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IMPACTS DE L'UTILISATION DES TERRES SUR LE ZOOPLANCTON DES PLAINES INONDABLES : UNE EXPÉRIENCE À L'ÉCHELLE DE L'ÉCOSYSTÈME

IMPACTS OF LAND USE ON FLOODPLAIN ZOOPLANKTON: AN ECOSYSTEM-SCALE EXPERIMENT

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RÉSUMÉ

Les plaines inondables constituent des environnements uniques soumis à des inondations périodiques; elles favorisent ainsi une forte production de zooplancton, souvent cruciale pour la pêche. Toutefois, des changements d'affectation des sols causés par l'expansion et l'intensification de l'agriculture dans les plaines inondables pourraient affecter les communautés zooplanctoniques par la perte d'habitat, l'érosion des sols et l'augmentation conséquente de la turbidité et du lessivage des produits agrochimiques. Ces altérations de l'habitat pourraient affecter les réserves d'œufs du zooplancton ainsi que leurs stades adultes via la dégradation de la qualité de l'eau, compromettant ainsi leur santé générale. Cette thèse, combinant des observations de terrain et des approches expérimentales, vise à démontrer les impacts de l'utilisation des terres/l'intensification de l'agriculture sur les communautés de zooplancton dans la plaine inondable d'un grand fleuve. Nous avons mené une expérience unique à l'échelle de l'écosystème, en manipulant l'utilisation des terres dans la plaine inondable. Nous avons comparé les impacts des zones humides naturelles (marais d'érables et prairies humides) avec des prairies cultivées (anciennes et récentes) et des cultures agricoles (p. ex. maïs et soja) (pratiques améliorées et pratiques conventionnelles) dans quatre régions de la plaine inondable du Lac Saint-Pierre, en étudiant les communautés de zooplancton de la colonne d'eau ainsi que leurs banques d'œufs dans les sols. Les pratiques améliorées incluent des méthodes telles que les cultures de couverture, les cultures intercalaires, le semis direct et les bandes tampons pérennes; tandis que les pratiques conventionnelles incluent les pratiques conventionnelles intensives.

Nous avons commencé par évaluer l'impact de différents types d'occupation des sols sur l'abondance, la biomasse et la diversité du zooplancton, comparativement à celui des terres agricoles dans la colonne d'eau lors des crues printanières. Nous n'avons observé aucun impact significatif de l'utilisation des sols à une échelle locale sur le zooplancton; les effets étaient davantage liés aux différentes zones inondables (quatre secteurs), et influencés par la qualité de l'eau, suggérant la nécessité d'intégrer l'utilisation des terres à une échelle spatiale plus large dans ce type d'étude. Nous avons ensuite étudié les impacts de l'utilisation des sols et du régime des crues sur les réserves d'œufs de zooplancton via i) le comptage direct des œufs et ii) l'incubation des sols pour l'émergence du zooplancton à partir de stades de dormance. Pour l'émergence à partir de phases de dormance, les zones humides naturelles ont présenté une émergence plus importante que les terres cultivées, les cultures fourragères ayant un résultat intermédiaire. Les ostracodes, les rotifères et les copépodes étaient les principaux groupes émergents des sols. De plus, la durée de l'inondation n'a influencé qu'un seul groupe : les ostracodes, avec une augmentation de l'émergence durant les deux premières semaines, suivie d'une diminution entre la troisième et la cinquième semaine. Ces résultats ont clairement illustré l'impact du changement de l'utilisation des sols sur la résilience du zooplancton dans les plaines inondables, sans distinctions significatives entre les pratiques améliorées et conventionnelles. Les résultats suggèrent néanmoins que les prairies cultivées constituent un meilleur compromis que les pratiques conventionnelles. Elles pourraient améliorer le recrutement des communautés de

zooplancton à partir des stades de dormance, protéger la biodiversité et ainsi soutenir la production durable de zooplancton dans les plaines inondables.

Enfin, nous avons évalué la réponse écotoxicologique de l'utilisation des terres de la plaine inondable sur *Daphnia magna,* en analysant leur interaction potentielle avec les rayonnements ultraviolets naturels (UVR). Nous avons effectué deux expériences : i) une expérience en plein air afin d'évaluer les impacts de l'utilisation des terres et des rayons UVR, en exposant *D. magna* aux lixiviats de sol provenant de trois types de terres différents (érablière marécageuse naturelle, ancienne culture prairie et culture conventionnelle) et aux rayons UVR (sans UV, avec UV-A et UV-AB); ii) une expérience en laboratoire où *D. magna* sont exposées uniquement aux lixiviats du sol provenant d'un plus large gradient d'utilisation des terres (naturel : érablières marécageuses et prairies humides, prairies : cultures anciennes et récentes, agriculture : cultures améliorées et conventionnelles (soja et maïs). Les expériences réalisées à l'extérieur n'ont révélé aucun impact de l'utilisation des terres ni des rayons UVR sur le comportement natatoire, la reproduction ou les paramètres physiologiques. Toutefois, un impact significatif de l'utilisation des terres sur la survie de *D. magna* a été observé, avec les cultures conventionnelles favorisant sa survie. Dans le cas, de l'expérience en laboratoire, l'utilisation des terres provenant des cultures conventionnelles et des érablières marécageuses naturelles ont démontré une amélioration de la survie de *D. magna*, tandis que les cultures améliorées réduisaient la fréquence cardiaque comparativement aux lixiviats d'autres occupations du sol.

Cette thèse reflète l'importance des changements dans les pratiques d'utilisation des terres en plaine inondable sur les communautés du zooplancton. Il s'agit de la première étude sur les effets interactions de l'utilisation des terres et des rayons UV naturels sur *D. magna*. L'utilisation des terres à l'échelle locale influence principalement les banques d'œufs de zooplancton, tandis qu'à l'échelle régionale, elle semble potentiellement affecter les communautés de la colonne d'eau par l'intermédiaire de la qualité d'eau. Toutefois, les résultats mitigés du chapitre écotoxicologique suggèrent la nécessité d'approfondir les recherches afin de mieux comprendre les effets sur d'autres aspects de la santé individuelle (p. ex. les variations des biomarqueurs). Les travaux présentés dans cette thèse suggèrent la nécessité de considérer les impacts de l'utilisation des terres à l'échelle locale et régionale sur la dynamique du zooplancton dans la plaine inondable lors de l'élaboration de stratégies de gestion durable, ce qui contribuerait à améliorer les conditions de ces milieux, favorisant ainsi la conservation de la biodiversité et la protection des écosystèmes des plaines inondables.

Mots-clés : émergence du zooplancton, Lac Saint-Pierre, intensification agricole, écologie des milieux humides, agroécologie, écotoxicologie, paramètres physiologiques, comportement de nage, invertébrés aquatiques, fleuve Saint-Laurent

ABSTRACT

Floodplain habitats are unique environments that undergo periodic inundation and are known to support high zooplankton production, which is often crucial for fisheries. However, changes in land use with expansion and intensification of agriculture in floodplains could affect zooplankton communities through habitat loss, soil erosion and resultant increase in turbidity and leaching of agrochemicals. These alterations to habitat could affect zooplankton egg banks as well as their adult stages via degradation of water quality, thus affecting their overall health. Using a combination of field observations and experimental approaches, this thesis aimed to demonstrate the impacts of land use /agricultural intensification on zooplankton communities in a large river floodplain. We used a unique ecosystem-scale experiment, wherein land use in the floodplain was manipulated. We compared the impacts of natural wetlands (maple swamps and wet meadows) with forage (old and recently sown), and agriculture i.e., corn and soya (agri-environmental and agri-conventional) croppings in four regions of Lake Saint-Pierre floodplain by studying water column zooplankton communities as well as their resting egg banks in soils. Here, agri-environmental cropping included practices such as cover cropping, intercropping, no tillage, and perennial buffer strips, while agri-conventional cropping included intensive conventional practices.

We first assessed impact of different land use types on zooplankton abundance, biomass, and diversity, compared to that of agricultural land use in water column during spring flooding. We found no clear impacts of land use at local scale on zooplankton; they were more associated with the regions of the floodplain (four sectors) and were influenced by water quality, thereby suggesting inclusion of land use at larger spatial scale in such studies. We then assessed the impacts of land use and flood regime on zooplankton egg bank by i) direct egg count and ii) incubation of soils for emergence of zooplankton from resting stages for different durations in the laboratory. In the case of emergence from resting stages natural wetlands were found to harbor higher emergence of zooplankton compared to agriculture soils, with forage croppings behaving intermediate. Ostracods, rotifers and copepods were the main groups that emerged from soils. Furthermore, inundation duration influenced only one group, i.e., ostracods with increase in emergence in first two weeks and thereafter decreased between third and fifth week. These results indicated clearly the impact of changes in land use on zooplankton resilience in floodplains, but with no difference between agri-environmental and agri-conventional practices, and that the forage practices could be a better compromise over agri-conventional ones. It could enhance recruitment of zooplankton communities from resting stages and protect biodiversity and help and thus support in sustaining production of zooplankton in floodplains.

Lastly, we evaluated ecotoxicological response of floodplain land use and natural ultraviolet radiation (UVR) on *Daphnia magna*. We performed two experiments: i) outdoor experiment to evaluate effects of land use and natural UVR by exposing *D. magna* to soil leachates from three different land use types (natural maple swamp forest, forage-old cropping and agri-conventional cropping) and natural UVR (no UV, UV-A and UV-AB);

ii) indoor experiment wherein *D. magna* were exposed to only soil leachates but from a larger land use gradient (natural: maple swamp and wet meadow, forage: old and recent cropping, agriculture: agri-environmental and agri-conventional cropping (soya and corn). Outdoor experiment revealed no impact of either land use or natural UVR on swimming behavior, reproduction or physiological endpoints. However, significant effect only of land use on survival of *D. magna* was observed with agri-conventional cropping favoring its survival. In case of indoor experiment, agri-conventional cropping and natural maple swamp forest land use was found to improve survival of *D. magna*, while agri-environmental cropping lowered the heart rate compared to other land use leachates.

This thesis highlights the importance of changes in land use practices in floodplain on zooplankton communities. This is the first-time study on interactive effects of land use and natural UVR on *D. magna*. Land use at local scale was found to influence mainly the zooplankton egg bank, while the land use at regional scale appeared to potentially affect the water column communities via water quality. However, mixed results from the ecotoxicological study suggest that further exploration is required to better understand the effects on other aspects of the individual health (e.g., changes in biomarkers). The work carried out in this thesis overall suggests the need to consider the impacts of land use both at local and larger spatial scale on zooplankton dynamics in floodplain when developing sustainable land use management in floodplain that would aid in improving the conditions and thus aid in conserving biodiversity and protect the floodplains ecosystem.

Keywords: zooplankton emergence, Lake Saint-Pierre, agriculture intensification, wetland ecology, agroecology, ecotoxicology, physiological endpoints, swimming behavior, aquatic invertebrates, St. Lawrence River

GENERAL INTRODUCTION

Floodplains are unique environments acting as temporary water bodies that undergo periodic inundations either through lateral connection with rivers and lakes or by precipitation or groundwater (Junk et al., 1989). Due to their alternating aquatic and terrestrial phases, floodplain areas have been termed “aquatic/terrestrial transition zones (ATTZ)” (Junk et al., 1989). Floodplains are characterized by seasonal flow variability, whereby high flows build the hydrological connection between the main channel and the inundated floodplain (Górski et al., 2013). This lateral hydrological connectivity varies spatio-temporally and has a strong influence on the physicochemical and biological properties of these key habitats (Sackreiter, 2019). These factors together play an important role in the exchange of matter and fauna between the floodplain and the main channel (Dias et al., 2017), thus exhibiting a significant role in structuring the biota therein (Chaparro et al., 2023; Górski et al., 2013). The expansion and contraction of the flood can either increase the heterogeneity of the floodplains, as reported for glacial floodplains (Malard et al., 2000) or lead to homogeneity, as has been reported for Danubian floodplain systems (Tockner et al., 2000). In tropical and subtropical floodplains, seasonal floods occurring under warm conditions may persist for several months, thus leading to longer periods of aquatic connectivity and favorable temperatures for supporting high primary and consumer production (Hamilton, 2009). In contrast, temperate floodplains experience greater seasonal variability in temperature, and the seasonal timing of inundation and its interaction with temperature and hydrological connectivity determine the ecological effects of flooding (Bayley, 1995; Junk et al., 1989).

Large river floodplains are rich in biodiversity and exhibit high biological productivity across most regions of the world (Tockner & Stanford, 2002). Floodplain ecosystems can support high primary productivity. For example, mean net primary productivity of forested floodplains has been reported to range from approximately 508 g C m^{-2} yr^{-1} in temperate forested floodplains to 1123 g C m^{-2} yr^{-1} in tropical forested floodplains (Cleveland et al., 1999). Floodplains are also known to contribute substantial zooplankton biomass to the riverine food web. For example, Furst et al. (2014) estimated that up to 6.3 ± 1.6 tonnes

of zooplankton (dry weight) per day have been reported to be exported from the Chowilla floodplain(Kirk & Gilbert, 1990). Increased DOC in floodplain riverine systems have been found to support zooplankton abundances via bacterial and microbial pathways (Hitchcock et al., 2025; Mitrovic et al., 2014) to the River Murray in Australia. They are also recognized as biodiversity hotspots (Ahearn et al., 2006; Sparks, 1995) and provide multiple ecosystem services (Schindler et al., 2016). The flood regime (duration and magnitude) drives their productivity (Górski et al., 2013; Junk et al., 1989) and biodiversity (Tockner & Stanford, 2002). The rise and fall of the flood determine the extent of the area that would be flooded, which then determines the time spent by the biota (either terrestrial or aquatic) in the area, which, in turn, affects the annual biological production in the floodplains (Bayley & Sparks, 1989). Floodplains serve as a source of primary and secondary production, thus acting as a subsidy to main water channels such as rivers and lakes (Farly et al., 2019; Henning & Rogers, 2004). The increased lateral connectivity to the main water channel can facilitate fish migration to the floodplain for spawning (e.g., salmonids, and perch), wherein the floodplain serves as an essential rearing habitat for feeding and refuge (Henning & Rogers, 2004). Thus, especially the early ontogenetic life stages of fish are highly benefited from the abundant food resources available, such as zooplankton, which thus improve their growth rates (Farly et al., 2019; Pratt et al., 2023; Sommer et al., 2001), before returning to the main channel (Junk et al., 1989). The *Flood Pulse Concept* proposed by Junk and co-workers acknowledges that the flood pulse is the principal driving force that controls the biota in riverine floodplains through lateral connectivity (Junk et al., 1989). Longer duration and a predictable flood pulse allow the organisms to adapt and develop strategies to derive benefits from the highly productive ATTZ (Junk et al., 1989). Larger floods tend to inundate larger areas, providing a greater quantity and variety of food resources for fish (Pratt et al., 2023). Because small body-sized, calorie-dense and found at high densities, zooplankton are a major and easily available food supporting juvenile fish survival within these habitats (Faggotter et al., 2013; Pratt et al., 2023). Thus, they constitute an essential linkage between basal resources and top consumers (Keckeis et al., 2003) and play a significant role in the energy flow and nutrient cycling in floodplains (Degerman et al., 2018; Fantin-Cruz et al., 2011).

Floodplain secondary production is also suggested to exceed that of adjacent water bodies during flooding (Tockner & Stanford, 2002).

Zooplankton in the floodplain

The ecological structure and functioning of zooplankton communities in floodplains are mainly governed by the interplay of seasonal flow, flood pulses, lateral connectivity and the amount of inundated area (Chaparro et al., 2021; Fantin-Cruz et al., 2011; Górski et al., 2013). The degree of hydrological connectivity, macrophyte cover, detritus source, soil texture in the bottom sediments and water transparency strongly influence the community composition and secondary production in the floodplain (Zilli & Paggi, 2013). The presence of dense vegetation in the floodplain can support high abundances of zooplankton such as cladocerans* and copepods, and macroinvertebrates, as well as their high diversity, while more sparse vegetation influences the abundances of only certain taxa (Flinn et al., 2005; Nhiwatiwa et al., 2017). These zooplankton in the floodplain are, in general, also very sensitive to other environmental factors controlled by the variability in physico-chemical properties of the water column that are driven by the flow regime, e.g., dissolved organic carbon (Mitrovic et al., 2014), turbidity and dissolved oxygen (Galir Balkić et al., 2018; Ning et al., 2013). More precisely, zooplankton such as rotifers and copepods are found to be sensitive to floodplain hydrology and site-specific water quality variables (Galir Balkić et al., 2018). Thus, with short life cycles, high reproduction rates and being sensitive to environmental conditions, zooplankton serve as ideal candidates for evaluating the health of the aquatic systems (Florescu et al., 2026).

Dominant microinvertebrate taxa in floodplains are represented by rotifers, cladocerans, copepods (Baranyi et al., 2002; Bomfim et al., 2018; Shiel et al., 1998), and ostracods (Ezcurra et al., 2007). These invertebrates colonise the floodplains either by active dispersion from neighbouring habitats, passive dispersion with water inflow, or emergence from the flooded soils (Jenkins & Boulton, 2003; Smock, 1999). Higher water flow during floods increases the passive dispersal of zooplankton (Gonzalez,

* Despite this taxonomic term is not accepted anymore, we did not replace it with '*Diplostraca*' to be consistent with its use in our Chapter 2, which has already been published.

2009) and tends to homogenise both environmental variables as well as the zooplankton assemblages across the region (Bozelli et al., 2015). Increased zooplankton abundance with the dominance of copepods during the wet period and subsequent decline during the dry period has been observed in tropical floodplains (Sendek & Aynalem, 2020). The emergence patterns of zooplankton from soils could vary depending on environmental conditions/cues such as flood regime, photoperiod and temperature (Chaki et al., 2021; Maharjan et al., 2026; Vandekerkhove et al., 2005). Higher abundances of total zooplankton hatchlings (rotifers, copepods, cladocerans and ostracods) in the floodplain have been reported when exposed to warm temperatures (Maharjan et al., 2026), and they also varied between the hatchling collection weeks (Chaki et al., 2021; Maharjan et al., 2026). Furthermore, the initial flood pulse of invertebrate emergence and dominance from the soils could be significantly impacted by the sediment quality as well (Dietz-Brantley et al., 2002).

Dormancy in zooplankton as an adaptation to thrive through changing conditions

In such dynamic or fluctuating environments, many species undergo dormancy as an adaptation to survive through the harsh conditions (Wisnoski et al., 2019). Their ability to diapause by producing resting stages that remain dormant and viable for long periods allows them to cope with dry periods (Thorp & Covich, 2009; Williams, 2006). This dormancy could either be as quiescence state, which is controlled by exogenous factors and is triggered by adverse environmental conditions) or a diapause state, which is an internally programmed mechanism and induced by cues including temperature and photoperiod (Radzikowski, 2013). Diapause is characterized by a reduction in metabolic rate and development, allowing the organisms to survive through temporary environmental stress periods (Mushegian & Tougeron, 2019), while also influencing their responses to such cues (Alekseev, 2025). These dormant forms may include dormant eggs (e.g., monogonont rotifers and copepods), ephippia in cladocerans (Hairston et al., 2000), and instar stages in the case of copepods (Bruno et al., 2001; Hairston, 1996) and ostracods (Williams et al., 2015; Zhai et al., 2024). Thus, the accumulation of such resting eggs/stages in the sediments over time forms a so-called ‘egg bank’, which can stay viable for decades or more in the soils (Hairston, 1996). Such egg banks constitute a potential

reservoir of high genetic variations (Brendonck & De Meester, 2003) and emerge when triggered by environmental cues announcing suitable conditions, such as the onset of the next flooding cycle, and thus help to rebuild the water column zooplankton community (Brendonck & De Meester, 2003b) thereby contributing to the productivity in the floodplains that can subsidize the main river channel (Farly et al., 2021). Studies suggest that floodplain habitats harbour abundant and diverse egg bank communities (Chaparro et al., 2021; Ning & Nielsen, 2011). Today, several factors pose threats to these reservoirs of diversity, and these floodplain subsidies are expected to decrease in the future, given scenarios of shorter spring floods due to climate change (Burn & Whitfield, 2016).

Anthropogenic and environmental stressors

Floodplains, being very fertile and easily accessible, have been undergoing tremendous pressure due to increasing human activities, thereby potentially altering their ecosystem services (Jakubínský et al., 2021). Heavily modified floodplains are generally subjected to short flood pulses and could be unpredictable as well (Junk et al., 1989). This could, in turn, affect the organisms with limited adaptations to benefit from the ATTZ (Junk et al., 1989). In addition to climate change, the increasing anthropogenic pressure could also significantly affect zooplankton productivity in floodplains. For example, human encroachment through the expansion of agricultural activities in the floodplains has led to degradation and loss of floodplain wetlands (Hudon et al., 2018). Increasing human settlement and demand for food have caused alterations to these natural habitats, thereby reducing the habitat complexity and thus the biodiversity of the region (Tockner & Stanford, 2002). A reduction in natural floodplain forest cover has been reported, for example, in New Zealand (Fahey et al., 2004), and across the globe, along 520 major river basins, a huge loss of natural floodplains due to agriculture has been reported between 1992 and 2019 (Rajib et al., 2023). The diminishing water quality due to agricultural intensification and increased pesticide use is also expected to have a significant impact on aquatic organisms, including zooplankton communities and eventually affect the forthcoming egg banks (Plangklang & Athibai, 2021). For example, pesticides such as neonicotinoids exhibit high solubility in water and relatively long half-lives in both water and soils (Morrissey et al., 2015). Neonicotinoids such as Clothianidin,

Thiacloprid and Imidacloprid are among those widely used pesticides around the world (Simon-Delso et al., 2015). Furthermore, they have been found to affect non-target aquatic organisms (Finnegan et al., 2017; Hébert et al., 2021).

