified both morphologically as well as genetically (Bakran-Lebl et al., 2022, 2024). In Vienna (Austria), a growing metropolis in Central Europe (Pamer, 2019), *Aedes japonicus* was first recorded in the year 2011 (Schoener et al., 2019), followed by *Aedes albopictus* in 2020 (Bakran-Lebl et al., 2021). Both alien species are by now considered established with overwintering populations (Bakran-Lebl et al., 2025). Thus far, no reports of either species have been received from the Donau-Auen National Park, which extends into the city boundaries. Zittra & Waringer (2014) conducted a mosquito inventory of the National Park back in 2011, including water-filled tree holes. Nevertheless, a comprehensive faunal inventory of the phytotelmata in this region has so far been entirely missing. This circumstance, coupled with the spread of non-native species, prompted me to investigate these microhabitats in further detail.

A comparative field survey of water-filled treeholes (dendrotelmata) and ovitraps was performed in the Vienna Prater, an urban park near the city center, and in the Donau-Auen National Park near Orth an der Donau, in the rural outskirts of Vienna. The following questions were addressed: (1) which abiotic characteristics are typical for dendrotelmata, (2) which animal taxa live in there, (3) do any differences exist between urban versus rural communities, and (4) whether certain taxa prefer artificial microhabitats? According to the literature, I

assumed that nutrient-rich, oxygen-poor conditions prevail (Verdonschot et al., 2008; Walker et al., 1991). It can therefore be concluded that animals specialising in astatic microhabitats are to be found, which either breathe atmospheric oxygen, such as Culicidae (Alvarez-Costa et al., 2024; Becker et al., 2020), Syrphidae (Gossner & Petermann, 2022; E. L. Rotheray, 2013) and Scirtidae (Klausnitzer, 2009; Schmidl et al., 2008), as well as those that respire dissolved oxygen and are known to survive hypoxia. Among these are representatives of the Chironomidae (Grazioli et al., 2016; Hoback & Stanley, 2001; Pinder, 1995). Based on the results of Sommer & Petermann (2026), I assumed that urbanisation is linked to a change in the mosquito community. Findings of *Aedes japonicus* should therefore be associated with rural conditions, whereas *Aedes albopictus* is mainly expected in urban areas (Li et al., 2014; Mogi et al., 2020). The investigations by Mogi et al. (2024) have also shown that *Aedes japonicus* prefers artificial containers to treeholes. Accordingly, it is assumed that specimens are most likely found in ovitraps.

3. Methods

3.1 Study area

The study sites are located in two wooded areas: the Vienna Prater (48.1973°N, 16.4311°E), a park near the center of the metropolis, and a floodplain forest within the Donau-Auen National Park near the town of Orth an der Donau (48.1443°N, 16.6928°E), outside of Vienna (Figure 1). Situated in temperate Central Europe, this area has annual precipitation ranging from 495 mm (Groß-Enzersdorf) to 565 mm (Wien Innere Stadt) and mean annual air temperatures between 11.4 °C (-10.9 to 36.4 °C) and 12.8 °C (-5.4 to 37.2 °C), as recorded by nearby meteorological stations for the year 2025 (GeoSphere Austria, 2025).

The areas are approximately 20 kilometers apart and differ substantially in their urbanisation (Figure 1). With over two million citizens, Vienna is one of the largest cities in Europe, with inner districts characterised by residential buildings and industry (European Environment Agency, 2019; Pamer, 2019). The district of Leopoldstadt, Vienna's second municipal district, which contains the Prater, has a population density of over 5800 people per km² (City of Vienna, 2025). In contrast, Orth an der Donau has a population of just over two thousand and a density of 67 people per km² (Federal State of Lower Austria, 2025). The surrounding landscape is characterised by intensive agricultural production (European Environment Agency, 2019; Niedermayr et al., 2018), with exception of the national park situated between the town and the Danube. In both cases the study area is used for recreational purposes (Arnberger et al., 2021; O'Brien, 1981).

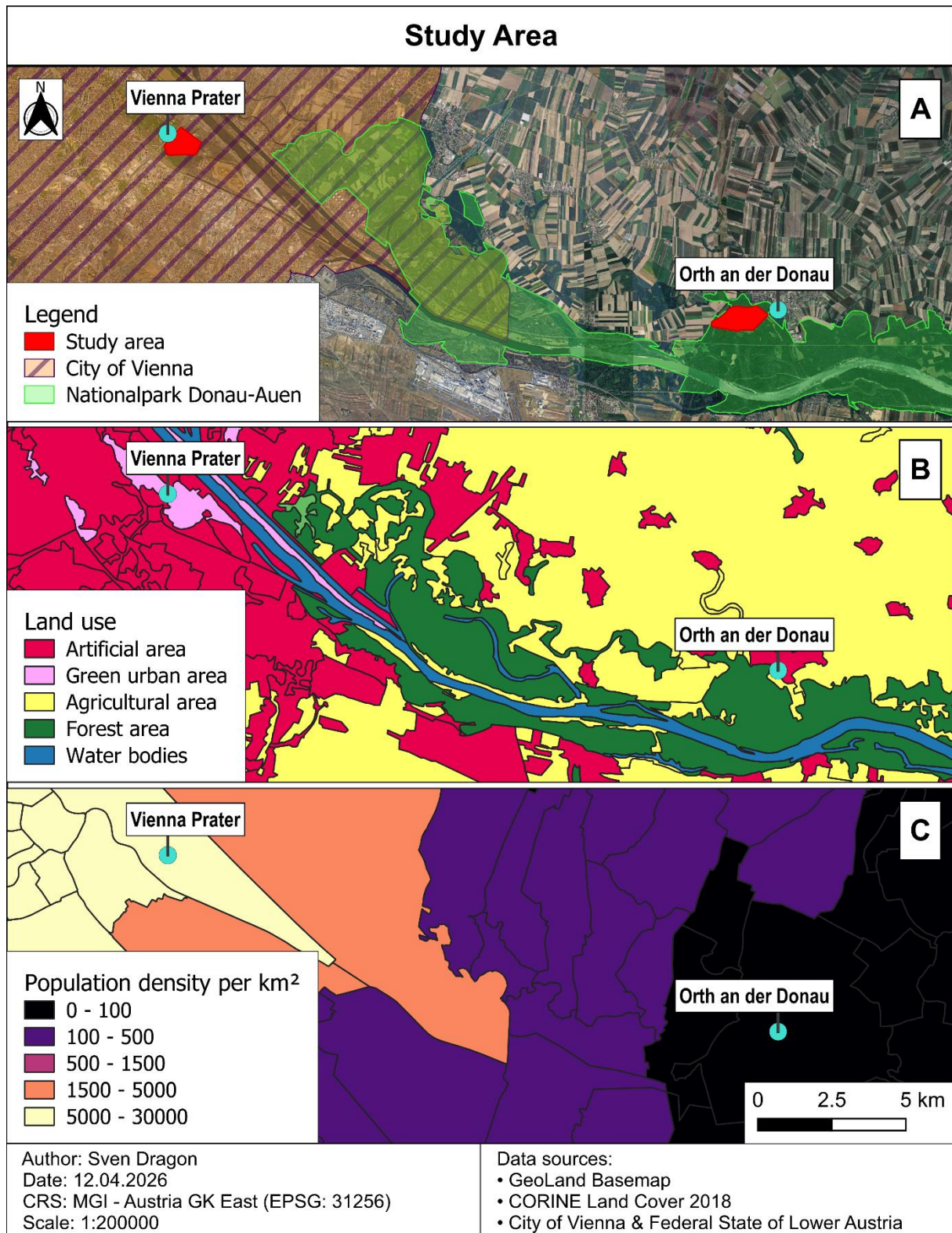


Figure 1: Map of the study area illustrating the urbanisation gradient between the locations. Part A shows the boundaries of Vienna and the Donau-Auen National Park, as well as the two study locations. In Part B, the region's land use is displayed based on the CORINE Land Cover dataset (European Environment Agency, 2019). For this purpose, the CLC class level 1 is refined to CLC class level 2 in case of green urban area (Class 1: artificial areas) and forest area (Class 3: forest and semi-natural areas). Part C shows the human population density in people per square kilometer for the political administrative units.

For Vienna, census data for the city districts (City of Vienna, 2025) were used. In Lower Austria, census data for the municipalities (Federal State of Lower Austria, 2025) were used.

3.2 Study design

This study is based on comparative field surveys conducted in 2025, during which both abiotic and biotic parameters were assessed. A distinction was made between two location types, rural (Orth) versus urban (Prater), along with two types of microhabitat (Figure 2), treeholes (dendrotelmata) and plastic buckets (ovitraps). For each type, five replicates were planned in three seasons (spring, summer, autumn). The seasonal sampling took place in May (Orth: 26 May; Prater: 28 May), July (Orth: 29 July; Prater: 31 July) and October (Orth: 06 October; Prater: 09 October). To avoid any potential interference from previous sampling, tree holes were sampled independently, each only once, whereas the plastic buckets were refilled with autoclaved rainwater and sampled repeatedly (paired sampling).

In addition, a one-time sampling of leaf axils from *Dipsacus fullonum* Linnaeus, 1758 was conducted in July at an open area on the so-called Schlossinsel, an outdoor adventure area at the National Park Centre in Orth an der Donau. Due to the small sample size ($n = 5$) and the research questions focusing on dendrotelmata, this data was excluded from further analysis and is available in the appendix of this work (Table A1–A4). The five ovitraps, deployed in July as a comparable control group, were not included in the limnochemical analysis, but their fauna data were retained for subsequent assessments. Exclusions were still made in comparative statistical tests across locations or seasons, to ensure the comparability with other ovitraps that had been positioned in wooded areas for a longer period.

3.3 Field work

The mapping of dendrotelmata started in February 2025. A standardised documentation protocol for documentation was prepared using QGIS (version 3.34, Open Source Geospatial Foundation) and QField (version 3.4; see Montagnetti & Guarino, 2021). Information such as coordinates, height and plant species was recorded directly in the field. Based on the method described by Bakran-Lebl et al. (2022), five black ovitraps with a volume of 1 liter were set up in each area close to dendrotelmata and secured with wire (Figure 2). The position remained unchanged throughout the entire sampling period. About two weeks before sampling, they were refilled if required and equipped with wooden mouth spatulas to monitor mosquito oviposition (Bakran-Lebl et al., 2024).

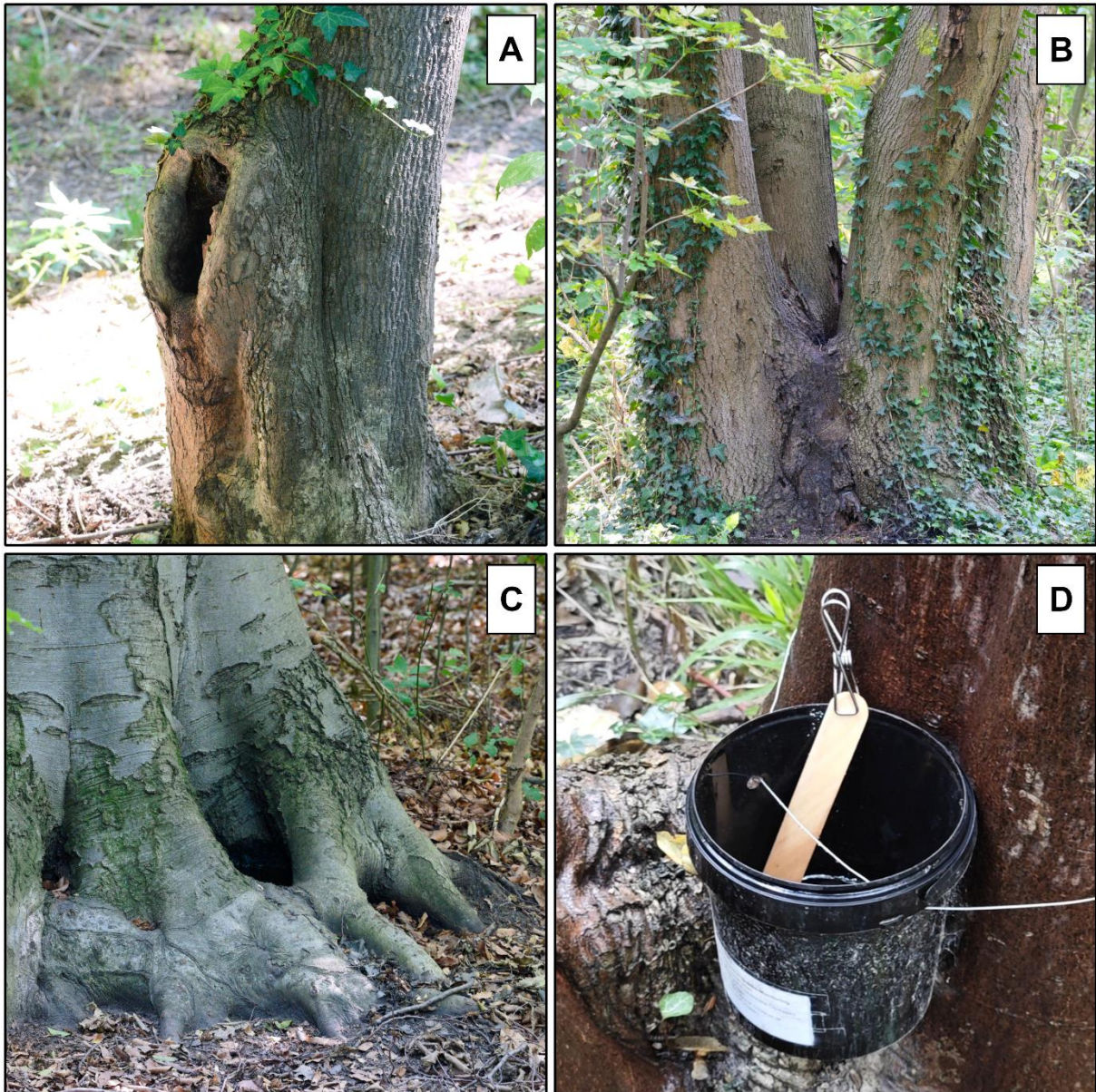


Figure 2: Categorisation of microhabitat types into dendrotelmata (A–C) and plastic buckets (D). The dendrotelmata were further subdivided into branch hollows (A), coppice stools (B) and trunk pools (C). The ovitraps (D) were equipped with wooden spatulas to monitor mosquito oviposition.

On the sampling days, the microhabitats were visited and initially examined in-situ for oxygen content, conductivity and pH using a digital multi-parameter device (WTW Multi 3630 IDS, Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany). The water was then pumped out using a hand pump (Beijing Jinxinxing Medical Device Factory, Beijing, China) and the volume was measured in a measuring flask. Approximately 5 ml of the raw sample was transferred into a sterile plastic tube for subsequent eDNA metabarcoding. The remaining sample was then filtered through a 500 μm hand net to separate insects and other macroorganisms. This was followed by filtration through a 33 μm plankton net to collect zoo- and phytoplankton. This plankton fraction was transferred into a flask, while the filtrated water ($< 33 \mu\text{m}$) was bottled separately for further analysis in the laboratory. The substrate

remaining in the microhabitats was collected with a spoon and stored, along with the > 500 µm filtered macroorganisms, in a container in 96% EtOH. In addition, the canopy cover was recorded using a fisheye camera (Coolpix 4500, Nikon Corporation, Tokyo, Japan) with a FC-E8 0.21x converter lens, later analysed using the Gap Light Analyzer (GLA) software (version 2.0, Simon Fraser University & Cary Institute of Ecosystem Studies; Frazer et al., 1999). Also temperature loggers (HOBO Pendant, Onset Computer Corporation, Bourne, USA) and wildlife cameras (Zecre PH770-5S, Shenzhen Zecre Technology Co. Ltd., Shenzhen, China) were deployed sporadically at selected sites within the national park area to document temperature fluctuations and interactions with vertebrates. The sample tubes and mouth spatulas collected from the ovitraps were kept cool using ice packs and transported to the laboratory in the Biology Building at the University of Vienna. The water samples, as well as the plankton fractions, were stored in the fridge at 4 °C, the mosquito eggs were frozen at -10 °C, whilst the ethanol-preserved macrofauna was kept at room temperature, protected from light.

3.4 Laboratory work

3.4.1 Limnochemistry

Water samples were filtered through 0.45 µm cellulose nitrate filters (47mm, Sartorius GmbH, Göttingen, Germany) to remove large particles. The DOC concentration was then measured based on high-temperature oxidation at 720 °C using a TOC analyzer (TNM-L ROHS, Shimadzu Corporation, Kyoto, Japan) equipped with an autosampler (ASI-L, Shimadzu Corporation, Kyoto, Japan) and a non-dispersive infrared (NDIR) detector. Inorganic carbon was removed via internal HCl injection. A reference standard of 20 mgL⁻¹ was prepared for automatic multi-point calibration and fresh Milli-Q water was used for blank controls. The sample filtrate required dilution with Milli-Q in a ratio of 1:10 (1+9) prior to measurement. Total nitrogen (TN) was also measured using the TOC-L analyser (reference standard 7.5 mgL⁻¹), with diluting the sample 1:4. Dissolved inorganic carbon (DIC) was determined using an acid-based hardness titration kit (MQuant Carbonate Hardness Test, Merck KGaA, Darmstadt, Germany). Major anions (chloride, sulfate, nitrate, nitrite, and phosphate) were quantified by ion chromatography (Dionex Inuvion IC System, Thermo Fisher Scientific Inc., Waltham, USA) using an IonPac AS14A analytical column (4 × 250 mm) and a corresponding AG14A guard column (4 × 50 mm) from the same manufacturer, following the DIN EN ISO 10304-1 specifications (Deutsches Institut für Normung e.V., 2009). The cations (sodium, potassium, calcium, magnesium, and ammonium) were analyzed with an IonPac CS12A analytical column (4 × 250 mm) and a CG12A guard column (4 × 50 mm), in accordance with ÖNORM DIN EN ISO 14911 (Austrian Standards International, 1999).

3.4.2 Identification of evertebrates

The morphological identification of the fauna relied on appropriate literature, support from specialised taxonomists and suitable optical equipment (SMZ1500 with HR Plan Apo 1x, Nikon Corporation, Tokyo, Japan). The total abundance was determined by counting all individuals, without applying any subsampling approach. Water beetles of the family Scirtidae were determined according to Klausnitzer (2009). For the mosquito larvae (Culicidae), Becker et al. (2020) was used. Additionally, the identification guide by Farajollahi & Price (2013) was consulted to distinguish between the non-native *Aedes* species. For biting midges (Ceratopogonidae), information from Mauch (2017) as well as Mauch & Mauch (2022) was checked. The non-biting midges (Chironomidae) were first identified to the genus level with Andersen et al. (2013) and further to species level using Orendt & Bendt (2020). Moth flies (Psychodidae) were addressed according to Jaume-Schinkel et al. (2022) and identified following Vaillant (1971, 1989). The soldier flies (Stratiomyidae) were determined following Rozkošný (2000) and Krivosheina & Mamaev (1967). Hoverflies (Syrphidae) were identified according to G. Rotheray (1993) as well as G. Rotheray & Gilbert (1999). And the muscid flies (Muscidae) were examined using Krivosheina (2019).

The mosquito eggs collected from the ovitraps were morphologically pre-sorted for *Aedes* occurrence and then identified using multiplex PCR according to Reichl et al. (2024). The analysis was conducted at the University of Veterinary Medicine, Vienna, using the innuPREP DNA Mini Kit 2.0 (Analytik Jena, Jena, Germany) for DNA extraction in compliance with the manufacturer's protocol. A PCR reaction contained then 9.675 µL of nuclease-free water, 5.0 µL of GoTaq Green Buffer (Promega Corporation, Madison, USA), 0.2 µL dNTP mix containing dUTP (25 mM), 0.8 µL each of the primers AediniUni-F (universal forward primer), ALB-R, JAP-R, KOR-R and GEN-R (specific reverse primers; see Bang et al., 2021 and Reichl et al., 2024), 0.125 µL (1 U) GoTaq DNA polymerase (Promega Corporation) and 1 µL template DNA. The thermal profile was as described by Reichl et al. (2024): 94 °C for 5 minutes, followed by 94 °C for 30 seconds, 56 °C for 30 seconds, and 72 °C for 30 seconds over 35 cycles, with a final extension at 72 °C for 5 minutes. Expected amplicons: *Ae. albopictus* 398 bp, *Ae. koreicus* 321 bp, *Ae. geniculatus* 272 bp and *Ae. japonicus* 120 bp. The products were separated on 2% agarose in 0.5x TBE at 100 V (90–120 min) and visualised using a Gel Doc 2000 (Bio-Rad, Hercules, USA), size reference was provided by the GeneRuler 100 bp DNA Ladder (Thermo Fisher Scientific Inc.).

3.4.3 eDNA metabarcoding

For the eDNA analysis, around 5 ml of raw sample was vacuum-filtered through 1.2 µm glass fiber filters (24 mm, grade 693, VWR International, Leuven, Belgium). The filters were wrapped in aluminium foil and stored at -80 °C in an ultra-freezer until further processing.

The subsequent extraction and sequencing were conducted by the Centre for Microbiology and Environmental Systems Science (CeMESS) at the University of Vienna. A DNeasy PowerSoil Pro Kit (QIAGEN, Hilden, Germany) was used for extraction according to the manufacturer's instructions, modified by 40 seconds of mechanical bead beating (6.0 m/s) for cell lysis in 800 µl CD1 buffer and an enzymatic proteinase K incubation (25 µl, 20 mg/ml, QIAGEN: Cat. No. 19131) for 4 hours on a thermoshaker (56 °C , 550 rpm). In line with the kit protocol, the lysate was clarified with CD2 buffer, adjusted to the binding conditions of the silica filter membrane using CD3 solution, and then the DNA was washed (EA, C5) using MB spin columns. The elution step to purify the DNA was subsequently performed using just 50 µl of solution C6.

The amplicon sequencing was based on a two-step barcoding approach as described by Pjevac et al. (2021). In the first-step PCR the V9 region of the 18S rRNA gene (target gene) was amplified using the established eukaryotic primers TAREuk454FWD1 (forward primer) and TAREukREV3mod (reverse primer) (Obertegger et al., 2019). These products were subsequently purified, normalised and served then as templates for the second-step, barcoding PCR. In this step, 12 bp barcode sequences for the sample assignment were added to each template. The resulting barcoded amplicons were purified again, quantified using a Qubit fluorometer (Thermo Fisher Scientific Inc.), pooled in equal quantities and checked for fragment lengths. These amplicon pools were then processed for library preparation using the TrueSeq Nano Kit (Illumina Inc., San Diego, USA), omitting the fragmentation step, before being sequenced on an Illumina MiSeq system (2x 300 cycles) from the same manufacturer in paired-end mode (Pjevac et al., 2021).

This was followed by raw data processing and amplicon sequence variant (ASV) inference. The raw data were separated into individual samples (demultiplexed), barcodes as well as primers were trimmed and the sequences were processed using a DADA2-based pipeline (JMF-flavor; see Callahan et al., 2016). The processing steps included quality filtering, separate denoising of both read ends, merging of read pairs and removal of chimeric sequences (artefacts). A sample filter of ≥ 1000 reads per sample was applied, reducing the dataset to 60 samples (651518 reads). The taxonomic assignment of the 18S ASVs was then finally performed against the eukaryotic reference database SILVA SSU Ref (release 138.2; Quast et al., 2012).

3.5 Statistics

Statistical analyses were performed in R (version 4.5.0, R Core Team, 2025) within RStudio (version 2026.01.1, Build 403, Posit Software, Boston, USA), using the R Markdown format (version 2.30, see Xie et al., 2019) for documentation. Data preparation and visualisation were carried out using packages from the *tidyverse* extension (Wickham et al., 2019), in particular *ggplot2* (Wickham, 2016). The *vegan* package (Oksanen et al., 2026) was utilised to conduct multivariate analyses, together with *MASS* (Venables & Ripley, 2002) and *mvabund* (Wang et al., 2012).

Based on respective literature (Kitching, 1971; Walker et al., 1991), the dendrotelmata samples were additionally grouped into different types for further statistical analysis. I have subdivided them into three types (Figure 2A–C): branch hollows, trunk pools and so-called coppice stools (Coxhead & Slater, 2022). The former two correspond to the categories defined by Kitching (1971), whilst the latter type (which Kitching also included in the “rot holes”) is defined separately according to an old forest management practice historically employed in the study area (Buckley, 2020).

3.5.1 Abiotic characteristics

Within the framework of descriptive statistics, the frequencies, measures of location and variability were determined. The interquartile range (IQR) of spring values was used to derive a ratio that illustrates seasonal trends in the variability of limnochemical parameters. Relations between the parameters were assessed using a Spearman correlation matrix. To investigate differences in the variance of water chemistry, a principal component analysis (PCA) based on z-standardised parameters was conducted (Legendre & Legendre, 1998). Redundancy was avoided by selecting the parameters based on their correlations, followed by a skewness correction through logarithmic transformation. The normal distribution was checked using the Shapiro-Wilk test. The PCA results were then visualised using biplots with a scaling factor of two and 95% confidence ellipses (type = “norm”).

For inferential statistics, the significance level was set at $\alpha = 0.05$. The *p* values were adjusted using the Benjamini-Hochberg (BH) method to control the false discovery rate (FDR) at 5% in order to mitigate the risk arising from multiple testing (Benjamini & Hochberg, 1995). Abiotic differences between groups were tested using euclidean distances via a permutational multivariate analysis of variance (PERMANOVA, 999 permutations), whereby effects were tested sequentially according to model order (Borcard et al., 2018).

The same input parameters as used in the PCA were applied in a combined PERMANOVA (dendrotelmata and ovitraps; blocked permutations), which included the factors microhabitat type (dendrotelmata vs. ovitraps), season and location. Interaction effects were further explored using two separate models, testing microhabitat type $\times$ season and season $\times$ location. The homogeneity of the dispersion, a fundamental requirement of PERMANOVA analyses (Borcard et al., 2018), was tested using the *betadisper* function (vegan) with 999 permutations.

3.5.2 Fauna analyses

Analyses of the fauna were based solely on taxa classified as aquatic, excluding terrestrial occurrences. The total abundance and species richness were complemented by the Shannon index to assess the species diversity across samples (Daly et al., 2018; Morris et al., 2014). Differences between microhabitat types, seasons, locations and dendrotelmata types were analysed using non-parametric tests (Legendre & Legendre, 1998). The Wilcoxon test was conducted for pairwise comparisons (e.g. rural vs. urban), whilst the Kruskal–Wallis test for comparisons between multiple groups (e.g. branch hollow vs. trunk pool vs. coppice stool). Where the Kruskal-Wallis tests yielded significant results, pairwise post-hoc tests were performed using the Dunn approach (Dunn, 1964).

Non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities (Borcard et al., 2018) was performed to illustrate the differences in community composition (Dexter et al., 2018). The confidence ellipses were plotted based on a t-distribution (type = "t"). The differences were tested using sequential PERMANOVA analyses based on Bray-Curtis distances calculated from total abundances. A combined PERMANOVA analysis (dendrotelmata and ovitraps; blocked permutations) was conducted including the factors microhabitat type (dendrotelmata vs. ovitraps), season and location. Interaction effects were further explored by testing microhabitat type $\times$ season and season $\times$ location. A stratified PERMANOVA model (dendrotelmata only) was calculated based on the dendrotelmata types. In addition, taxa were also compared for group effects without using distance measures, employing multivariate generalised linear models (mGLM). For this purpose, the *manyglm* function (mvabund) was used, which enables the simultaneous modelling of multiple species and combines individual GLMs into a multivariate test (Wang et al., 2012). A negative binomial model (microhabitat type + season + location) based on total abundances was created. Significance was determined using 999 pit-trap resamples (Warton et al., 2017). For taxa showing significant effects, the direction of the response was determined from the estimated model coefficients and the observed abundances. Furthermore, an indicator species analysis was carried out to identify characteristic taxa among the various dendrotelmata types, between the locations and in comparison of microhabitats, using the *multipatt* function (999

permutations) according to Cáceres & Legendre (2009). Only taxa with ≥ 10 individuals were included, whilst empty samples were removed. The analysis is based on an abundance matrix, with the indicator values derived from the components of specificity and fidelity. A taxon is considered strongly indicative if it occurs exclusively within a group and is represented in a large number of its sample units (maximum indicator value = 100%).

The relationship between the species community and the environment was investigated using canonical correspondence analysis (CCA) based on chi-square metrics of total abundances. The suitability of a unimodal method was tested within the framework of a detrended correspondence analysis (DCA; *decorana* function in *vegan*). Environmental variables were selected a priori based on ecological interpretability and evidence from the literature (Gossner et al., 2026; Schmidl et al., 2008). In order to ensure comparable scaling, the environmental parameters were z-standardised. To reduce multicollinearity among correlated parameters, a stepwise selection was performed based on variance inflation factors (VIF, threshold: ≤ 10). The significance of the global model, individual predictors and the canonical axes was assessed using permutation tests (999 permutations). Triplots with double scaling were used for graphical representation, overlapping labels were adjusted using the *ggrepel* package.

3.5.3 eDNA metabarcoding

The eDNA dataset was analysed by initially filtering out ASVs with a threshold of fewer than 20 reads per sample in order to reduce potential noise (Vecchi, 2025; Watts et al., 2026). The taxa were harmonised at genus level to account for differences in the taxonomic resolution between eDNA and morphological identification. Derivation based on the number of reads was avoided in order to prevent method-specific biases in the abundance estimation (Bylemans et al., 2019). Instead, a presence/absence matrix was generated to compare the two identification methods simply based on the occurrence frequency of aquatic taxa.

4. Results

4.1 Sample overview

A total of 31 dendrotelmata and 31 ovitrap samples were obtained, whereby five samples originated from the added Schlossinsel ovitraps and therefore were excluded from abiotic analyses (Table A5–A7). The reduced sample size was mainly due to dessication, particularly during the autumn sampling, which affected four ovitraps, one in Orth and three in the Prater. An additional dendrotelmata sample was collected in the urban area, also in October. Among the sampled dendrotelmata were 7 branch hollows, 8 trunk pools and 16 coppice stools (Figure 2A–C). Branch hollows were sampled exclusively within the urban setting. Trunk pools (Orth:

n = 6; Prater: n = 2) and coppice stools (Orth: n = 9; Prater: n = 7) were recorded at both locations, with higher numbers in Orth.

The composition of plant hosts also differed between the two sampling locations. In Orth, *Carpinus betulus* Linnaeus, 1758 was the dominant species, accounting for around half (n = 8) of all sampled dendrotelmata. Other taxa included *Tilia* sp. (n = 3), *Fraxinus excelsior* Linnaeus, 1758 (n = 2) and *Populus alba* Linnaeus, 1758 (n = 2). In contrast, dendrotelmata in the Prater were predominantly related to *Acer* sp., which comprised for over two-thirds (n = 11) of the samples. The remaining samples were distributed among *C. betulus* (n = 2), *F. excelsior* (n = 2) and *Aesculus hippocastanum* Linnaeus, 1758 (n = 1).

4.2 Abiotic characteristics

4.2.1 Descriptive overview

Overall, the limnochemical conditions of dendrotelmata were characterised by low oxygen availability and high nutrient concentrations (Table A8–A11). Dissolved oxygen was limited across both sites (Orth: median 0.35 mgL⁻¹ [IQR: 0.25–0.54]; Prater: median 0.44 mgL⁻¹ [IQR: 0.11–0.74]), whereas nutrients such as dissolved organic carbon (Orth: 100.87 mgL⁻¹ [61.96–144.67]; Prater: 109.99 mgL⁻¹ [58.53–187.30]), total nitrogen (Orth: 8.40 mgL⁻¹ [5.39–11.76]; Prater: 14.15 mgL⁻¹ [9.22–18.78]) and orthophosphate (Orth: 9.30 mgL⁻¹ [3.75–15.25]; Prater: 11.00 mgL⁻¹ [4.70–20.90]) were elevated. Measured pH values ranged from 5.7 to 7.8 and, similar to nutrient concentrations, were slightly higher in the Prater (7.3 [6.9–7.3]) than in Orth (6.9 [6.6–7.1]). Conductivity was also higher in the urban location, with a median of 917 µS/cm [447–1123], whereas the value in Orth was 487 µS/cm [314–628].

A comparison of the three dendrotelmata types reveals striking differences. Branch hollows were even lower in oxygen and had the highest nutrient concentrations. The median dissolved oxygen was only 0.03 mgL⁻¹ [0.02–0.41], dissolved organic carbon 480.40 mgL⁻¹ [160.29–1378.67], total nitrogen at 11.22 mgL⁻¹ [6.68–39.59] and orthophosphate at 32.00 mgL⁻¹ [14.80–41.30]. The pH value was clearly alkaline at 8.5 [7.75–8.65] and the conductivity was 4760 µS/cm [1357–6100]. However, with 110 ml [82–168], their volume was also lower than that of trunk pools (213 ml [110–1122]) or coppice stools (341 ml [164–1028]). Water temperatures measured in-situ also varied noticeably between the different types. The large coppice stools (15.2 °C [13.1–17.9]) showed higher temperatures than branch hollows (14.3 °C [13.8–16.5]) or trunk pools (13.8 °C [12.6–15.9]).

Regarding the seasons, the dendrotelmata differed particularly in terms of temperature. The water temperatures peaked in summer (18.3 °C [17.9–19.0]), with intermediate values in spring

(14.6 °C [13.6–15.3]) and lower values in autumn (12.4 °C [10.9–13.5]). During all seasons, higher temperatures were measured in the Vienna Prater (Prater: spring 15.2 °C, summer 18.2 °C, autumn 12.8 °C; Orth: spring 13.5 °C, summer 18.0 °C, autumn 10.8 °C). But the seasonal influence was also evident in other parameters, whose interquartile ranges (IQR) increased markedly from spring to autumn. Examples include conductivity (IQR ratio = 7.6), dissolved inorganic carbon (IQR ratio = 6.7) and nitrite (IQR ratio = 6.7), which clearly demonstrated greater variability in autumn.

4.2.2 Characteristics of ovitraps

The ovitraps (Figure 2D), installed at the beginning of the year, differed substantially from the dendrotelmata (Table A12–A16). Across all samples ($n = 26$), dissolved oxygen was around ten times higher, with a median of 3.56 mgL⁻¹ [IQR: 1.75–5.50]. The nutrient concentrations of dissolved organic carbon (37.79 mgL⁻¹ [16.48–53.57]), total nitrogen (5.59 mgL⁻¹ [3.59–6.97]) and orthophosphate (1.40 mgL⁻¹ [0.25–4.58]) were clearly lower. The pH value was almost neutral (7.1 [6.9–7.5]) and the conductivity was only 181 µS/cm [84–351].

But a seasonal comparison reveals, that the ovitraps increasingly converged with the limnochemical conditions of dendrotelmata. A striking example is the median conductivity, which was still 64 µS/cm [40–86] in spring, had risen to 236 µS/cm [191–356] by summer and reached 431 µS/cm [320–499] in autumn, while the opposite trend can be seen for oxygen (spring: 6.33 mgL⁻¹ [5.02–7.03]; autumn: 1.08 mgL⁻¹ [0.10–2.87]). The initially homogeneous conditions in spring were thus increasingly characterised by high variability in autumn. Striking examples include orthophosphate (IQR ratio = 16.7), dissolved organic carbon (IQR ratio = 12.8) and total nitrogen (IQR ratio = 8.5). Yet despite the increased nutrient concentrations and heterogeneous variability in autumn, the values of ovitraps still differed substantially from those of the dendrotelmata.

Differences between the microhabitats also become apparent in terms of temperature conditions. Looking at two temperature loggers, which provided a complete record for September, the temperature fluctuations of an ovitrap (OT_003_Orth) and a coppice stool (DT_012_Orth) can be seen (Figure 3). Both were located in the same area, just a few metres apart, yet the median daily range (min–max) differed greatly. Whilst the dendrotelmata fluctuated by only about 1.95 °C [1.41–2.61], the fluctuations in the black plastic bucket were almost twice as high at 3.94 °C [2.86–5.56], which was closer to air temperature (8.65 °C [6.02–12.00]).

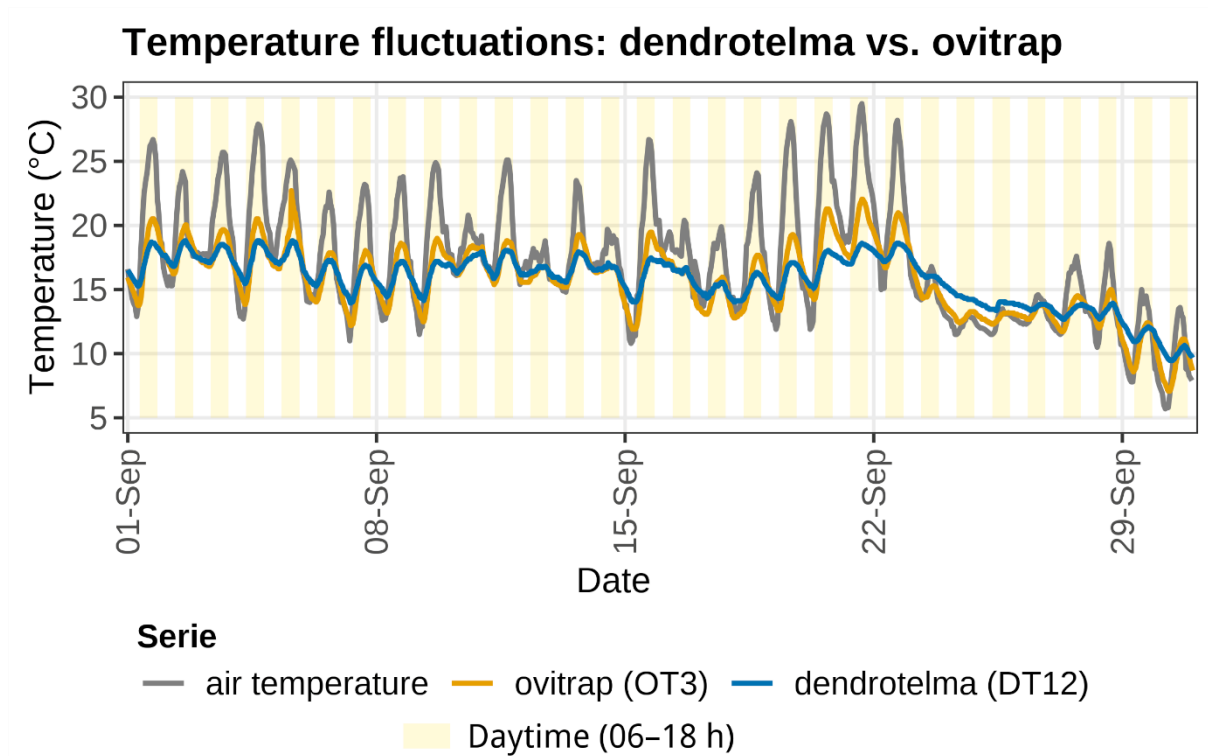


Figure 3: Temperature fluctuations recorded in a dendrotelma and an ovitrap using temperature loggers at 30-minute intervals during September in Orth an der Donau. The air temperature measured in Groß-Enzersdorf (GeoSphere Austria, 2024) was used for further comparison. Air temperature showed the greatest fluctuations, followed by the ovitrap, with the dendrotelma exhibiting the smallest temperature changes.

4.2.3 Correlations

The Spearman correlation revealed a strong relationship between conductivity and several solutes, including orthophosphate ($\rho = 0.816$, $p \text{ adj} < 0.001$), dissolved organic carbon ($\rho = 0.812$, $p \text{ adj} < 0.001$) and particularly dissolved inorganic carbon ($\rho = 0.971$, $p \text{ adj} < 0.001$). Strong positive correlations were also found for most ions ($\rho = 0.827\text{--}0.947$, all $p \text{ adj} < 0.001$). The exception to this pattern were nitrogen compounds. Ammonium ($\rho = 0.354$, $p \text{ adj} < 0.001$) and nitrite ($\rho = 0.439$, $p \text{ adj} < 0.001$) showed only moderate positive correlations, whilst nitrate correlated slightly negatively with conductivity ($\rho = -0.313$, $p \text{ adj} = 0.002$). Only total nitrogen had a stronger positive relationship ($\rho = 0.646$, $p \text{ adj} < 0.001$). In contrast to the other major ions, sulphate showed no apparent correlation with conductivity. Meanwhile, dissolved oxygen reversed the trend and correlated strongly negative with conductivity (mgL^{-1} : $\rho = -0.741$, $p \text{ adj} = < 0.001$).

The canopy cover of tree crowns showed only weak correlations to water chemistry ($\rho = 0.216\text{--}0.256$, all $p \text{ adj} = < 0.05$), with higher shading being associated with slightly increased dissolved organic carbon and orthophosphate concentrations as well as lower oxygen levels (Figure A1).

4.2.4 PCA

Based on the z-standardised parameters conductivity, pH, temperature, oxygen and total nitrogen (pH untransformed, the others log-transformed), the principal component analysis resolved two distinct axes explaining 79.1% of the variance (PC1 = 56.5%, PC2 = 22.6%). PC1 had strongly negative loadings for conductivity (loading -1.745), pH (-1.437) and total nitrogen (-1.405), whereas oxygen (+1.493) loaded highly positive and temperature contributed only weakly (+0.374). In relative terms, PC1 was driven by conductivity ($\approx 32.2\%$), oxygen ($\approx 23.6\%$), pH ($\approx 21.8\%$) and total nitrogen ($\approx 20.9\%$), with temperature contributing only $\approx 1.5\%$. The PC2 axis was dominated by temperature (-1.709; $\approx 77.3\%$), followed by pH (-0.811; $\approx 17.4\%$), while oxygen (-0.361; $\approx 3.4\%$), conductivity (-0.171; $\approx 0.8\%$) and total nitrogen (+0.203; $\approx 1.1\%$) contributed only marginally. Accordingly, PC1 represents a nutrient gradient opposed to oxygen availability, while PC2 primarily captures the temperature impact.

The biplots (Figure 4A–B) show differences between microhabitat types, seasons and locations. Dendrotelmata are mainly on the negative side of PC1 (nutrient-rich, oxygen-poor) whilst ovitraps occur predominantly on the positive side (nutrient-poor, oxygen-rich). Visually, dendrotelmata are more widely scattered, whilst ovitraps tend to cluster more closely together (Figure 4A). A gradient within the dendrotelmata types is evident: branch hollows have lower PC1 scores and trunk pools higher ones, whilst coppice stools lie in between and show a slight division according to the location (rural/urban). Overall, no clear visual separation of locations is apparent. The distribution along the PC2 axis reflects seasonal temperature differences (Figure 4B). Summer samples have lower PC2 scores (warmer), autumn samples have higher scores and spring samples lie in between. Ovitrap samples show pronounced seasonal shifts along PC1 (higher PC1 scores in spring; lower PC1 scores in summer/autumn), whilst dendrotelmata exhibited more moderate seasonal dynamics.

PCA biplot: limnochemistry

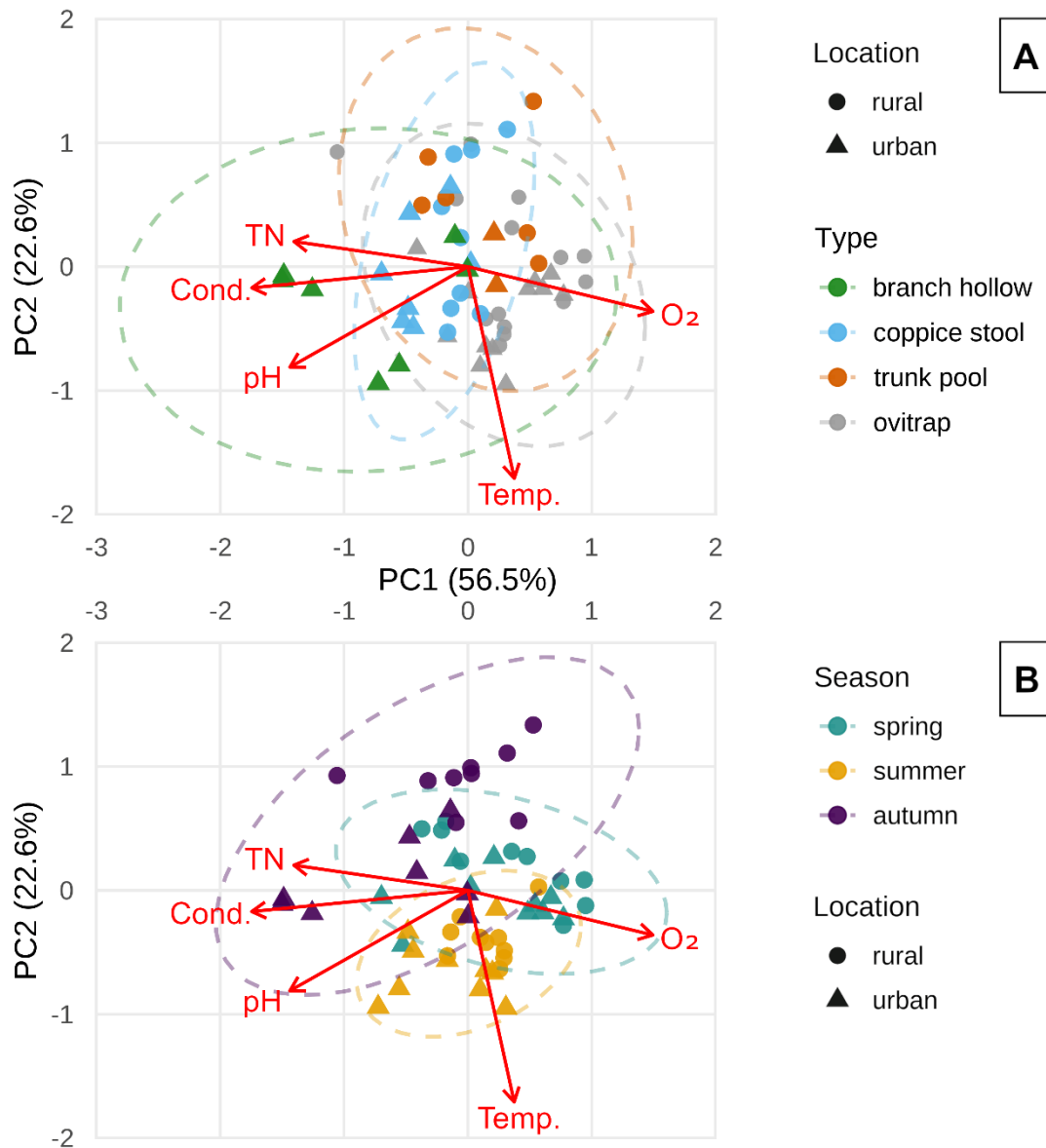


Figure 4: Principal component analysis (PCA) of limnochemical variables (abbreviations: TN = total nitrogen, Cond = conductivity, Temp = temperature, O₂ = dissolved oxygen). Biplots of PC1 vs. PC2 show sample scores and variable loadings (scaling 2). Samples are displayed as points (rural) and triangles (urban), while vectors indicate the direction and strength of variable contributions. Ellipses represent the 95% confidence regions within groups, assuming multivariate normal distributions. Plot A illustrates microhabitat types (dendrotelmata, ovitraps) and dendrotelmata types, whereas plot B refers to the seasons. Along PC1, a separation of microhabitat types is evident: dendrotelmata exhibit negative PC1 scores (nutrient-rich, oxygen-poor), whilst ovitraps show positive values. Within dendrotelmata, branch hollows plot lower on PC1, trunk pools higher, coppice stools intermediate. In terms of seasonality, summer samples tend to lower scores (warmer), while spring/autumn samples have higher ones. The two axes (PC1, PC2) together explain 79.1% of the total variance (PC1: 56.5%; PC2: 22.6%).

4.2.5 PERMANOVA

The abiotic PERMANOVA analyses using the same z-standardised parameters confirmed distinct group differences. The microhabitat type (dendrotelmata vs. ovitraps) explained a significant proportion of the variation ($F = 17.03$, $R^2 = 0.166$, $p = 0.005$), followed by a seasonal effect that was also significant ($F = 12.00$, $R^2 = 0.235$, $p = 0.005$) and a smaller but significant location effect ($F = 9.29$, $R^2 = 0.091$, $p = 0.005$). The interaction model for microhabitat type and season additionally revealed significant microhabitat-specific seasonal dynamics ($F = 3.02$, $R^2 = 0.055$, $p = 0.045$). In the interaction model for season and location, no significant location differences were detected.

The dispersion check revealed significant differences in multivariate dispersion among seasons ($p = 0.017$), meaning that the prerequisite for PERMANOVA is not fulfilled and a cautious interpretation is required. No significant differences in dispersion were detected among microhabitat types ($p = 0.208$) or locations ($p = 0.369$).

4.3 Fauna analyses

Unless stated otherwise, fauna analyses included all 31 ovitrap samples, taking into account the five additional samples collected during summer on the Schlossinsel at the National Park Centre in Orth. For inferential comparisons (microhabitat, location, season), they were excluded to ensure comparability with the dendrotelmata setup.

4.3.1 Community composition of aquatic insects

All dendrotelmata ($n = 31$) and the majority of ovitrap samples ($n = 23$ of 31) contained a combined total of 6068 aquatic individuals, of which 4467 could be identified at least to genus level (Table A17–A21). The rest were mainly very small larvae or pupae. There were also carcasses of about 650 terrestrial animals (Figure A2), which will not be addressed further here (Table A22–A25). The recorded aquatic community consisted of larvae from 15 insect taxa belonging to two orders, Coleoptera and Diptera (Table 1). The marsh beetles (Coleoptera: Scirtidae) comprised two species, *Prionocyphon serricornis* (Müller, 1821) and *Sacodes flavicollis* (Kiesenwetter, 1859). However, the majority of the diversity ($\approx 87\%$) was represented by dipteran families. Mosquitoes (Culicidae) comprised five species: *Aedes geniculatus*, *Anopheles plumbeus* and *Culex pipiens* s.l. / *Cx. torrentium*, as well as the non-native species *Aedes japonicus* and *Aedes albopictus*. The biting midges (Ceratopogonidae) belonged to the genus *Dasyhelea* sp. Kieffer, 1911. A single species was found for both the non-biting midges (Chironomidae), including *Metriocnemus cavicola* Kieffer, 1921, and the moth flies (Psychodidae), with *Clogmia cf. albipunctata* (Williston, 1893). The soldier flies

(Stratiomyidae) were represented by three taxa: *Beris* sp. Latreille, 1802, *Pachygaster* sp. Meigen, 1803 as well as *Odontomyia annulata* (Meigen, 1822). And furthermore, *Myathropa florea* (Linnaeus, 1758), a hoverfly (Syrphidae), and *Phaonia exoleta* (Meigen, 1826), a muscid fly (Muscidae), were recorded.

Table 1: Total abundance of each recorded taxon by rural and urban location.