In addition to their potential direct effects, in natural environments, such contaminants present in water and soils can interact with different environmental factors, potentially modulating their toxicity. Among these, natural ultraviolet radiation (UVR) can potentially interact with xenobiotics to have direct effects on aquatic organisms (Paquet-Walsh et al., 2019; Wolinski et al., 2020). Further, since the water column in the floodplains is very shallow, the impact of UVR could be potentially higher compared to the main river channels. UVR can have a significant impact on zooplankton either through DNA damage or photooxidative stress by altering the toxicity of the contaminants in the aquatic systems (Rautio & Tartarotti, 2010). UVR can make the compound more toxic through photoactivation (Huovinen et al., 2001) or through photodegradation, their toxicity could be reduced as well (Beketov et al., 2011). However, most studies in the literature have documented the detrimental effects of UVR, such as mortality in zooplankton (e.g., Zagarese & Williamson, 2000).

Context of the thesis

The available literature strongly suggests that zooplankton in floodplains are structured by a combination of factors and are exposed to various stressors either due to changes in flood regime, changes in UVR owing to climate change or changes in land use due to expansion of human activities to make ends meet, thus leading to tremendous alterations in habitat structure and properties of the floodplains (Hudon et al., 2018; Jobin & Brodeur, 2023). These stressors could act individually or through interactions that could significantly affect the zooplankton communities in the floodplains, with differences in their effects across taxa. However, most studies available in the literature have focused either on limited land use comparisons, such as between forest and agriculture only (e.g., Frisch et al., 2009) or on individual stressors such as pesticides or UVR on zooplankton, keeping aside the possible interactive effects between the factors influencing the zooplankton community. For example, most studies focus on the effects of

commercially available contaminants, especially pesticides (e.g., 2, 4-D, imidacloprid, glyphosate) on model organisms (mostly the zooplankter, *Daphnia magna*), wherein such compounds have been found to affect the survival, fecundity and physiological endpoints of the organism (Cuhra et al., 2013; Man et al., 2023). Combined effects of contaminants and UVR have been studied across different aquatic organisms such as phytoplankton (e.g., Pelletier et al., 2006), fish (e.g., Hakkinen et al., 2003), and aquatic invertebrates (e.g., Barron, 2017), revealing synergistic, antagonistic, or additive effects depending on the organisms. However, relatively few studies have examined the combined effects of contaminants and UVR on zooplankton, with some reporting synergistic (e.g., Beketov et al., 2011) while others have reported antagonistic effects (Luo et al., 2018). Moreover, most of these involved the exposure of zooplankton to artificial UVR lamps in laboratory conditions.

Hence, the present study was designed to address the effects of land use across a relatively wide gradient of land uses (natural, forage and agriculture), across flood regimes, and by explicitly addressing the potential interactions between natural UVR and soil leachates on zooplankton dynamics in a large river floodplain. This study was conducted in the Lake Saint-Pierre (LSP) floodplain in Quebec, which is the largest floodplain along the St. Lawrence River (SLR) system, Canada. The site is also recognized as a UNESCO Biosphere Reserve and as a RAMSAR site. It experiences 5-9 weeks of flooding, with differences in the spatial and temporal extent (Watson et al., 2024). Despite LSP is less regulated among the fluvial lakes of the SLR system, its floodplain has undergone dramatic changes in land use with a shift in agricultural practices from perennial to intensive agriculture since the 1950s (Dauphin & Jobin, 2016a). Approximately 22.8% of the floodplain area is today occupied by agriculture (Jobin & Brodeur, 2023) (Figure 1).

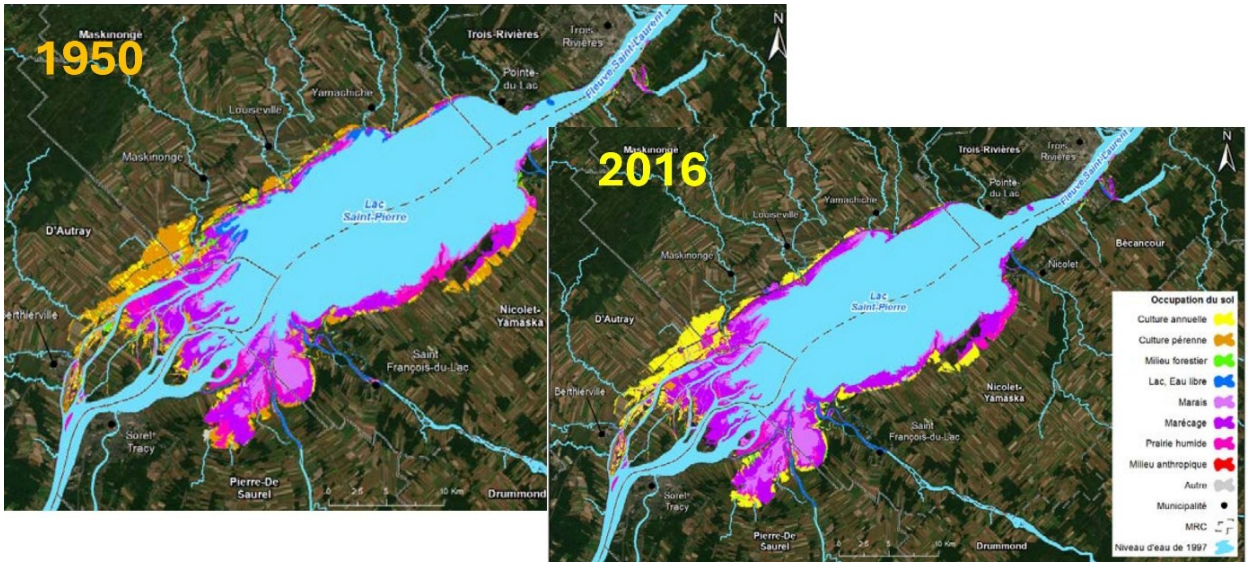


Figure 1. Maps illustrating changes in land use between 1950 to 2016 within the 2-year flood reoccurrence zone of Lake Saint-Pierre Floodplain. Modified from Jobin and Brodeur (2023).

The observed expansion of agriculture in the LSP floodplain and the concomitant shift to conventional, intensive cropping (corn/soy) practices involving heavy pesticide usage, machinery for tillage, and mowing, caused a severe degradation of the natural vegetation that was otherwise available for the wildlife (Rioux et al., 2009). Such habitat deterioration has also led to diminishing water quality and reduced natural habitats that once served as spawning and nursery grounds for fish during spring flooding (Jobin & Brodeur, 2023; Richard et al., 2011), thereby affecting the floodplain food webs and biodiversity (Hudon et al., 2018). A collapse of a commercial yellow perch (*Perca flavescens*) fishery in the LSP was reported for the same period, partially owing to such degradation of the environment (Giacomazzo et al., 2023; Jobin & Brodeur, 2023). The collapse of the yellow perch fishery could also be in part attributed to the decrease in their prey, which is affected by the diminished water quality due to increased pesticides such as neonicotinoids (TCRLSP, 2017). The last study available on the zooplankton from the LSP floodplain dates back to 1982 by R. Savignac (Savignac, 1982), who reported poor conditions in agricultural fields due to ploughing and mowing activities, with a concomitant decrease in zooplankton biomass compared to less disturbed environments such as abandoned fields and ditches. Therefore, taking into account the worsening environmental conditions in the floodplains, the Quebec government established in 2018 the “Multidisciplinary Hub of Expertise on sustainable management of the Littoral Zone of

Lake Saint-Pierre" (Pole d'expertise multidisciplinaire en gestion durable du littoral du Lac Saint-Pierre) to restore the natural habitats in the LSP floodplain and to support fisheries associated with it. This ambitious and innovative program involved 30 researchers from multiple research groups in ecology, agronomy, and socio-economics, with the aim of coming up with strategies for sustainable management of land in the LSP floodplain by comparing results obtained from different research groups across different land use types. Some of these land uses were manipulated based on the willingness of the landowners to implement the suggested agri-environmental agriculture practices (Watson et al., 2024).

Aim and Objectives

The main aim of this thesis was to evaluate the impact of changes in land use on zooplankton egg banks in a large river floodplain using a unique ecosystem-scale experimental approach with manipulation of land use in the floodplain. Three major land use types, each with two subtypes, were implemented in four regions of the LSP floodplain (namely, Baie-du-Febvre (BAIE), St. Barthelemy (BART), Île Dupas (DUPA) and Pierreville (PIER)). Thus, a comparison of land use effects was made between natural (maple swamp and marsh), forage cropping (old and recent), and agriculture (corn/soy) cropping (agri-environmental and conventional).

The main hypothesis of the thesis was that natural wetlands would support higher zooplankton abundance, diversity and biomass, a greater number of hatchlings emerging from the resting egg bank and improved zooplankton survival and performance. In contrast, conventional agricultural cropping would have negative effects, whereas agri-environmental cropping was expected to mitigate them. Forage croppings would behave intermediate between natural wetlands and agricultural croppings (Figure 2).

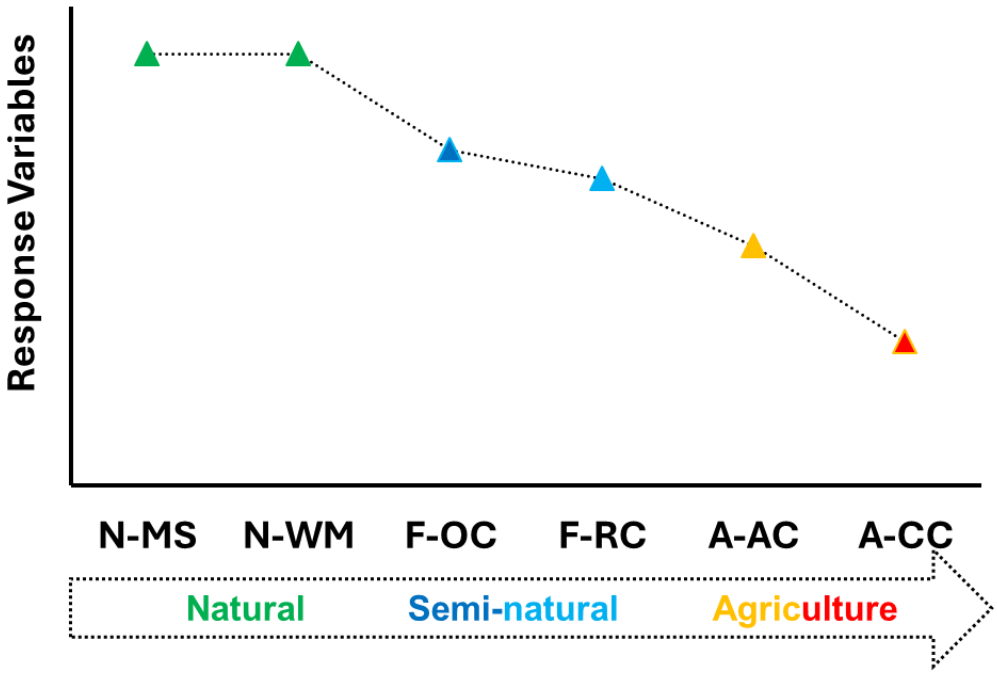


Figure 2. Hypotheses of the thesis, wherein the response variables include (i) water column zooplankton, (ii) hatchling abundances from the resting egg bank, and (iii) survival and performance of model zooplankter, *Daphnia magna*. Monotonous decline along the gradient is expected across the land use gradient, but the pattern of decline can change with a different shape. Land use gradient: 1) Natural-Maple Swamp (N-MS), 2) Natural-Wet Meadow (N-WM), 3) Forage-Old Cropping (F-OC), 4) Forage-Recent Cropping (F-RC), 5) Agriculture-Agri-environmental Cropping (A-AC), and 6) Agriculture-Conventional Cropping (A-CC). Land use nomenclature adapted from Watson et al., 2024.

This hypothesis was tested through specific objectives, which formed the three chapters of the thesis:

Objective 1: To assess the impact of land use and water quality on water column zooplankton in a large river floodplain **(Chapter I)**.

Hypotheses

H1: Natural wetlands would support higher abundance, biomass and diversity of zooplankton over agricultural land use, which would impart a negative influence.

H2: Water quality in the study area would significantly affect zooplankton.

This objective was achieved by studying the water column zooplankton communities for their abundance, biomass, and diversity during the spring flooding of 2019 and 2022 across the land use gradient.

Objective 2: To evaluate the impact of land use and flood regime on zooplankton resilience through the egg bank **(Chapter II)**.

Hypotheses

H1: Natural wetlands will favour a higher abundance of resting eggs as well as of the emerging zooplankton from the resting stages over agricultural soils, and the forage croppings would be intermediate.

H2: Higher inundation duration and frequency would favour higher abundances of resting eggs as well as the emergence from resting stages.

This objective was achieved by i) directly quantifying the resting egg bank across the land use gradient and ii) the emergence of zooplankton from resting stages across the land use gradient and flood regime through a series of soil incubation experiments in the laboratory.

Objective 3: To evaluate the impact of land use and natural ultraviolet radiation (UVR) on *Daphnia magna* through an ecotoxicological approach **(Chapter III)**.

Hypotheses

H1: Interaction between land use and natural UVR would significantly affect *D. magna* survival, reproduction, performance, and swimming behavior either synergistically or antagonistically.

H2: Natural UVR would have detrimental effects on *D. magna*.

H3: Natural wetland leachates would influence *D. magna* positively, while those from agricultural soils would have a negative influence. However, agri-environmental land use leachates will have a lower impact than agri-conventional leachates.

This objective was achieved by assessing the response of *D. magna* in terms of its survival, reproduction, physiological performance and swimming behavior on exposure to leachates prepared in the laboratory from soils across a land use gradient, both in the presence of natural UVR (outdoor experiment) as well as its absence (indoor experiment).

These three chapters would fill the existing knowledge gap on zooplankton communities and their egg bank in the LSP floodplain. A conceptual diagram is presented here that shows connections between the three chapters (Figure 3).

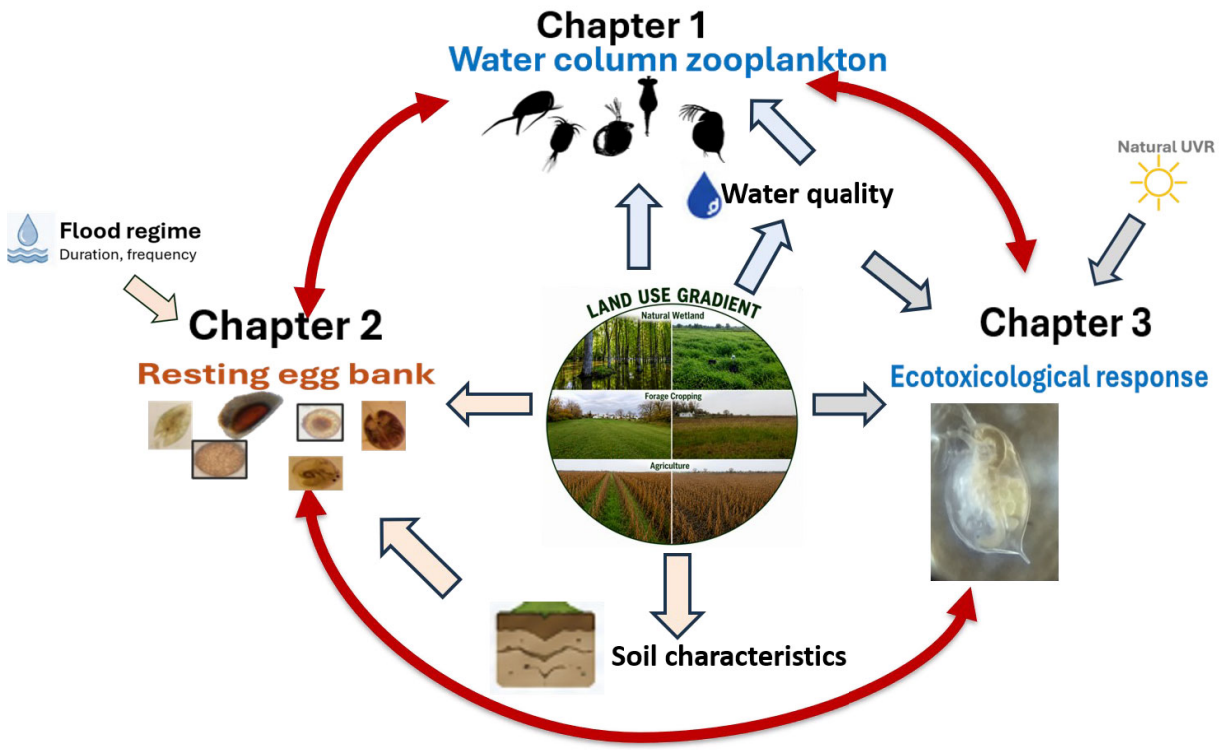


Figure 3. A conceptual diagram representing the connection between different objectives and chapters of the thesis.

This thesis will also provide new insights into the impact of land use practices across a wide land use gradient on aquatic organisms that play a significant role in the floodplain food web and productivity. A combination of both observational and experimental approaches used in the three chapters would help derive robust conclusions, thereby suggesting the incorporation of such studies on a long-term basis, which would aid in developing mitigation measures to protect and restore natural wetlands and biodiversity in the floodplains. A general discussion is presented at the end of these three chapters that would contribute to recommendations for the development of sustainable land use practices in the floodplains.

CHAPTER I

EFFECTS OF LAND USE AND WATER QUALITY ON ZOOPLANKTON COMMUNITIES IN A LARGE RIVER FLOODPLAIN: AN ECOSYSTEM-SCALE EXPERIMENT

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Abstract

Seasonal floodplains are productive habitats that contribute strongly to fluvial ecosystem functioning, but their biotic integrity is increasingly threatened by anthropogenic stressors such as land use. To better understand these impacts, zooplankton communities were analyzed across a land use gradient in a large river floodplain in Canada. Through an ecosystem-scale experiment in partnership with agricultural producers, we evaluated the impact of various land use types on zooplankton abundance, biomass, and diversity in the water column during spring flooding. While different regions of the floodplain varied strongly in terms of zooplankton community structure, local (plot-scale) land use had only a limited effect on zooplankton abundance, biomass, and diversity. Only harpacticoid abundance responded to variation in land use, being more abundant in natural wetlands. Cultivated fields with or without agroecological practices (e.g., cover crops, intercropping) intended to improve floodplain water quality showed no measurable differences in terms of zooplankton assemblages. However,

water quality variables linked to water sources at a larger scale within the floodplain had a clear impact on zooplankton communities. Conductivity, chlorophyll *a*, pH, dissolved organic carbon (DOC), and turbidity all influenced zooplankton, with each major group responding to different variables. Our results indicate that floodplain zooplankton communities are shaped by water quality, which can itself be decoupled from land use within the floodplain itself. Thus, land use planning and management intended to improve floodplain water quality and biotic integrity need to consider upstream land use in watersheds that outflow into floodplains.

Keywords: agroecology, global change, Lake Saint-Pierre, wetland ecology, aquatic invertebrates, St. Lawrence River

Introduction

Floodplains are temporary aquatic habitats that are extremely complex, rich in biodiversity, and provide numerous ecosystem services (Petsch et al., 2023). They serve as hotspots for the exchange of matter between terrestrial and aquatic systems, which are significantly influenced by flooding regimes (Junk et al., 1989; Opperman et al., 2017). Indeed, lateral connectivity and hydrological regimes in the floodplains influence the physico-chemical properties and biota therein (Opperman et al., 2017; Sackreiter, 2019). Zooplankton are an important component of floodplain wetland biodiversity and food webs, linking terrestrial and aquatic systems (Farly et al., 2021; Junk et al., 1989) and subsidizing higher trophic levels in the main river channel (Bunn et al., 2003; Jardine et al., 2015). In addition, the extensive vegetation cover in floodplains is known to support a high number of zooplankton species (Brito et al., 2020; Lansac-Tôha et al., 2009). Generally, rotifers, copepods, ostracods, and cladocerans are the zooplankton taxa commonly found in floodplain wetlands (Pereira et al., 2017; Siziba et al., 2013). These taxa are affected by, and respond differentially to, various environmental conditions (Gaiser & Lang, 1998). Because of their short life cycle and high reproduction rates, they can prove as excellent indicators of the quality of aquatic ecosystems (Castilho-Noll et al., 2023; Ovaskainen et al., 2019). Therefore, studying zooplankton dynamics can serve as a useful tool for evaluating changes in wetland ecosystems (Lougheed & Chow-Fraser, 2002).

Floodplain wetlands and their hydrological regimes are severely threatened due to various anthropogenic activities and climate change (Amaral et al., 2024; Davidson, 2014). For example, construction of levees for flood control leads to a reduction in wetland extent (Richter et al., 2003), and construction of dams leads to flow reduction, causing changes in aquatic communities over time (Simoes et al., 2015; Winemiller et al., 2016). Climate change can also have a negative impact on the floodplains by affecting the flooding regime (spatial extent, intensity and duration) (Karim et al., 2016; Schneider et al., 2011). Increasing human population and associated increase in demand for food and housing have led to expansion of agriculture and other human development activities in floodplains (Roggeri, 2013). Indeed, floodplains (being highly fertile areas) are facing large-scale alterations due to the expansion and intensification of agriculture and

urbanization, leading to the degradation of wetland habitats (Tockner & Stanford, 2002). Rajib et al. (2023) quantified alterations in floodplains due to anthropogenic activities along 520 major river basins worldwide between 1992 and 2019 and found that there has been a significant loss of natural floodplains (forest, grassland and wetland) owing to agricultural practices and other developmental activities. For instance, agricultural intensification and the use of fertilizers and machinery have impacted wetland habitats worldwide, often accompanied by a decrease in the biodiversity of both terrestrial (Newbold et al., 2016) and aquatic organisms (Dos Santos et al., 2025).

Changes in land use also lead to landscape homogenization (de Arruda Ramos et al., 2025). For example, New Zealand has reported a decrease in the natural forest cover from 75 to 23% in floodplains since European settlement (Fahey et al., 2004). In Quebec, Canada, there has been a dramatic change in agricultural practices over recent decades with the intensification of agriculture, i.e. a switch from perennial to annual crops, which has severely affected floodplain water quality (Jobin & Brodeur, 2023). This, in turn, impacted floodplain food webs and biodiversity along the Saint-Lawrence River (Farly et al., 2019; Hudon et al., 2018). For example, a decrease in zooplankton biomass has been reported in agricultural fields with ploughing and mowing activities relative to nearby abandoned fields and ditches when flooded (Savignac, 1982).

While it is widely recognized that land use can significantly alter invertebrate community composition in aquatic systems (J. D. Gilbert et al., 2017; Ono et al., 2020), it remains unclear whether communities respond more to local land use (within the floodplain) vs larger-scale land use affecting the water quality of streams that contribute to seasonal floods. In hydrologically dynamic environments such as floodplains, land use at larger scales might matter more for local diversity than plot-scale land use, given the important exchange of water and organisms among neighbouring plots that may differ in land use. Some studies have shown that local (plot-scale) conditions impact zooplankton communities either by affecting the active zooplankton (Bomfim et al., 2023) or their egg banks in the floodplains (Gleason et al., 2003a). In contrast, other studies have found effects of landscape cover at a larger scale on floodplain zooplankton (Fernández et al., 2009). However, studies comparing the effects of different land use types at the local vs.

regional level are limited, yet these would be important to understand the interactions between aquatic habitats and terrestrial landscapes (Angeler et al., 2008; Van Egeren et al., 2011). This question has important management implications, as many floodplain conservation measures focus on land use within the floodplain itself, ignoring upstream land use that might nonetheless affect local water quality due to water inflow.

To narrow these knowledge gaps, the present study aimed to evaluate the impact of land use and environmental variables on zooplankton communities in a large river floodplain, considering both local (plot-scale) land use and water quality driven by larger-scale, upstream watershed land use. Working in the largest floodplain complex along the St. Lawrence River, Canada, zooplankton communities from natural wetlands (swamps and marshes) were compared with communities from flooded fields implementing either a moderate form of land use (old and recent forage croppings) or an intensive form of land use (soy-corn monocultures with or without agroecological practices such as cover crops and intercropping). Land use in the plots was manipulated experimentally in collaboration with agricultural producers, converting intensive monoculture plots into forage and agroecological cropping to test whether these forms of less-intensive land use had milder impacts on aquatic communities during spring floods. We hypothesised that land use at the local scale (plot-scale) would have a strong influence on zooplankton communities (Savignac, 1982). More specifically, we hypothesised that 1) natural wetlands would have a higher abundance, biomass, and diversity of zooplankton than agricultural fields; 2) more intensive land use would have greater negative impacts on zooplankton than less intensive land use; and 3) water quality at the local scale (irrespective of land use, e.g., distinct water masses in the system) will also have a significant influence on zooplankton communities.

Methods

Study area and sampling design

The present study was conducted in the Lake Saint-Pierre (LSP; 46°12’ N, 72°49’ W) floodplain, the largest floodplain along the Saint-Lawrence River (Canada). The site is a UNESCO Biosphere Reserve and a RAMSAR wetland of international importance.

LSP experiences spring flooding for 5 – 9 weeks, with varying spatial extent of inundation among years (Watson et al., 2024). LSP floodplains have undergone dramatic land use alterations with intensification of agriculture over the years, which have been described in detail elsewhere (Dauphin & Jobin, 2016a; Jobin & Brodeur, 2023). Briefly, in recent decades, perennial crops and grasslands used as pastures have been gradually replaced by row crop monocultures (soya, corn), leading to increases in pesticide loadings and turbidity. Declining water quality has been linked to biodiversity change, e.g., there has been a collapse of an important commercial yellow perch (*Perca flavescens*) fishery in LSP, and higher turbidity and declining aquatic vegetation are usually invoked as causal mechanisms (Giacomazzo et al., 2023; Jobin & Brodeur, 2023). This decline could also be due to a decrease in the availability of prey such as zooplankton, which could also be driven by water quality (TCRLSP, 2017).

To better understand the impacts of changing land uses on the LSP social-ecological system, the government of Quebec launched in 2018 the *Multidisciplinary Hub of Expertise on the sustainable Management of the Littoral Zone of Lake Saint-Pierre* (in French: “Pole d’expertise multidisciplinaire en gestion durable du littoral du Lac Saint-Pierre”). This multidisciplinary project involved researchers in agronomy, ecology, and agricultural economics working together to identify synergies and trade-offs among biodiversity, water and soil quality, agricultural yield, and economic/well-being indicators. To that end, an ecosystem-scale experiment was laid out in collaboration with agricultural producers, whereby six land use types were implemented in four different regions of the LSP floodplain.

Watson et al. (2024) described the experiment and project in detail. Briefly, sampling in the floodplain was conducted during the spring flooding of 2019 and 2022 in four blocks (regions of the floodplain), namely Baie-du-Febvre (BAIE), Pierreville (PIER), Saint-Barthelemy (BART), and Île Dupas (DUPA) (Figure 1).

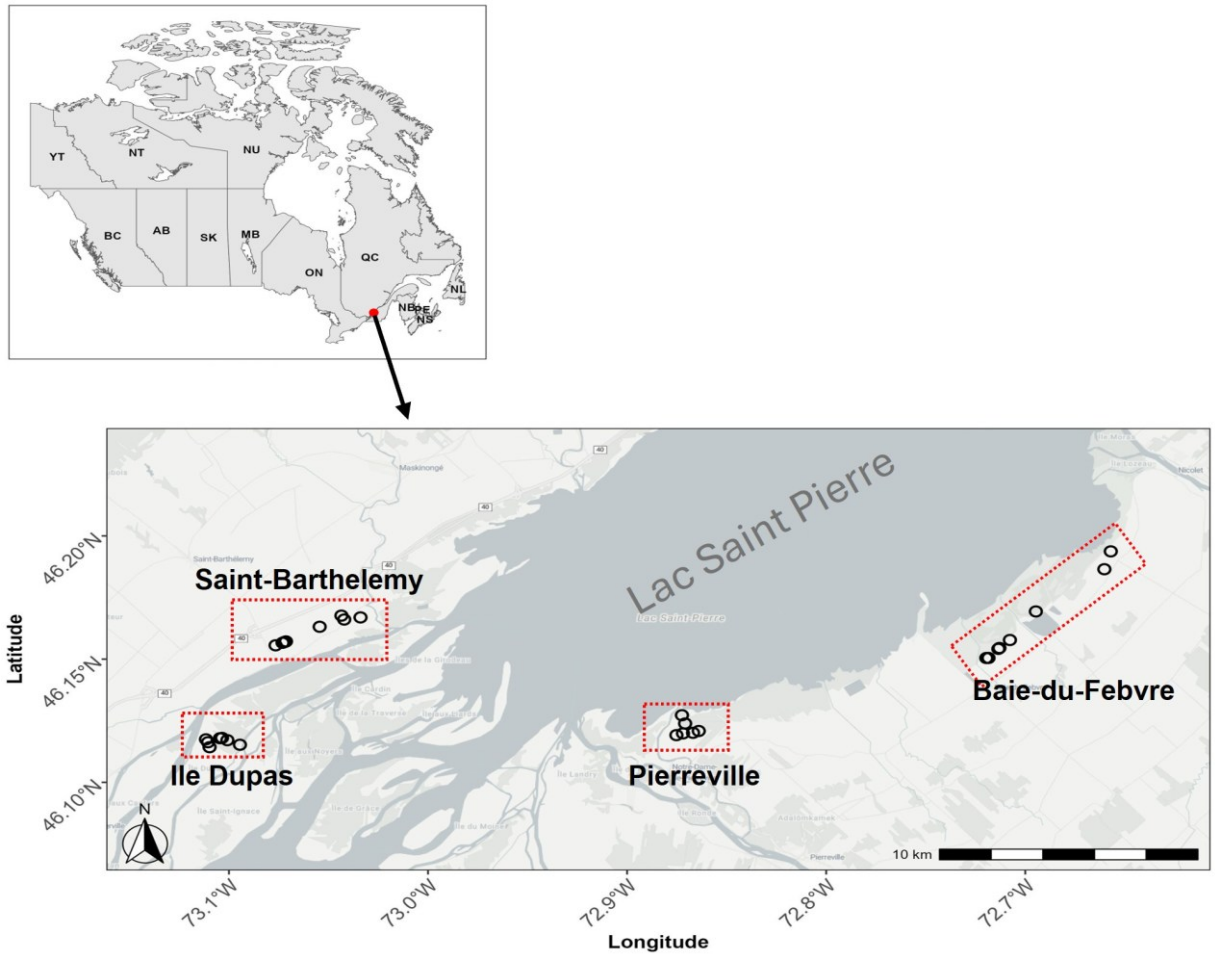


Figure 1. Study area depicting zooplankton sampling locations within four blocks (Baie-du-Febvre, Pierreville, St. Barthelemy and Ile Dupas) in the Lake Saint-Pierre Floodplain (Quebec, Canada) during spring 2019 and 2022. Each block includes six types of land use or land cover. In order from the most natural to the most intensive form of land use, these include: 1) Natural-Maple Swamp (N-MS), 2) Natural-Wet Meadow (N-WM), 3) Forage-Old Cropping (F-OC), 4) Forage-Recent Cropping (F-RC), 5) Agriculture-Agri-environmental Cropping (A-AC), and 6) Agriculture-Conventional Cropping (A-CC). Land use nomenclature adapted from Watson et al., 2024.

Each of these blocks housed three major land use types, namely, natural wetlands (N), forage fields (F), and cropland/agricultural fields (A). Each of these land use types included two subtypes: 1) natural maple swamps (N-MS) and natural wet meadows (N-WM), ii) old forage cropping (F-OC) with 5+ years without ploughing and recently sown forage cropping (F-RC) implemented in converted soy/corn fields, and iii) agri-environmental cropping (A-AC) and conventional cropping (A-CC) of corn and soy, whereby agri-environmental cropping includes measures to diminish impacts on water quality (intercropping during the growing season; cover crops at the end of the growing season). More details on these land use types can be found in Badesab et al. (2026).

In 2019, due to a shorter spring flood, zooplankton samples were collected at 18 sites (N-MS: 4, N-WM = 3, F-OC = 3, F-RC = 2, A-CC = 6), while in 2022, sampling was possible at 27 sites (N-MS: 4, N-WM = 3, F-OC = 3, F-RC = 4, A-AC = 6, A-CC = 7) (total = 45 samples). In 2019, the A-AC treatment was not included in the analysis since the spring sampling was carried out before the implementation of agri-environmental practices (Table S1). All sites were located at the same elevation to control for flood duration.

Zooplankton sampling and environmental variables

Water column zooplankton were collected at all sites using a bucket filled with 20 L of site water, which was then filtered through a 63 µm mesh. The concentrated samples were preserved using 90% ethanol. Samples were then sent for taxonomic analysis to a professional laboratory (IdentaZoop), where all pelagic crustacean taxa were counted and identified to the lowest possible level (usually species). Only 2022 samples were measured for the mean body size of each taxon at each site, and biomass was estimated using published length-mass relationships. Samples were shipped back to our laboratory at UQTR, where they were further screened for the abundance of groups omitted by IdentaZoop (rotifers, ostracods). Only the total abundance of these groups was counted without species identification or length measurement.

We also measured various physicochemical parameters at each site. Water pH, conductivity (µS cm^{-1}), temperature (°C) and oxygen (mg L^{-1}) were measured with a YSI multiparameter probe (Yellow Spring Instruments, OH). Turbidity (FNU) was measured using a HANNA HI9829 probe. Water samples collected were acidified with sulfuric acid, filtered using 0.7 µm GF/F filters (47 mm diameter), and then analyzed for TN (µg L^{-1}) and TP (µg L^{-1}) using a Lachat's QuikChem flow injection analyzer (QuickChem 8500 series). Dissolved organic carbon (DOC, mg L^{-1}) was measured using a Sievers M9/M9e total organic carbon (TOC) analyzer (Suez 2018). Concentration of chlorophyll *a* (µg L^{-1}) was measured by filtering a water sample through a GF/F filter (47 mm diameter), extracting chlorophyll on the filter using 90% acetone, and then measuring its concentration/fluorescence with Turner Design AU fluorometer (Turner Designs, SD;

Arar and Collins, 1997). See Campeau et al. (2024) for additional information on abiotic measurements.

Data analysis

Land use effects on zooplankton community descriptors were tested using generalized linear mixed models (GLMMs). All data analyses were performed using R version 4.3.2 (R core team, 2023). GLMMs were fitted with the package 'glmmTMB' (Brooks et al., 2017). We fitted separate models for each response variable: abundance of each major group (Calanoida, Cyclopoida, Harpacticoida, calanoid copepodites, cyclopoid copepodites, nauplii, Cladocera, Rotifera and Ostracoda), alpha diversity indices (richness, evenness, and Shannon diversity) computed with the R package 'vegan' (Oksanen, 2015), total zooplankton biomass, and community weighted mean body size (CWMBS; calculated with crustaceans other than ostracods). For the latter two variables, only 2022 samples were included, while all other variables had samples from both 2019 and 2022. Land use was included as a fixed effect (a factor with six levels), and blocks (BAIE, BART, PIER, DUPA) and individual site nested with block were used as random intercepts. For biomass and CWMBS (based on 2022 data only, and thus with a single sample per site), the site random effect was omitted. To properly use the appropriate distributions in models, we checked for overdispersion and zero-inflation accordingly with the DHARMa package (Hartig, 2016). A Gamma or Tweedie error distribution was chosen depending on the presence of zero-inflation. The effect of land use on zooplankton was tested with a likelihood ratio test comparing the full model with a reduced model omitting the land use effect. When we found a significant effect of land use, the estimated marginal means of each group were calculated using the emmeans package (Lenth, 2022). Then, multiple pairwise *post hoc* comparisons between the land use types were made, adjusting *p* values using the 'False Discovery Rate' (FDR) method at alpha = 0.05. The pairwise tests were fitted and interpreted using the 'multcomp' and 'multcompView' packages (Graves et al., 2019; Hothorn et al., 2016).

We also visualized differences in zooplankton community composition among land use types and floodplain regions (blocks) using nonmetric multidimensional scaling

(NMDS). The ordination was performed with the 'metaMDS' function from 'vegan'. We tested for the effect of land use and block on community composition using a permutational multivariate ANOVA (PERMANOVA) implemented in the function 'adonis2' of the 'vegan' package. The community composition matrix was Hellinger-transformed prior to multivariate analyses. We also repeated these analyses (NMDS and PERMANOVA) with the biomass instead of abundance, using 2022 samples only. Finally, to evaluate the effect of water quality (irrespective of local land use), we fitted GLMMs with the same set of response variables listed above, again using blocks and sites as random effects, but using five water quality parameters as fixed effects instead of the land use factor. These 5 variables were conductivity (log-transformed), pH, turbidity (log-transformed), DOC (log-transformed), and chlorophyll *a* (log-transformed). Nutrients were omitted from the analysis since they were highly collinear with DOC. Variance inflation factors were below 2 for all models, confirming that the five remaining covariates were weakly correlated. All parameters were scaled to a mean of 0 and unit variance to compare effect sizes. The results of these GLMMs and LMMs were visualized by extracting estimates with the *tidy* () function from broom.mixed package (Bolker et al., 2022) and *ggplot* () function of the package 'ggplot2'(Wickham, 2016).

Results

Zooplankton recorded in the LSP floodplain included Cladocera, Rotifera, Ostracoda and Copepoda, copepodites of calanoid and cyclopoid, nauplii of calanoid, cyclopoid and harpacticoid. Cyclopoid copepodites and nauplii were highly dominant (81.3% of all individuals). When excluding copepodites and nauplii, the remaining 18.7% of individuals were dominated by Cladocera (65.3%), followed by adult Cyclopoida (15.8%), Rotifera (13.8%), Ostracoda (4.4%), Harpacticoida (0.6%), and finally adult Calanoida (0.1; Figure S1). Among cladocerans, *Ceriodaphnia* sp. dominated the group (25.7%), followed by *Bosmina longirostris* (13.8%), *Simocephalus serrulatus* (10.7%), *Daphnia catawba* (7.8%), *Scapholeberis mucronata* (2.4%), *Daphnia pulicaria* (2.2%), and *Chydorus sphaericus* (1.3%). Among adult Cyclopoida, *Acanthocyclops* sp. dominated the group (7.4%), *followed by Diacyclops bicuspidatus* (5.1%), and *Cyclops scutifer* (2.9%).

Local (site-level) land use showed a significant influence only on harpacticoid abundance (GLMM, effect of land use, $p = 0.015$; Figure 2a-i). Post hoc tests revealed that natural maple swamps (N-MS) had the highest abundance, differing significantly from all land uses except natural wet meadows (N-WM; Figure 2c). Forage fields with old cropping (F-OC) and cultivated fields with conventional agricultural practices (A-CC) had the lowest abundance and differed significantly from the two types of natural wetlands. The two types of land use, whereby soy/corn fields were manipulated experimentally to implement less impactful cultures (F-RC and A-AC), had intermediate abundances and differed only from natural swamps (Figure 2c).

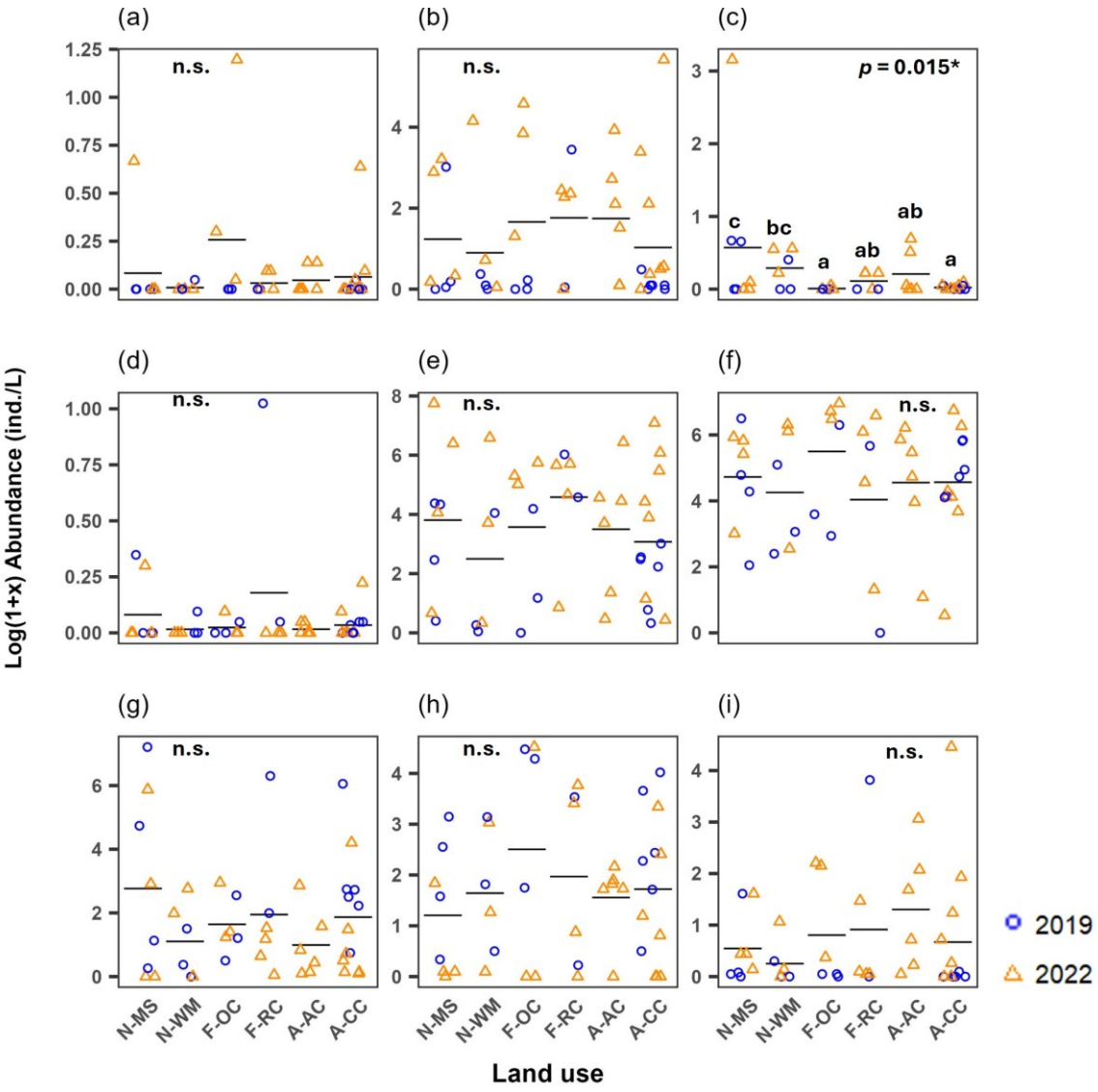


Figure 2. Abundance of major zooplankton groups across different land uses for the two sampling years (2019 and 2022). (a) adult Calanoida, (b) adult Cyclopoida, (c) adult Harpacticoida, (d) calanoid copepodites, (e) cyclopoid copepodites, (f) nauplii, (g) Cladocera, (h) Rotifera, and (i) Ostracoda. Land use treatment: Natural-Maple Swamp (N-MS), Natural Wet Meadow (N-WM), Forage-Old Cropping (F-OC), Forage-Recent Cropping (F-RC), Agriculture-Agri-environmental Cropping (A-AC), and Agriculture-Conventional Cropping (A-CC). Symbols represent samples (site-year combinations) while horizontal bars represent the mean of all samples from a given level of the land use treatment. *p* value and n.s. (non-significant) refer to the effect of land use in GLMM. ind.: individuals.