Order	Taxon	rural (Orth)	urban (Prater)
Coleoptera	<i>Prionocyphon serricornis</i>	711	239
Coleoptera	<i>Sacodes flavicollis</i>	0	9
Diptera	<i>Aedes albopictus</i>	0	8
Diptera	<i>Aedes geniculatus</i>	489	107
Diptera	<i>Aedes japonicus</i>	53	10
Diptera	<i>Anopheles plumbeus</i>	60	98
Diptera	<i>Beris</i> sp.	1	0
Diptera	<i>Clogmia cf. albipunctata</i>	36	185
Diptera	<i>Culex pipiens</i> s.l.	47	96
Diptera	<i>Dasyhelea</i> sp.	302	494
Diptera	<i>Metriocnemus cavicola</i>	677	417
Diptera	<i>Myathropa florea</i>	48	279
Diptera	<i>Odontomyia annulata</i>	0	73
Diptera	<i>Pachygaster</i> sp.	0	9
Diptera	<i>Phaonia exoleta</i>	11	8

4.3.2 nMDS

The non-metric multidimensional scaling, based on untransformed Bray-Curtis distances, resulted in a two-dimensional visualisation of the samples with a stress value of 0.202. The nMDS plots show substantial overlaps between the groups (Figure 5A–B). Yet, a noticeable difference between dendrotelmata and ovitraps samples is evident (Figure 5A). Dendrotelmata are further subdivided into rural and urban samples, whereas ovitraps show no such location substructure. The seasons display no noticeable subdivisions, but a slightly greater variation is observed in the summer and autumn samples (Figure 5B).

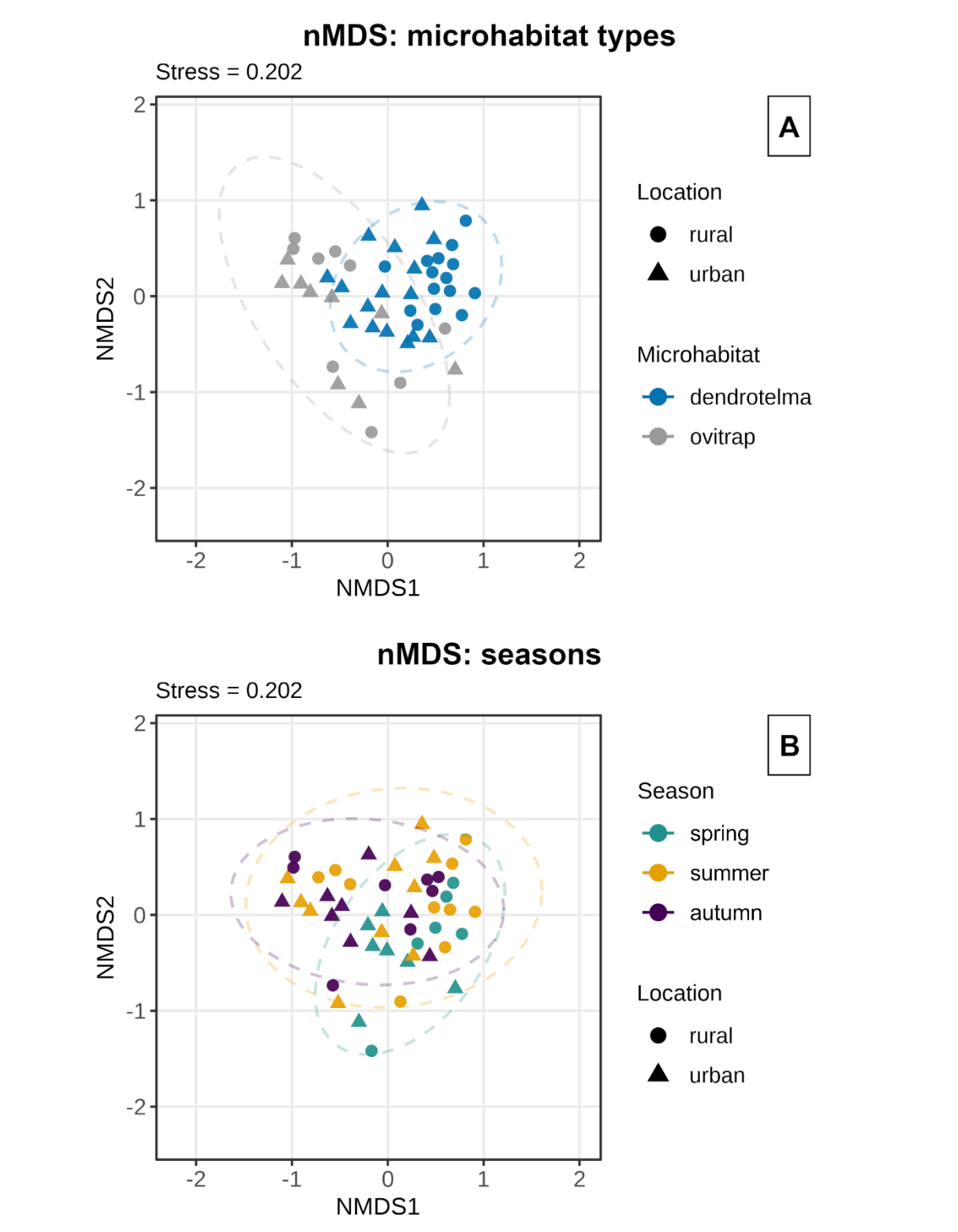


Figure 5: Non-metric multidimensional scaling (nMDS) of the community composition in dendrotelmata and ovitraps based on Bray-Curtis dissimilarities. Samples are displayed as points (rural) and triangles (urban). Ellipses represent the 95% confidence regions within groups, assuming t-distributions. Plot A illustrates the distribution according to microhabitat types (stress = 0.202), whereas plot B refers to the seasons (stress = 0.202). In both cases there are substantial overlaps between the groups, but while the microhabitat types show a clear division into dendrotelmata and ovitraps, the seasons display no distinct separation. Dendrotelmata also show a sub-division into rural and urban samples.

4.3.3 PERMANOVA

The faunal PERMANOVA analyses based on total abundances confirmed a significant difference between dendrotelmata and ovitraps ($F = 7.82$, $R^2 = 0.135$, $p = 0.001$), as well as seasonal effects ($F = 2.02$, $R^2 = 0.070$, $p = 0.007$) and a smaller location effect ($F = 2.13$, $R^2 = 0.037$, $p = 0.021$). The interaction model for microhabitat type and season indicated significant seasonal differences ($F = 2.28$, $R^2 = 0.074$, $p = 0.004$), but the interaction between season and location showed no significant result. The stratified model with regard to dendrotelmata types revealed a significant difference between them ($F = 2.54$, $R^2 = 0.143$, $p = 0.003$). The location effect remained significant ($F = 2.17$, $R^2 = 0.061$, $p = 0.040$), but the seasonal effect could not be maintained as significant in this model ($F = 1.65$, $R^2 = 0.092$, $p = 0.059$).

Dispersion homogeneity was ensured. The microhabitat types ($p = 0.399$), seasons ($p = 0.111$), locations ($p = 0.789$) and dendrotelmata types ($p = 1.000$) showed no significant differences with regard to their dispersion.

4.3.4 mGLM

The multivariate GLM analysis revealed significant community differences for microhabitat type (Dev = 105.61, $p = 0.001$), the seasons (Dev = 80.68, $p = 0.001$) and between locations (Dev = 56.64, $p = 0.001$). No significant result was found for the interaction between microhabitat type and season. The taxon-specific analysis revealed several significant differences in abundance with regard to microhabitat types. The marsh beetle *Prionocyphon serricornis* (Dev = 47.560, p adj = 0.001) and the mosquito *Aedes geniculatus* (Dev = 11.94, p adj = 0.018–0.025) were assigned to dendrotelmata, whereas *Dasyhelea* sp. (Dev = 13.81, p adj = 0.008–0.012) exhibited significantly higher abundances in ovitraps. With regard to seasons, significantly higher abundances were observed in summer/autumn for *Clogmia cf. albipunctata* (Dev = 13.59, $p = 0.026$ –0.036) and *Anopheles plumbeus* (Dev = 13.06, $p = 0.030$ –0.040), whilst other taxa showed no significant effect. With regard to the locations, a significant effect was observed for *Prionocyphon serricornis* (Dev = 9.68, p adj = 0.038–0.046) and *Aedes geniculatus* (Dev = 10.03, p adj = 0.035–0.042) with both occurring more frequently in the rural area. By contrast, the abundance of *Myathropa florea* (Dev = 9.39, p adj = 0.040–0.046) was significantly higher in the Prater.

4.3.5 Indicator species analysis

The indicator species analysis with regard to microhabitat type retained a significant preference for dendrotelmata in case of *Prionocyphon serricornis* (IndVal = 0.95, p adj = 0.001). For *Aedes geniculatus*, the result (IndVal = 0.80) lost its significance following the BH

correction (p adj = 0.073), although only 20 of the overall 579 individuals (dendrotelma: 12 [4–29], n = 22; ovitrap: 2 [1–6], n = 4, both rounded) were found in ovitraps. For *Dasyhelea* sp., there was a significant preference for ovitraps (IndVal = 0.87, p adj = 0.003), with 115 specimens found in dendrotelmata and 678 in ovitraps. Focusing on location, the BH-corrected analysis revealed only a single significant result, thereby assigning *Dasyhelea* sp. (IndVal = 0.83, p adj = 0.020) to an urban distribution in the Prater. In contrast, *Aedes geniculatus* was initially classified as rural (IndVal = 0.81), but was no longer significant after the adjustment (p adj = 0.100). The same fate befell *Clogmia* cf. *albipunctata*, which showed a trend towards urban distribution (IndVal = 0.67) but without a significant result (p adj = 0.100). No significant results at all were found for ovitraps. A comparison of dendrotelmata types showed a significant preference for branch hollows for both *Odontomyia annulata* (IndVal = 0.66, p adj = 0.042) and *Clogmia* cf. *albipunctata* (IndVal = 0.74, p adj = 0.044). In the case of *Metriocnemus cavicola* coppice stools and trunk pools were preferred (IndVal = 0.94, p adj = 0.044). For *Anopheles plumbeus*, a tendency towards branch hollows (IndVal = 0.66) was no longer supported as significant after BH correction (p adj = 0.060).

4.3.6 Shannon diversity index

The Shannon index, indicating the species diversity of samples, showed differences between the groups. The Wilcoxon test revealed that dendrotelmata (median 1.01 [IQR: 0.816–1.316]) had a significantly higher Shannon diversity (p < 0.001) than ovitraps (0.596 [0.103–0.888]). A Kruskal-Wallis test also revealed significant differences (p = 0.031) between the various dendrotelmata types. The Dunn post-hoc test resulted in a significant difference (p adj = 0.023) between the branch hollows (1.37 [1.144–1.717]) and the coppice stools (0.930 [0.747–1.134]). No significant result was found for trunk pools (0.932 [0.859–1.257]). There was also no significant difference between the locations, although the median Shannon diversity was slightly higher in the Prater (rural: 0.788 [0.596–1.016]; urban: 1.01 [0.826–1.311], p = 0.089).

4.3.7 Frequency of occurrence across microhabitats

The frequency of occurrence highlights the differences between microhabitats in terms of community composition (Figure 6). While *Prionocyphon serricornis* (90%), *Metriocnemus cavicola* (87%), *Aedes geniculatus* (71%), *Myathropa florea* (68%) and *Dasyhelea* sp. (52%) were predominant within the majority of the dendrotelmata, the most common taxa in the ovitraps were *Dasyhelea* sp. (42%), *Myathropa florea* (32%), *Metriocnemus cavicola* (23%), *Anopheles plumbeus* (19%) and *Aedes japonicus* (19%). Thus, *Aedes japonicus* (19% vs. 6%) belongs to the taxa that were more frequently found in ovitraps than dendrotelmata, along with *Culex pipiens* s.l. / *Cx. torrentium* (6% vs. 3%), *Aedes albopictus* (3% vs. 0%) and *Beris* sp.

(3% vs. 0%). Whilst the larvae of the two marsh beetles, *Prionocyphon serricornis* and *Sacodes flavicollis*, along with *Odontomyia annulata*, were found exclusively in dendrotelmata, those of the Asian tiger mosquito *Aedes albopictus* and *Beris* sp. were found solely in ovitraps.

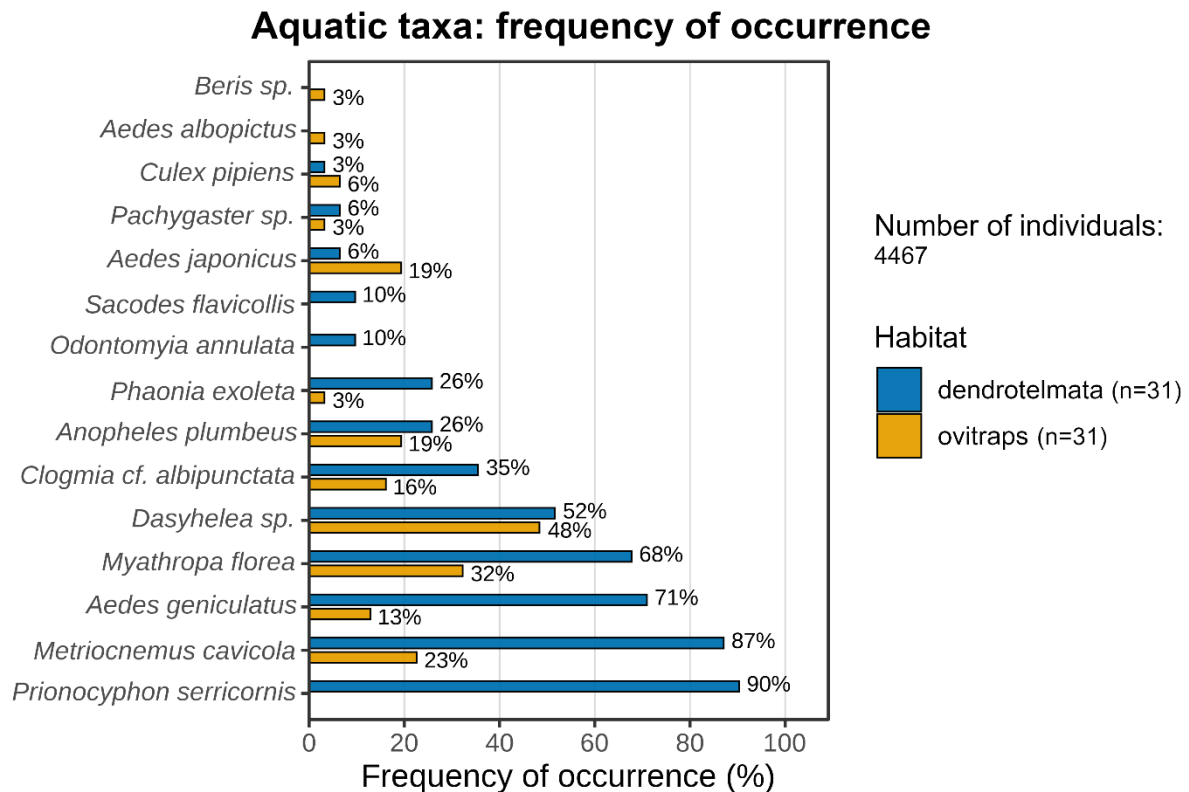


Figure 6: Frequency of occurrence (%) of the 15 aquatic taxa recorded in dendrotelmata (n = 31) and ovitraps samples (n = 31). The figure shows the relative occurrence of taxa in all samples for each microhabitat type. The composition and ranking of taxa differ between dendrotelmata and ovitraps.

4.3.8 Relationship between species and environment

The relationship between species composition and environmental conditions in dendrotelmata and ovitraps was investigated using a canonical correspondence analysis, as the decorana analysis resulted in a gradient length of 3.375 standard deviation units along the first axis. Multicollinearity remained below the threshold of ≤ 10 VIF, thereby integrating conductivity (5.18), pH (4.70), oxygen concentration (1.33), volume (1.21) and temperature (1.20) into the model. The overall model was significant ($F = 3.28$, $p = 0.001$) and exhibited a total inertia of 4.361, of which 1.291 (29.6% of the total variation) was attributed to the explained (constrained) inertia and 3.071 to the unexplained (unconstrained) inertia. The determination coefficient ($R^2 = 0.296$) decreased to $R^2 = 0.191$ after the adjustment. Of this explained variation, the first two canonical axes together covered about 74.3%. CCA1 (44.4%, $p = 0.001$) and CCA2 (30.0%, $p = 0.002$) were significant, while the remaining axes were not.

In the sequential tests, conductivity ($Chi^2 = 0.374$, $F = 4.74$, $p = 0.002$) and dissolved oxygen ($Chi^2 = 0.374$, $F = 4.75$, $p = 0.001$) showed the strongest effects, with pH ($Chi^2 = 0.187$, $F = 2.38$, $p = 0.039$) and temperature ($Chi^2 = 0.181$, $F = 2.29$, $p = 0.028$) also being significant. Volume showed only a tendency ($Chi^2 = 0.175$, $F = 2.23$, $p = 0.059$). The intersite values demonstrate that CCA1 correlated strongly negatively with oxygen (-0.766) and positively, though more weakly, with volume (0.327). Associations with pH (-0.203), temperature (-0.077) and conductivity (0.004) are minor. In contrast, CCA2 correlated mainly positively with conductivity (0.901) and pH (0.775). The impact of oxygen (-0.313), temperature (-0.245) and volume (-0.097) remained small.

The triplot (Figure 7) illustrates a gradient along the CCA1 axis, with positive scores corresponding to lower oxygen and larger volumes. Taxa in this sector include *Metriocnemus cavicola* (CCA1: +0.41, CCA2: -0.37), *Prionocyphon serricornis* (CCA1: +0.57, CCA2: +0.06), *Aedes geniculatus* (CCA1: +0.48, CCA2: -0.33) and *Myathropa florea* (CCA1: +0.38, CCA2: +0.15). Conversely, taxa with negative scores on CCA1 include *Aedes albopictus* (CCA1: -2.22, CCA2: -0.59), *Aedes japonicus* (CCA1: -1.85, CCA2: -0.84), *Culex pipiens* s.l. / *Cx. torrentium* (CCA1: -0.87, CCA2: -0.42), *Dasyhelea* sp. (CCA1: -1.37, CCA2: -0.16) and *Beris* sp. (CCA1: -0.65, CCA2: -0.21). The oxygen-rich ovitrap samples are decisive here. Along CCA2, positive values correspond to higher conductivity and more alkaline conditions. Taxa positioned here include *Odontomyia annulata* (CCA1: -0.20, CCA2: +3.08), *Sacodes flavicollis* (CCA1: -0.34, CCA2: +2.66), *Anopheles plumbeus* (CCA1: -0.33, CCA2: +1.68), *Clogmia cf. albipunctata* (CCA1: +0.05, CCA2: +0.93), *Phaonia exoleta* (CCA1: +0.19, CCA2: +0.75) and *Pachygaster* sp. (CCA1: -0.18, CCA2: +0.46). In this context, it is worth noting that *Odontomyia annulata* and *Sacodes flavicollis* were found exclusively in branch hollows, which were characterised by particularly nutrient-rich and oxygen-poor conditions.

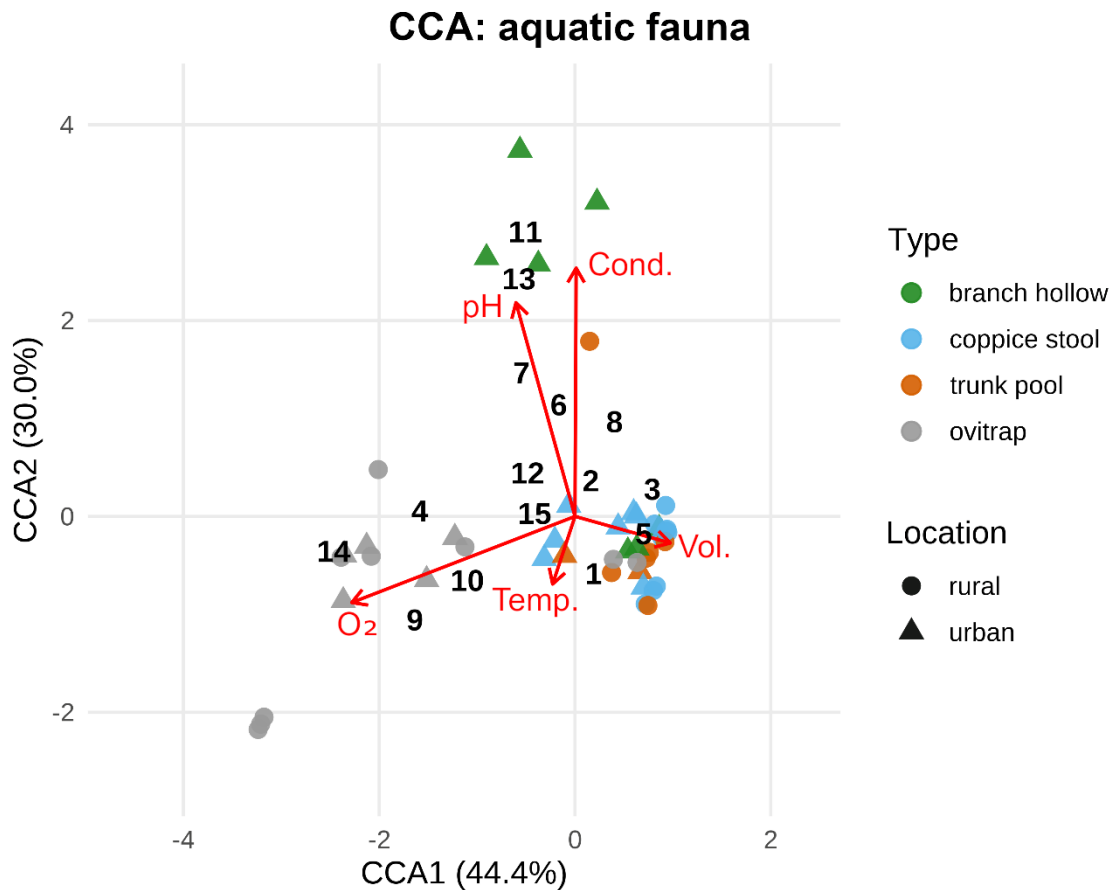


Figure 7: Canonical correspondence analysis (CCA) illustrating the relationship between species community and environmental variables. The triplot shows sampling sites represented by circles (rural) and triangles (urban), with the colours indicating the microhabitat and dendrotelmata type. The physicochemical parameters are represented as arrows indicating the direction and strength of the environmental gradients (abbreviations: Cond = conductivity, Temp = temperature, O₂ = dissolved oxygen, Vol = Volume). The first two canonical axes explained 44.4% and 30.0% of the constrained variation. Taxa are indicated by numbers: (1) *Metriocnemus cavicola*, (2) *Myathropa florea*, (3) *Prionocyphon serricornis*, (4) *Dasyhelea* sp., (5) *Aedes geniculatus*, (6) *Clogmia* cf. *albipunctata*, (7) *Anopheles plumbeus*, (8) *Phaonia exoleta*, (9) *Aedes japonicus*, (10) *Culex pipiens* s.l. / *Cx. torrentium*, (11) *Odontomyia annulata*, (12) *Pachygaster* sp., (13) *Sacodes flavicollis*, (14) *Aedes albopictus*, (15) *Beris* sp.

4.3.9 Oviposition activity in ovitraps

Three ovitraps in the Prater contained eggs of both *Aedes geniculatus* and *Aedes albopictus* (Table A26–A27). The tiger mosquito was detected exclusively in the urban area, with two occurrences in summer and one in autumn. In contrast, eggs of *Aedes geniculatus* were found both in urban (n = 8) and rural (n = 9) sites, throughout all three seasons, making it the most frequently observed of all the species studied and the only one with confirmed oviposition already in spring. Eggs of *Aedes japonicus* were detected only in a few rural samples (n = 4) in summer, whilst *Aedes koreicus* was not detected at all. Of the 35 ovitrap samples collected, 20 contained eggs, with more detections in the rural area (rural: 12; urban: 8) and a peak in oviposition observed during summer.

4.4 eDNA metabarcoding

4.4.1 Comparison of morphological and eDNA results

The eDNA analysis (18S primer) identified a total of 1314 distinct amplicon sequence variants (ASVs), with 70 laboratory replicates (JMF-ID) linked to 68 sampling sites (including the *Dipsacus* and ovitrap samples). The insert lengths ranged from 304 to 468 bp (median 378 bp). Alignment with the SILVA reference database assigned the ASVs to a total of 898 eukaryotic genera, the vast majority of which were terrestrial. Whilst a collective of 12 aquatic insect genera were identified morphologically across all 31 sampled dendrotelmata (Table 1), the eDNA survey (≥ 20 reads) detected only 5 of these genera in just 12 dendrotelmata (Table A28–A31).

Compared to the morphological identification, fewer aquatic insects were detected and they were also less frequently found. Up to nine different genera were observed morphologically within a single dendrotelma, whereas the eDNA survey identified a maximum of two different genera in a single sample. Among the aquatic genera detected in dendrotelmata using eDNA were *Prionocyphon*, *Metriocnemus*, *Aedes*, *Anopheles* and *Culex* (Figure 8). With the exception of the last genus, all were detected less frequently with eDNA than by morphological identification. Whilst specimens of *Prionocyphon* were morphologically slightly the most common, *Metriocnemus* was by far the most frequently genus detected via eDNA.