Further, multivariate analyses confirmed that land use did not affect overall community composition. Indeed, NMDS ordination showed that samples clustered according to blocks but not land use (Figure 3), with no significant interaction between them. PERMANOVA confirmed these patterns (p = 0.002 for block; p = 0.63 for land use),

which were also visible in the 2022 biomass data (p = 0.001 for block; p = 0.82 for land use; Figure S2).

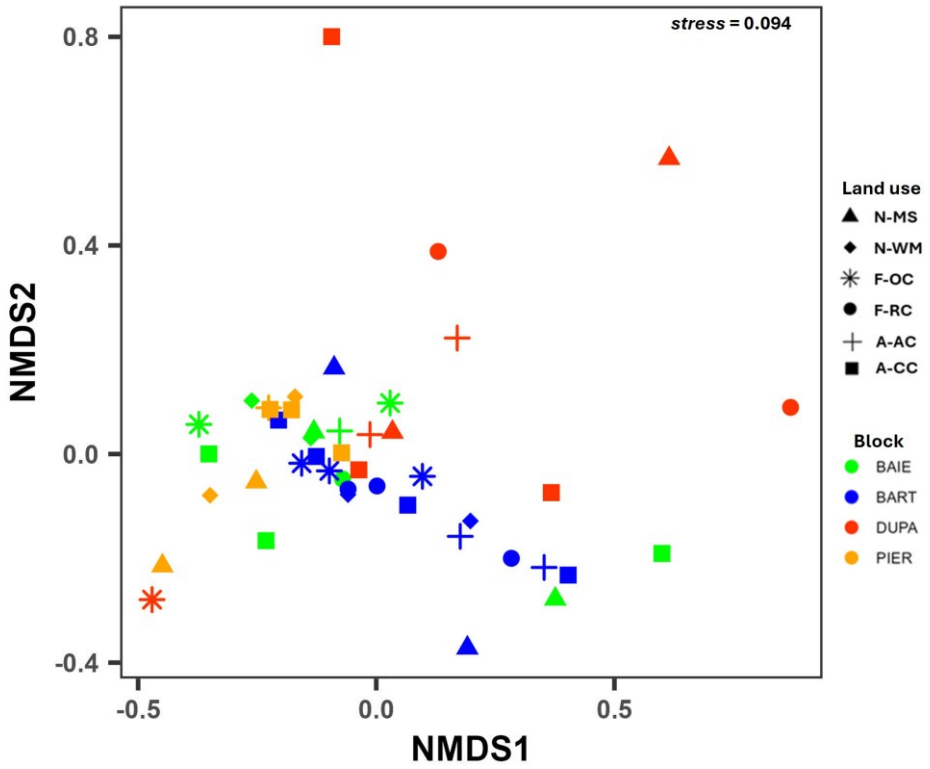


Figure 3. NMDS plot showing effect of land use and block (regions of floodplain for both years together) on zooplankton community composition (Hellinger-transformed species abundances). Samples from both sampling years were included. Symbols denote land use classes, whereas colors represent blocks. PERMANOVA results: p = 0.002** for block; p = 0.63 for land use.

Finally, none of the alpha diversity indices, nor biomass or community-weighted mean body size (CWMBS) varied with land use (Figure 4; p > 0.05 for all GLMMs).

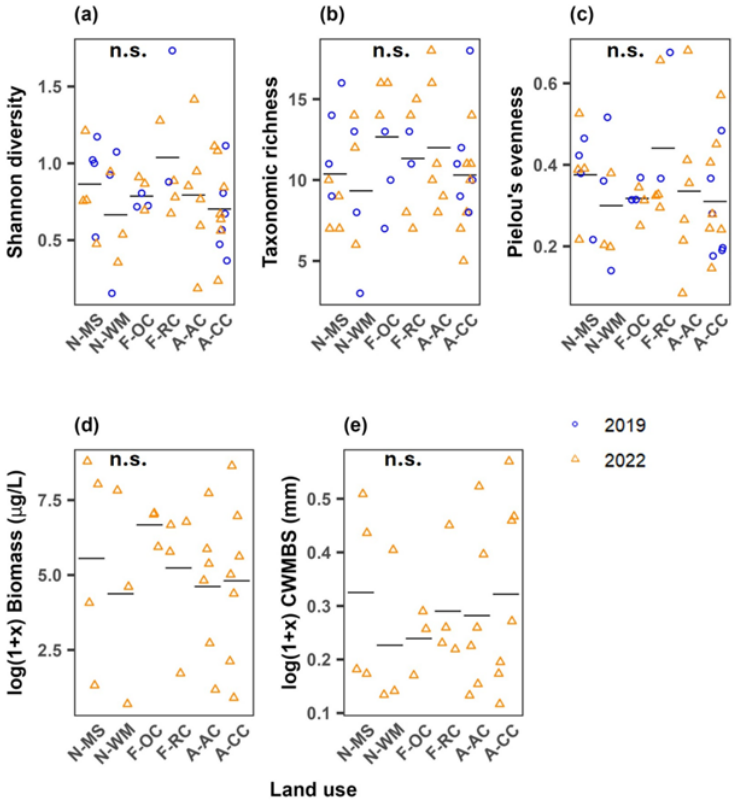


Figure 4. Zooplankton diversity, biomass, and body size as a function of land use. (a) Shannon diversity; (b) Taxonomic richness; (c) Pielou's evenness; (d) total zooplankton biomass (µg/L); (e) community weighted mean body size (CWMBS) (mm). Note that biomass and body size data were collected in 2022. n.s. denotes non-significant effect of land use in GLMM.

While plot-level land use had little impact on communities, variation in water quality strongly influenced many taxa and community descriptors (Figure 5). Inter-block variations in physico-chemical variables are presented in Figure S3. Abundance of cyclopoid adults and copepodites increased with water conductivity and DOC and decreased with pH (Figure 5A). Nauplii abundance was further influenced by (increased with) chlorophyll *a* and conductivity and decreased with pH. Harpacticoid abundance decreased with conductivity and turbidity, but increased with DOC. In contrast, cladoceran abundance decreased with chlorophyll *a* and pH, but increased with conductivity. Rotifers were most affected by chlorophyll *a* (positive effect) and DOC (negative effect), with pH and turbidity also having smaller but significant effects. Finally, ostracod abundance followed the same pattern as cyclopoids, with abundance increasing with conductivity and DOC and decreasing with pH. Among community descriptors, conductivity influenced total biomass significantly (positive effect), and to some extent species richness (positive effect) and

evenness (negative effect) (Figure 5B). Shannon index and community weighted mean body size were not influenced by any of the water quality parameters.

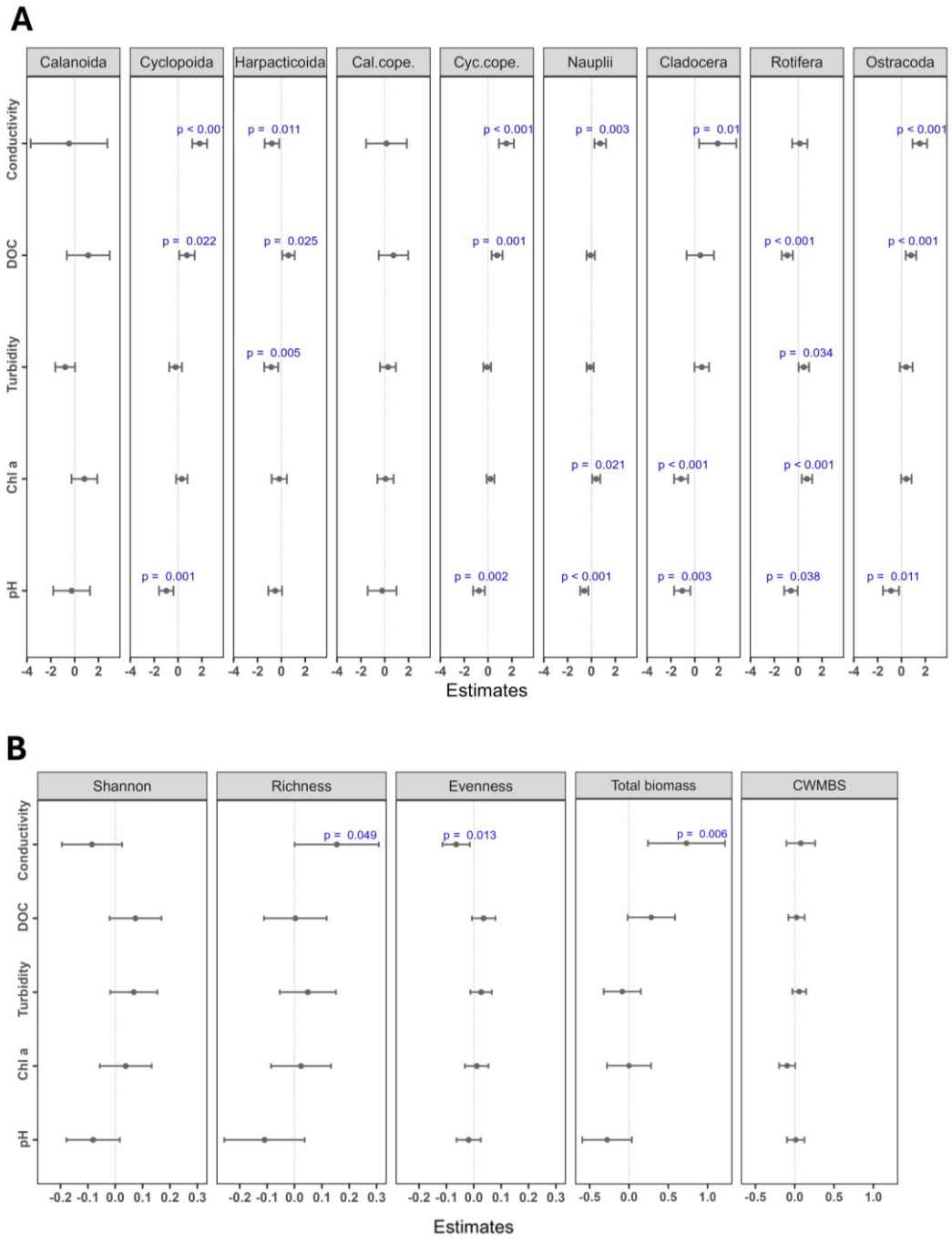


Figure 5. Forest plots showing the effect of 5 water quality variables on the abundance of all major zooplankton groups (A) and on 5 community descriptors (B). Estimates are coefficients from Tweedie GLMMs for abundances and LMMs for biomass and community weighted mean body size (CWMBS). All predictors were standardized to compare effect sizes. Error bars indicate confidence intervals. A dashed line is shown at 0 to aid interpretation. DOC: dissolved organic carbon, Chl *a*: Chlorophyll *a*, Cal.cope.: calanoid copepodites, Cyc.cope.: cyclopoid copepodites.

Discussion

We report results from a landscape-scale study where we characterized zooplankton communities of a large river floodplain in which land use was manipulated in collaboration with agricultural producers. Sites varied in land use and land cover, including natural wetlands and a gradient of land use intensity going from less intensive to more intensive forms of land use. Contrary to our expectations, local land use in the floodplain plots showed very little to no significant impact on zooplankton abundance, diversity indices, total biomass, and community weighted mean body size, most likely due to horizontal mixing of water among neighbouring fields and wetlands. However, a clear block effect was visible for most variables, indicating that zooplankton communities vary significantly within different regions of the same (relatively large) floodplain. Additionally, water quality parameters had a strong structuring effect on communities. While we cannot unambiguously attribute a cause for the observed variation in water quality, and thus zooplankton communities, we hypothesize that land use in watersheds draining onto the floodplain is a key factor.

Floodplain land use and zooplankton communities

Our first assumption that local land use (in the floodplain) would have a significant impact on the zooplankton community did not hold true except for harpacticoid abundance. These results contrast with Barbosa et al. (2025), who found a significant impact of localized land use on zooplankton in agricultural, floodplain landscapes. Another study reported higher abundances of cladocerans, copepods and nauplii from inundated forests compared to pasture, suggesting a key role of dense vegetation (Górski et al., 2013). A study comparing zooplankton in agroecological and conventional rice fields reported significant differences in abundance and diversity between these land uses (Romero et al., 2022). More specifically, they found higher values for richness, evenness and abundance of various groups in agroecological fields, while higher dominance due to smaller species in conventional crop fields, suggesting a positive influence of agroecological practices. In contrast, in this experiment, we found no influence of agroecological practices on any zooplankton metrics.

Despite the lack of results, it is known that local floodplain land use alters water physicochemical properties, in addition to affecting the availability of food and shelter for zooplankton (Fares et al., 2020). However, during inundation, environmental conditions and biological assemblages can be homogenized due to water movement, thereby masking local effects of land use (Nwonumara & Okogwu, 2013; Simoes et al., 2013). Several studies have indeed found homogenizing effects of floods on communities and their associated environmental drivers (Bozelli et al., 2015; Padial et al., 2014; Thomaz et al., 2007). Floods tend to increase zooplankton dispersal (Penha et al., 2017), with smaller organisms being more easily dispersed than larger ones (Padial et al., 2014). Thus, future work will distinguish the impacts of land use on various size fractions in our system. Flooding frequency is also known to have a significant influence on zooplankton communities (Baranyi et al., 2002); however, all of our sampling sites belonged to the 0-2 year flood recurrence zone and were located at the same elevation, and thus had roughly similar flooding frequency and connectivity with the main channel. A comparison of land uses at different elevations subjected to different flood regime (duration and frequency) might help uncover local effects of land use, e.g., in areas with a weaker connection (and thus presumably mixing) with the main river channel. However, differences between the overall flood regime of the St. Lawrence and other large rivers might explain the discrepancy between our results and those from other, more impacted floodplains where connectivity with the main river channel is generally weaker. Moreover, our sampling focused on a single date per site during each inundation year. As is evident in the literature, there exist differences in communities between rising and receding floods in the floodplains (Savignac, 1982). Incorporating both phases of flooding might therefore be beneficial to understand the dynamics of zooplankton in the floodplain.

Importantly, despite zooplankton communities did not show any response to land use in this study, we have evidence suggesting it can impact zooplankton (Savignac, 1982). Furthermore, Badesab et al. (2026) found strong impacts of land use on the emergence of hatchlings from the soil egg bank from the same sampling sites as this study, wherein natural wetlands were found to have significantly higher abundances of hatchlings compared to agricultural sites. This suggests that land use impacts soil properties (e.g., structure, contaminants), resting egg viability, and thus the emergence of

zooplankton from resting stages. Thus, even if water mixing masks the effects of land use on communities during spring inundation, agricultural fields would nonetheless be expected to export less zooplankton to the water column than natural wetlands and therefore contribute less to zooplankton standing stock biomass in this system. This would suggest that if all natural wetlands were to be converted to agriculture, total zooplankton density across the entire floodplain would decline.

Water quality and zooplankton communities

Copepods, cladocerans, and rotifers were found to be abundant and diverse in our study, similarly to what has been observed in other floodplain wetlands (Chaparro et al., 2019; Siziba et al., 2013). These major taxa can all be affected by various physicochemical and biotic variables (Schöll et al., 2012). In the present study, five main water quality variables (conductivity, DOC, turbidity, pH and Chl *a*) influenced zooplankton communities in line with several other studies. For example, conductivity has been reported to significantly influence cyclopoids (Perbiche-Neves et al., 2021), ostracods (Castillo-Escriva et al., 2017; Liberto et al., 2012) and cladocerans (Çakıroğlu et al., 2014). Cladoceran abundance has been reported to increase with high conductivity in a flood-controlled tropical floodplain wetland (Dube et al., 2017). Zooplankton biomass and/or richness also increased with conductivity in Chilean lakes and ponds (Soto & De Los Rios, 2006) and Turkish lakes (Çakıroğlu et al., 2014). pH was found to be negatively correlated with most zooplankton groups, which is in agreement with results from the Yangtze River floodplain lakes (Lu et al., 2021) and pond ostracods (Liberto et al., 2012). Some cladoceran species have been reported to prefer low pH conditions (Kattel, 2012), as was found in our study as well.

Chlorophyll *a* as an indicator of phytoplankton biomass/food availability for zooplankton has also been found to significantly influence zooplankton in various studies (e.g., Yuan & Pollard, 2018). In our study, we found an inverse relationship between Chl *a* and cladoceran abundance, with only nauplii showing a positive, albeit weak, relationship with Chl *a*. This is a puzzling result for which we currently do not have an explanation. Turbidity was found to be positively correlated with rotifer abundance but negatively

correlated with copepod (harpacticoid) abundance. Thorp & Mantovani (2005) have reported that copepods are more sensitive to turbidity than rotifers, the latter being raptorial or microphagous feeders whose feeding mechanisms are less impacted by suspended particles (Kirk & Gilbert, 1990). Increased DOC in floodplain riverine systems have been found to support zooplankton abundances via bacterial and microbial pathways (Hitchcock et al., 2025; Mitrovic et al., 2014), which is partially in agreement with our study, where rotifers, ostracods, cyclopoids, and harpacticoids, but not cladocerans, were positively influenced by DOC.

While we did not map the hydrology of our study system, we presume that variation in water quality variables was mainly associated with different water masses from the neighbouring watersheds with different land uses. Over 20 different streams of various sizes contribute to the flooding of our sampling plots, and these differ in watershed land cover (Campeau et al., 2024). Thus, an obvious future direction for this work would be to quantify watershed land use in all of these floodplain tributaries and determine whether such upstream land use affects local (floodplain) water quality. Few studies have considered the regional-scale impacts of land use on zooplankton. For example, Shen et al. (2021) studied the impact of urbanization on zooplankton at different spatial scales and reported that urbanization inhibits zooplankton biodiversity at some, but not all, scales. Furthermore, they also reported that wetland water quality correlated positively with species richness. A study by Fernández et al. (2009) showed that copepods were not affected by either local water quality or landscape features at different spatial scales, but that cladocerans responded to local water quality conditions (Fernández et al., 2009).

Conclusions

Overall, our results suggest that zooplankton communities in the floodplain are influenced by a combination of factors. We did not find any impact of land use at the local scale, but the effects of block (region) and water quality were clear. Future work should aim to clarify the drivers of water quality variation in this system, taking a regional-scale perspective. When combined with the results of Badesab et al. (2026) reporting a strong effect of local land use on zooplankton emergence in the same system, our results

suggest the need to incorporate land use and environmental factors at both the local and the watershed scales to determine more precisely the drivers of floodplain zooplankton communities. This would aid further in developing more effective mitigation measures for the conservation of biodiversity and sustainable management of floodplain ecosystems.

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Author contribution

Conceptualisation: SB, AB, VF, GC. Developing methods: SB, AB, VF, GC. Conducting the research: SB, GB. Data analysis: SB, AB, VF. Data interpretation: SB, AB, VF. Preparation of figures & tables: SB, AB, VF. Writing: SB, AB, VF.

Data availability statement

The data will be made available on the Borealis repository upon acceptance of the manuscript for publication.

Conflict of interest

The authors declare no conflict of interest.