4.4.2 eDNA-based detection of Rotifera and Nematoda

There was no detailed morphological identification of the rotifers and nematodes. Although sporadic Bdelloidea and Nematoda were observed in the plankton samples, a semi-quantitative or even quantitative assessment was not feasible due to the low number of occurrences. However, the eDNA analysis provided more comprehensive results, with 17 ASVs assigned to Rotifera and 37 ASVs to Nematoda (Table A32–A33). Both groups were detected in the majority of dendrotelmata samples (Rotifera: 81%; Nematoda: 52%), whilst there were fewer occurrences in ovitraps (Rotifera: 48%; Nematoda: 13%) (Figure 9). Five genera of rotifers were listed, the most common being *Rotaria* Scopoli, 1777 (Bdelloidea), found in 14 out of 31 dendrotelmata (total reads: 2540), with the remaining genera found only sporadically. The nematodes included 12 genera, the most frequently detected being *Eumonhystera* Andr ssy, 1981, but still occurring only in a few samples (4 out of 31 dendrotelmata, total reads: 834).

eDNA vs. morphology: detection of taxa

Denominator: 31 shared dendrotelmata - eDNA threshold ≥ 20 reads

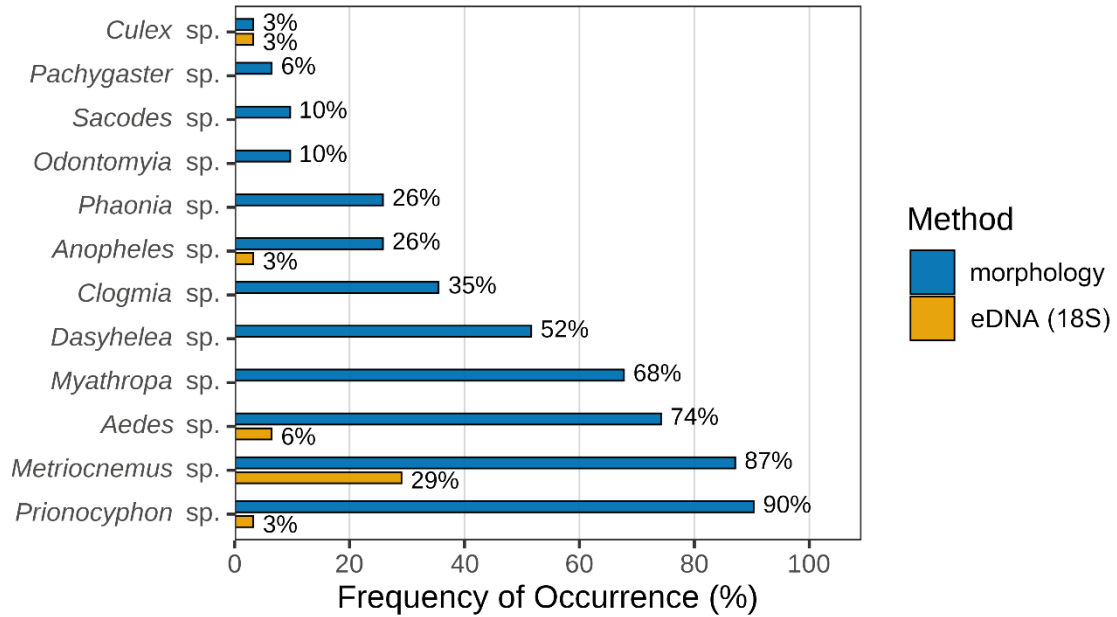


Figure 8: Comparison between eDNA and morphological recordings in terms of the frequency of occurrence (%) among aquatic taxa found in dendrotelmata ($n = 31$). The figure shows the relative occurrence of taxa in all samples for each method, whereby the composition as well as the ranking of taxa differ between morphological and eDNA records.

eDNA: detections of Rotifera & Nematoda

18S primers - eDNA threshold ≥ 20 reads

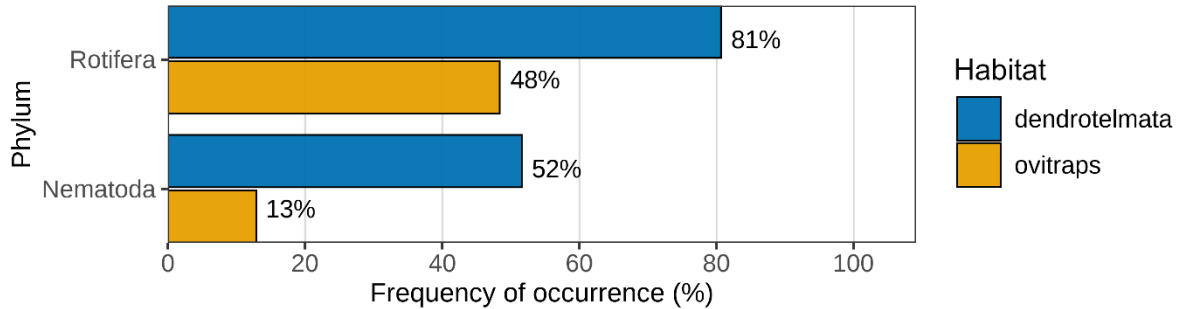


Figure 9: Frequency of occurrence (%) of the two phyla, Rotifera and Nematoda, recorded in dendrotelmata ($n = 31$) and ovitraps samples ($n = 31$). The figure shows the relative occurrence of taxa across all samples for each microhabitat type.

4.5 Vertebrate interactions with dendrotelmata

Wildlife cameras deployed at a subset of sites within the national park area recorded the presence of numerous vertebrates visiting the microhabitats. Due to the non-standardised sampling effort and limited spatial coverage, these data are presented as qualitative observations only. Across all monitored sites, several vertebrate taxa were detected interacting with the water bodies, including mammals, birds and amphibians. A summary of detections is provided in Table 2. It is worth noting that mammals and birds were observed mainly drinking

or simply inspecting the microhabitats. But in the case of *Bufo bufo* (Linnaeus, 1758), the toads were found completely hidden inside the dendrotelmata, specifically trunk pools.

Table 2: Vertebrate taxa recorded interacting with the microhabitats of dendrotelmata and ovitraps in the National Park Donau-Auen using sporadically deployed wildlife cameras. The table includes all taxa observed inspecting or directly interacting with the sampled microhabitats during the study period.

Trivial name	Taxonomic designation	Dendrotelma	Ovitrap
Common toad	<i>Bufo bufo</i>	✓	
Eurasian jay	<i>Garrulus glandarius</i>	✓	
Eurasian otter	<i>Lutra lutra</i>	✓	
European badger	<i>Meles meles</i>	✓	✓
Great spotted woodpecker	<i>Dendrocopos major</i>		✓
Great tit	<i>Parus major</i>	✓	✓
Marten	<i>Martes</i> sp.	✓	✓
Murid	Muridae	✓	✓
Nuthatch	<i>Sitta europaea</i>	✓	
Red fox	<i>Vulpes vulpes</i>	✓	✓
Red squirrel	<i>Sciurus vulgaris</i>	✓	✓
Robin redbreast	<i>Erithacus rubecula</i>	✓	
Roe deer	<i>Capreolus capreolus</i>	✓	
Thrush	Turdidae	✓	✓
Wild boar	<i>Sus scrofa</i>	✓	✓

In addition, several samples showed signs of nutrient input caused by vertebrates, mainly in form of bird feces, which could be linked to elevated phosphate concentrations. This pattern was especially pronounced in one ovitrap sample (OT_003_Orth). Whilst the orthophosphate level in summer was at 4.1 mgL⁻¹ (volume: 790 mL; dissolved oxygen: 2.25 mgL⁻¹), the concentration rose to 22.7 mgL⁻¹ in autumn following obvious faecal deposition (volume: 600 mL; dissolved oxygen: 0.02 mgL⁻¹).

5. Discussion

5.1 Dendrotelmata as habitats

As demonstrated in the abiotic analyses (Section 4.2), dendrotelmata are characterised by exceptionally nutrient-rich, oxygen-poor yet variable conditions. They emerge as a special habitat, particularly when compared to other lentic systems (Dodds, 2002; Mayer et al., 1997). Frequent desiccation of dendrotelmata throughout the year, as well as overflow during rainfall, highlighted the extreme dynamics of these microhabitats as a result of their restricted water volume. These fluctuations were nicely described in the work done by Verdonchot et al. (2008). During their study period, the average oxygen concentration remained relatively constant at just 0.64 mgL^{-1} , but spiked to 6.35 mgL^{-1} following rainfall. Nutrient concentrations, which increased in dry periods through evaporation, were diluted again during rainfall, but also new nutrients were flushed into the system via stemflow.

Furthermore, there is the occasional impact of vertebrates (see Table 2). Some of them are known to regularly interact with phytotelmata. They mainly use them as a drinking resource, for bathing or in some cases also for feeding (Gossner et al., 2020; Kirsch et al., 2021), with some tropical amphibians, such as poison dart frogs, even using them as a breeding habitat (Lehtinen et al., 2004; Ryan & Barry, 2011; Schiesari et al., 2003). As a result, these vertebrates not only affect the water volume, but can also cause allochthonous nutrient input (Batanero et al., 2017; Green & Elmberg, 2014). In some of the samples examined in this study, bird faeces was present, resulting in raised phosphate levels. A substance that is generally considered to be the limiting factor for primary production in most larger, unpolluted freshwater ecosystems (Dodds, 2002).

But not only enriched stemflow (Mabrouk et al., 2022; Van Stan et al., 2021), leaf litter (Paradise, 2004; Paradise & Dunson, 1998) or vertebrate excretions (Batanero et al., 2017) can be regarded as nutrient inputs, also terrestrial animals drowning in phytotelmata can be considered as such, since their remains will be decomposed (Carpenter, 1982; Kitching, 1971). The carnivorous pitcher plants of the genus *Nepenthes* Linnaeus, 1758 are known for explicitly luring prey into their phytotelmata, where they are then digested and the released nutrients are absorbed by the plant (Adlassnig et al., 2011; Lam et al., 2018). A carnivorous function of phytotelmata has also been hypothesised for the native teasel plants (Shaw & Shackleton, 2011), although this assumption remains controversial (Vecchi, 2025). This influx of nutrients via terrestrial animals was also observed in the microhabitats investigated for this study. About one tenth of invertebrates found in the samples (Section 4.3.1) were terrestrial carcasses.

Therefore, the aquatic fauna of dendrotelmata has a plentiful supply of food at its disposal. During decomposition processes, organic material is broken down by shredders and microbes, leading to the accumulation of detritus in various particle sizes (Gossner & Petermann, 2022; Schmidl et al., 2008; Walker et al., 1991). Dissolved nutrients are also rebounded as biomass through microbial metabolism (Russo et al., 2016; Verdonschot et al., 2008). These microorganisms and the detritus thus form the nutritional foundation for the aquatic community in dendrotelmata (Paradise et al., 2008; Petermann & Gossner, 2022).

5.2 Types of dendrotelmata

Already Kitching (1971) had noticed that dendrotelmata are not uniform, rather they can be divided into several types. He distinguished between so-called “pans”, meaning water bodies on the undamaged bark of a tree, and the “rot holes”, referring to tree holes with damaged bark, in which the injured tree is confronted with fungal infestation and further decomposition processes. In both types of dendrotelmata, organic matter accumulate, forming a layer of leaf litter with a bed of decayed material beneath. Walker et al. (1991) also referred to this classification in their study on nutrient dynamics and found that the types are clearly distinguishable from one another by their limnochemical properties. With the exception of nitrite, the nitrogen compounds were significantly more concentrated in pans than in rot holes, whereas nitrite and phosphate were higher in rot holes, although not significant.

The present study has also demonstrated that different types of dendrotelmata differ from each other. I distinguished three types: the branch hollows, which basically correspond to rot holes, the trunk pools found in undamaged bark depressions (particularly on the trunks of hornbeams), and the so-called coppice stools. The last type is a distinctive structure that mainly arises from the old forestry practice of coppicing (Buckley, 2020), although comparable formations can also occur naturally, for example as a result of windthrow (Joys et al., 2004). In coppicing, deciduous trees are cut back to the ground, causing several new shoots to emerge during the regeneration process, which may form a sort of basin (Coxhead & Slater, 2022).

As the PCA analysis showed (Figure 4A), branch hollows were the nutrient-richest and the oxygen-poorest samples. In contrast, trunk pools were comparatively nutrient-poor and oxygen-rich, thus more similar to the ovitrap samples. The coppice stools fell between the branch hollows and the trunk pools. However, the size of dendrotelmata should be considered here, as concentrations ultimately depend on volume (Section 4.2.1). The volumes of the branch hollows was clearly smaller than that of the large coppice stools, resulting in a smaller dilution.

5.3 Aquatic insect community in dendrotelmata

The larvae of 13 aquatic insect taxa were found in dendrotelmata (see Section 4.3.1), belonging to just two orders: Coleoptera and Diptera. Most of these insects have already been discovered in water-filled treeholes throughout Central Europe, for example in Slovakia (Oboňa & Dominiak, 2014; Oboňa & Svitok, 2012), the Czech Republic (Devetter, 2004) and in Germany (Gossner, 2018; Schmidl et al., 2008) they have been found. Dendrotelmata outside of Europe essentially have a comparable taxonomic composition as well. The same insect orders and families have also been reported from North America (Copeland, 1989; Verdonschot et al., 2008), South America (Campos et al., 2011; Yanoviak et al., 2006), Africa (Copeland et al., 1999; Noutcha et al., 2018), Asia (Mogi, 2004; Watanabe et al., 2023) and Oceania (Blakely et al., 2012; Kitching & Callaghan, 1982). Although biodiversity is higher in tropical regions, with orders such as dragonflies (Odonata) or true bugs (Hemiptera) also occurring in the phytotelmata of rainforests (Fincke & Hedström, 2008; Greeney, 2001; Mogi, 2004).

This modest community composition is likely due to the fact that the taxa within these communities are broadly specialised to the harsh conditions of these astatic microhabitats, conditions in which many other animals fail to thrive (Carpenter, 1982; Paradise et al., 2008; Petermann & Gossner, 2022; Sota, 1993). Mosquitoes (Culicidae) are an excellent example in this regard. Their larvae are equipped with a breathing tube (siphon) that allows them to respire atmospheric oxygen directly from the air, thus making them independent of the dissolved oxygen within the water (Alvarez-Costa et al., 2024; Becker et al., 2020). Thanks to their rapid development time, which lasts from just a few days to weeks, depending on the species and temperature, they are able to preempt desiccation (Barrera & Medialdea, 1996; Becker et al., 2020). Treehole-dwelling mosquitoes have even adapted their oviposition to the dynamic hydrology of dendrotelmata. One example is *Anopheles plumbeus*, which does not lay its eggs directly on the water surface, but instead attaches them to the side walls. The larvae then hatch only after the treehole has been flooded (Becker et al., 2020).

But the situation becomes particularly striking with regard to those taxa, which are dependent on the dissolved oxygen available in the water, thus being exposed to the extreme oxygen deficiency of dendrotelmata. The family of non-biting midges (Chironomidae) is considered one of the most diverse freshwater groups, with their larvae inhabiting virtually all types of aquatic environments, including phytotelmata (Pinder, 1995; Sæther, 1995). Some of their representatives are known to be adapted to hypoxic conditions, such as life within sediments (Grazioli et al., 2016). This is particularly true for the genus *Chironomus* with some species known to produce the respiratory protein haemoglobin, which is highly unusual for insects

(Herhold et al., 2020; Hoback & Stanley, 2001). However, this adaptation primarily affects members of the subfamily Chironomini (Grazioli et al., 2016). The subfamily Orthoclaadiinae, which also includes the treehole-dwelling *Metriocnemus cavicola* (Orendt & Bendt, 2020; Pillot, 2014), is generally considered sensitive to oxygen deficiency. Its greatest diversity is found in cold and oxygen-rich waters (Cranston, 2004; Pinder, 1995). Although it is known that some chironomid species can also rely on anaerobic energy production via alcoholic fermentation or simply move into normoxic water if necessary (Hoback & Stanley, 2001), the extent to which this applies to *Metriocnemus cavicola* appears still to be unstudied. While Schmidl et al. (2008) reported that the larvae in their samples preferred more open waters, presumably to ensure oxygen supply, the paper by Gossner & Petermann (2022) concludes that *Metriocnemus cavicola* tolerates low-oxygen situations very well. The canonical correspondence analysis (CCA) in this study also shows a tendency towards more oxygenated conditions (Figure 7), but higher temperatures appear to have a great effect too (Section 4.3.8). This seems actually contradictory, as higher temperatures are typically associated with lower oxygen concentrations (Dodds, 2002). One explanation for this could be that *Metriocnemus cavicola* simply prefers larger, better oxygenated dendrotelmata, which, by virtue of their size, are more exposed to sunlight and therefore warmer. The indicator species analysis with regard to the dendrotelmata types provided evidence of this (Section 4.3.5). Here, *Metriocnemus cavicola* showed a significant preference for coppice stools and trunk pools, which were indeed more oxygen-saturated than branch hollows. And the bigger coppice stools, in turn, were the warmest of all dendrotelmata. These results would thus support the findings of Schmidl et al. (2008), who reported a preference for more open waters.

5.4 Faunal differences between different dendrotelmata types

Not only did the abiotic conditions differ between the different types of dendrotelmata, their faunal composition and total abundances also varied. The PERMANOVA analysis (Section 4.3.3) showed that a considerable proportion of variation is explained by the dendrotelmata type ($R^2 = 14.3\%$). Branch hollows appear to be truly exceptional within the dendrotelmata, featuring their own distinct fauna assembly (Figure 7) and a significantly higher Shannon diversity (Section 4.3.6). The indicator species analysis showed a significant preference for this type in case of the moth fly (Psychodidae) *Clogmia cf. albipunctata* and the soldier fly (Stratiomyidae) *Odontomyia annulata*, which was found exclusively in branch hollows. For the mosquito *Anopheles plumbeus*, only an insignificant tendency was observed, but the larvae were nevertheless found primarily in branch hollows.

A special species that should definitely be addressed here is *Sacodes flavicollis*. As Klausnitzer (2009) points out, this species has its centre of distribution in the Mediterranean region, like

European marsh beetles (Scirtidae) in general. It is the sole representative of this genus in Europe and its distribution remains poorly explored, although dendrotelmata are confirmed as larval habitats. In Austria only a few instances of larvae have been reported thus far (Holzinger et al., 2014; Jäch et al., 2013). Of the nearly one thousand Scirtidae larvae counted in this study, only nine individuals were identified as *Sacodes flavicollis* (Section 4.3.1). All of them were found in branch hollows in the Vienna Prater. Studies from Germany did not report this rare species at all (Gossner, 2018; Gossner & Petermann, 2022; Schmidl et al., 2008). However, as there are also occasional reports from the Czech Republic and Poland (Klausnitzer, 2009), there is no reason to assume that *Sacodes flavicollis* reaches its northern distribution limit in Vienna. Given the small number of individuals found, it would be inappropriate to generalise about possible ecological preferences. Nevertheless, it would now be interesting to know whether the species is associated with specific types of dendrotelmata (Figure 7). Accordingly, in future it would be advisable to look out for branch hollows in the national park area as well.

So why are some taxa found primarily in branch hollows, which are highly nutrient-rich but also extremely hypoxic? It is known that the larvae of the soldier fly *Odontomyia annulata* can develop in water as well as in moist rotting wood, with a slow development period of up to three years (Roháček, 2020; Rozkošný, 2000). In the context of dendrotelmata, with their limited water volume, this means that the larvae are regularly confronted with desiccation. However, they benefit from a strategy known as dormancy, in which their metabolism is greatly reduced and development is paused, enabling them to survive desiccation events (Washko & Bogan, 2024). A useful trait, particularly in the case of branch hollows, which had the lowest water volumes of all dendrotelmata types (Section 4.2.1). In contrast, the non-native moth fly *Clogmia cf. albipuncata* has a much faster development time of around 17 days and is therefore less likely confronted with desiccation (Zittra et al., 2020). The larvae inhabit exceptionally nutrient-rich habitats, ranging from bat guano to bathroom sinks and sewage treatment plants (Oboňa & Ježek, 2012; Vaillant, 1971). It is therefore not surprising that they have also been found in dendrotelmata such as the branch hollows (Section 4.3.5). In Slovakia, larvae have already been reported from treeholes (Ježek et al., 2012; Oboňa & Ježek, 2012), whilst reports from Austria have so far been based mainly on discoveries of adult imagines (Zittra et al., 2020). Strikingly, the dendrotelmata samples in this study contained only the morphotype of *Clogmia cf. albipuncata*. Native psychodid species were not found at all, although it is known that representatives of genera such as *Lepiseodina* or *Psychoda* would actually be expected in Central European dendrotelmata (Jaume-Schinkel et al., 2022; Oboňa et al., 2021; Schmidl et al., 2008). Oboňa & Ježek (2012) already classify *Clogmia cf. albipuncata* as “invasive”, referring to non-native species with negative impacts on native communities (Blackburn et al., 2011; Francis & Chadwick, 2015). Thus, it is reasonable to conclude that the limited occurrence

of psychodid specimens restricted to *Clogmia cf. albipunctata* supports this assumption. I therefore concur with the suggestion of Ježek et al. (2012), who call for further investigations to assess the impact of *Clogmia cf. albipunctata* on the native treehole biodiversity.

5.5 Impact of urbanisation

A key research question in this study was the impact of urbanisation on dendrotelmata and their inhabitants. Analyses of abiotic characteristics revealed minor but significant differences between the locations (Section 4.2.5). The median nutrient values were slightly higher in the urban area (Section 4.2.1) and as can be seen from the PCA biplots (Figure 4), a subtle location gradient for coppice stools is apparent. Urban waters are often affected by increased salt and nutrient inputs, for example through road salt runoff or sewage disposal (Hassall, 2014; Oertli & Parris, 2019). However, such input pathways are unlikely in the case of treeholes. One aspect that might be of interest here instead is the shift in vertebrate density within cities. Some animals, such as the Eurasian red squirrel (*Sciurus vulgaris* Linnaeus, 1758), benefit from the additional food sources provided by urban landscapes and occur in greater numbers in city parks than they do in natural habitats (Wist & Dausmann, 2024). For urban dendrotelmata, this could imply increased vertebrate interactions and consequently increased allochthonous nutrient input (Section 4.5).

The fauna analyses also revealed a difference between the locations. Despite there was no significant difference in Shannon diversity, the PERMANOVA revealed a small yet significant shift in community composition ($R^2 = 3.7\%$). The mGLM analyses likewise detected significant abundance differences, although microhabitat type and season showed stronger effects. These location differences are taxon-specific: the marsh beetle *Prionocyphon serricornis*, the mosquito *Aedes geniculatus* and the hoverfly *Myathropa florea* were significantly affected (Section 4.3.4). The first two were found primarily in the rural national park area, whereas *Myathropa florea* was more frequently found in the Prater (Table 1). The results of the indicator species analysis present a slightly different situation here (Section 4.3.5). A significant preference was only identified for *Dasyhelea* sp., in this case for the Prater. For *Aedes geniculatus*, following the BH correction, only a non-significant trend towards rural sites remained. With a trend towards urban settings, the non-native species *Clogmia cf. albipunctata* met a similar fate.

The results are therefore largely consistent with those of Sommer & Petermann (2026), who studied the aquatic community in artificial microhabitats (1-liter plastic buckets) in the vicinity of the Central Austrian city Salzburg. They concluded that urbanisation does not affect neither the abundance nor the species richness of these microhabitats, but it changes the species

community. The abundance of *Aedes japonicus* decreased significantly with increasing urbanisation, whilst *Culex pipiens* s.l. / *Cx. torrentium* showed a non-significant trend towards urban conditions. In the present study, although not significant, *Aedes japonicus* also occurred more frequently in rural samples, whilst *Culex pipiens* s.l. / *Cx. torrentium* was found more frequently in the Prater (Table 1). Such a gradient applies not only to larvae, but also to eggs (Section 4.3.9). Oviposition by *Aedes japonicus* was observed only in Orth, whereas eggs of *Aedes albopictus*, like the larvae, were found only in the urban area. The main factors driving this gradient could be the cold tolerance of *Aedes japonicus* (Kampen & Werner, 2014; Kaufman & Fonseca, 2014) and the urban heat island effect in cities, which benefits anthropophilic species including *Culex pipiens* s.l. / *Cx. torrentium* as well as *Aedes albopictus* (Duval et al., 2023; Townroe & Callaghan, 2014). Other reasons might include increased interspecific competition, higher predation pressure in forests or the availability of suitable blood-feeding hosts, as discussed by Mogi et al. (2020, 2024). In their studies on the impact of urbanisation on treehole-dwelling mosquito species in Japan, they also observed that *Aedes japonicus* occurs predominantly in rural areas in or near the forest, whereas *Aedes albopictus* clearly dominates in urban areas.

But how can the significant location differences of *Prionocyphon serricornis* and *Myathropa florea* be explained? Compared with mosquitoes, whose responses to urbanisation have been extensively studied due to their medical relevance (Garrido et al., 2025; Kolimenakis et al., 2021; Perrin et al., 2022), there is little information available for other aquatic invertebrates (Gál et al., 2019). As described by Keinath et al. (2023), the entire amphibiotic life cycle of aquatic insects must be considered. They thus respond not only to aquatic but also to terrestrial environmental changes, for example in terms of reproduction during their adult stage. In addition, different taxonomic groups have varying demands. Nocturnal and diurnal taxa are affected by urban light pollution in different ways, for example (Ganguly & Candolin, 2023; Van Koppenhagen et al., 2026). In case of hoverflies (Syrphidae), which are important pollinators as imagines, they are generally known to cope well with urban conditions as long as there is sufficient food in form of flowering plants (Lequerica Tamara et al., 2023; Wittische et al., 2024).