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Supplementary material

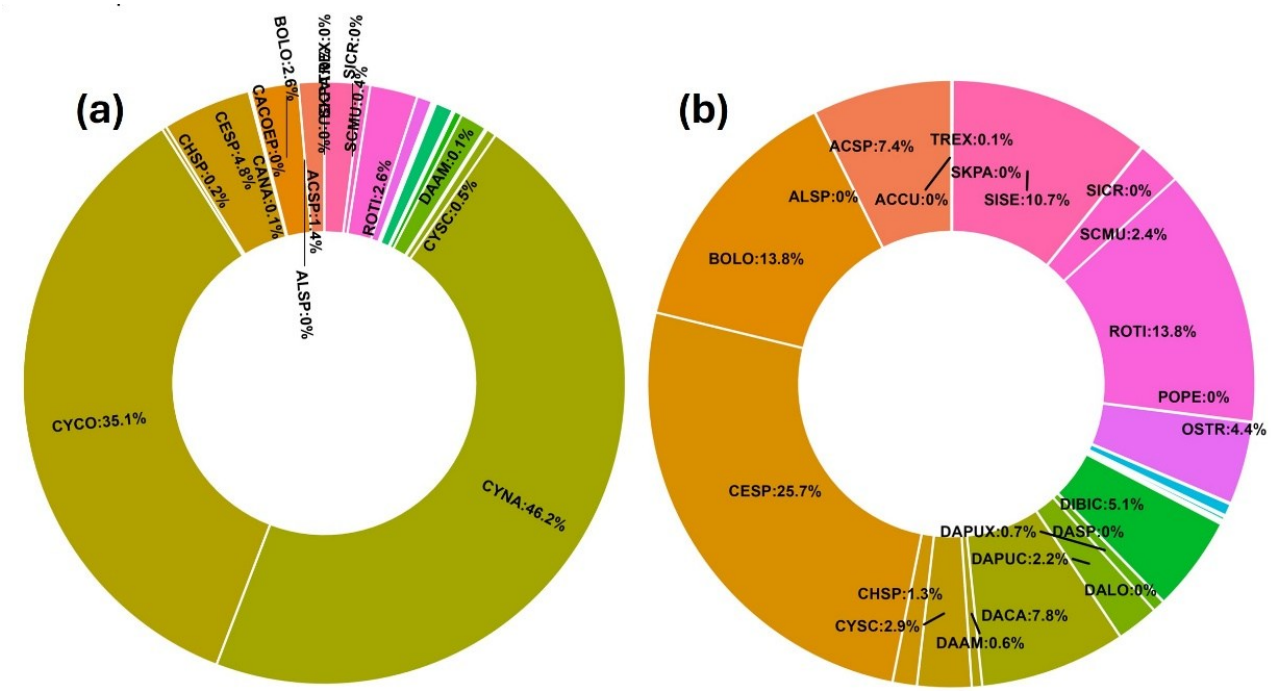


Figure S1. Percent contribution of zooplankton taxa to total abundance, either. (a) including copepodites and nauplii, or (b) excluding copepodites and nauplii. Rotifera (ROTI); Ostracoda (OSTR); *Bosmina longirostris* (BOLO); *Chydorus sphaericus* (CHSP); *Daphnia pulicaria* (DAPUC); *Simocephalus serrulatus* (SISE); *Ceriodaphnia* sp. (CESP); *Scapholeberis mucronata* (SCMU); *Eurytemora affinis* (EUAF); *Acanthocyclops* sp. (ACSP); *Cyclops scutifer* (CYSC); *Diacyclops bicuspidatus* (DIBIC); *Eubosmina longispina* (EULO); *Tropocyclops extensus* (TREX); *Leptodiaptomus minutus* (LEMI); *Macrothrix laticornis* (MALA); *Eucyclops elegans* (EUEL); *Daphnia catawba* (DACA); *Skistodiaptomus pallidus* (SKPA); *Eucyclops agilis* (EUAG); *Microcyclops* sp. (MISP); *Sida crystallina* (SICR); *Megafenestra nasuta* (MENA); *Mesocyclops edax* (MEED); *Orthocyclops modestus* (ORMO); Harpacticoida sp. (HASP); *Diacyclops thomasi* (DITH); *Daphnia ambigua* (DAAM); *Daphnia pulex* (DAPUX); *Moina macrocopa* (MOMA); *Diaphanosoma birgei* (DIBIG); *Acantholeberis curvirostris* (ACCU); *Daphnia longiremis* (DALO); *Onychodiaptomus birgei* (ONBI); *Macrocyclops albidus* (MAAL); *Daphnia* sp. (DASP); *Eurycercus* sp.(EUSP); *Polyphemus pediculus* (POPE); *Diacyclops nanus* (DINA); *Alona* sp. (ALSP); Calanoid nauplii (CANA); Cyclopoid copepodites (CYCO); Cyclopoid nauplii (CYNA); Calanoid copepepodites including Epischura copepodites (CACOEP); Harpacticoida nauplii (HANA).

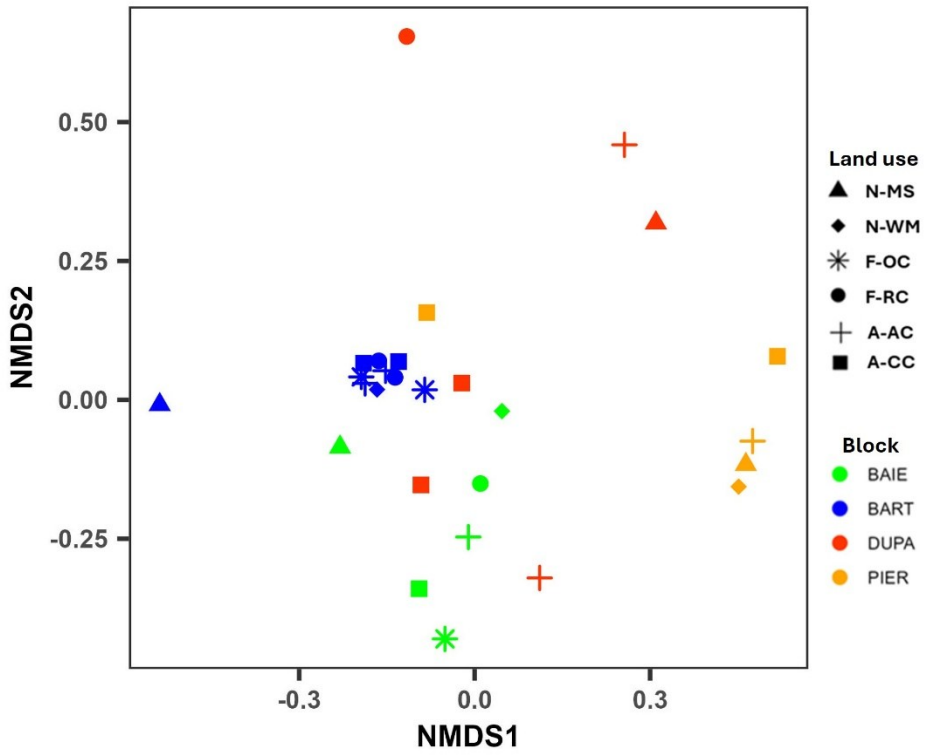


Figure S2. NMDS plot showing the effect of land use and block (regions of floodplain) on zooplankton biomass during spring 2022. Symbols denote land use classes whereas colors represent blocks. PERMANOVA results: p = 0.001*** for block; p = 0.82 for land use.

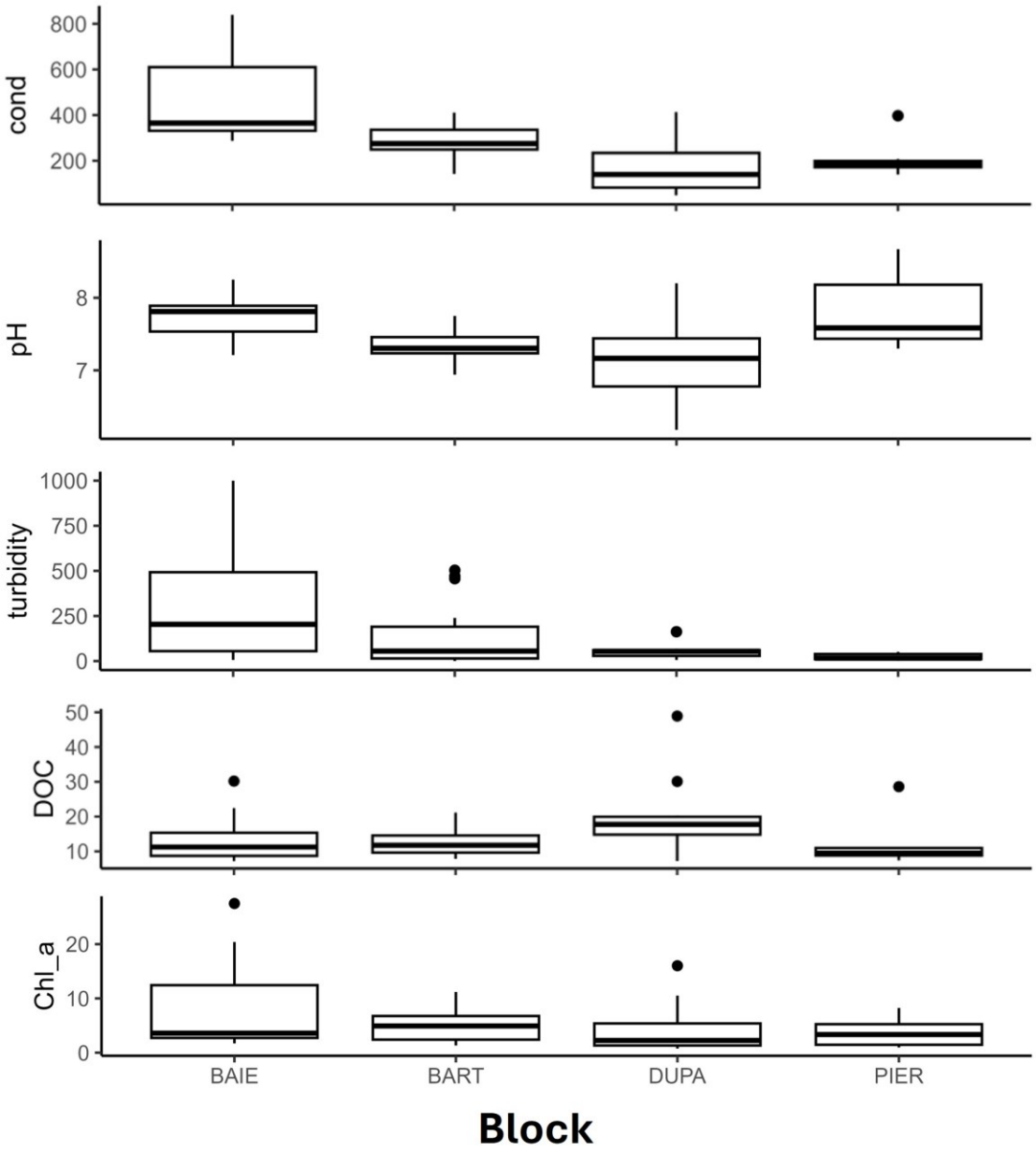


Figure S3. Variation in water quality variables across blocks.

Table S1. Details of sample collection during spring flooding.

Year	Land use	Block			
		BAIE (*n*)	BART (*n*)	DUPA (*n*)	PIER (*n*)
2019	N-MS	1	1	1	1
	N-WM	1	1	-	1
	F-OC	1	1	1	-
	F-RC	-	1	1	-
	A-AC	-	-	-	-
	A-CC	2	2	1	1
2022	N-MS	1	1	1	1
	N-WM	1	1	-	1
	F-OC	1	2	-	-
	F-RC	1	2	1	-
	A-AC	1	2	2	1
	A-CC	1	2	2	2

CHAPTER II

IMPACTS OF LAND USE AND FLOOD REGIME ON ZOOPLANKTON EGG BANKS IN A LARGE RIVER FLOODPLAIN

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Abstract

Zooplankton egg banks are crucial in rebuilding zooplankton populations in temporary water bodies when favourable conditions return after dry periods. However, their abundance, viability and hatching success depend on many factors, with changes in land use and flooding regimes being potentially crucial drivers. Here, we studied a large-river floodplain to compare the egg banks of soils across a land use gradient and at different elevations, the latter affecting inundation frequency and duration. We performed experimental manipulations at both the ecosystem scale (land use in the floodplain) and in the laboratory (incubation of soils of different origins). Six land use types were considered: i) natural maple swamp, ii) natural wet meadow, iii) old forage cropping, iv) recently sown forage cropping, v) agri-environmental corn/soybean cropping, and vi) conventional corn/soybean cropping implemented in collaboration with agricultural producers. Egg banks were characterized through both i) direct egg counts and ii) by

counting the individuals emerging following the incubation of soils in the laboratory, testing the effects of land use, and flooding regime (duration, frequency) on hatching success.

We found no significant difference in the abundance of resting eggs of different taxa in soils across the land use gradient in frequently inundated sites at low elevation. In contrast, at high elevation where inundation periods are less frequent and shorter, rotifer and cladoceran egg density varied across land uses, with higher abundance in old forage cropping compared to agricultural cropping. Ostracods, rotifers and copepods were the most abundant taxa that hatched in the laboratory. Their abundance varied across land use types, with natural soils supporting higher abundances than agricultural soils, and forage cropping showing intermediate abundances. Frequently inundated sites (low elevation) had higher abundances of hatchlings than the less frequently inundated (high elevation) sites. Inundation duration in incubators strongly influenced ostracod hatching only, with an overall increase after two weeks of inundation and a decrease thereafter for most soil types.

Different taxa dominated the egg and hatchling counts. For example, cladocerans were common in the egg bank but not in hatchling samples, while ostracods were absent from the former but dominated the latter. This apparent paradox suggests that egg viability varied along the land use gradient (e.g. due to agricultural practices during summer months), that the cues required for hatching differed across taxa, or that stress (land use) modulates the likelihood that ostracods enter dormancy as eggs vs juveniles/adults. Natural wetland habitats in floodplains favour the resilience of zooplankton communities facing a disturbance (i.e., the dry period) via a high potential recovery through emergence of resting stages. In contrast, alterations to these habitats due to agricultural intensification in floodplains hampers zooplankton community resilience via decreased emergence success. Agricultural practices leading to changes in soil properties, which influence the viability of resting stages, are the plausible explanations for this phenomenon. It is paramount to conserve natural wetlands and implement sustainable land use practices in floodplains, to allow egg banks to rebuild zooplankton communities in floodplains and sustain their productivity and ecosystem services.

Introduction

Floodplains are temporary water bodies or aquatic habitats that have lateral connectivity with the main river channel and that undergo periodic drying (Junk et al., 1989). These highly dynamic systems are among the world's most productive and biodiverse freshwater ecosystems (Reis et al., 2017; Tockner & Stanford, 2002). Different zooplankton taxa such as rotifers, cladocerans, copepods, and ostracods are generally abundant in floodplains (Pereira et al., 2017; Siziba et al., 2013). These contribute significantly to the high production of these ecosystems and serve as an important food source for higher trophic levels (Bunn et al., 2003; Jardine et al., 2013). For example, early life stages of fishes spawning in floodplains are highly reliant upon zooplankton production from the floodplain itself (Farly et al., 2019; Górski et al., 2013). To survive in such temporary aquatic environments, zooplankton have evolved adaptations to enter dormancy during long dry periods, including production of resting stages that remain dormant and viable for many years (Gyllström & Hansson, 2004; Schröder, 2001; Williams, 2006). These dormant forms are commonly found in rotifers, copepods, ostracods, and cladocerans, and include dormant eggs (e.g. rotifers, ostracods and copepods), ephippia (cladocerans), larval instars (e.g. copepods) and aestivating adults (e.g. ostracods) (Bruno et al., 2001; Williams, et al., 2015; Zhai et al., 2024). The accumulation of such dormant forms in floodplain sediments constitutes a reservoir of resting stages (hereafter "egg bank", a general term we use here to refer to both eggs and other resting stages). By integrating over long time periods, egg banks comprise high genetic variation (Brendonck & De Meester, 2003a) and they can contribute significantly to re-building the zooplankton community in the water column with the onset of the next flooding cycle or when favourable conditions return (Battauz et al., 2014; Brendonck & De Meester, 2003a; Schröder, 2001). Thus, egg banks contribute significantly to the productivity of floodplains and potentially subsidize adjacent main river channels (Farly et al., 2019).

Floodplain egg banks could be affected by anthropogenic stressors such as floodplain land use and hydrological alterations. Indeed, lateral connectivity and hydrology (e.g. the duration, timing, and flooding magnitude) strongly influence floodplain physico-chemical properties and biota (Chaparro et al., 2023; Sackreiter, 2019), and their

exchange of matter and organisms with the main river channel (Dias et al., 2017; Junk et al., 1989). For example, higher and longer-lasting floods often enhance fish spawning and recruitment, with fish thereby returning to the main river channel once flood waters recede (Junk et al., 1989). Flood characteristics and lateral connectivity also affect ecosystem services such as flood and erosion control, water quality, groundwater recharge, wildlife habitat, and recreation opportunities (Petsch et al., 2023) as well as overall ecosystem functioning (Jakubínský et al., 2021; Petsch et al., 2023). However, human disturbances can affect floodplain connectivity, hydrology, and extent (Davidson, 2014). For example, the construction of levees to control flooding has led to the expansion of agriculture and the decline in the extent of floodplains in both Europe and North America (Richter et al., 2003). Climate change might further exacerbate floodplain loss through its negative impacts on inundation duration and intensity in some regions (Schneider et al., 2011). However, how human impacts on the hydrological regime of floodplains will influence zooplankton egg banks has not been fully explored yet.

Floodplains are also increasingly affected by land use. Being highly fertile and accessible, floodplains have long been used and impacted by human activities, altering the services they provide (Jakubínský et al., 2021). Urbanization and expansion of agriculture in floodplains can lead to a loss of biodiversity and habitat complexity (Buijse et al., 2002; Tockner & Stanford, 2002). A recent study by Rajib et al. (2023) on floodplain alterations from 1992 to 2019 along 520 major river basins (15 million km^2) across the globe, revealed a significant loss of natural floodplains to agriculture (460,000 km^2) and other developments (140,000 km^2). For example, tropical floodplains are under immense pressure due to rapid population increase and infrastructure development (Roggeri, 2013), thereby decreasing the extent of natural habitats. In New Zealand, a decrease in natural forest cover from 75 to 23% has been reported for floodplains (Fahey et al., 2004). In Quebec, Canada, floodplains along the Saint-Lawrence River have experienced significant agricultural intensification since the 1950s, whereby grasslands and perennial crops are being replaced with annual crops (intensive soy and corn monocultures), affecting water quality and fish spawning habitat during spring floods (Jobin & Brodeur, 2023), with cascading effects on floodplain food webs and biodiversity (Farly et al., 2019;

Hudon et al., 2018). Conventional, intensive agricultural practices (with pesticides, tillage, and fertilization) have degraded natural habitats available for wildlife (Rioux et al., 2009). Ploughing causes destruction of natural vegetation used as spawning grounds by some fishes (Richard et al., 2011). Agricultural intensification in floodplains and the associated diminished water quality (e.g. higher pesticide loads) may also impact zooplankton standing stocks and egg banks, thus leading to a reduction in zooplankton biomass and/or diversity and, in turn, to the size of the forthcoming egg banks (Gleason et al., 2003b; Plangklang & Athibai, 2021). While relatively few studies have been conducted on the response of floodplain egg banks to land use, studies conducted in other temporary water bodies have indeed found negative impacts of agriculture. Frisch et al. (2009) studied the zooplankton propagule banks from different sections of Mediterranean temporary stream in laboratory-controlled conditions and found that the zooplankton hatchling abundances were lower in agricultural sections in comparison to reference (forested) sections. Fernandez et al. (2009) studied the association of zooplankton egg bank with local habitat features and landscape features (land use percentage) in ponds using microcosms and found that land use impacted some taxa. However, it remains unclear whether more sustainable agricultural practices, such as the use of cover crops or intercropping, can mitigate the negative impacts of intensive land use on zooplankton egg banks, especially in floodplains.

Unveiling the effect of land use and inundation duration on zooplankton egg banks is key to understanding the potential resilience (i.e., the ability to cope with or recover from disturbances; Bernhardt & Leslie, 2013) of zooplankton communities facing environmental change. Some studies have looked at zooplankton resilience in floodplains (e.g., Górski et al., 2013), but these have tended to focus on single drivers (e.g. extreme flood and drought phases; Golec-Fialek et al., 2021), types of vegetation or environments (Odriozola et al., 2020; Pérez-Martínez et al., 2013), or taxonomic groups (Frisch & Threlkeld, 2005; Gilbert, 2017; Panarelli et al., 2020; Rosa et al., 2020). Hatching success of resting eggs is influenced by a combination of environmental factors which could be region- or habitat-specific and not governed by any single variable, prompting the need for broad-scale comparisons across habitat types and taxa (Brendonck, 1996). Moreover, to our

knowledge, only a few studies have directly characterized the abundance of zooplankton resting stages in floodplains or temporary wetlands (Waterkeyn et al., 2011; Zhai et al., 2024; Rahman et al., 2025), and fewer still have compared such data to hatching success in the laboratory.

To narrow these knowledge gaps, this study aimed to i) quantify zooplankton resting eggs in floodplain soils across a land use gradient from natural to conventional (intensive) agriculture and ii) evaluate the interactive impact of land use and flood regime (duration and frequency) on zooplankton hatching from the egg bank (for simplicity, we use the term “hatching” to refer to emergence of zooplankton from both eggs and other dormant stages). To that end, natural wetlands were compared with farmed fields in four regions of a large floodplain complex along the Saint-Lawrence River, Canada, also comparing sites with frequent vs. rare inundation. Our treatments include a wide range of land use practices (natural, forage, agri-environmental, and conventional agriculture) that were implemented in collaboration with agricultural producers. We hypothesized that land use and flooding regime (frequency and duration) would have a strong influence on the resilience of zooplankton by affecting their resting eggs and hatching success. More specifically, we hypothesised that 1) natural soils would harbor higher abundance of resting eggs compared to forage and agriculture soils; 2) abundance of hatchlings would be higher in natural wetlands, intermediate in forage fields and lowest in agricultural fields, mimicking the pattern seen for resting eggs; and lastly 3) longer inundation duration and higher inundation frequency would support higher hatchling abundances of all zooplankton groups.

Methods

Study area and sampling design

Lake Saint-Pierre (LSP; 46°12’ N, 72°49’ W), the largest fluvial lake along the St. Lawrence River in Canada, is a biodiversity hotspot, a UNESCO Biosphere Reserve, and a Ramsar wetland of international importance due to its extensive seasonal floodplain (Jobin & Brodeur, 2023). LSP experiences annual spring flooding and gets inundated for 5 – 9 weeks, with the spatial extent of the inundation varying strongly across years

(Watson et al., 2024). Over recent decades, land use alterations have been dramatic in the region, with both agricultural expansion and intensification affecting LSP (Hudon et al., 2018; Jobin & Brodeur, 2023). For example, around 50% of the area covered by perennial crops (pasture and hay fields) that were present in the 1950's were converted to annual crops such as intensive corn and soya by the end of the 1990's (Dauphin & Jobin, 2016), a trend that continued until recently (Jobin & Brodeur, 2023). This resulted in increased pesticide contamination and turbidity, impaired water quality, and a loss of wetland habitats, all of which have been invoked to explain the recent collapse of a commercially-important yellow perch (*Perca flavescens,* Mitchill, 1814) fishery (Dauphin & Jobin, 2016b). This might also be related to lower productivity of aquatic invertebrates - a key food source for early ontogenic stages of yellow perch in the tilled or mowed field compared to the natural wetlands (TCRLSP, 2017). Therefore, considering the need to take urgent measures to protect and restore these wetland habitats and their associated fisheries, the Quebec government established in 2018 the *Pôle d'expertise multidisciplinaire en gestion durable du littoral du Lac Saint-Pierre* (Multidisciplinary Hub of Expertise on the sustainable Management of the Littoral Zone of Lake Saint-Pierre in Quebec), a collaborative project involving multiple research groups in ecology, agronomy, and agricultural economics. The aim of this research group was to identify compromises and solutions for sustainable land management in the LSP floodplain by comparing a large suite of environmental, social, and economic indicators across various land use types, some of which were manipulated in collaboration with landowners (Watson et al., 2024).

Sampling locations were selected based on accessibility during both spring and autumn periods and landowners' willingness to participate in the project and implement new agri-environmental practices. Thirty experimental units (locations) were selected following a randomized block design with four blocks corresponding to regions of the floodplain, namely Baie-du-Febvre (BAIE; $n = 8$), Pierreville (PIER; $n = 6$), Saint-Barthelemy (BART; $n = 9$), and Île Dupas (DUPA; $n = 7$) (Figure 1).

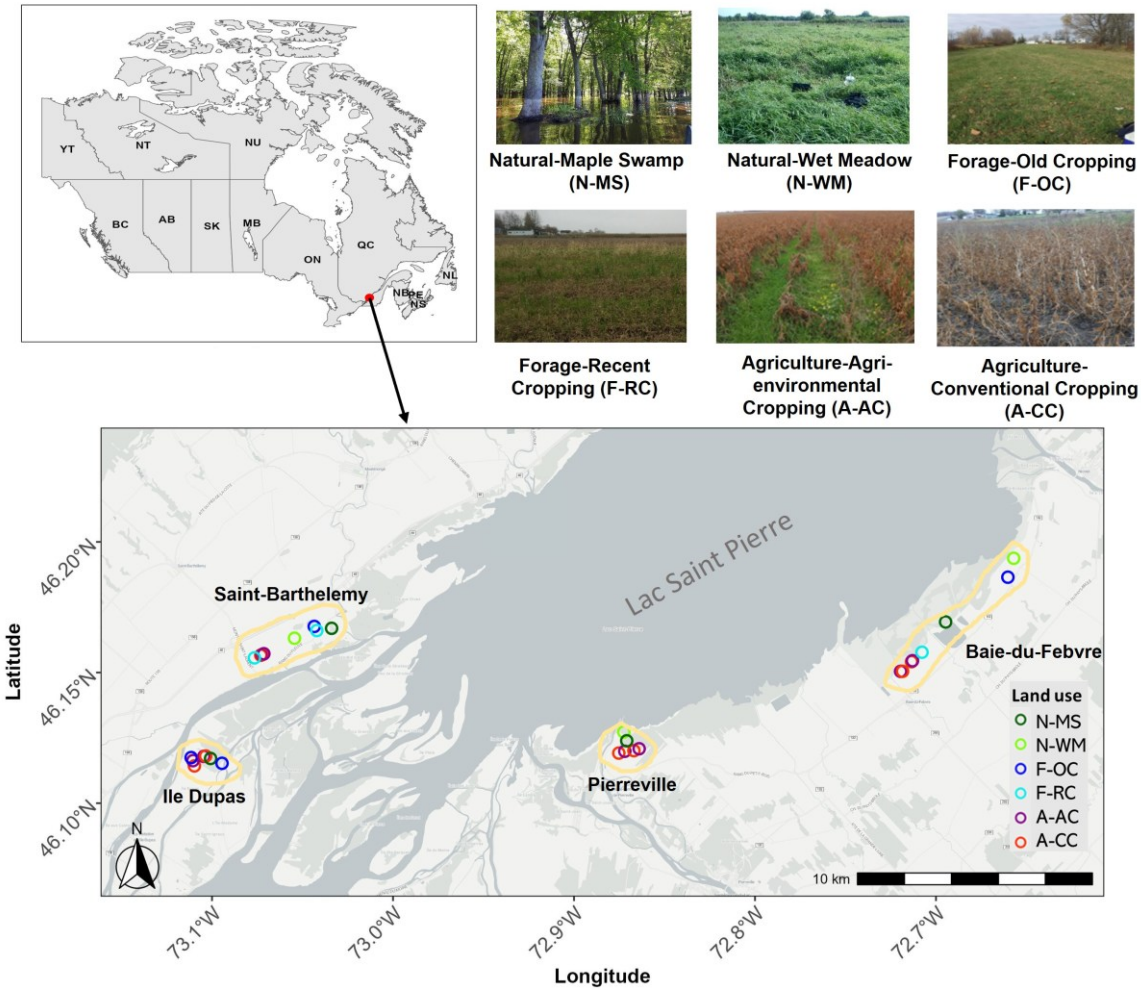


Figure 1. Study area depicting 30 sampling locations within four blocks (Baie-du-Febvre, Pierreville, St. Barthelemy and Ile Dupas) in the Lake Saint-Pierre Floodplain (Quebec, Canada). Each block includes 6 types of land use: 1) Natural-Maple Swamp (N-MS), 2) Natural Wet Meadow (N-WM), 3) Forage-Old Cropping (F-OC), 4) Forage-Recent Cropping (F-RC), 5) Agriculture-Agri-environmental Cropping (A-AC), and 6) Agriculture-Conventional Cropping (A-CC). Land use image credits: Jim Félix-Faure, Geneviève Berger, Shahin Badesab; Land use nomenclature adapted from Watson et al., 2024.

Six land use types were considered: i) natural maple swamp (N-MS; *n* = 4), ii) natural wet meadow (N-WM; *n* = 3), iii) old forage cropping (F-OC; *n* = 4), iv) recently sown forage cropping (F-RC, *n* = 3), and v) agri-environmental cropping of annual crops (A-AC; *n* = 8) and vi) conventional cropping of annual crops (A-CC; *n* = 8) (nomenclature adapted from Watson et al., 2024). The N-MS plots were dominated by silver maple; N-WM were natural, uncultivated grasslands; F-OC were forage grown for more than five years without ploughing; F-RC were newly-established grasslands sown for the project, within the last five years; A-AC included annual crops (soybean-corn rotations) with inter-cropping,

cover cropping, and/or perennial buffer strips implemented since 2018, while the A-CC included annual crops without any improved practices. For more details on land use classification, see Watson et al. (2024). Since site selection depended on accessibility and willingness of landowners to implement agri-environmental practices, not all land use types could be represented in each block. Thus, the design is nearly but not fully balanced: for example, BART and BAIE had some land use types with more than one replicate, whereas in DUPA and PIER some were absent. Each plot also had a low elevation sampling location which flooded almost every year and a high elevation sampling location that floods less frequently (Watson et al., 2024).

Soil sampling and abiotic measurements

Soil samples for egg bank characterization were collected in three replicates from each location from the top 10 cm, using a core sampler/dibble (~7 cm diameter) (Brendonck & De Meester, 2003a; Catlin et al., 2016). A composite sample was prepared by pooling the three replicates collected at the same site. The field campaigns were carried out during dry periods on three occasions: autumn 2019 (low elevation only), spring 2020, shortly after flood waters receded (low elevation only), and autumn 2020 (at both low and high elevations). Dry soil samples were then transferred to plastic self-sealing bags, labeled, and stored at 4 °C in the dark until further use. Details of soils collected are given in Table 1.

Table 1. Details of sample collection and analyses.

Assessment/ Experiment	Year	Season	Elevation	No. of sites	Incubators	No. of observations	Additional information
1. Abundance of resting eggs	2019	autumn	low	18	NA	18	See Figure 2a-c
	2020	spring	low	23	NA	23	See Figure 2d-f
	2020	autumn	low	27	NA	27	See Figure 2g-i
	2020	autumn	high	20	NA	20	See Figure 2j-l
2. Hatching experiment 1: Series I	2019	autumn	low	30	30	690 (30 x 23 days)	30 days of incubation. Repeat sampling of the incubators once every 1-2 days. See Figure 3a-c
Hatching experiment 1: Series II	2019	autumn	low	30	30	30	30 days of incubation. One sampling on day 30. See Figure 3d-f
3. Hatching Experiment 2: Series III	2020	autumn	low	30	150	150 (30 x 5 weeks)	7-35 days of incubation. 5 incubators per site for 1, 2,3,4,or 5 weeks of inundation. See Figure 4
Hatching experiment 2: Series IV	2020	spring	low	29	29	29	28 days of incubation. One sample on day 28. See Figure S2
	2020	autumn	high	20	20	20	28 days of incubation. One sampling on day 28. Ten sites were not sampled. See Figure S3

*NA= Not Applicable

Water samples for water quality variables were collected during spring flooding in 2019 (n = 22) and soil samples for quantifying soil abiotic variables were collected only once in autumn 2019 (n = 30) (See Supplementary material, section: Environmental variables for more details).

Abundance of resting eggs in the soils

Eggs were extracted from the soil samples collected across the land use gradient during autumn 2019 at low elevation (N-MS, *n* = 1; N-WM, *n* = 1; F-OC, *n* = 3; F-RC, *n* = 3; A-AC, *n* = 5; A-CC, *n* = 5), spring 2020 at low elevation (N-MS, *n* = 2; N-WM, *n* = 2; F-OC, *n* = 4; F-RC, *n* = 3; A-AC, *n* = 7; A-CC, *n* = 5) and autumn 2020 at both low elevation (N-MS, *n* = 3; N-WM, *n* = 2; F-OC, *n* = 4; F-RC, *n* = 3; A-AC, *n* = 7; A-CC, *n* = 8) and high elevation (F-OC, *n* = 2; F-RC, *n* = 2; A-AC, *n* = 8; A-CC, *n* = 8) (Table 1). The number of soil samples used for egg extraction was smaller than that used in the emergence experiments (30); indeed, the soils were used for the emergence experiments first, and the assessment of resting egg abundance was carried out on the remaining amount of soil. In addition, at high elevation, ten sites out of 30 were not available. All seven natural sites were absent at high elevation; these land use types only occur at low elevations in the LSP floodplain, as much of the higher elevation sites have been cleared for agriculture. Three other high elevation sites had to be excluded due to sample mislabelling during fieldwork. Eggs were extracted using the sugar floatation method (Marcus, 1990; Onbé, 1978; Vandekerkhove et al., 2004a, 2004b). An aliquot of 15 g of soil from each site was centrifuged at 2700 rpm for three mins after adding a sugar solution in a 1:1 ratio (1000 g table sugar in 1000 mL distilled water) (Araújo et al., 2013). The supernatant was washed with distilled water on a 35 µm mesh to remove sugar residues. This cycle was repeated three times to extract the maximum/all possible resting eggs and store them in 70% ethanol (Waterkeyn et al., 2011). Eggs were then identified using available keys (Bailey et al., 2003; Maia-Barbosa et al., 2003; Vandekerkhove et al., 2004a, 2004b).

Hatching experiments

Hatching experiment 1: Effects of land use on zooplankton emergence

This experiment used composite soil samples collected in autumn 2019 at low elevation (*n* = 30). The soil was sieved through 4 mm mesh to separate large particles, split into two sub-samples, and then transferred to separate glass jars (700 mL) to form a 2-cm layer of soil at the jar bottom, without any prior isolation of eggs (Catlin et al., 2016). One jar per composite soil sample was used for each incubation series (I & II) described

below. The jars were filled 2 cm above the soil with filtered water (10 µm mesh) from the Saint-Lawrence River to remove all metazoans. Jars were placed randomly within a 2 x 6 m fish raceway in the UQTR wet laboratory. Samples were incubated at 12-14 °C with a luminosity of 100-140 lux and a 16:8 h light/dark cycle to mimic the light conditions in southern Quebec during spring. The incubation experiment ran for 31 days. Jars were periodically moved randomly within the raceway to reduce small differences in light intensity across the raceway. On every sampling occasion, hatchlings (i.e., individuals emerging from eggs or aestivating resting stages) were collected by removing the supernatant water using a pipette and filtering it through a 80 µm mesh (the 35-80 µm fraction was also checked, but resulted in virtually no zooplankton). Hatchlings retained on the mesh were transferred to 60 ml plastic containers and fixed in 70% ethanol. Hatchlings were identified and counted using a stereomicroscope. At the end of the experiment, the leftover soils in the incubators were then dried at 60 °C for 24 hours or more until constant weight was achieved and then weighed to calculate soil dry weight (FAO, 2023).

Using identical incubation and sampling methods, we conducted two incubation series that both aimed to test for the effect of land use. The two series, however, varied in their temporal resolution (Table 1):

Incubation series I: Cumulative daily hatching. Jars were sampled every day for the first 15 days and then every other day between day 16 and day 31 (n = 30 jars x 23 times = 690 samples). This labor-intensive incubation series was meant to quantify hatchling abundance without mortality (e.g. due to starvation) or species interactions.

Incubation series II: Snapshot sample at four weeks. Sampling occurred only once on day 30 (last day) of the incubation (n = 30 jars). This series was expected to represent the outcome of all processes (emergence, reproduction, competition, and mortality) occurring in the jars during the incubation period and was also meant to test whether land use effects could be detected with a single snapshot sample.

Hatching experiment 2: Combined effects of land use and flood regime on zooplankton emergence

Two other incubation series were used to test whether flood regime interacts with land use to influence emergence, with flood regime defined as either inundation duration manipulated experimentally (series III) or inundation frequency *in situ* linked to site elevation (series IV). These incubations were made under the same experimental conditions (light and temperature) as experiment 1, but we standardized wet weight of soils (100 g) to account for variation in sample dry weights observed during experiment 1, where soil volume was standardized.

Incubation series III: Hatching snapshot at weekly intervals over five weeks. The soils collected from the 30 sites at low elevation during autumn 2020 were split into 5 jars (n = 30 x 5 weeks = 150 jars) and filled with filtered water from the St. Lawrence River. In order to simulate different inundation durations, one replicate jar per soil was sampled after 1, 2, 3, 4 or 5 weeks of incubation. Note that the observations for week 4 from this experiment are directly comparable with the results of incubation series II from Hatching Experiment 1, since the experimental conditions are similar. This series was also meant to reveal if a similar pattern can be obtained along the land use gradient despite potential interannual variations in environmental conditions.

Incubation series IV: Effects of inundation frequency and sampling season on hatching (soils from 2020 only). In order to test the effect of inundation frequency *in situ* we compared the soils collected in autumn at low elevation (data from week 4 of series III) with soils collected at the same time but at higher elevation by using elevation as a proxy for flood regime. Furthermore, we compared the soils collected in autumn at low elevation with soils collected at the same place in spring of the same year. These extra soil samples collected during autumn (at high elevation, n = 20) and spring (at low elevation, n = 29) in 2020 were also incubated for four weeks.

Data analysis

To test the effects of land use on abundance of resting stages in soils and emergence of zooplankton from resting egg banks, we used generalized linear mixed

models (GLMMs). All statistical analyses were performed using the R software (v4.3.2). The R package glmmTMB was used for fitting the GLMMs as it can handle various distributions (Poisson, negative binomial) and zero-inflation (Brooks et al., 2017). For hatching experiment 1 (incubation series I and II), land use type was used as a fixed factor (N-MS; n = 4, N-WM: n = 3, F-OC: n = 4, F-RC: n = 3, A-AC: n = 8, A-CC: n = 8), while the 'block' (the 4 regions of the floodplain, coded as BAIE, PIER, BART, and DUPA with eight, six, nine, and seven sites respectively) was included as a random factor. Although final dry weight apparently did not influence hatchling abundance (Figure S1), we nonetheless wanted to correct for among-jar differences in soil weight by including log-transformed dry weight as an offset in the model. Separate models were fitted for each taxonomic group (rotifers, ostracods, copepods) and incubation series. For incubation series III (hatching experiment 2), inundation duration (weeks, coded categorically), land use, and their interaction were added in the models as fixed factors. When no interaction was found in the global test, a simpler additive model was used. The same offset (with dry weight) was used for hatching experiment 2, for consistency with the models described above. To check for overdispersion and zero-inflation and select the appropriate distribution for the models (i.e. Poisson or negative binomial, and/or zero-inflation), we used the DHARMa package (Hartig, 2016). When land use was found significant, we then: 1) calculated estimated marginal means (EMMs) using the emmeans package (Lenth, 2022); and 2) performed multiple pairwise *post hoc* comparisons among land use types, adjusting *p*-values with the 'False Discovery Rate' (FDR) method at alpha = 0.05. Pairwise tests were fitted and interpreted using the 'multcomp' (Hothorn et al., 2016) and 'multcompView' packages in R (Graves et al., 2019), and results are illustrated as letters above boxes in Figures 2-4.

Results

Resting egg abundance in soils

Resting eggs were represented mainly by Rotifera, Copepoda, and Cladocera. The total abundance of resting eggs varied greatly between years and elevations (Figure 2).

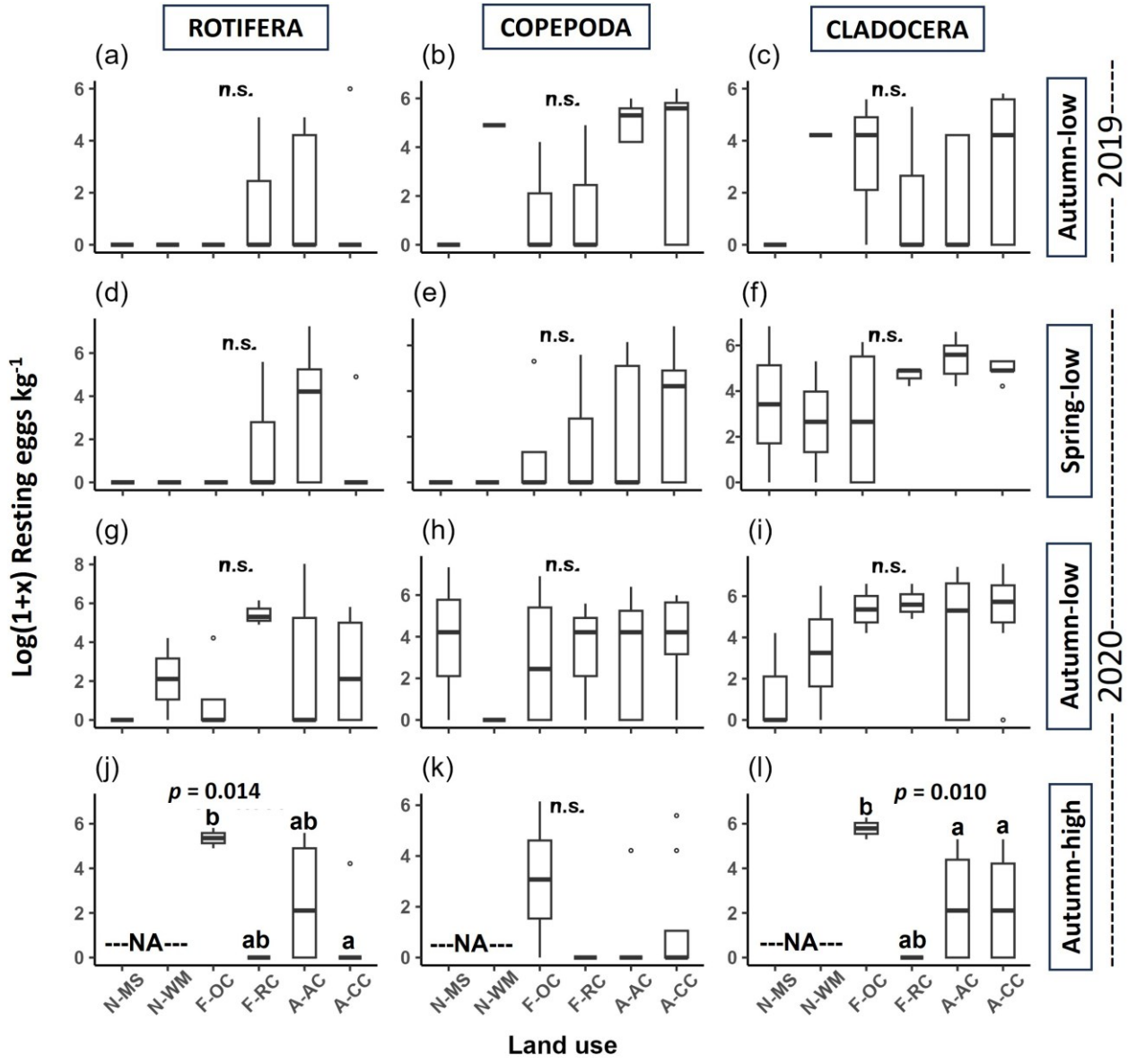


Figure 2. Abundance of resting eggs of Rotifera (a, d, g, j), Copepoda (b, e, h, k) and Cladocera (c, f, i, l) in soils collected during autumn 2019 (a-c), spring 2020 (d-f), and autumn 2020 (g-i) from low elevation, and during autumn 2020 (j-l) from high elevation. *p*- values and n.s. indicate the results of GLMMs testing for the effect of land use on abundance of resting eggs. NA in autumn 2020 (j-l): not available, as these sites were not sampled. Land use nomenclature as in Figure 1.