At this point it is worth discussing the Vienna Prater as an urban location. The first issue is the definition of urbanity, as there is no universal standard. However, the United Nations (UN) Statistical Commission refers to the degree of urbanisation method. According to this method, urban centres are defined as grid cells with an area of 1 km² and a population density of at least 1500 inhabitants per km², whereas grid cells with fewer than 300 inhabitants per km² are considered rural (Dijkstra et al., 2021). Based on this simplified method, classifying the Vienna Prater as urban would arguably be legitimate (Figure 1). The city district in which the Vienna Prater is located has a high population density of over 5800 people per km² (City of Vienna,

2025) and the land use is classified under artificial areas (Class 1) in the CORINE Land Cover dataset (European Environment Agency, 2019). Nevertheless, the multivariate approach by Suarez-Rubio & Krenn (2018) has demonstrated that quantifying urbanisation is often more complex than might be assumed. They applied a total of 17 metrics, which were divided into the categories of demographic variables, physical variables and landscape metrics. According to their findings, the Prater is not categorised as urban, but rather as green space. The approach taken by Sommer & Petermann (2026), which involves several numerical variables such as sealed surface or human population to assess the degree of urbanisation within defined buffer zones around the microhabitats, therefore appears to be a more reliable measure. After all, despite the nearby population density and widespread light as well as noise pollution (Payer, 2007; Puschnig et al., 2014), the Vienna Prater is a large, relatively undisturbed green space rather than the concrete wasteland found elsewhere. In this regard, the definition of urbanisation considered in this study remains debatable given the complexity of this topic.

5.6 Forest management practices

An environment in which dendrotelmata are certainly affected is cultivated forestry. Studies on water-filled treeholes in Germany have shown that increasing management intensity is associated with negative impacts on the dendrotelmata fauna (Gossner et al., 2016, 2026; Petermann et al., 2020). Historically, the Vienna Prater was part of the Danube floodplains (Haidvogel et al., 2018), which was used as a private hunting reserve by the former feudal nobility and eventually became a public recreational area in the 18th century (O'Brien, 1981). As part of the hydroengineering remodelling, the Prater area was separated from the original floodplains and remained as an island between the Danube Canal and the new riverbed of the Danube (Haidvogel et al., 2018). Intensive forestry was not practised and the main forest remained as a relict of the former floodplains. However, the park was also affected to a certain extent during the 2nd World War (O'Brien, 1981) and park trees such as the horse chestnut, native to southern Europe, were sporadically introduced (Adler et al., 2003). The area of today's Donau-Auen National Park was also part of the historically contiguous floodplains and was used as a hunting ground, but to a certain extent also for minor forestry, prior to the establishment of the national park in the 1990s (Haidvogel et al., 2018; Klasz et al., 2013; Knoll & Reiter, 2017). Both locations are therefore comparable as they are based on the original floodplain forests and have been spared from intensive forestry, meaning that effects such as those described by Petermann et al. (2020) can be neglected.

5.7 Microhabitat $\neq$ microhabitat

Numerous studies have used artificial microhabitats like plastic buckets (respectively ovitraps) to infer the conditions in natural dendrotelmata (Bartel et al., 2025; Petermann et al., 2016; Ptatscheck & Traunspurger, 2014). In some cases, they are simply referred to as “artificial treeholes” (Bartel et al., 2025; Ptatscheck & Traunspurger, 2014), whilst in others they are even equated directly with natural treeholes, at least in title (Watanabe et al., 2023). The advantage of these artificial vessels certainly resides in the experimental manipulability and standardisation of factors such as nutrient input or water volume (Yanoviak & Fincke, 2005). However, as the results of this study confirm, plastic buckets cannot be equated with natural dendrotelmata, neither in terms of their abiotic characteristics (Section 4.2.2) nor with regard to the fauna (Section 4.3.7). Nutrients had to accumulate over the entire year and even then, the water chemistry was not comparable to their natural counterparts, as the dendrotelmata exhibited substantially higher nutrient and lower oxygen concentrations as well as greater variability. Although in corresponding studies the artificial vessels are usually supplied with nutrients such as leaf litter right from the start (Bartel et al., 2025; Watanabe et al., 2023), they nevertheless differ in major aspects. Petermann et al. (2016) also found that the artificial vessels not only had higher oxygen concentrations but also much warmer water temperatures than natural treeholes. The recorded values from the temperature loggers clearly illustrate this fact (Figure 3), a black plastic bucket simply has a different temperature regime than a water body isolated by plant structures. These habitat structures themselves are also important differences. The structured bark of dendrotelmata serves as oviposition surface for treehole-dwelling mosquitoes (Bakran-Lebl et al., 2024; Becker et al., 2020), whilst serving as a shelter for many other species (Kitching, 1971; Yanoviak & Fincke, 2005), which is not possible with the smooth surface of plastic buckets. But above all, an important characteristic of phytotelmata is undermined, namely the interaction with the host plant. The experiments by Carpenter (1982) demonstrated the importance of plant-specific stemflow, as the water chemistry of a dendrotelma varies between tree species, but also depending on the specific type of dendrotelma (Walker et al., 1991). All these natural heterogeneities fall victim to the experimental homogeneity of artificial vessels.

Yet the fauna of artificial microhabitats appears to derive from the same species inventory. Although the statistical analyses clearly showed that dendrotelmata were more species-rich and also differed significantly in their abundance patterns, the natural dendrotelmata and the artificial ovitraps nevertheless shared a majority of 10 out of a total of 15 insect taxa found (Section 4.3.7). What is the explanation for this overlap of species? After all, also artificial ovitraps are astatic microhabitats that are affected by fluctuating water levels and desiccation. This means that the ecological suitability is already limited for many species, but not in the

case of the aquatic treehole fauna. However, on closer inspection, the composition of the community differed distinctly (Figure 6). For instance, no marsh beetles were found in the ovitraps and the biting midges of the genus *Dasyhelea*, which appeared in dendrotelmata merely as the fifth frequently occurring taxon, clearly dominated in the ovitraps. The mGLM analysis and the indicator species analysis support this with significant results. Barely anything is known about the larval ecology of biting midges, although several representatives of *Dasyhelea* are reported to inhabit phytotelmata (Dominiak, 2012). As noted by Oboňa & Dominiak (2014), the species of this genus can only be identified by their adult stage. Two species have been recorded in the phytotelmata of Slovakia, *Dasyhelea flavifrons* Guérin, 1833 and *Dasyhelea bilineata* Goetghebuer, 1920, which have been found both in dendrotelmata (Oboňa & Dominiak, 2014) and in the leaf axils of *Dipsacus* plants (Oboňa et al., 2024). This suggests that these species do not have any specific preferences for different types of phytotelmata, which implies that the colonisation of other microhabitats, such as ovitraps, are to be expected.

The mosquito community showed differences between microhabitats as well (Figure 6), although there were no significant results. Larvae of *Aedes japonicus* were found more frequently in the artificial microhabitats as were larvae of *Aedes albopictus*, which were found exclusively in one single ovitrap at the urban study area (Table 1). However, due to the limited occurrence with only eight individuals, an ecological interpretation remains difficult in this case, but this observation is still in line with the results of other studies that consistently report a preference of artificial and urban habitats for *Aedes albopictus* (Bartlett-Healy et al., 2012; Li et al., 2014; Mogi et al., 2020, 2024). When considering the results of the canonical correspondence analysis (CCA) for the remaining four taxa, the striking differences in species-environment relationships are evident, which can also be attributed to the difference between dendrotelmata and ovitraps (Figure 7). Whilst *Aedes geniculatus* and *Anopheles plumbeus*, which can be described as characteristic treehole-dwelling species, were also found in conditions with lower oxygen levels and higher nutrient concentrations, the opposite is true for *Culex pipiens* s.l. / *Cx. torrentium* and *Aedes japonicus*, which were more frequently found in the ovitraps. Within its natural range in Asia, *Aedes japonicus* is often associated with the microhabitat of rook pools (Kaufman & Fonseca, 2014; Mogi et al., 2024). This is also an astatic microhabitat with fluctuating hydrology, but one that is richer in oxygen and poorer in nutrients compared to dendrotelmata (Jocque et al., 2010). This observation is therefore consistent with the findings of the CCA analysis and would also explain why *Aedes japonicus* prefers the more saturated ovitraps to the hypoxic dendrotelmata. The common house mosquito *Culex pipiens* s.l. / *Cx. torrentium* inhabits a wide variety of habitats, ranging from vegetation-rich ponds to still areas of flowing water, but its larvae can also be found in microhabitats such as ovitraps or treeholes (Becker et al., 2020; Townroe & Callaghan, 2014; Zittra et al., 2016). The

representatives of this species complex can therefore be described as generalists and it can be assumed that the specific conditions in dendrotelmata do not correspond to their niche optimum. It is therefore not surprising that they were found more frequently in the ovitraps.

5.8 Aquatic insects detected by eDNA metabarcoding

The results of the eDNA analysis (18S primer) showed only modest success in terms of taxonomic resolution (Section 4.4.1). Of 31 dendrotelmata samples, aquatic insects were detected in only 12 of them and only 5 of the overall 12 morphologically identified genera were found (Figure 8). However, several methodological challenges of this study need to be discussed. Firstly, the filtered water volume. Studies dealing with larger freshwater ecosystems, such as rivers or groundwater, usually use several litres of sample water for their eDNA analyses (Bylemans et al., 2019; Pont et al., 2023; Retter et al., 2024; Van Der Heyde et al., 2023). Such volumes are simply not available in the case of microhabitats such as dendrotelmata. Depending on the type of dendrotelmata, the median water volume ranged between 100 and 400 ml, but a large proportion of this was required for the limnochemical analyses (Section 3.4.1). Accordingly, the approach of Vecchi (2025) served as a guide, who also filtered only 5 ml of sample water for his eDNA analyses, although he limited his taxonomic analysis to family level. Some might argue now that the sample volume must be based on the available DNA concentration (Brasseur et al., 2023; Watts et al., 2026) and that the concentration is much more diluted in large systems such as rivers or groundwater than it is in small dendrotelmata.

This brings us to the next challenge, the condition of the DNA material. The degradation of genetic samples can pose an obstacle for successful eDNA analyses (Deiner et al., 2017; Watts et al., 2026), particularly due to enzymatic or microbial activity (Barnes et al., 2014). And exactly such microbial decomposition processes play a central role in the dynamics of dendrotelmata (Verdonschot et al., 2008; Walker et al., 1991). It can therefore be assumed that the quality of the eDNA samples has already been affected and thus complicated the analyses.

In addition there is another challenge, the status of the reference database. Metabarcoding is basically the comparison of DNA sequences extracted from environmental samples with existing sequences, which have been digitised using sequencing methods such as Sanger or Illumina, then stored in a database and assigned to specific taxa (Deiner et al., 2017; Valentini et al., 2009; Watts et al., 2026). Consequently, the reference database is a bottleneck for the success of eDNA analyses. One of the problems that arises here, is that while there are extensive references for well-studied taxonomic groups such as fish (Pont et al., 2023), less

well-researched taxonomic groups, such as the insects found in treeholes, are only scarcely covered (Sire et al., 2025). For this study, this meant that the identification at species level was not possible anyway. This was partly because most species were not recorded in the database, but also because the 18S universal primers are considered unsuitable for taxonomically resolving most animals (particularly insects) to species in the first place (Giebner et al., 2020). For insects, CO1 primers such as Lep-F are generally used, as these regions exhibit a higher evolutionary rate and thus ensure sufficient resolution for the identification of many insect species (Creedy et al., 2025; Hebert et al., 2003; Valentini et al., 2009; Wilson, 2012). The eDNA analyses in this study were therefore conducted at the genus level. For most of the genera identified morphologically, there were entries in the SILVA reference database (release 138.2) (Quast et al., 2012). The only genera not listed were *Myathropa*, *Sacodes* and *Pachygaster*. Therefore, for the remaining genera it can be assumed that, with sufficient DNA concentration and successful amplification, corresponding ASVs were to be expected.

5.9 Meiofauna detected by eDNA metabarcoding

Nevertheless, the results of this analysis also highlight the strengths of eDNA metabarcoding. The number of experienced taxonomists, who are even capable of performing morphological identification on larvae belonging to challenging insect orders such as the Diptera, is extremely limited and is currently even in decline (Cerretti et al., 2026). Metabarcoding has the potential to serve as a supportive complement in biomonitoring and to mitigate this shortage of taxonomists to some extent (Sire et al., 2025).

But metabarcoding also has the advantage of detecting tiny organisms that are otherwise difficult to sample or completely inaccessible (Deiner et al., 2017; Van Der Heyde et al., 2023). The sampling method used in this study (Section 3.3) proved unsuitable for the morphological recording of Rotifera and Nematoda individuals. In their investigations of the Rotifera fauna in bromeliad phytotelmata, Koste et al. (1991) provided a suitable methodological description. They stirred the contents of the phytotelmata prior to sampling to dislodge the detritus and wash off the rotifers. Furthermore, live examinations were carried out, as species identification in Rotifera is often only possible whilst they are feeding (Ricci & Melone, 2000). For several reasons such a method would not have been appropriate within the scope of this study. After all, stirring up the water sample causes changes in the water chemistry, which would have negated a representative limnochemical analysis. Moreover, a rapid live examination would have been difficult to implement, as the number of dendrotelmata sampled and the necessity of conducting the water chemistry analyses as promptly as possible left no time for such examinations.

It is therefore encouraging that at least eDNA metabarcoding was able to detect these two animal groups. Rotifera and Nematoda were detected in the majority of dendrotelmata samples (Section 4.4.2). Based on their frequency of occurrence, they are the most frequently detected taxa in the eDNA results. This is consistent with the findings of Ptatscheck & Traunspurger (2015), who observed that Rotifera and Nematoda constitute the majority of individuals in artificial microhabitats (ovitraps). Thanks to their dispersal via wind and other animals (phoresy), they reach new microhabitats and recently flooded phytotelmata quite rapidly (Bartlow & Agosta, 2021; Ptatscheck & Traunspurger, 2014). Alongside aquatic insects, Rotifera and Nematoda therefore also belong to the species inventory of local dendrotelmata. Consequently, future species identification will require dedicated studies using methods specifically adapted to Rotifera and Nematoda.

6. Conclusions

Dendrotelmata are dynamic, nutrient-rich and oxygen-poor microhabitats that harbour a highly specialised fauna. Their community composition shifts with increasing urbanisation, leading to taxon-specific responses. Four taxa showed significant location differences: *Prionocyphon serricornis* and *Aedes geniculatus* were more frequent at the rural location, whilst *Myathropa florea* and *Dasyhelea* were associated with the urban setting. With regard to the non-native mosquito species, a contrary but non-significant trend was observed. *Aedes albopictus* was associated with the urban location, whereas *Aedes japonicus* tended towards rural sites. Both non-native species predominantly colonised ovitraps.

Although dendrotelmata and ovitraps share a largely similar species inventory, they differ significantly in their abiotic properties, species diversity and species composition. Moreover, different types of dendrotelmata vary in water chemistry and fauna, which highlights the relevance of microhabitat heterogeneity within treeholes. In terms of methodology this study demonstrated that, under the given conditions, eDNA metabarcoding was less effective in detecting aquatic insects than morphological identification, but could instead confirm additional animal groups (Rotifera, Nematoda).

Overall, this study demonstrates that urbanisation affects dendrotelmata. Furthermore, it is evident that ovitraps are ecological surrogates with limitations and cannot substitute dendrotelmata from an ecological perspective. But they are still useful as specific monitoring tools for certain taxa such as non-native mosquitoes. eDNA metabarcoding shows promise as a complementary tool but requires methodological refinement to capture the biodiversity of these microhabitats more reliably. For nature conservation this means that the preservation of natural treehole structures is vital and that taxonomic expertise remains important.

7. Literature

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8. Appendix

8.1 Voucher specimens and sequence records

The two Scirtidae species, *Prionocyphon serricornis* (Sample ID: ABOL-25-1208) and *Sacodes flavicollis* (Sample ID: ABOL-25-1236), were sequenced and deposited in the BOLD database as reference records (Ratnasingham & Hebert, 2007). The corresponding voucher specimens were deposited at the Natural History Museum Vienna.

8.2 Supplementary figures

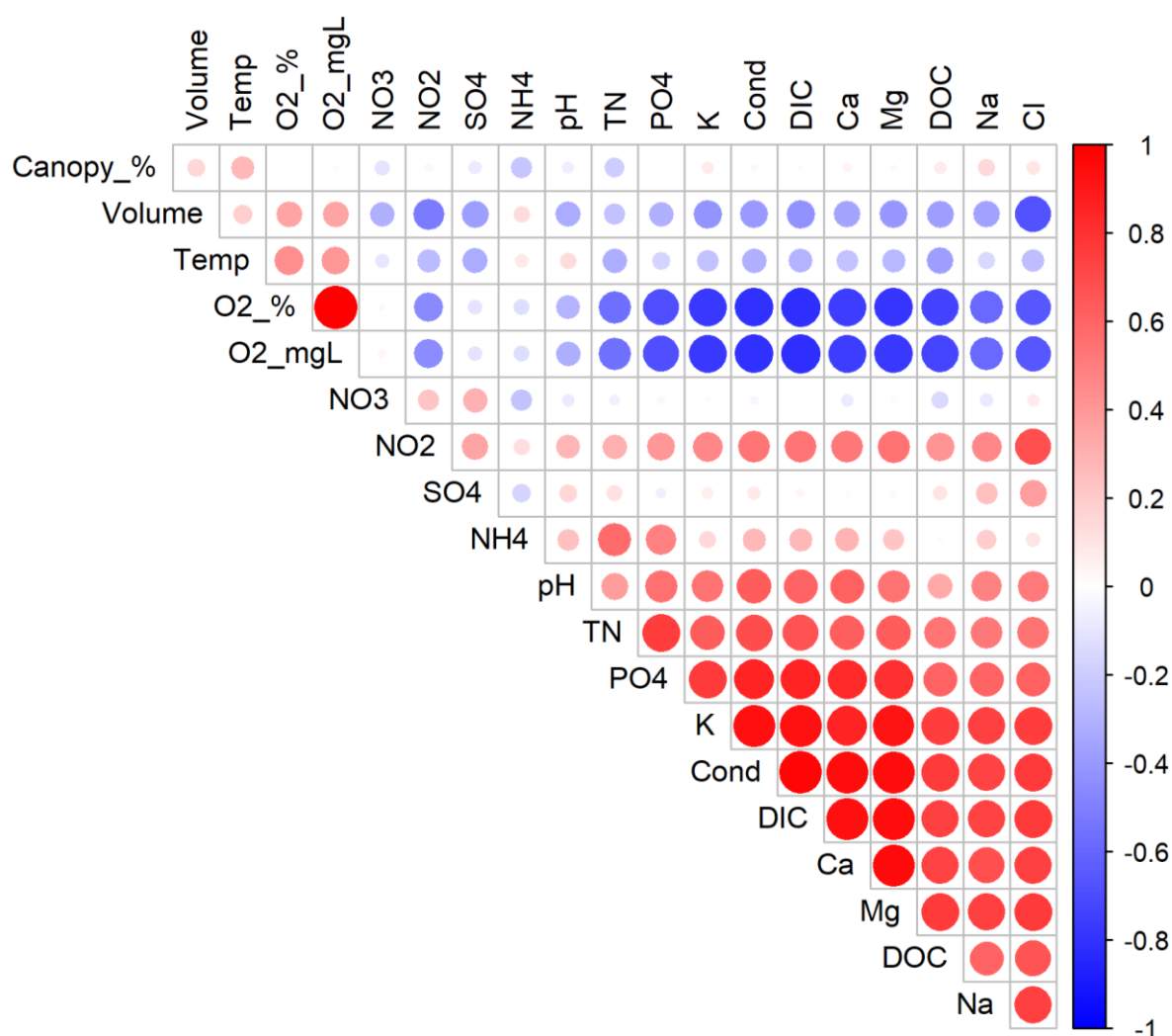


Figure A1: Spearman correlation matrix (Corrplot) of the hydrochemical parameters (abbreviations: Temp = temperature, O₂ = dissolved oxygen, NO₃ = nitrate, NO₂ = nitrite, SO₄ = sulphate, NH₄ = ammonium, TN = total nitrogen, PO₄ = orthophosphate, K = potassium, Cond = conductivity, DIC = dissolved inorganic carbon, Ca = calcium, Mg = magnesium, DOC = dissolved organic carbon, Na = sodium, Cl = chloride) . Blue dots indicate positive and red dots negative correlations.

Taxonomic composition of phytotelmata fauna

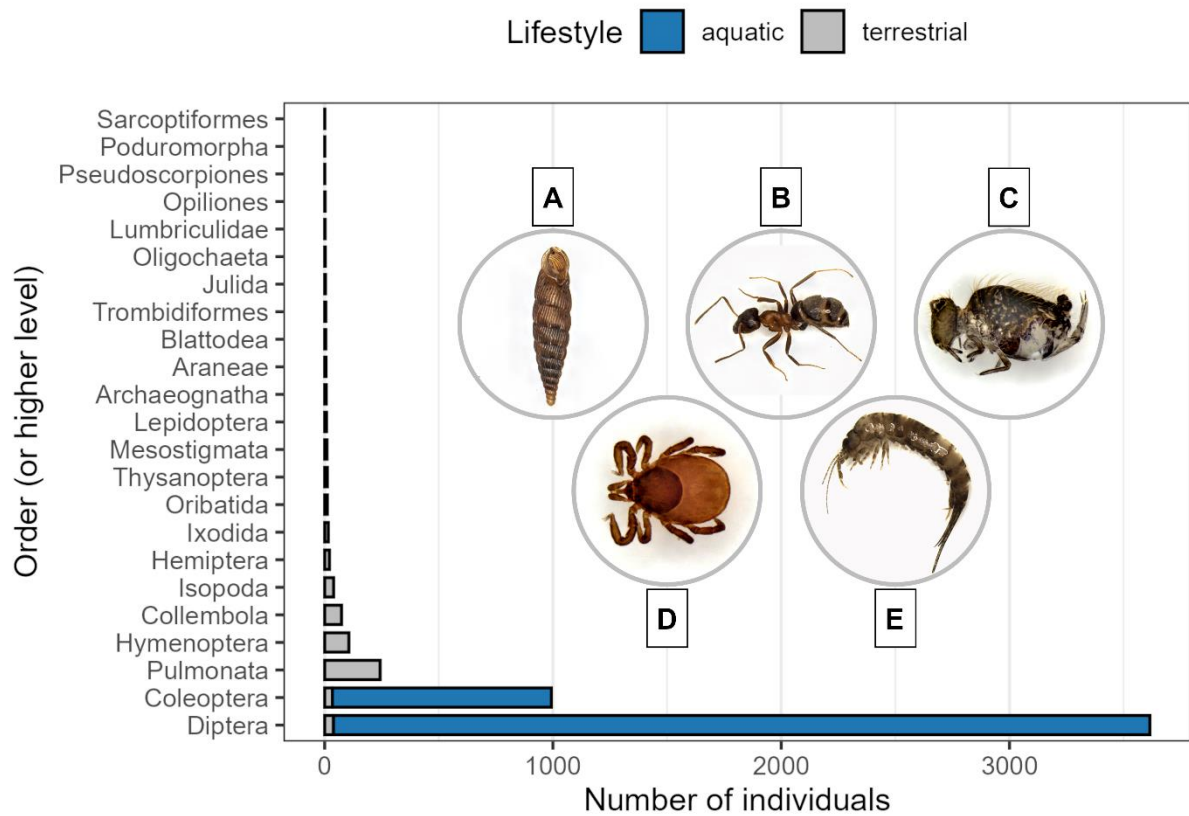


Figure A2: Bar chart showing the number of individuals per order (or higher taxonomic level) and lifestyle. Examples for terrestrial taxa include: (A) Pulmonata, (B) Hymenoptera, (C) Collembola, (D) Ixodidae and (E) and Archaeognatha.