More precisely, at sites with frequent inundation, egg density ranged between 0 – 1066 ind. kg^{-1} (259 ± 269 ind. kg^{-1}) during autumn 2019 (Figure 2a-c), 0 – 1800 ind. kg^{-1} (423 ± 483 ind. kg^{-1}) shortly after the spring of 2020 (Figure 2d-f), and 0 – 3733 ind. kg^{-1} (800 ± 878 ind. kg^{-1}) during autumn 2020 (Figure 2g-i). There was no significant difference in the abundance of resting eggs across land use types at frequently inundated sites for any of the taxa, but in most cases, we observed a tendency to have more eggs

in the agricultural compared to the natural sites (Figure 2a-i). At sites with less frequent inundation, soils collected in autumn 2020 showed a lower abundance of eggs, ranging from 0 to 867 ind. kg^{-1} (180 ± 261 ind. kg^{-1}). The abundance of resting eggs differed significantly among land use types for rotifers (p = 0.014, Figure 2j) and cladocerans (p = 0.010, Figure 2l), with higher abundance of rotifers in F-OC than A-CC, while cladocerans were higher in F-OC than in both agricultural soil types (A-AC as well as A-CC).

Hatching experiments

Hatching experiment 1: Effects of land use on zooplankton emergence

Incubation series I: Cumulative daily hatching. The groups that dominated the hatchlings emerging from the soil egg banks were Ostracoda, Rotifera, and Copepoda (Figure 3a-c). The total number of hatchlings that emerged ranged between 46 ind. kg^{-1} and 1537 ind. kg^{-1} (386 ± 316 ind. kg^{-1}), with a median value of 315 ind. kg^{-1} across all samples (n = 30 x 23 observations). Significant differences across land use types were found for Ostracoda (p = 0.037, Figure 3a) and Rotifera (p = 0.022, Figure 3b). Post-hoc tests showed that more ostracods emerged from N-WM than in the A-AC and F-OC, while rotifers emerged in higher abundances from N-WM than A-AC and A-CC, and also from F-OC than in A-AC. We did not find any significant impact of land use on copepod hatchlings (p = 0.252) (Figure 3c).

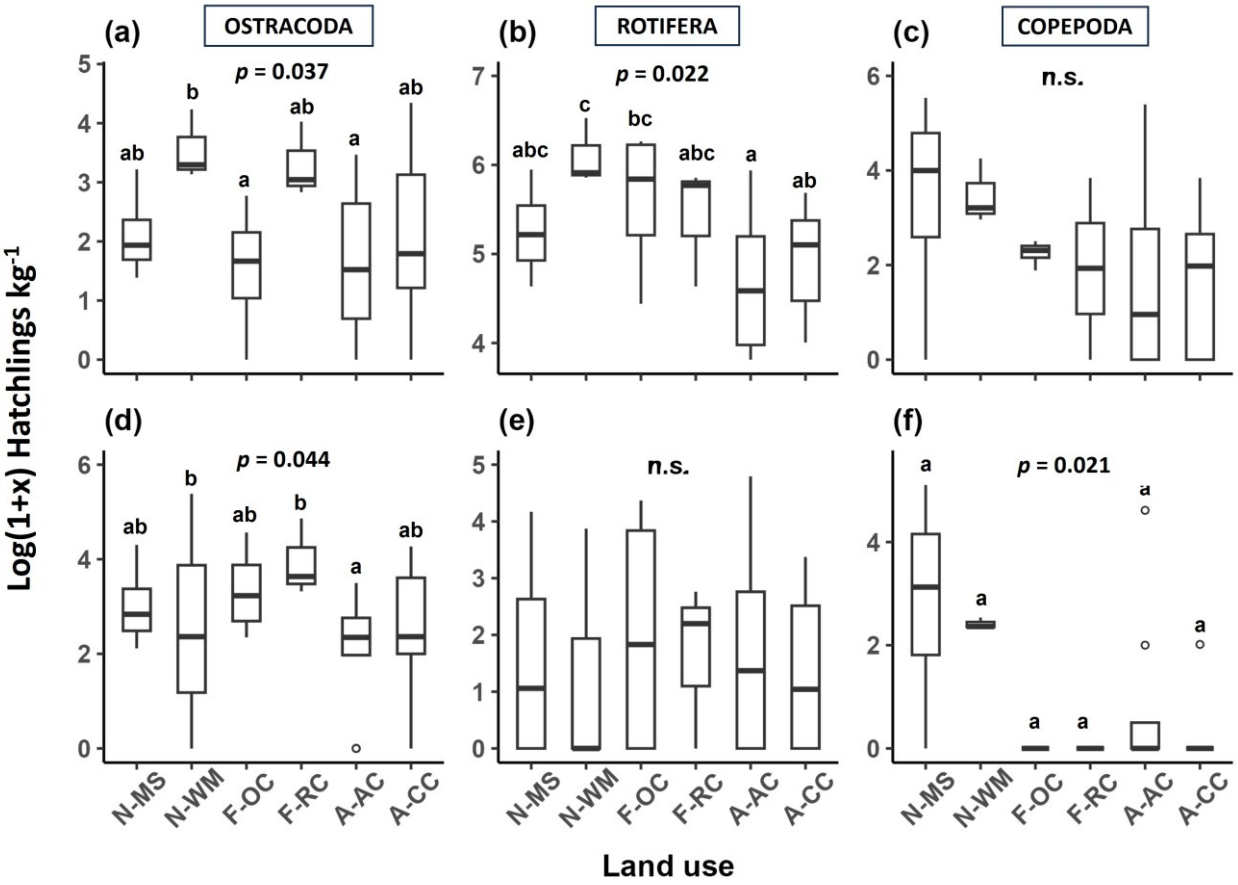


Figure 3. Results of incubation experiment 1 (series I and II). Abundance of Ostracoda (a, d), Rotifera (b, e) and Copepoda (c, f) hatchlings that emerged from soils collected during autumn 2019 at low elevation: cumulative hatching over four weeks (a-c; incubation series I); snapshot of hatching (after four weeks) at the end of week 4 (d-f; incubation series II). *p*- values and n.s. indicate the results of GLMMs testing for the effect.

Incubation series II: Hatching snapshot after four weeks. After 1 month of (undisturbed) incubation, the total number of hatchlings in the jars ranged between 6 ind. kg^{-1} and 273 ind. kg^{-1} (61 ± 66 ind. kg^{-1}), with a median of 33 ind. kg^{-1} (Figure 3d-f). Fewer rotifers were found with this incubation method than with the daily sampling (Figure 3b vs 3e), but abundances were comparable between the two methods for Ostracoda and Copepoda. Significant differences in abundance between land use types were found for ostracods ($p = 0.044$, Figure 3d) and copepods ($p = 0.021$, Figure 3f), but not rotifers ($p = 0.847$). For example, copepod abundance was very low in all soils except a few samples from natural wetlands (Figure 3f). *Post hoc* tests revealed some significant differences between land use types for ostracods (e.g. lower abundance in A-AC than N-WM or F-RC) but not for copepods.

Hatching experiment 2: Effects of land use and flood regime on zooplankton emergence

Incubation series III: Hatching snapshot at weekly intervals.

Ostracoda, Rotifera, and Copepoda also dominated the abundance of hatchlings in this incubation series, with tardigrades, nematodes, and oligochaetes seldom encountered. The total number of hatchlings that emerged from the soil ranged from 0 to 1623 ind. kg^{-1} (154 ± 216 ind. kg^{-1}), with a median of 75 ind. kg^{-1} (Figure 4).

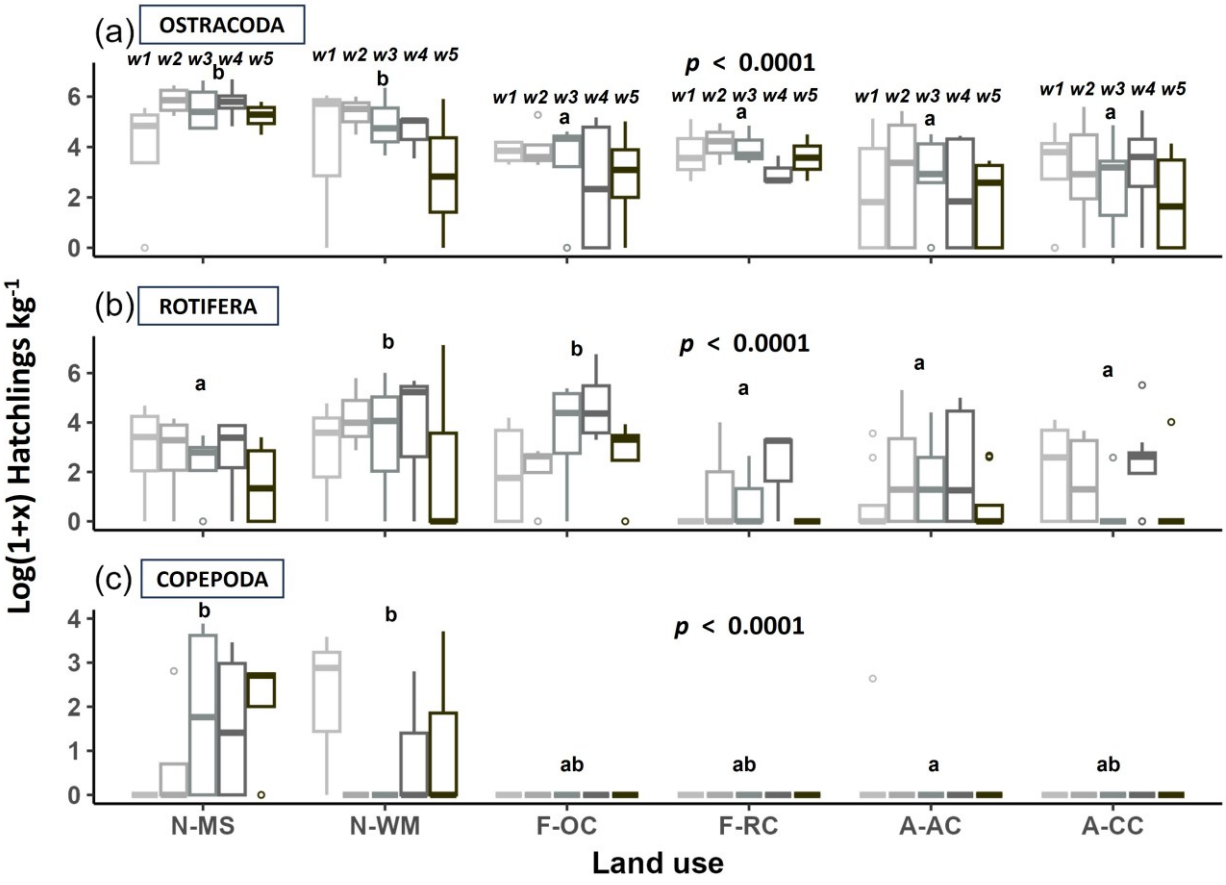


Figure 4. Results of incubation experiment 2, series III. Abundance of Ostracoda (a), Rotifera (b), and Copepoda (c) hatchlings that emerged from soils collected during autumn 2020 at low elevation, a year after implementation of experimental land use treatment. Colors (w1-w5) indicate hatchling abundances from week 1 to week 5. *p*- values refer to the main effect of land use in taxon-specific GLMMs. Small letters represent groupings identified by *post hoc* tests, with groupings defined by land use (not inundation duration; see results). Land use nomenclature as in Figure 1.

There was no significant interaction between land use types and inundation duration (1 to 5 weeks) on hatchling abundance, but a significant impact of land use was found for all three groups ($p < 0.0001$; Figure 4), confirming the results of experiment 1 with an even greater sample size. For Ostracoda and Copepoda, *post hoc* tests revealed that natural wetlands had higher abundance than forage or agricultural soils, while for Rotifera, the highest abundance was in N-WM and F-OC. The impact of inundation duration was only significant for ostracod abundance, which showed a non-linear change over time ($p = 0.009$). After two weeks, the median ostracod hatchling abundance increased up to 72 ind. kg^{-1}, whereas after that it began to decrease, reaching 25 ind. kg^{-1} after five weeks of incubation.

Incubation series IV: Effects of inundation frequency and sampling season on hatching. Hatchling abundance in frequently inundated soils collected during the spring of 2020, shortly after the flood, did not reveal any significant difference across land use types, although ostracods emerged only from N-WM and Cladocera from F-OC (Figure S2). Similarly, no significant effect of land use was found for hatchlings emerging from less frequently inundated soils collected in autumn 2020, although cladocerans hatched only from A-AC (Figure S3). Unexpectedly, soils from both of these sampling occasions had cladocerans but no copepods emerging during the experiment, which contrasts with the other incubation series. We also note that hatchling abundance was generally lower at the high elevation, less frequently inundated sites than the low elevation, more frequently inundated sites (Figure S3 vs. Figures 3-4). Unexpectedly, we did not find any relationship between hatchling abundance and resting eggs (Figure S4).

Discussion

Despite a mismatch between the observed abundance of resting eggs and hatchlings, our results overall support the hypothesis that land use and flooding influence zooplankton resilience in floodplains. Our results clearly suggest that, despite a relatively homogeneous distribution of resting eggs among land use types in frequently inundated fields, clear differences exist in terms of hatching potential along the land use gradient analyzed here, with little evidence that agroecological practices can reduce impacts of

intensive agriculture. This result could depend on how long these practices have been implemented, and it is possible that in our case, this time window was relatively short, since these were implemented only since 2018. Inundation duration had little influence on the outcome of our hatching experiments, yet we did find that high elevation sites that inundate less frequently and for shorter periods had fewer eggs and hatchlings than the frequently inundated low elevation sites. Finally, our study showed some puzzling results, namely that some groups were present in the egg bank and not in the hatching experiments and vice-versa.

Composition of egg and hatchling samples and effects of incubation methods

Hatchling samples were dominated by rotifers, ostracods, and copepods. Rotifers and microcrustaceans such as ostracods, copepods and cladocerans are known to be important in ephemeral water bodies as they serve as important food sources for many predators, including invertebrates, larval and young fish, and water birds (Bass et al., 1997; Boulton et al., 2014). Studies in temporary water bodies have reported dominance of different taxa that emerged from desiccation-resistant stages. For example, hatchlings from a temporary pool were composed mainly of rotifers, cladocerans, and copepods (Araújo et al., 2013), while hatchlings from a seasonal wetland influenced by agriculture were dominated by ostracods, copepods, and cladocerans (Gleason et al., 2003b). Higher hatchling abundances of ostracods and rotifers in the present as well as in some other studies, could reflect their capacity to survive desiccation periods through resting stages. Such tolerance has been observed in ostracods from seasonal wetlands (Strachan et al., 2016), *Artemia* sp. (Vargas et al., 2024) and in rotifers (Ricci & Caprioli, 2005).

Egg samples, in contrast, were dominated by rotifers, copepods, and cladocerans, but no ostracod eggs were found. The absence of ostracod eggs in the soils, but their emergence in the hatching experiment, indicates the possibility of them diapausing as desiccation-resistant instar stages rather than eggs (Strachan et al., 2014; Wang et al., 2025; Zhai et al., 2024). We inspected soils with a high-power microscope after removing eggs with the sugar flotation method but did not find any aestivating ostracods. We nonetheless assume that there were some in the soils as we see no other routes

through which ostracods could have colonized our incubators (we used filtered lake water and new, sterile incubators). For taxa that were found both as eggs and hatchlings (rotifers and copepods), we did not find any clear relationship between resting egg and hatchling abundance. We do not have an explanation for this finding, but variations in embryo survival probability and resting egg viability could be important factors. A similar mismatch has been reported across other life stages, for example between hatchling abundance and active water column zooplankton from Brazilian lakes (Santangelo et al., 2015). For cladocerans, their high abundance as eggs but rarity as hatchlings could also be due to incubation conditions. We aimed to use an incubation method that favored most groups (e.g. constant light, photoperiod, and temperature were controlled as these factors have been reported to be important in terminating dormancy; Vandekerkhove et al., 2005). However, some species or taxa might have required a distinct hatching protocol. For example, some researchers have shown that pre-refrigeration at *ca*. 6 °C (as was done in this experiment) could help in increasing the hatching rates for rotifers, while it could lower the hatching success for some cladocerans such as *Daphnia laevis* (Maia-Barbosa et al., 2003). Similar observations have been made by Santangelo et al., 2011 for other cladoceran species. Constant light/photoperiod and temperature can trigger higher hatching rates for cladocerans resting eggs (Guimarães et al., 2024). However, different environmental cues (e.g., temperatures, longer incubation periods) may be required by different populations and species for terminating dormancy (Radzikowski et al., 2018). Furthermore, environmental variability during the flooded season could also explain the differences in zooplankton emergence from the egg bank (Florencio et al., 2020). Incubating soils without prior isolation of the resting eggs was successfully used elsewhere (Day et al., 2010) but others have suggested that incubation of isolated eggs can yield higher hatching success (Vandekerkhove et al., 2004b). Furthermore, not all viable eggs that are present in the soils will hatch; rather, it could just be a fraction that hatches when exposed to suitable cues, while others remain in the soil (Pinceel et al., 2017).

We also found that the cumulative method with collection of daily hatchlings yielded much higher hatchling abundances (for rotifers) than one snapshot sample after a month

of incubation. Collecting hatchlings daily quantified the potential production or success of zooplankton emergence, while the snapshots (at the end of one month or weekly) could be a consequence of various processes such as reproduction, mortality, competition, predation, and other interactions over time. This suggests that depending on the research question, the method to be chosen could vary in similar studies. The less labour-intensive methods of incubation series III (with weekly samples) represented a compromise that was sufficient to detect impacts of land use without the need for daily sampling.

Effects of land use

In contrast to our first hypothesis, we found no significant difference in the abundance of resting eggs of different taxa across land use types at low elevation, frequently inundated sites although effects were seen at high elevation. This could be due to homogeneous flooding and colonization by active zooplankton, leading to similar egg production across the land use gradient (Rosa et al., 2020). However, as predicted by our second hypothesis, significant differences in hatchling abundance were observed across land use types, with a stronger influence on ostracods and rotifers. In most cases, the natural wetland soils (N-MS and N-WM) had higher hatchling abundance than agricultural soils (A-AC and A-CC), while the forage cropping (F-OC and F-RC) exhibited an intermediate response. However, among these three groups, copepods emerged only in the natural habitats (N-MS and N-WM), which suggests stronger habitat sensitivity. One possible explanation for this pattern might be related to the fact that this taxon, in contrast to ostracods and rotifers, can reproduce only sexually, making it more difficult to rebuild a viable population after the dry season. However, we did not find any significant difference in the abundance of their eggs across the land use gradient, and more targeted studies are needed to test this hypothesis. Besides this, our results confirm that land use is an important modulator of zooplankton abundance, as has been shown in other aquatic ecosystems such as boreal lakes (Grosbois et al., 2023) and in a Mediterranean temporary stream (Frisch et al., 2009). We found no evidence that converting soy and corn fields with intensive (conventional) practices into new (recently sown) pastures had beneficial effects, nor did agroecological practices such as intercropping or cover crops. Thus, conserving natural wetland habitats or old forage grasslands (without ploughing for

5+ years) with abundant vegetation seems necessary to promote the resilience of floodplain zooplankton. However, we note that agroecological practices in our field experiment were implemented only recently, in 2018, which may not have allowed sufficient time for positive effects on zooplankton to emerge. A study based on the active (water column) zooplankton from flooded rice fields has shown that agroecological practices could improve water quality and support both higher abundance and diversity of zooplankton (Romero et al., 2022). Therefore, it would be advisable to revisit the present study sites later to reassess differences among fields with conventional vs. agroecological practices.

Previous studies have found that the vegetation in natural habitats can support higher zooplankton production (Catlin et al., 2016), and that variation in physicochemical conditions, hydrology, and the density of organisms plays a crucial role in triggering the production of resting eggs as well as the termination of their dormancy (Palazzo et al., 2008; Strachan et al., 2016; Vargas et al., 2019). However, these hypotheses are not supported by our results, since we did not find any difference in egg bank size along the land use gradient. This suggests that egg viability is a more reasonable explanation for our results. For instance, agricultural practices such as cultivation and soil reworking with farm equipment could have negative effects on invertebrate egg banks (Euliss & Mushet, 1999). In more vegetated areas, during dry periods shade provided by fringing meadows and trees can also keep soils cooler, richer in organic matter, more porous, and better able to retain moisture than soils at open or exposed sites (Strachan et al., 2016). In this study, soil porosity and organic content indeed decreased from natural environments towards agricultural sites (S. Badesab pers. obs.), which could have affected egg viability (Strachan et al., 2016). Furthermore, other studies suggest that the presence of pesticides in the environment can disrupt resting eggs and their hatching success, but that impacts vary across taxa (Portinho et al., 2018, 2021). However, in another study, we found that the concentration of all measured pesticides in our study sites was either very low or too small to be detected. Nonetheless, water quality criteria are usually based on bioassays with adults from model species, and pesticide concentrations below known toxicity levels could affect egg banks. Additional lab exposure experiments with eggs are warranted.