Taxa occurring in dendrotelmata

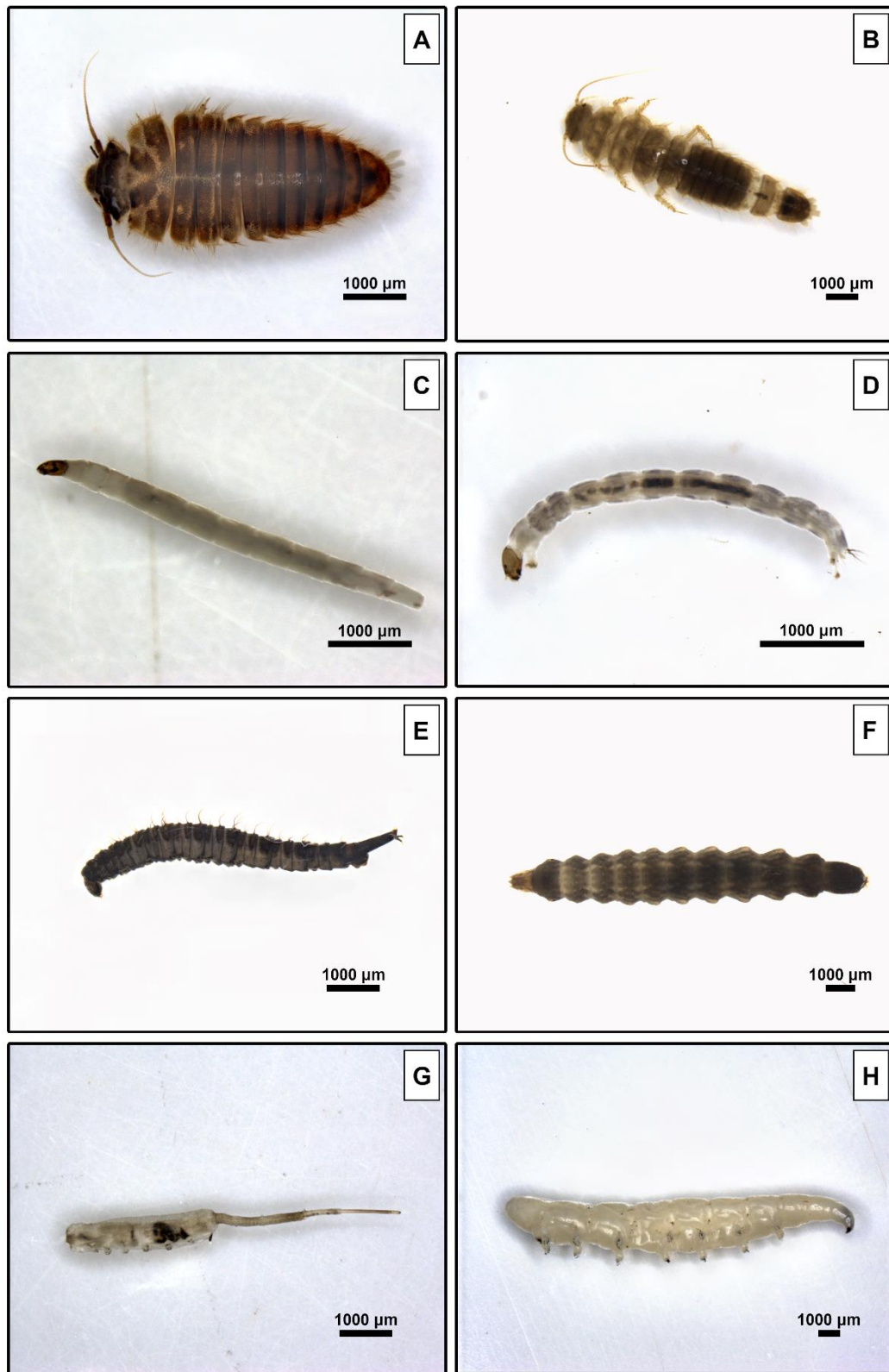


Figure A3: Overview of eight different aquatic insects found in dendrotelmata. Shown are larvae of: (A) *Sacodes flavicollis* (Scirtidae), (B) *Prionocyphon serricornis* (Scirtidae), (C) *Dasyhelea* sp. (Ceratopogonidae), (D) *Metriocnemus cavicola* (Chironomidae), (E) *Clogmia cf. albipunctata*

(Psychodidae), (F) *Odontomyia annulata* (Stratiomyidae), (G) *Myathropaflorea* (Syrphidae) and (H) *Phaonia exoleta* (Muscidae). Scale: 1000 μ m.

Mosquitoes occurring in microhabitats

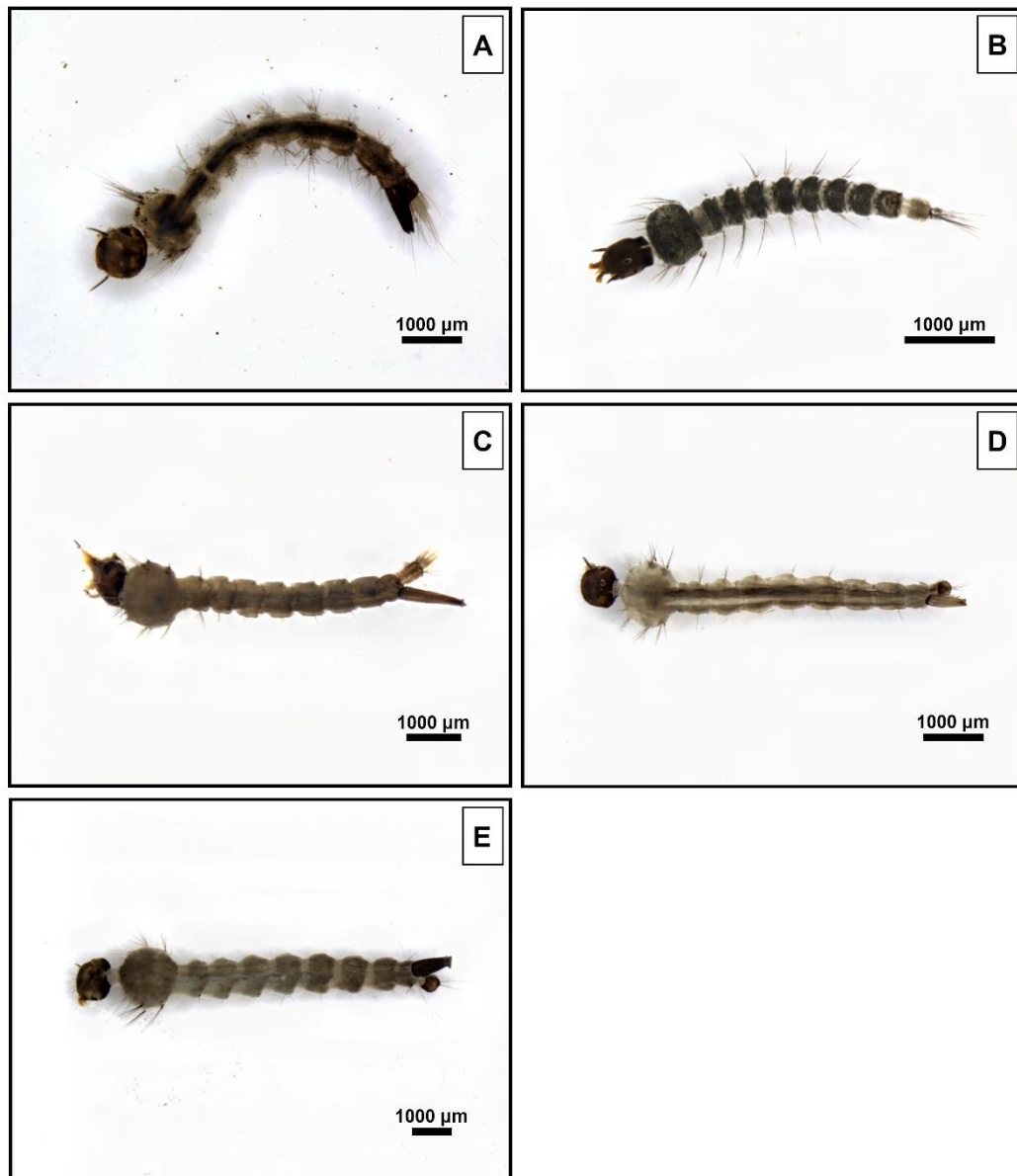


Figure A4: Overview of five different mosquito species (Culicidae) found in microhabitats. Shown are larvae of: (A) *Aedes geniculatus*, (B) *Anopheles plumbeus*, (C) *Culex pipiens* s.l. / *Cx. torrentium*, (D) *Aedes japonicus* and (E) *Aedes albopictus*. Scale: 1000 μ m.

Mammal interactions with dendrotelmata

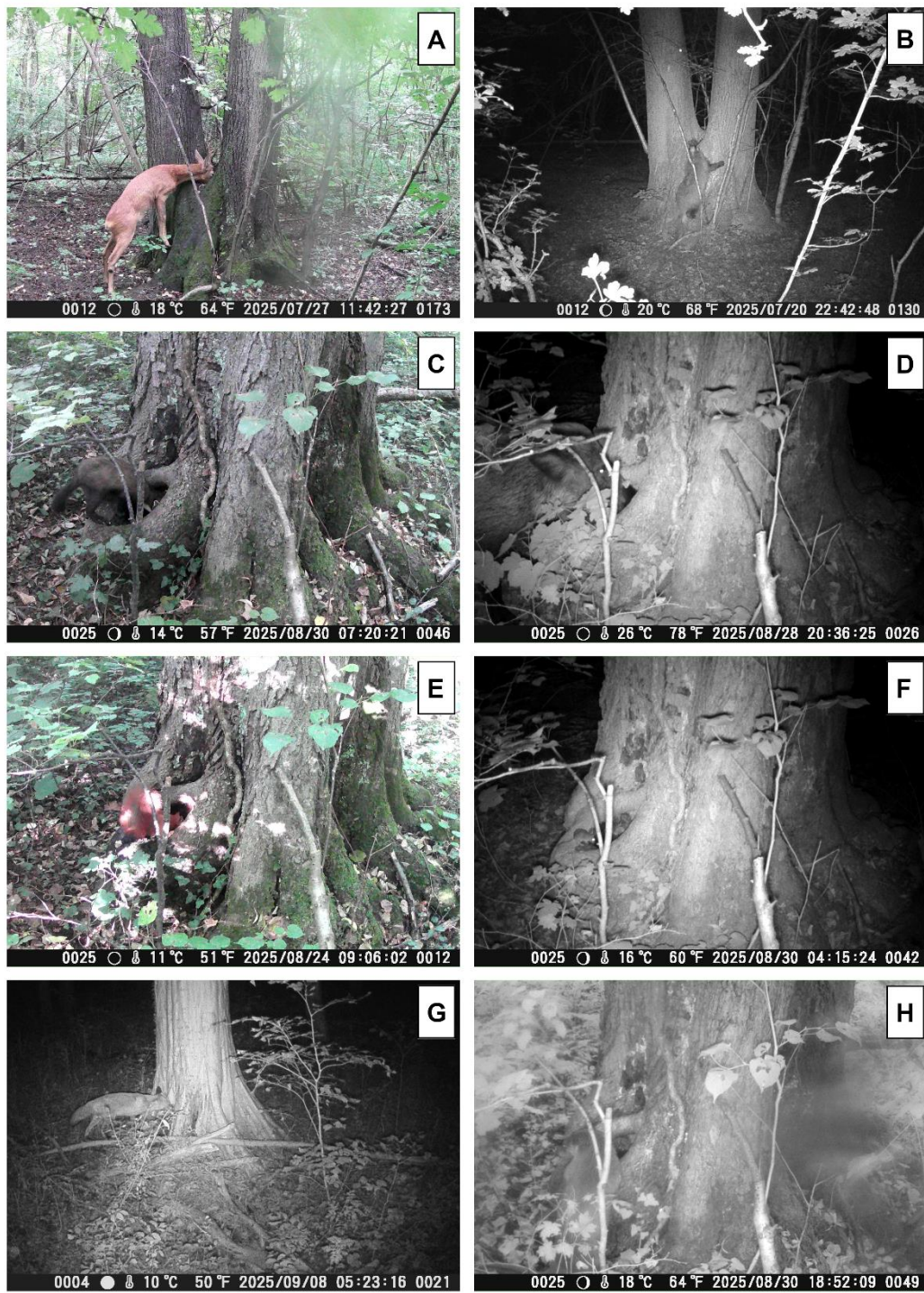


Figure A5: Overview of different mammals interacting with dendrotelmata. Shown are: (A) Roe deer, (B) European badger, (C) Marten, (D) Wild boar, (E) Red squirrel, (F) Murid, (G) Red fox and (H) Eurasian otter.

Avian interactions with dendrotelmata

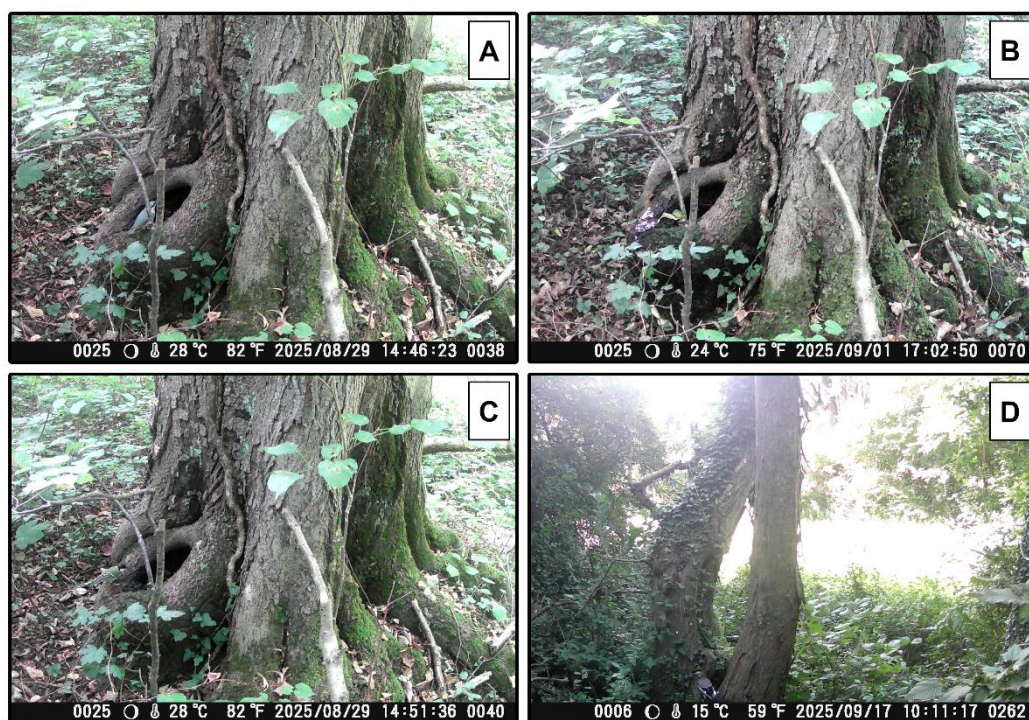


Figure A6: Overview of different birds interacting with dendrotelmata. Shown are: (A) Nuthatch, (B) Robin redbreast, (C) Great tit and (D) Eurasian jay.

8.3 Supplementary tables

Table A1: General site information regarding the plant hosts and their phytotelmata for the *Dipsacus* samples.

Microhabitat code	Microhabitat type	Habitat type	Location	Urbanisation degree	Longitude	Latitude	Plant host	Height (m)	Cardinal direction
DF_001_Orth	herbaceous axillary leaf	natural	Orth	rural	16.6998	48.1434	Dipsacus fullonum		undirected
DF_002_Orth	herbaceous axillary leaf	natural	Orth	rural	16.6998	48.1434	Dipsacus fullonum		undirected
DF_003_Orth	herbaceous axillary leaf	natural	Orth	rural	16.6998	48.1434	Dipsacus fullonum		undirected
DF_004_Orth	herbaceous axillary leaf	natural	Orth	rural	16.6997	48.1435	Dipsacus fullonum		undirected
DF_005_Orth	herbaceous axillary leaf	natural	Orth	rural	16.6997	48.1435	Dipsacus fullonum		undirected

Table A2: Dataset for the hydrochemical analysis of the *Dipsacus* samples (Part 1).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (μS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
DF_001_Orth	Summer	Orth	2025-07-29	2025-08-01	64	8.0	19.5	819.0	7.27	78.7	35.11
DF_002_Orth	Summer	Orth	2025-07-29	2025-08-01	146	7.6	20.7	178.9	9.77	106.5	35.11
DF_003_Orth	Summer	Orth	2025-07-29	2025-08-01	150	7.8	19.3	232.0	6.23	68.6	35.11
DF_004_Orth	Summer	Orth	2025-07-29	2025-08-01	66	8.5	19.7	94.3	11.56	127.4	35.11
DF_005_Orth	Summer	Orth	2025-07-29	2025-08-01	118	7.9	19.1	154.9	9.97	109.2	35.11

Table A3: Dataset for the hydrochemical analysis of the *Dipsacus* samples (Part 2).

Microhabitat code	Season	DOC (mg/L)	DIC (mmol/L)	Dissolved nitrogen (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Nitrate (mg/L)	Nitrite (mg/L)	Sulfate (mg/L)	Ammonium (mg/L)	Phosphate (mg/L)
DF_001_Orth	Summer	45.92	1.7	5.32	1.9	75.1	19.4	3.5	63.3	0.1	0.2	2.0	2.8	14.9
DF_002_Orth	Summer	43.08	1.7	2.27	1.4	51.3	17.6	3.3	31.6	0.0	0.1	0.8	0.0	14.9
DF_003_Orth	Summer	45.00	2.2	2.55	1.6	51.3	24.1	4.2	27.5	0.0	0.1	1.9	0.0	15.8
DF_004_Orth	Summer	32.75	1.1	2.58	2.1	43.2	7.5	1.9	30.9	0.0	0.1	0.7	0.2	7.8
DF_005_Orth	Summer	89.33	1.4	2.65	4.6	51.2	9.8	2.5	29.3	0.1	0.1	2.4	0.0	13.0

Table A4: Dataset for the fauna inventory of the *Dipsacus* samples.

Microhabitat code	Season	Location	Sampling date	Identification date	Dasyhelea sp.
DF_001_Orth	Summer	Orth	2025-07-29	2025-08-16	347
DF_002_Orth	Summer	Orth	2025-07-29	2025-08-17	313
DF_003_Orth	Summer	Orth	2025-07-29	2025-08-17	301
DF_004_Orth	Summer	Orth	2025-07-29	2025-08-18	256
DF_005_Orth	Summer	Orth	2025-07-29	2025-08-18	242

Table A5: General site information regarding the plant hosts and their phytotelmata for the dendrotelmata samples (Part 1).

Microhabitat code	Microhabitat type	Habitat type	Location	Urbanisation degree	Longitude	Latitude	Plant host	Height (m)	Cardinal direction
DT_003_Orth	coppice stool	natural	Orth	rural	16.6924	48.1438	Fraxinus excelsior	1.10	undirected
DT_004_Orth	coppice stool	natural	Orth	rural	16.6898	48.1412	Carpinus betulus	0.35	undirected
DT_005_Orth	coppice stool	natural	Orth	rural	16.6899	48.1411	Carpinus betulus	0.60	West
DT_009_Orth	trunk pool	natural	Orth	rural	16.6825	48.1403	Carpinus betulus	0.30	
DT_012_Orth	coppice stool	natural	Orth	rural	16.6831	48.1404	Tilia sp.	0.70	
DT_013_Orth	trunk pool	natural	Orth	rural	16.6790	48.1389	Carpinus betulus	0.20	Southwest
DT_014_Orth	coppice stool	natural	Orth	rural	16.6788	48.1393	Tilia sp.	0.30	undirected
DT_018_Orth	coppice stool	natural	Orth	rural	16.6741	48.1422	Populus alba	1.35	undirected
DT_020_Orth	trunk pool	natural	Orth	rural	16.6806	48.1429	Carpinus betulus	0.20	
DT_022_Orth	trunk pool	natural	Orth	rural	16.6844	48.1426	Tilia sp.	0.40	East
DT_023_Orth	coppice stool	natural	Orth	rural	16.6928	48.1435	Fraxinus excelsior	0.50	North
DT_024_Orth	trunk pool	natural	Orth	rural	16.6740	48.1392	Carpinus betulus	0.40	North
DT_025_Orth	coppice stool	natural	Orth	rural	16.6912	48.1413	Carpinus betulus	0.80	undirected
DT_026_Orth	trunk pool	natural	Orth	rural	16.6829	48.1407	Carpinus betulus	0.20	Southeast
DT_027_Orth	coppice stool	natural	Orth	rural	16.6706	48.1396	Populus alba	0.60	undirected

Table A6: General site information regarding the plant hosts and their phytotelmata for the dendrotelmata samples (Part 2).

Microhabitat code	Microhabitat type	Habitat type	Location	Urbanisation degree	Longitude	Latitude	Plant host	Height (m)	Cardinal direction
DT_001_Prater	coppice stool	natural	Prater	urban	16.4269	48.1998	Acer sp.	0.40	undirected
DT_002_Prater	branch hollow	natural	Prater	urban	16.4271	48.1997	Fraxinus excelsior	0.30	West
DT_005_Prater	coppice stool	natural	Prater	urban	16.4281	48.1993	Acer sp.	1.00	undirected
DT_006_Prater	coppice stool	natural	Prater	urban	16.4319	48.1957	Acer sp.	1.10	South
DT_009_Prater	trunk pool	natural	Prater	urban	16.4329	48.1946	Carpinus betulus	0.20	South
DT_011_Prater	branch hollow	natural	Prater	urban	16.4277	48.1946	Acer sp.	0.40	Northwest
DT_013_Prater	branch hollow	natural	Prater	urban	16.4273	48.1948	Acer sp.	0.40	Southeast
DT_014_Prater	trunk pool	natural	Prater	urban	16.4326	48.1947	Carpinus betulus	0.30	South
DT_015_Prater	coppice stool	natural	Prater	urban	16.4271	48.1951	Fraxinus excelsior	0.60	undirected
DT_016_Prater	coppice stool	natural	Prater	urban	16.4261	48.1947	Acer sp.	0.40	undirected
DT_017_Prater	branch hollow	natural	Prater	urban	16.4346	48.1959	Acer sp.	1.30	Northwest
DT_018_Prater	coppice stool	natural	Prater	urban	16.4355	48.1962	Aesculus hippocastanum	1.00	South
DT_019_Prater	coppice stool	natural	Prater	urban	16.4351	48.1939	Acer sp.	0.50	undirected
DT_020_Prater	branch hollow	natural	Prater	urban	16.4351	48.1939	Acer sp.	0.30	Northeast
DT_021_Prater	branch hollow	natural	Prater	urban	16.4310	48.1942	Acer sp.	0.50	Northwest
DT_022_Prater	branch hollow	natural	Prater	urban	16.4273	48.1950	Acer sp.	1.8	South

Table A7: General site information regarding the ovitrap samples.

Microhabitat code	Microhabitat type	Habitat type	Location	Urbanisation degree	Longitude	Latitude	Plant host	Height (m)	Cardinal direction
OT_001_Orth	plastic bucket	artificial	Orth	rural	16.6927	48.1436	Ovitrap	0.4	North
OT_002_Orth	plastic bucket	artificial	Orth	rural	16.6888	48.1399	Ovitrap	0.2	South
OT_003_Orth	plastic bucket	artificial	Orth	rural	16.6827	48.1404	Ovitrap	0.6	Southwest
OT_004_Orth	plastic bucket	artificial	Orth	rural	16.6719	48.1407	Ovitrap	0.1	Northwest
OT_005_Orth	plastic bucket	artificial	Orth	rural	16.6818	48.1432	Ovitrap	0.5	North
OT_006_Orth	plastic bucket	artificial	Orth	rural	16.6998	48.1434	Ovitrap	0.2	undirected
OT_007_Orth	plastic bucket	artificial	Orth	rural	16.6998	48.1434	Ovitrap	0.2	undirected
OT_008_Orth	plastic bucket	artificial	Orth	rural	16.6998	48.1434	Ovitrap	0.2	undirected
OT_009_Orth	plastic bucket	artificial	Orth	rural	16.6997	48.1435	Ovitrap	0.2	undirected
OT_010_Orth	plastic bucket	artificial	Orth	rural	16.6997	48.1435	Ovitrap	0.2	undirected
OT_001_Prater	plastic bucket	artificial	Prater	urban	16.4275	48.1992	Ovitrap	0.4	South
OT_002_Prater	plastic bucket	artificial	Prater	urban	16.4312	48.1960	Ovitrap	0.2	South
OT_003_Prater	plastic bucket	artificial	Prater	urban	16.4335	48.1946	Ovitrap	0.1	West
OT_004_Prater	plastic bucket	artificial	Prater	urban	16.4307	48.1939	Ovitrap	0.3	Northwest
OT_005_Prater	plastic bucket	artificial	Prater	urban	16.4273	48.1949	Ovitrap	0.3	East

Table A8: Dataset for the hydrochemical analysis of the dendrotermata samples (Part 1).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (µS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
DT_003_Orth	Spring	Orth	2025-05-26	2025-05-29	498	6.90	13.5	647	0.23	0.50	88.37
DT_004_Orth	Spring	Orth	2025-05-26	2025-05-29	300	7.30	13.8	442	0.23	2.43	93.36
DT_009_Orth	Spring	Orth	2025-05-26	2025-05-29	135	6.90	13.1	402	0.54	5.20	96.40
DT_013_Orth	Spring	Orth	2025-05-26	2025-05-29	115	7.10	13.1	639	0.48	4.50	92.41
DT_020_Orth	Spring	Orth	2025-05-26	2025-05-29	95	6.40	15.4	120.4	3.24	32.8	90.54
DT_001_Prater	Spring	Prater	2025-05-28	2025-05-29	55	7.80	16.9	1924	0.74	7.80	86.72
DT_002_Prater	Spring	Prater	2025-05-28	2025-05-29	330	6.90	14.6	751	0.71	7.10	87.30
DT_005_Prater	Spring	Prater	2025-05-28	2025-05-29	240	7.00	15.6	494	1.49	15.30	87.17
DT_006_Prater	Spring	Prater	2025-05-28	2025-05-29	670	7.80	14.8	2340	0.20	2.10	84.61
DT_009_Prater	Spring	Prater	2025-05-28	2025-05-29	1830	6.80	14.5	281	1.18	11.60	88.19
DT_005_Orth	Summer	Orth	2025-07-29	2025-08-01	132	6.90	18.6	487	0.48	5.40	80.99
DT_012_Orth	Summer	Orth	2025-07-29	2025-08-01	4100	7.20	17.8	622	0.53	5.70	85.61
DT_018_Orth	Summer	Orth	2025-07-29	2025-08-01	310	7.10	17.3	495	0.35	3.80	97.99
DT_023_Orth	Summer	Orth	2025-07-29	2025-08-01	2100	7.20	19.2	634	0.35	3.90	79.47
DT_024_Orth	Summer	Orth	2025-07-29	2025-08-01	290	6.20	18.0	84.2	0.26	2.3	81.86

Table A9: Dataset for the hydrochemical analysis of the dendrotelmata samples (Part 2).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (µS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
DT_011_Prater	Summer	Prater	2025-07-31	2025-08-01	165	8.50	18.4	6120	0.02	0.40	83.92
DT_013_Prater	Summer	Prater	2025-07-31	2025-08-01	64	7.80	19.6	1892	0.11	1.20	85.51
DT_014_Prater	Summer	Prater	2025-07-31	2025-08-01	2370	6.70	17.4	409.0	0.74	7.9	85.66
DT_015_Prater	Summer	Prater	2025-07-31	2025-08-01	3200	7.30	18.2	1123	0.11	1.20	86.45
DT_016_Prater	Summer	Prater	2025-07-31	2025-08-01	106	7.30	19.2	1049	0.09	1.20	83.71
DT_014_Orth	Autumn	Orth	2025-10-06	2025-10-10	3108	6.80	10.0	473	2.65	23.50	85.49
DT_022_Orth	Autumn	Orth	2025-10-06	2025-10-10	886	7.06	10.9	636.0	0.03	0.3	86.62
DT_025_Orth	Autumn	Orth	2025-10-06	2025-10-10	372	6.44	9.8	226	1.68	14.80	85.13
DT_026_Orth	Autumn	Orth	2025-10-06	2025-10-10	88	5.68	10.9	101.3	0.17	1.8	83.47
DT_027_Orth	Autumn	Orth	2025-10-06	2025-10-10	662	6.79	10.8	569	0.30	2.90	90.23
DT_017_Prater	Autumn	Prater	2025-10-09	2025-10-10	110	8.80	13.5	6080	0.02	0.20	90.06
DT_018_Prater	Autumn	Prater	2025-10-09	2025-10-10	175	6.90	12.4	447	0.44	4.20	84.97
DT_019_Prater	Autumn	Prater	2025-10-09	2025-10-10	90	7.30	13.3	917	0.04	0.40	88.72
DT_020_Prater	Autumn	Prater	2025-10-09	2025-10-10	60	8.70	14.1	4760	0.03	0.40	86.84
DT_021_Prater	Autumn	Prater	2025-10-09	2025-10-10	170	7.70	13.5	821	2.28	21.90	86.33
DT_022_Prater	Autumn	Prater	2025-10-09	2025-10-10	100	8.60	14.3	7490	0.02	0.20	88.37

Table A10: Dataset for the hydrochemical analysis of the dendrotelmata samples (Part 3).

Microhabitat code	Season	DOC (mg/L)	DIC (mmol/L)	Dissolved nitrogen (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Nitrate (mg/L)	Nitrite (mg/L)	Sulfate (mg/L)	Ammonium (mg/L)	Phosphate (mg/L)
DT_003_Orth	Spring	141.03	6.8	12.30	3.4	102.6	49.1	15.3	26.4	0.8	0.2	1.7	6.6	9.3
DT_004_Orth	Spring	59.81	4.3	3.85	0.9	27.7	30.0	7.1	16.8	7.9	0.2	7.0	35.8	11.6
DT_009_Orth	Spring	60.48	4.6	22.59	2.2	40.9	29.3	9.7	31.5	0.3	0.1	2.1	19.4	18.0
DT_013_Orth	Spring	160.77	5.7	33.08	3.6	50.3	66.4	21.9	45.0	0.1	0.2	3.8	23.5	76.2
DT_020_Orth	Spring	58.63	1.5	8.42	2.4	30.8	16.1	4.5	30.3	11.3	0.2	4.3	2.4	2.0
DT_001_Prater	Spring	198.27	11.8	18.78	60.1	458.8	73.2	18.8	51.6	3.4	0.6	47.2	8.0	19.8
DT_002_Prater	Spring	112.88	7.4	11.22	8.0	166.1	37.5	10.3	34.1	2.3	0.2	2.2	6.0	5.3
DT_005_Prater	Spring	6.29	4.5	10.20	7.8	94.1	35.0	8.8	23.9	0.2	0.1	4.3	3.5	4.7
DT_006_Prater	Spring	23.52	17.4	18.94	41.2	486.3	112.9	34.1	137.1	1.0	0.6	7.9	9.2	21.7
DT_009_Prater	Spring	208.79	2.7	6.00	5.3	53.5	14.3	4.4	12.2	0.0	0.0	3.1	0.0	0.1
DT_005_Orth	Summer	63.43	5.4	5.42	3.3	51.0	41.9	15.0	19.8	0.4	0.1	1.0	3.1	7.6
DT_012_Orth	Summer	100.87	6.3	11.19	2.0	58.5	76.1	14.4	18.2	0.2	0.1	1.0	10.5	5.5
DT_018_Orth	Summer	77.52	4.9	7.86	2.0	58.3	51.1	14.0	24.3	0.2	0.1	1.6	6.4	11.9
DT_023_Orth	Summer	199.08	4.5	11.63	11.3	109.9	41.4	10.8	39.9	0.1	0.1	5.1	8.1	17.9
DT_024_Orth	Summer	51.26	1.1	3.03	1.7	16.3	10.8	3.0	18.3	4.5	0.0	2.1	0.0	1.3

Table A11: Dataset for the hydrochemical analysis of the dendrotelmata samples (Part 4).

Microhabitat code	Season	DOC (mg/L)	DIC (mmol/L)	Dissolved nitrogen (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Nitrate (mg/L)	Nitrite (mg/L)	Sulfate (mg/L)	Ammonium (mg/L)	Phosphate (mg/L)
DT_011_Prater	Summer	1595.43	71.6	1.38	53.0	2310.8	130.5	103.8	44.8	0.4	0.5	1.6	0.0	47.0
DT_013_Prater	Summer	207.70	21.2	10.55	87.3	316.6	89.8	70.3	77.0	0.8	0.6	2.2	1.5	46.6
DT_014_Prater	Summer	58.53	3.8	4.47	9.5	51.8	27.4	9.2	11.3	0.2	0.1	3.0	3.2	8.3
DT_015_Prater	Summer	131.70	12.1	20.72	5.5	140.6	107.8	20.6	10.8	0.1	0.1	0.7	18.5	20.9
DT_016_Prater	Summer	109.99	10.3	16.72	4.9	233.9	64.8	18.5	46.3	0.1	0.2	1.6	11.6	54.2
DT_014_Orth	Autumn	115.17	4.0	11.88	1.9	45.3	45.2	13.1	16.8	0.2	0.2	0.7	7.9	24.3
DT_022_Orth	Autumn	100.78	5.8	5.36	1.0	107.3	50.6	13.0	16.9	0.2	0.1	0.5	0.3	12.6
DT_025_Orth	Autumn	116.55	1.6	5.48	2.5	25.3	25.3	7.3	22.6	0.0	0.2	2.7	0.0	0.7
DT_026_Orth	Autumn	172.61	2.9	3.39	6.8	32.8	14.7	3.4	58.2	0.0	0.2	3.9	0.0	0.2
DT_027_Orth	Autumn	148.31	5.1	8.40	1.4	73.1	50.0	15.3	14.9	0.4	0.1	0.9	3.1	9.0
DT_017_Prater	Autumn	1161.90	57.0	53.64	74.0	1921.0	104.0	53.0	114.0	3.0	1.0	10.0	0.0	36.0
DT_018_Prater	Autumn	187.30	3.2	14.15	0.0	63.0	18.0	5.0	41.0	2.0	0.0	6.0	0.0	11.0
DT_019_Prater	Autumn	101.40	7.7	9.22	0.0	78.0	58.0	14.0	130.0	1.0	1.0	6.0	0.0	4.0
DT_020_Prater	Autumn	480.40	38.0	25.53	188.0	889.0	45.0	29.0	102.0	2.0	1.0	7.0	0.0	23.0
DT_021_Prater	Autumn	45.26	8.1	2.80	4.1	186.3	35.1	12.4	27.4	0.7	0.1	1.6	0.0	6.6
DT_022_Prater	Autumn	2552.80	64.0	70.24	61.0	2387.0	139.0	77.0	71.0	2.0	0.0	5.0	0.0	32.0

Table A12: Dataset for the hydrochemical analysis of the ovitrap samples (Part 1).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (µS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
OT_001_Orth	Spring	Orth	2025-05-26	2025-05-29	730	6.70	14.8	97.8	0.91	9.2	89.56
OT_002_Orth	Spring	Orth	2025-05-26	2025-05-29	610	6.50	15.8	37.2	7.70	79.4	87.32
OT_003_Orth	Spring	Orth	2025-05-26	2025-05-29	720	6.60	15.9	49.1	5.61	57.8	88.55
OT_004_Orth	Spring	Orth	2025-05-26	2025-05-29	730	6.60	16.9	35.3	6.71	70.7	92.17
OT_005_Orth	Spring	Orth	2025-05-26	2025-05-29	685	6.94	17.4	31.8	7.86	83.2	89.12
OT_001_Prater	Spring	Prater	2025-05-28	2025-05-29	605	6.90	16.9	50.5	7.13	75.1	90.65
OT_002_Prater	Spring	Prater	2025-05-28	2025-05-29	630	7.00	16.4	83.2	6.35	65.7	86.83
OT_003_Prater	Spring	Prater	2025-05-28	2025-05-29	655	6.90	16.5	76.9	6.31	65.8	88.41
OT_004_Prater	Spring	Prater	2025-05-28	2025-05-29	600	6.70	16.5	86.9	1.72	17.9	88.59
OT_005_Prater	Spring	Prater	2025-05-28	2025-05-29	500	7.00	16.7	90.2	4.82	50.5	88.64
OT_001_Orth	Summer	Orth	2025-07-29	2025-08-01	710	7.20	18.1	219.0	2.11	22.3	88.71
OT_002_Orth	Summer	Orth	2025-07-29	2025-08-01	750	6.90	18.8	164.2	0.92	10.2	85.45
OT_003_Orth	Summer	Orth	2025-07-29	2025-08-01	790	7.10	18.6	177.0	2.25	24.5	90.42
OT_004_Orth	Summer	Orth	2025-07-29	2025-08-01	835	7.40	18.6	207.0	3.86	41.8	95.25
OT_005_Orth	Summer	Orth	2025-07-29	2025-08-01	800	7.20	18.6	185.5	3.64	39.6	94.53

Table A13: Dataset for the hydrochemical analysis of the ovitrap samples (Part 2).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (µS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
OT_006_Orth	Summer	Orth	2025-07-29	2025-08-01	624	7.10	19.6	47.7	7.85	86.8	35.11
OT_007_Orth	Summer	Orth	2025-07-29	2025-08-01	870	6.90	22.4	59.2	6.75	79.0	35.11
OT_008_Orth	Summer	Orth	2025-07-29	2025-08-01	774	6.70	20.8	44.0	7.04	79.8	35.11
OT_009_Orth	Summer	Orth	2025-07-29	2025-08-01	810	7.10	20.3	49.2	8.70	97.6	35.11
OT_010_Orth	Summer	Orth	2025-07-29	2025-08-01	850	7.10	21.5	45.4	8.51	97.3	35.11
OT_001_Prater	Summer	Prater	2025-07-31	2025-08-01	118	7.40	18.6	372.0	3.48	37.8	89.41
OT_002_Prater	Summer	Prater	2025-07-31	2025-08-01	480	7.70	17.7	553.0	2.50	26.8	86.42
OT_003_Prater	Summer	Prater	2025-07-31	2025-08-01	136	7.50	18.4	307.0	3.87	41.8	87.54
OT_004_Prater	Summer	Prater	2025-07-31	2025-08-01	90	7.60	19.8	252.0	5.18	57.5	91.03
OT_005_Prater	Summer	Prater	2025-07-31	2025-08-01	480	7.30	20.2	375.0	1.35	15.2	92.06
OT_001_Orth	Autumn	Orth	2025-10-06	2025-10-10	578	6.91	9.8	366.0	0.34	3.1	93.99
OT_002_Orth	Autumn	Orth	2025-10-06		0						89.86
OT_003_Orth	Autumn	Orth	2025-10-06	2025-10-10	600	7.63	10.3	1263.0	0.02	0.2	89.99
OT_004_Orth	Autumn	Orth	2025-10-06	2025-10-10	750	7.51	11.0	305.0	3.21	29.4	88.27
OT_005_Orth	Autumn	Orth	2025-10-06	2025-10-10	804	6.96	11.8	168.2	1.82	16.9	88.54

Table A14: Dataset for the hydrochemical analysis of the ovitrap samples (Part 3).

Microhabitat code	Season	Location	Sampling date	Laboratory date	Volume (mL)	pH	Temperature (°C)	Conductivity (µS/cm)	Dissolved O2 (mg/L)	Dissolved O2 (%)	Canopy cover (closed, %)
OT_001_Prater	Autumn	Prater	2025-10-09		0						89.81
OT_002_Prater	Autumn	Prater	2025-10-09		0						87.12
OT_003_Prater	Autumn	Prater	2025-10-09		0						86.80
OT_004_Prater	Autumn	Prater	2025-10-09	2025-10-10	90	7.80	14.6	500.0	4.65	46.5	88.59
OT_005_Prater	Autumn	Prater	2025-10-09	2025-10-10	125	7.60	14.6	495.0	0.02	0.3	87.38

Table A15: Dataset for the hydrochemical analysis of the ovitrap samples (Part 4).

Microhabitat code	Season	DOC (mg/L)	DIC (mmol/L)	Dissolved nitrogen (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Nitrate (mg/L)	Nitrite (mg/L)	Sulfate (mg/L)	Ammonium (mg/L)	Phosphate (mg/L)
OT_001_Orth	Spring	24.90	1.4	6.59	0.0	20.1	3.2	1.7	7.0	0.5	0.2	3.9	5.2	1.2
OT_002_Orth	Spring	15.05	0.9	2.07	0.0	7.6	2.6	0.8	5.5	4.0	0.0	2.0	0.0	0.1
OT_003_Orth	Spring	10.44	0.9	3.69	0.0	9.4	2.9	0.9	5.6	3.8	0.1	2.5	1.6	0.4
OT_004_Orth	Spring	10.32	0.9	1.76	0.0	6.0	4.4	1.6	5.1	2.9	0.0	3.5	0.0	0.2
OT_005_Orth	Spring	16.06	0.9	3.73	0.0	11.1	4.8	1.6	9.6	6.3	0.1	4.2	0.4	0.2
OT_001_Prater	Spring	10.97	0.5	2.44	0.0	9.7	3.8	1.3	6.3	4.3	0.1	2.3	0.1	0.0
OT_002_Prater	Spring	14.15	0.9	3.31	0.0	12.2	5.5	1.3	5.8	0.6	0.0	2.4	2.4	0.6
OT_003_Prater	Spring	15.13	0.7	6.05	0.0	9.4	3.1	1.0	4.7	2.2	0.1	2.5	3.2	0.5
OT_004_Prater	Spring	41.35	0.7	1.78	0.0	14.4	5.5	2.9	6.2	0.0	0.1	2.8	0.0	0.1
OT_005_Prater	Spring	19.68	1.1	5.65	0.0	15.2	4.4	1.4	8.2	0.6	0.1	2.9	4.3	2.3
OT_001_Orth	Summer	43.21	2.2	10.58	1.2	28.9	13.6	4.9	8.6	0.1	0.0	1.1	10.4	2.3
OT_002_Orth	Summer	34.22	1.7	8.12	1.5	21.4	11.5	3.2	12.6	0.2	0.0	0.6	9.1	3.5
OT_003_Orth	Summer	22.70	2.0	6.60	0.6	16.2	15.8	2.7	6.3	0.1	0.0	1.3	7.7	4.1
OT_004_Orth	Summer	17.72	2.3	6.01	2.0	12.5	20.0	3.2	8.4	0.1	0.0	1.0	7.0	4.8
OT_005_Orth	Summer	46.15	2.1	7.07	1.7	20.3	16.4	3.5	8.9	0.2	0.0	1.2	6.5	1.1
OT_006_Orth	Summer	13.20	0.8	1.26	17.9	10.9	7.6	3.9	55.4	0.7	0.2	6.5	0.2	0.0

Table A16: Dataset for the hydrochemical analysis of the ovitrap samples (Part 5).

Microhabitat code	Season	DOC (mg/L)	DIC (mmol/L)	Dissolved nitrogen (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Nitrate (mg/L)	Nitrite (mg/L)	Sulfate (mg/L)	Ammonium (mg/L)	Phosphate (mg/L)
OT_007_Orth	Summer	17.01	0.7	1.47	0.0	11.2	6.0	1.4	9.7	0.3	0.1	3.1	0.4	0.1
OT_008_Orth	Summer	17.80	0.4	1.44	0.0	7.2	3.7	1.0	5.4	0.3	0.0	2.5	0.4	0.4
OT_009_Orth	Summer	20.57	0.6	1.49	0.0	6.6	4.4	1.1	5.9	0.2	0.0	2.2	0.0	0.2
OT_010_Orth	Summer	23.11	0.8	1.13	0.0	6.9	5.0	1.2	5.3	0.0	0.0	1.2	0.0	0.1
OT_001_Prater	Summer	42.00	3.1	6.66	2.6	68.2	22.2	8.8	38.3	0.4	0.2	1.9	6.3	4.7
OT_002_Prater	Summer	85.92	4.9	14.91	3.8	81.8	40.0	11.0	18.4	0.1	0.0	2.0	11.3	31.2
OT_003_Prater	Summer	64.52	2.8	5.13	0.7	50.8	25.9	7.6	18.9	0.1	0.1	2.3	0.4	4.2
OT_004_Prater	Summer	42.13	2.8	3.56	1.8	38.8	27.1	6.3	24.5	0.2	0.1	2.7	2.0	0.5
OT_005_Prater	Summer	54.98	3.0	7.13	2.3	70.8	17.9	6.1	21.3	0.1	0.0	1.3	6.5	14.2
OT_001_Orth	Autumn	99.01	2.7	4.44	7.5	59.0	15.9	11.0	13.3	0.4	0.0	19.2	0.0	0.1
OT_002_Orth	Autumn													
OT_003_Orth	Autumn	116.58	8.3	74.12	65.9	53.7	40.7	12.9	129.4	0.0	0.6	5.3	77.6	22.7
OT_004_Orth	Autumn	29.44	2.7	14.56	2.6	14.4	23.4	3.4	11.6	0.1	0.0	8.2	18.2	8.8
OT_005_Orth	Autumn	63.36	1.6	2.25	0.0	21.1	17.6	4.8	7.9	0.1	0.0	2.0	0.0	0.0
OT_001_Prater	Autumn													
OT_002_Prater	Autumn													
OT_003_Prater	Autumn													
OT_004_Prater	Autumn	343.06	3.5	5.52	3.0	50.3	43.0	8.3	67.3	0.3	0.3	9.2	4.6	1.6
OT_005_Prater	Autumn	49.33	5.0	5.42	2.1	44.8	51.8	8.5	34.6	0.2	0.2	4.2	3.6	5.6

Table A17: List of abbreviations for taxon tables.

Taxon	Abbreviation
<i>Aedes albopictus</i>	Ae. alb.
<i>Aedes geniculatus</i>	Ae. gen.
<i>Aedes japonicus</i>	Ae. jap.
<i>Anopheles plumbeus</i>	An. plu.
<i>Beris</i> sp.	B. sp.
<i>Clogmia cf. albipunctata</i>	C. alb.
<i>Culex pipiens</i> s.l.	Cx. pip.
<i>Dasyhelea</i> sp.	D. sp.
<i>Metriocnemus cavicola</i>	M. cav.
<i>Myathropa florea</i>	M. flo.
<i>Odontomyia annulata</i>	O. ann.
<i>Pachygaster</i> sp.	P. sp.
<i>Phaonia exoleta</i>	P. exo.
<i>Prionocyphon serricornis</i>	P. ser.
<i>Sacodes flavicollis</i>	S. fla.

Table A18: Dataset for the fauna analysis of the dendrotelmata samples showing individual abundances per taxon (Part 1).

Microhabitat code	Season	Location	Ae. gen.	Ae. jap.	An. plu.	C. alb.	Cx. pip.	D. sp.	M. cav.	M. flo.	O. ann.	P. sp.	P. exo.	P. ser.	S. fla.
DT_003_Orth	Spring	Orth	0	0	0	0	0	0	38	2	0	0	1	64	0
DT_004_Orth	Spring	Orth	21	0	0	0	0	0	23	0	0	0	0	115	0
DT_009_Orth	Spring	Orth	18	0	0	0	0	0	9	0	0	0	5	5	0
DT_013_Orth	Spring	Orth	6	0	0	0	0	0	15	2	0	0	3	3	0
DT_020_Orth	Spring	Orth	27	0	0	0	0	0	93	2	0	0	0	0	0
DT_002_Prater	Spring	Prater	0	0	0	0	0	0	5	3	0	0	0	9	0
DT_001_Prater	Spring	Prater	0	0	0	0	0	15	19	1	0	0	2	7	0
DT_005_Prater	Spring	Prater	13	0	0	0	0	4	2	26	0	0	0	0	0
DT_006_Prater	Spring	Prater	3	0	0	0	0	15	12	20	0	0	0	1	0
DT_009_Prater	Spring	Prater	34	0	0	0	0	2	1	10	0	0	0	1	0
DT_005_Orth	Summer	Orth	10	0	0	0	0	2	301	1	0	0	0	14	0
DT_012_Orth	Summer	Orth	97	0	0	0	0	0	1	0	0	0	0	210	0
DT_018_Orth	Summer	Orth	90	0	0	1	0	0	57	4	0	0	0	14	0
DT_023_Orth	Summer	Orth	147	0	0	0	0	1	7	0	0	0	1	24	0
DT_024_Orth	Summer	Orth	8	0	0	0	0	0	4	0	0	0	0	18	0
DT_011_Prater	Summer	Prater	1	0	5	20	0	2	0	10	30	0	2	37	6
DT_013_Prater	Summer	Prater	3	0	0	4	0	0	17	2	0	0	0	0	0
DT_014_Prater	Summer	Prater	0	3	0	0	17	0	0	0	0	0	0	30	0
DT_015_Prater	Summer	Prater	18	3	0	66	0	0	214	152	0	0	0	75	0
DT_016_Prater	Summer	Prater	29	0	5	20	0	3	52	0	0	3	1	37	0

Table A19: Dataset for the fauna analysis of the dendrotelmata samples showing individual abundances per taxon (Part 2).

Microhabitat code	Season	Location	Ae. gen.	Ae. jap.	An. plu.	C. alb.	Cx. pip.	D. sp.	M. cav.	M. flo.	O. ann.	P. sp.	P. exo.	P. ser.	S. fla.
DT_014_Orth	Autumn	Orth	5	0	0	0	0	0	3	16	0	0	0	70	0
DT_025_Orth	Autumn	Orth	10	0	7	0	0	0	49	2	0	0	0	76	0
DT_027_Orth	Autumn	Orth	31	0	0	1	0	0	2	2	0	0	0	64	0
DT_022_Orth	Autumn	Orth	0	0	26	7	0	4	1	10	0	0	0	28	0
DT_026_Orth	Autumn	Orth	0	0	0	0	0	3	13	0	0	0	0	6	0
DT_017_Prater	Autumn	Prater	1	0	52	27	0	15	0	0	0	0	0	20	2
DT_020_Prater	Autumn	Prater	0	0	8	6	0	15	1	1	8	0	0	3	1
DT_021_Prater	Autumn	Prater	3	0	0	1	0	3	13	0	0	0	0	13	0
DT_022_Prater	Autumn	Prater	0	0	23	23	0	21	0	8	35	0	3	2	0
DT_022_Prater	Autumn	Prater	0	0	0	0	0	0	0	0	0	2	0	0	0
DT_018_Prater	Autumn	Prater	1	0	1	0	0	0	40	3	0	0	0	1	0
DT_019_Prater	Autumn	Prater	0	0	0	0	0	7	1	17	0	0	0	3	0

Table A20: Dataset for the fauna analysis of the ovitrap samples showing individual abundances per taxon (Part 1).

Microhabitat code	Season	Location	Ae. alb.	Ae. gen.	Ae. jap.	An. plu.	B. sp.	C. alb.	Cx. pip.	D. sp.	M. cav.	M. flo.	P. sp.	P. exo.
OT_001_Orth	Spring	Orth	0	0	0	0	0	0	0	0	0	1	0	0
OT_002_Prater	Spring	Prater	0	0	0	0	0	0	0	0	6	0	0	0
OT_005_Prater	Spring	Prater	0	0	0	0	0	0	0	0	0	3	0	0
OT_001_Orth	Summer	Orth	0	0	8	1	0	0	47	14	11	0	0	0
OT_002_Orth	Summer	Orth	0	2	0	0	0	8	0	0	46	0	0	0
OT_003_Orth	Summer	Orth	0	0	0	0	1	0	0	0	3	2	0	0
OT_004_Orth	Summer	Orth	0	16	0	2	0	0	0	55	0	0	0	0
OT_005_Orth	Summer	Orth	0	0	0	17	0	0	0	19	1	0	0	1
OT_006_Orth	Summer	Orth	0	0	1	0	0	0	0	0	0	0	0	0
OT_007_Orth	Summer	Orth	0	0	13	0	0	0	0	1	0	0	0	0
OT_008_Orth	Summer	Orth	0	0	31	0	0	0	0	1	0	0	0	0
OT_010_Orth	Summer	Orth	0	0	0	0	0	0	0	1	0	0	0	0
OT_001_Prater	Summer	Prater	8	0	0	0	0	0	0	1	0	4	0	0
OT_002_Prater	Summer	Prater	0	0	0	0	0	8	79	38	0	3	0	0
OT_003_Prater	Summer	Prater	0	1	3	0	0	4	0	54	0	2	0	0
OT_004_Prater	Summer	Prater	0	0	1	0	0	0	0	46	0	0	0	0
OT_005_Prater	Summer	Prater	0	0	0	3	0	0	0	8	26	6	0	0

Table A21: Dataset for the fauna analysis of the ovitrap samples showing individual abundances per taxon (Part 2).

Microhabitat code	Season	Location	Ae. alb.	Ae. gen.	Ae. jap.	An. plu.	B. sp.	C. alb.	Cx. pip.	D. sp.	M. cav.	M. flo.	P. sp.	P. exo.
OT_001_Orth	Autumn	Orth	0	0	0	0	0	19	0	0	0	4	0	0
OT_004_Orth	Autumn	Orth	0	1	0	0	0	0	0	116	0	0	0	0
OT_005_Orth	Autumn	Orth	0	0	0	7	0	0	0	85	0	0	0	0
OT_004_Prater	Autumn	Prater	0	0	0	1	0	0	0	157	0	2	0	0
OT_005_Prater	Autumn	Prater	0	0	0	0	0	6	0	85	8	6	4	0

Table A22: Dataset for the terrestrial fauna found in dendrotelmata samples showing individual abundances per taxon (Part 1). Abbreviations: Pse. = Pseudoscorpiones, Arc. = Archaeognatha, Col. = Coleoptera, Cmb. = Collembola, Dip. = Diptera, Hem. = Hemiptera, Hym. = Hymenoptera, Iso. = Isopoda, Ixo. = Ixodida, Jul. = Julida, Lep. = Lepidoptera, Lum. = Lumbriculidae, Mes. = Mesostigmata, Oli. = Oligochaeta, Ori. = Oribatida, Pul. = Pulmonata, Thy. = Thysanoptera, Tro. = Trombidiformes.

Microhabitat code	Season	Location	Pse.	Arc.	Col.	Cmb.	Dip.	Hem.	Hym.	Iso.	Ixo.	Jul.	Lep.	Lum.	Mes.	Oli.	Ori.	Pul.	Thy.	Tro.
DT_003_Orth	Spring	Orth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
DT_004_Orth	Spring	Orth	0	1	1	1	0	0	0	5	0	0	1	0	0	0	0	0	0	0
DT_009_Orth	Spring	Orth	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0
DT_013_Orth	Spring	Orth	0	0	0	4	0	0	0	4	1	0	1	0	0	0	0	4	0	0
DT_020_Orth	Spring	Orth	0	0	0	2	0	0	2	0	3	0	0	0	0	0	0	0	0	0
DT_002_Prater	Spring	Prater	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0
DT_001_Prater	Spring	Prater	0	0	0	1	0	0	2	2	0	1	0	0	0	0	0	2	0	0
DT_005_Prater	Spring	Prater	0	0	1	2	0	0	4	0	2	1	0	0	0	0	0	0	1	0
DT_006_Prater	Spring	Prater	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0
DT_009_Prater	Spring	Prater	0	0	0	4	1	1	4	0	1	0	2	1	0	0	0	1	0	0
DT_005_Orth	Summer	Orth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
DT_012_Orth	Summer	Orth	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	16	0	0
DT_018_Orth	Summer	Orth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0
DT_023_Orth	Summer	Orth	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Table A23: Dataset for the terrestrial fauna found in dendrotelmata samples showing individual abundances per taxon (Part 2). Abbreviations: Pse. = Pseudoscorpiones, Arc. = Archaeognatha, Col. = Coleoptera, Cmb. = Collembola, Dip. = Diptera, Hem. = Hemiptera, Hym. = Hymenoptera, Iso. = Isopoda, Ixo. = Ixodida, Jul. = Julida, Lep. = Lepidoptera, Lum. = Lumbriculidae, Mes. = Mesostigmata, Oli. = Oligochaeta, Ori. = Oribatida, Pul. = Pulmonata, Thy. = Thysanoptera, Tro. = Trombidiformes.

Microhabitat code	Season	Location	Pse.	Arc.	Col.	Cmb.	Dip.	Hem.	Hym.	Iso.	Ixo.	Jul.	Lep.	Lum.	Mes.	Oli.	Ori.	Pul.	Thy.	Tro.
DT_011_Prater	Summer	Prater	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	12	0	0
DT_013_Prater	Summer	Prater	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	25	0	0
DT_015_Prater	Summer	Prater	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59	0	1
DT_016_Prater	Summer	Prater	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	15	0	0
DT_014_Prater	Summer	Prater	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
DT_014_Orth	Autumn	Orth	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	4	0	0
DT_025_Orth	Autumn	Orth	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
DT_027_Orth	Autumn	Orth	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0
DT_022_Orth	Autumn	Orth	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	15	0	1
DT_026_Orth	Autumn	Orth	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
DT_017_Prater	Autumn	Prater	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
DT_021_Prater	Autumn	Prater	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	6	0	0
DT_022_Prater	Autumn	Prater	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
DT_019_Prater	Autumn	Prater	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	3	0	0

Table A24: Dataset for the terrestrial fauna found in ovitrap samples showing individual abundances per taxon (Part 1). Abbreviations: Ara. = Araneae, Ar. = Archaeognatha, Bla. = Blattodea, Col. = Coleoptera, Cmb. = Collembola, Dip. = Diptera, Hem. = Hemiptera, Hym. = Hymenoptera, Iso. = Isopoda, Ixo. = Ixodida, Lep. = Lepidoptera, Mes. = Mesostigmata, Opi. = Opiliones, Ori. = Oribatida, Pod. = Poduromorpha, Pul. = Pulmonata, Sar. = Sarcoptiformes, Thy. = Thysanoptera, Tro. = Trombidiformes.

Microhabitat code	Season	Location	Ara.	Arc.	Bla.	Col.	Cmb.	Dip.	Hem.	Hym.	Iso.	Ixo.	Lep.	Mes.	Opi.	Ori.	Pod.	Pul.	Sar.	Thy.	Tro.
OT_001_Orth	Spring	Orth	0	6	0	0	6	1	2	2	4	0	0	0	1	0	0	0	0	1	0
OT_002_Orth	Spring	Orth	1	0	0	1	7	2	0	1	3	0	1	0	0	0	0	1	0	0	0
OT_003_Orth	Spring	Orth	0	0	0	2	5	0	1	2	1	0	0	0	0	0	0	0	0	0	0
OT_004_Orth	Spring	Orth	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0
OT_005_Orth	Spring	Orth	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0
OT_001_Prater	Spring	Prater	0	0	0	1	0	0	2	10	0	0	1	0	0	0	0	0	0	0	0
OT_002_Prater	Spring	Prater	0	0	0	1	21	2	6	13	3	0	0	0	1	0	0	0	0	1	3
OT_003_Prater	Spring	Prater	0	0	0	1	1	3	2	11	0	0	1	0	0	0	0	0	0	3	0
OT_004_Prater	Spring	Prater	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	3	0
OT_005_Prater	Spring	Prater	0	0	0	0	9	0	1	3	0	1	0	0	0	0	0	0	0	0	0
OT_001_Orth	Summer	Orth	0	0	0	2	0	2	0	0	1	2	0	0	0	0	0	2	0	2	0
OT_002_Orth	Summer	Orth	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0
OT_003_Orth	Summer	Orth	0	0	0	1	0	0	0	2	1	2	0	0	0	0	1	8	0	0	0
OT_004_Orth	Summer	Orth	0	0	0	2	0	0	0	1	1	1	0	0	0	0	0	8	0	1	0
OT_005_Orth	Summer	Orth	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0

Table A25: Dataset for the terrestrial fauna found in ovitrap samples showing individual abundances per taxon (Part 2). Abbreviations: Ara. = Araneae, Ar. = Archaeognatha, Bla. = Blattodea, Col. = Coleoptera, Cmb. = Collembola, Dip. = Diptera, Hem. = Hemiptera, Hym. = Hymenoptera, Iso. = Isopoda, Ixo. = Ixodida, Lep. = Lepidoptera, Mes. = Mesostigmata, Opi. = Opiliones, Ori. = Oribatida, Pod. = Poduromorpha, Pul. = Pulmonata, Sar. = Sarcoptiformes, Thy. = Thysanoptera, Tro. = Trombidiformes.

Microhabitat code	Season	Location	Ara.	Arc.	Bla.	Col.	Cmb.	Dip.	Hem.	Hym.	Iso.	Ixo.	Lep.	Mes.	Opi.	Ori.	Pod.	Pul.	Sar.	Thy.	Tro.
OT_007_Orth	Summer	Orth	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
OT_008_Orth	Summer	Orth	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	2	0
OT_009_Orth	Summer	Orth	0	0	0	1	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0
OT_010_Orth	Summer	Orth	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
OT_001_Prater	Summer	Prater	1	0	4	0	0	1	0	7	1	0	0	0	0	0	0	0	0	0	0
OT_002_Prater	Summer	Prater	0	0	0	2	0	5	0	20	1	0	0	0	0	0	0	0	0	0	0
OT_003_Prater	Summer	Prater	1	0	0	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	0
OT_004_Prater	Summer	Prater	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
OT_005_Prater	Summer	Prater	2	0	0	1	0	1	0	8	0	0	0	0	0	2	0	5	0	0	0
OT_008_Orth	Summer	Prater	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
OT_010_Orth	Summer	Prater	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
OT_001_Orth	Autumn	Orth	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
OT_003_Orth	Autumn	Orth	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	10	0	0	0
OT_004_Orth	Autumn	Orth	0	0	0	4	0	2	2	0	4	0	0	4	0	3	0	10	0	0	0
OT_005_Orth	Autumn	Orth	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0
OT_004_Prater	Autumn	Prater	0	0	0	2	0	1	1	1	0	0	0	2	0	0	0	0	0	0	0
OT_005_Prater	Autumn	Prater	0	0	1	0	0	0	0	1	0	1	0	1	0	5	0	11	1	0	0

Table A26: Dataset for mosquito eggs (presence/absence) found in ovitrap samples per taxon (Part 1).

Ovitrap	Date_sampling	Season	Location	Aedes_albopictus	Aedes_geniculatus	Aedes_japonicus	Aedes_koreicus
CIM_OR_OT_1	2025-05-26	Spring	Orth	0	0	0	0
CIM_OR_OT_2	2025-05-26	Spring	Orth	0	1	0	0
CIM_OR_OT_3	2025-05-26	Spring	Orth	0	0	0	0
CIM_OR_OT_4	2025-05-26	Spring	Orth	0	1	0	0
CIM_OR_OT_5	2025-05-26	Spring	Orth	0	1	0	0
CIM_PR_OT_1	2025-05-28	Spring	Prater	0	0	0	0
CIM_PR_OT_2	2025-05-28	Spring	Prater	0	0	0	0
CIM_PR_OT_3	2025-05-28	Spring	Prater	0	0	0	0
CIM_PR_OT_4	2025-05-28	Spring	Prater	0	0	0	0
CIM_PR_OT_5	2025-05-28	Spring	Prater	0	0	0	0
CIM_OR_OT_1	2025-07-29	Summer	Orth	0	1	0	0
CIM_OR_OT_10	2025-07-29	Summer	Orth	0	0	1	0
CIM_OR_OT_2	2025-07-29	Summer	Orth	0	1	0	0
CIM_OR_OT_3	2025-07-29	Summer	Orth	0	0	0	0
CIM_OR_OT_4	2025-07-29	Summer	Orth	0	0	1	0
CIM_OR_OT_5	2025-07-29	Summer	Orth	0	1	0	0
CIM_OR_OT_6	2025-07-29	Summer	Orth	0	0	1	0
CIM_OR_OT_7	2025-07-29	Summer	Orth	0	0	0	0
CIM_OR_OT_8	2025-07-29	Summer	Orth	0	0	0	0
CIM_OR_OT_9	2025-07-29	Summer	Orth	0	1	1	0

Table A27: : Dataset for mosquito eggs (presence/absence) found in ovitrap samples per taxon (Part 2).

Ovitrap	Date_sampling	Season	Location	Aedes_albopictus	Aedes_geniculatus	Aedes_japonicus	Aedes_koreicus
CIM_PR_OT_1	2025-07-31	Summer	Prater	1	1	0	0
CIM_PR_OT_2	2025-07-31	Summer	Prater	0	1	0	0
CIM_PR_OT_3	2025-07-31	Summer	Prater	1	1	0	0
CIM_PR_OT_4	2025-07-31	Summer	Prater	0	1	0	0
CIM_PR_OT_5	2025-07-31	Summer	Prater	0	0	0	0
CIM_OR_OT_1	2025-10-06	Autumn	Orth	0	0	0	0
CIM_OR_OT_2	2025-10-06	Autumn	Orth	0	0	0	0
CIM_OR_OT_3	2025-10-06	Autumn	Orth	0	1	0	0
CIM_OR_OT_4	2025-10-06	Autumn	Orth	0	1	0	0
CIM_OR_OT_5	2025-10-06	Autumn	Orth	0	0	0	0
CIM_PR_OT_1	2025-10-09	Autumn	Prater	1	1	0	0
CIM_PR_OT_2	2025-10-09	Autumn	Prater	0	1	0	0
CIM_PR_OT_3	2025-10-09	Autumn	Prater	0	0	0	0
CIM_PR_OT_4	2025-10-09	Autumn	Prater	0	1	0	0
CIM_PR_OT_5	2025-10-09	Autumn	Prater	0	1	0	0

Table A28: Dataset for the eDNA metabarcoding of the dendrotelmata samples showing reads per taxon (Part 1).

Microhabitat code	Season	Location	Aedes	Anopheles	Culex	Dasyhelea	Metriocnemus	Prionocyphon
DT-003-Orth	Spring	Orth	0	0	0	0	20	0
DT-004-Orth	Spring	Orth	0	0	0	0	7	3
DT-009-Orth	Spring	Orth	0	0	0	0	6	0
DT-013-Orth	Spring	Orth	0	0	0	0	801	0
DT-020-Orth	Spring	Orth	0	0	0	1	19	0
DT-001-Prater	Spring	Prater	0	0	0	2	130	0
DT-002-Prater	Spring	Prater	0	0	0	0	0	0
DT-005-Prater	Spring	Prater	0	0	0	1	0	0
DT-006-Prater	Spring	Prater	0	0	0	0	0	0
DT-009-Prater	Spring	Prater	0	0	0	0	0	0
DT-005-Orth	Summer	Orth	0	0	0	0	11	1
DT-012-Orth	Summer	Orth	0	0	2	0	2	1
DT-018-Orth	Summer	Orth	0	0	0	0	16	0
DT-023-Orth	Summer	Orth	0	0	0	0	0	0
DT-024-Orth	Summer	Orth	0	0	0	0	1	0

Table A29: Dataset for the eDNA metabarcoding of the dendrotelmata samples showing reads per taxon (Part 2).

Microhabitat code	Season	Location	Aedes	Anopheles	Culex	Dasyhelea	Metriocnemus	Prionocyphon
DT-011-Prater	Summer	Prater	0	0	0	0	0	0
DT-013-Prater	Summer	Prater	0	0	0	0	42	0
DT-014-Prater	Summer	Prater	0	0	22	0	0	0
DT-015-Prater	Summer	Prater	0	0	0	1	403	50
DT-016-Prater	Summer	Prater	0	0	0	0	2520	2
DT-014-Orth	Autumn	Orth	0	0	0	0	1544	0
DT-022-Orth	Autumn	Orth	0	0	0	0	0	0
DT-025-Orth	Autumn	Orth	0	40	0	0	57	5
DT-026-Orth	Autumn	Orth	0	0	0	0	24	1
DT-027-Orth	Autumn	Orth	0	0	0	0	766	0
DT-017-Prater	Autumn	Prater	0	1	0	0	0	0
DT-018-Prater	Autumn	Prater	13701	0	0	0	2	0
DT-019-Prater	Autumn	Prater	0	0	0	0	0	0
DT-020-Prater	Autumn	Prater	0	0	0	0	0	0
DT-021-Prater	Autumn	Prater	28	0	0	0	16	0
DT-022-Prater	Autumn	Prater	0	0	0	0	0	0

Table A30: Dataset for the eDNA metabarcoding of the ovitrap samples showing reads per taxon (Part 1).

Microhabitat code	Season	Location	Aedes	Anopheles	Culex	Dasyhelea	Metriocnemus	Prionocyphon
OT-001-Orth	Spring	Orth	0	0	0	0	0	0
OT-002-Orth	Spring	Orth	0	0	0	0	0	0
OT-003-Orth	Spring	Orth	0	0	0	0	0	0
OT-004-Orth	Spring	Orth	0	0	0	0	0	0
OT-005-Orth	Spring	Orth	0	0	0	0	0	0
OT-001-Prater	Spring	Prater	0	0	0	0	0	0
OT-002-Prater	Spring	Prater	0	0	0	0	0	0
OT-003-Prater	Spring	Prater	0	0	0	0	0	0
OT-004-Prater	Spring	Prater	0	0	0	0	0	0
OT-005-Prater	Spring	Prater	0	0	0	0	0	0
OT-001-Orth	Summer	Orth	0	0	7232	0	20	0
OT-002-Orth	Summer	Orth	0	17871	0	0	343	0
OT-003-Orth	Summer	Orth	0	0	0	1	124	0
OT-004-Orth	Summer	Orth	0	0	0	1	323	0
OT-005-Orth	Summer	Orth	0	0	0	0	13	0

Table A31: Dataset for the eDNA metabarcoding of the ovitrap samples showing reads per taxon (Part 2).

Microhabitat code	Season	Location	Aedes	Anopheles	Culex	Dasyhelea	Metriocnemus	Prionocyphon
OT-006-Orth	Summer	Orth	0	0	0	0	0	0
OT-007-Orth	Summer	Orth	0	0	0	0	0	0
OT-008-Orth	Summer	Orth	0	0	0	0	0	0
OT-009-Orth	Summer	Orth	0	0	0	0	0	0
OT-010-Orth	Summer	Orth	0	1	0	0	0	0
OT-001-Prater	Summer	Prater	0	0	0	0	0	0
OT-002-Prater	Summer	Prater	0	0	0	1	17	0
OT-003-Prater	Summer	Prater	0	0	0	0	0	0
OT-004-Prater	Summer	Prater	0	0	0	2	0	0
OT-005-Prater	Summer	Prater	0	29	0	0	96	0
OT-001-Orth	Autumn	Orth	0	0	0	0	0	0
OT-003-Orth	Autumn	Orth	0	0	0	0	0	0
OT-004-Orth	Autumn	Orth	0	0	0	0	0	0
OT-005-Orth	Autumn	Orth	0	0	0	0	0	0
OT-004-Prater	Autumn	Prater	0	0	0	0	0	0
OT-005-Prater	Autumn	Prater	1358	0	0	1	0	203

Table A32: Dataset for the eDNA metabarcoding of Rotifera and Nematoda showing reads per dendrotermata sample.

Microhabitat code	Season	Location	Nematoda	Rotifera
DT-003-Orth	Spring	Orth	355	1124
DT-004-Orth	Spring	Orth	18	90
DT-009-Orth	Spring	Orth	14	209
DT-013-Orth	Spring	Orth	26	665
DT-020-Orth	Spring	Orth	23	613
DT-001-Prater	Spring	Prater	8	95
DT-002-Prater	Spring	Prater	4	165
DT-005-Prater	Spring	Prater	1	31
DT-006-Prater	Spring	Prater	3	62
DT-009-Prater	Spring	Prater	45	69
DT-005-Orth	Summer	Orth	91	528
DT-012-Orth	Summer	Orth	28	245
DT-018-Orth	Summer	Orth	22	1436
DT-023-Orth	Summer	Orth	0	42
DT-024-Orth	Summer	Orth	54	227
DT-011-Prater	Summer	Prater	5	2
DT-013-Prater	Summer	Prater	86	1882
DT-014-Prater	Summer	Prater	639	2050
DT-015-Prater	Summer	Prater	3	48
DT-016-Prater	Summer	Prater	119	2415
DT-014-Orth	Autumn	Orth	7	4
DT-022-Orth	Autumn	Orth	167	589
DT-025-Orth	Autumn	Orth	0	1549
DT-026-Orth	Autumn	Orth	112	54
DT-027-Orth	Autumn	Orth	0	4
DT-017-Prater	Autumn	Prater	11	0
DT-018-Prater	Autumn	Prater	27	297
DT-019-Prater	Autumn	Prater	63	8
DT-020-Prater	Autumn	Prater	0	0
DT-021-Prater	Autumn	Prater	1	3257
DT-022-Prater	Autumn	Prater	21	28

Table A33: Dataset for the eDNA metabarcoding of Rotifera and Nematoda showing reads per ovitrap sample.

Microhabitat code	Season	Location	Nematoda	Rotifera
OT-001-Orth	Spring	Orth	0	5
OT-002-Orth	Spring	Orth	0	0
OT-003-Orth	Spring	Orth	9	3
OT-004-Orth	Spring	Orth	0	0
OT-005-Orth	Spring	Orth	0	0
OT-001-Prater	Spring	Prater	0	0
OT-002-Prater	Spring	Prater	7	15
OT-003-Prater	Spring	Prater	33	14
OT-004-Prater	Spring	Prater	0	32
OT-005-Prater	Spring	Prater	27	1
OT-001-Orth	Summer	Orth	2	17
OT-002-Orth	Summer	Orth	1	0
OT-003-Orth	Summer	Orth	0	6
OT-004-Orth	Summer	Orth	22	6
OT-005-Orth	Summer	Orth	0	3635
OT-006-Orth	Summer	Orth	0	0
OT-007-Orth	Summer	Orth	18	54
OT-008-Orth	Summer	Orth	0	1173
OT-009-Orth	Summer	Orth	0	79
OT-010-Orth	Summer	Orth	0	29
OT-001-Prater	Summer	Prater	3	389
OT-002-Prater	Summer	Prater	2	49
OT-003-Prater	Summer	Prater	95	16
OT-004-Prater	Summer	Prater	16	57
OT-005-Prater	Summer	Prater	0	40
OT-001-Orth	Autumn	Orth	17	186
OT-003-Orth	Autumn	Orth	5	86
OT-004-Orth	Autumn	Orth	6	4
OT-005-Orth	Autumn	Orth	0	2594
OT-004-Prater	Autumn	Prater	4	4605
OT-005-Prater	Autumn	Prater	3	2081

9. Zusammenfassung (German abstract)

Phytotelmata sind aquatische Mikrohabitate in und auf Pflanzen, die zwar oft übersehen werden, jedoch eine spezialisierte Artengemeinschaft beherbergen. Obwohl sie auch im gemäßigten Zentraleuropa zu finden sind, ist die Ökologie der mit ihnen assoziierten Taxa noch relativ wenig erforscht. In dieser Arbeit untersuchte ich wassergefüllte Baumhöhlen (Dendrotelmata) in einem urbanen Park innerhalb der Stadt Wien und in einem ländlichen Auwald außerhalb der Metropole, um herauszufinden, wie Urbanisierung die Wasserchemie und die aquatische Fauna prägt. Für einen Vergleich zwischen Mikrohabitaten wurden an denselben Standorten Kunststoffbehälter (Ovitrap) aufgestellt. Ich erfasste limnochemische Parameter in drei Jahreszeiten, erhob Insektenlarven morphologisch, ergänzte die Bestimmung durch eDNA-Metabarcoding und analysierte die Datenstruktur multivariat.

Die abiotischen Bedingungen in Dendrotelmata waren nährstoffreich und sauerstoffarm, wobei die Umweltbedingungen und die Fauna signifikant durch Urbanisierung beeinflusst wurden. Vier Taxa wiesen signifikante Unterschiede auf: Der Sumpfkäfer *Prionocyphon serricornis* und die Stechmücke *Aedes geniculatus* waren häufiger am ländlichen Standort zu finden, während die Schwebfliege *Myathropa florea* und die Gnizen der Gattung *Dasyhelea* mit dem städtischen Umfeld assoziiert wurden. *Dasyhelea* zeigte auch eine signifikante Präferenz für Ovitrap, die sich grundlegend von natürlichen Dendrotelmata unterschieden, da sie höhere Sauerstoffkonzentrationen, geringere Nährstoffwerte, größere Temperaturschwankungen und eine andere Artenzusammensetzung aufwiesen. Die Beziehungen zwischen Arten und Umwelt wurden vor allem durch die Leitfähigkeit (Nährstoffkonzentration) und die Sauerstoffkonzentration erklärt. Ein Methodenvergleich zeigte, dass das eDNA-Metabarcoding aquatische Insektentaxa weniger umfassend nachweisen konnte als die morphologische Bestimmung, dafür jedoch zusätzlich Rotifera und Nematoda erfasste.

Diese Arbeit zeigt, dass Urbanisierung auch Mikrohabitate wie Dendrotelmata beeinflusst. Darüber hinaus zeigt sich, dass Ovitrap ein ökologischer Ersatz mit Einschränkungen und veränderten Artengemeinschaften sind, sich jedoch sehr wohl für das gezielte Monitoring gebietsfremder Stechmücken eignen. Um die Biodiversität dieser Mikrohabitate zu erfassen, bedarf das eDNA-Metabarcoding methodischer Weiterentwicklung. Für den Naturschutz bedeutet das, dass die Erhaltung natürlicher Baumhöhlenstrukturen von entscheidender Bedeutung ist und dass taxonomisches Fachwissen weiterhin wichtig bleibt.

Schlüsselwörter: Phytotelmata; Mikrohabitat; Urbanisierung; Metabarcoding; gebietsfremde Stechmücken