Effects of flood regime

Manipulating inundation duration in the lab had limited effects on hatching. The only clear effect was on the abundance of ostracod hatchlings, which declined between the first and the fifth week of incubation. This corroborates the results of a study carried out in a dry river floodplain, wherein ostracod hatchling abundance varied with inundation duration (Chaki et al., 2021). In our experiment, two weeks of inundation yielded the maximum number of ostracod emergences, and abundance decreased between weeks 2 and 5. An opposite trend has been reported for a dryland river floodplain study, where the total abundance of ostracods kept increasing after minimum abundance was observed for 3 weeks of inundation (Chaki et al., 2021). This difference might stem from methodological differences, whereby this latter study frequently removed newly emerged individuals from the incubators, thus avoiding competition and cannibalism, whereas we let hatchlings accumulate until a given sampling date, allowing interactions. We found no impact of inundation duration on rotifers and copepods, but Frisch & Threlkeld (2005) have reported an impact of flooding duration (four weeks) on copepods, which varied across species. Emergence and hatching time differences vary between and within species (Brock et al., 2003; Strachan et al., 2016). Additionally, the impact of the dry period would also vary depending on the habitat in which the organisms enter the dormancy phase (Strachan et al., 2016).

We nonetheless found an effect of inundation frequency by comparing frequently inundated (i.e., low elevation) sites and less frequently inundated (i.e., high elevation) sites from autumn 2020 for the same variables. The abundances of both eggs and hatchlings were lower at less frequently inundated sites, in line with the conceptual model of Jenkins and Boulton (2007), suggesting that loss of viable resting egg decreases strongly with increased inundation frequency. Less frequent inundation, and shorter inundation periods at high elevations when the fields do flood, would be expected to lead to lower egg deposition in soils. Thus, inundation frequency could act as a kind of disturbance (Carvalho & Wolf, 1989; Waterkeyn et al., 2011), with frequently inundated locations harbouring higher abundances of resting eggs (Jenkins & Boulton, 2007; Nielsen et al., 2013; Tronstad et al., 2005). Moreover, longer dry periods can disrupt the egg banks

and might reduce hatching success (Portinho & Perbiche-Neves, 2025). While our experiment was not specifically designed to test the effect of dry periods, we did include a comparison of spring vs autumn soils in incubation series IV focussing on frequently inundated (low elevation) sites. Egg and hatchling abundances were not higher in spring than autumn samples, suggesting that summer dry periods have limited impacts on egg viability overall. However, we did find stronger land use impacts in the autumn than in the spring, which aligns with the hypothesis that agricultural practices during the growing season can impair eggs. Lastly, although in spring hatchlings some patterns were visible (i.e., ostracods emerged only from natural wet meadows (N-WM) and cladocerans from old forage croppings (F-OC)) the land use impact was not significant, and additional sampling will be required to address seasonal effects.

Conclusions

Our results showed clearly that changes in land use influenced zooplankton resilience in floodplains by affecting their hatching dynamics, despite a rather homogeneous distribution of the egg bank across land use types. More precisely, natural wetland habitats present in floodplains favor the resilience of zooplankton communities facing a disturbance (i.e. the dry period) via a high potential recovery through hatching. On the other hand, human-altered sites such as fields with intensive agriculture are associated with lower hatching success, suggesting that zooplankton resilience is potentially hampered. Changes in soil variables and egg viability due to agricultural practices (e.g. soil compaction by machinery, lower organic matter, pesticides) are invoked as potential mechanisms explaining these findings. Therefore, there is a need for developing and implementing sustainable agricultural practices in floodplains (e.g. using perennial instead of annual crops) and to conserve natural wetland habitats, to improve the recovery of zooplankton communities from egg banks and sustain floodplain productivity and ecosystem services.

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Author contribution

Conceptualisation: SB, AB, VF. Developing methods: SB, AB. Conducting the research: SB, CF, AS. Data analysis: SB, AB, VF. Data interpretation: SB, AB, VF. Preparation of figures & tables: SB, AB, VF. Writing: SB, AB, VF, CF, AS.

Data availability statement

The data generated from this study are available in the Borealis repository: https://doi.org/10.5683/SP4/ YANKAC.

Conflict of interest

The authors declare no conflict of interest.

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Supplementary material

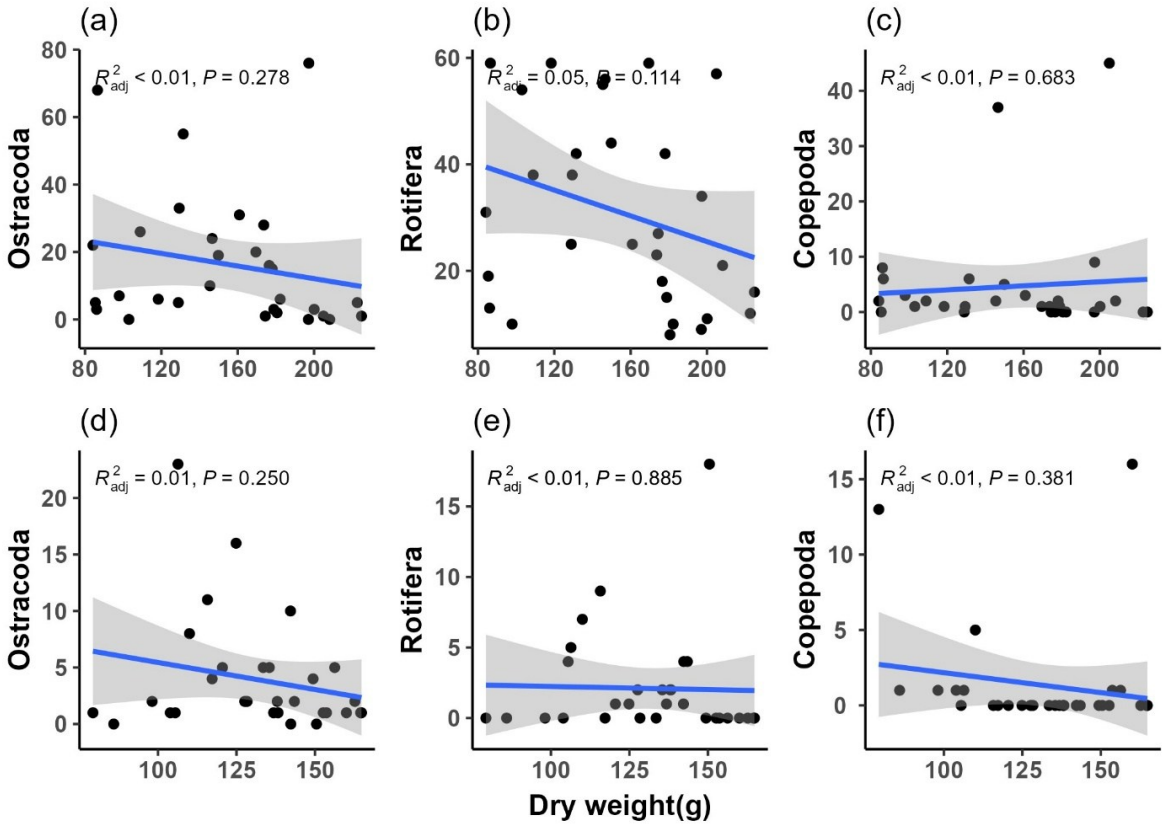


Figure S1. Scatter plot showing the relationship between soil dry weight (after incubation) and hatchlings' abundance in soils from autumn 2019. a-c: cumulative hatching (incubation series I) and d-f: snapshot (community) hatching (series II). For this experiment, soil volume was standardized, hence the variation in dry weight.

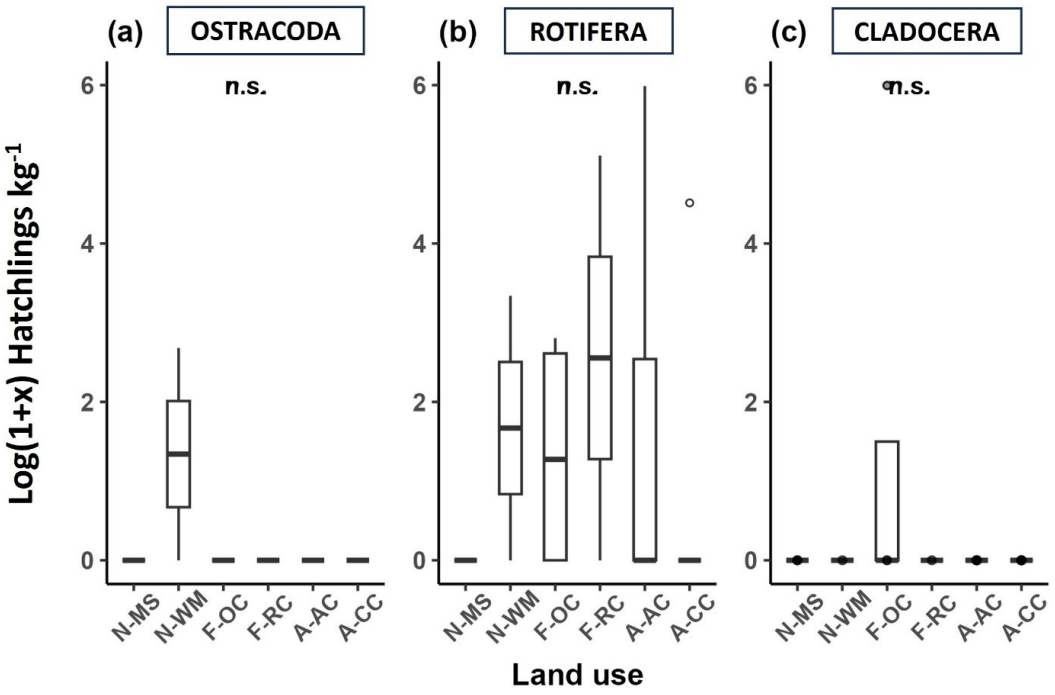


Figure S2. Abundance of zooplankton hatchlings a) Ostracoda, b) Rotifera, and c) Cladocera in soils during spring 2020 from low elevations. n.s. = non-significant effect of land use assessed with a GLMM.

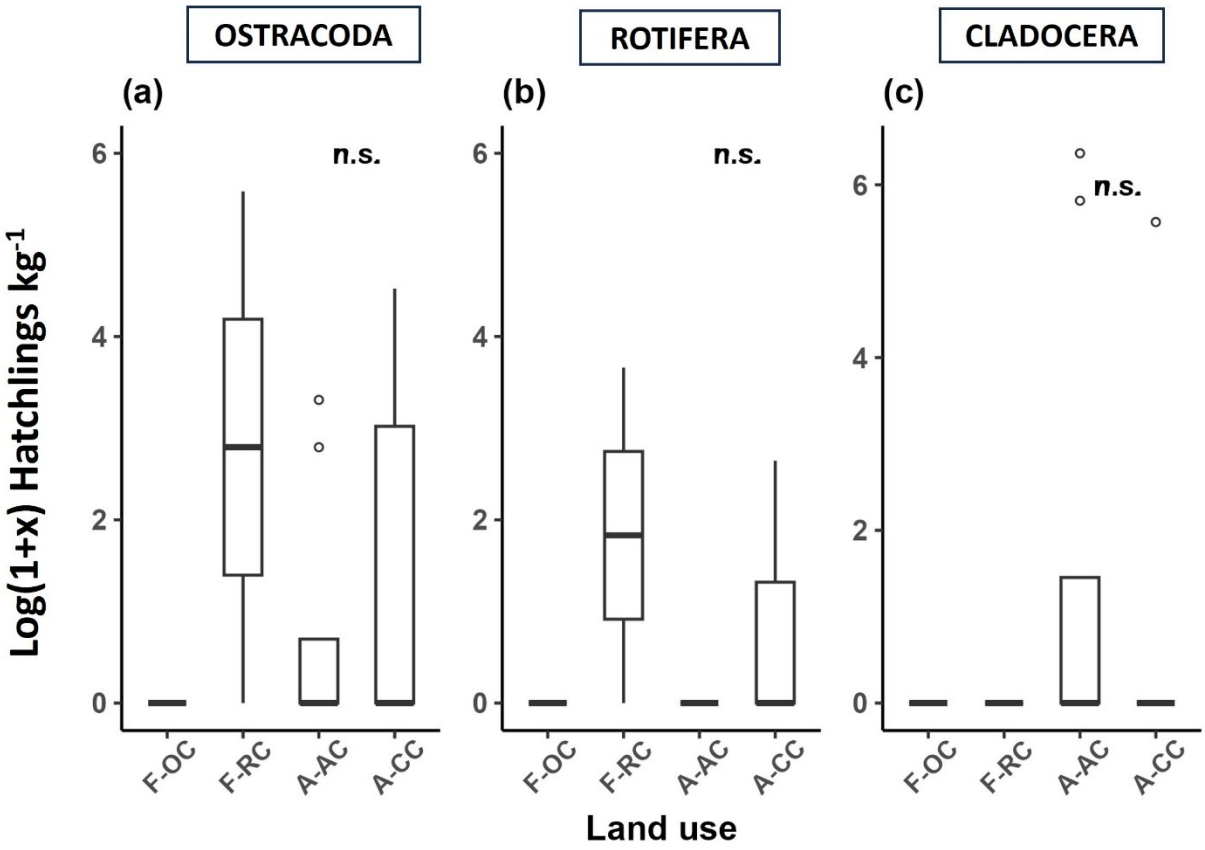


Figure S3. Abundance of zooplankton hatchlings a) Ostracoda, b) Rotifera, and c) Cladocera in soils during autumn 2020 from high elevations. Natural sites (N-MS and N-WM) were not available for high elevation sites. n.s. = non-significant effect of land use assessed with a GLMM.

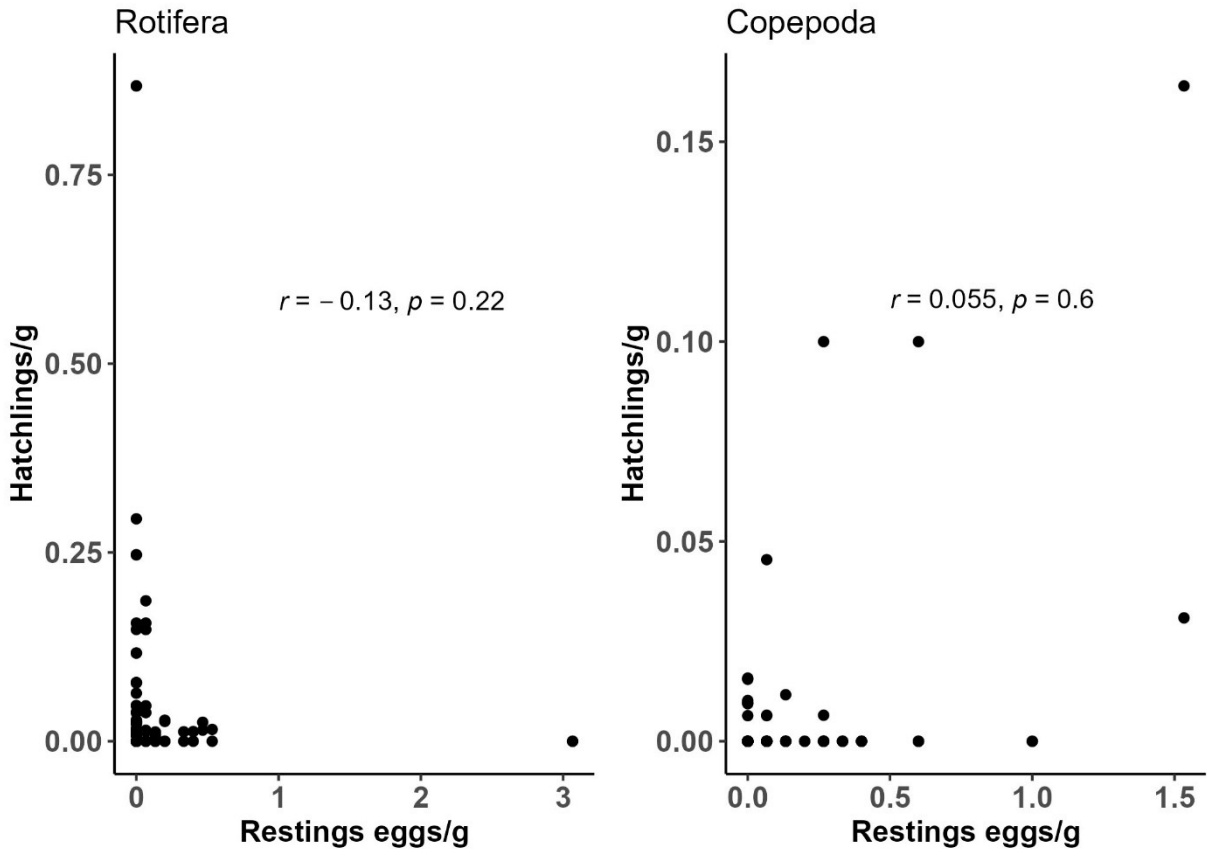


Figure S4. Linear regression for resting eggs (autumn 2019) and hatchlings abundance (autumn 2019 and 2020- incubation series II and III).

Environmental variables

To evaluate the effect of land use on environmental variables, water and soil samples were also collected at each sampling points during spring flooding (May-June 2019) and in autumn (September 2019). Water pH, conductivity (µS cm^{-1}), temperature (°C) and oxygen (mg L^{-1}) were measured with a YSI multiparameter probe (Yellow Spring Instruments, OH). Turbidity (FNU) was measured using a HANNA HI9829 probe and water samples collected for TN (µg L^{-1}) and TP (µg L^{-1}) analyses were fixed with sulfuric acid, and then were filtered using 0.7 µm GF/F filter paper (47mm diameter), and then analyzed using Lachat's QuikChem flow injection analyzer (QuickChem 8500 series). Dissolved organic carbon (DOC, mg L^{-1}) was measured using a Sievers M9/M9e total organic carbon (TOC) analyzer (Suez 2018). Concentration of chlorophyll *a* (µg L^{-1}) was measured by filtering the water through a GF/F filter (47mm diameter)

followed by extraction using 90% acetone and measuring the fluorescence using Turner Design AU fluorometer (Turner Designs, SD; Arar and Collins, 1997) (Campeau et al., 2024). Soil variables were measured in the top 10 cm of soil cores. Standard protocols were used to measure pH (water extract, v:v ratio 1/5, TC=20(°C) and redox potential (Eh (mV), current between a Platinum M241Pt electrode and REF321 reference electrode (Husson et al., 2016). Porosity (%) was calculated using the DaTF (apparent density in fine soil) with the following equation: 100-(1-[DaTF/2.65]), wherein a maximum density of 2.65 g cm^{-3} was considered. Water filled pore space (WFPS %) was calculated as the ratio between soil moisture (Hsol %) and porosity (%). Organic matter (OM %) was estimated following the loss on ignition method (after combustion at 550 °C). Carbon and total nitrogen (gC gN-1) were measured after acid fumigation using an elemental analyzer coupled to an isotope ratio mass spectrometer (EA-IRMS, Agilent technology, Santa Clara, CA, USA). Soil texture was measured using Fritsch analyzer 22 microtech plus. Finally, mean water level (m) during the spring flood was calculated using a digital elevation model and hydrometry data from: https://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/twl-mne/inventory-inventaire/interval-intervalle-fra.asp?user=isdm-gdsi&region=LAU&tst=1&no=15930, and mean summer normalized difference vegetation Index (NDVI) in 2019 was measured for each plot using satellite imagery (https://land.copernicus.eu/en/products/vegetation/). For additional information on environmental measurements (provided by other groups in the research cluster), see Campeau et al., (2024)

Data analysis

Redundancy analysis (RDA) was also used to study the relationship between zooplankton hatchling abundance and environmental variables (both water and soil). These analyses focused on experiments carried out on soils collected from low elevation sites during autumn 2019 only (as part of experiment 1). This was because the water and soil parameters were obtained from other collaborating research teams and were mostly available for 2019. Indeed, due to a short flooding period and sanitary measures implemented at the onset of the Covid-19 pandemic, no field campaign was carried out during the flooding period of 2020. For experiment 1, RDA analysis included soil as well

as water parameters (Flood level (m), pH, conductivity (µS cm^{-1}), temperature (°C) and oxygen (mg L^{-1}), Turbidity (FNU), TN (µg L^{-1}) and TP (µg L^{-1}), Dissolved organic carbon (DOC, mg L^{-1}), total organic carbon (TOC), chlorophyll a (µg L^{-1}), NDVI, Soil texture (Sand, silt, clay %), porosity (%), redox potential (Eh (mV)), soil pH (interstitial water), porosity (%), water filled pore space (WFPS %), organic matter (OM %), organic carbon (Corg %), and Carbon and total nitrogen (gC gN-1) as predictors, and hatchling abundance of Ostracoda, Rotifera, and Copepoda as the response matrix. RDA models were fitted with the *rda*() function in the vegan package in R (Oksanen, 2015).

Results

Using RDA analyses no significant influence of environmental variables was observed neither on abundance of resting eggs nor on the abundance of zooplankton hatchlings.

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CHAPTER III

ECOTOXICOLOGICAL RESPONSE OF *DAPHNIA MAGNA* TO FLOODPLAIN LAND USE AND NATURAL ULTRAVIOLET RADIATION

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Abstract

Floodplains are biodiversity hotspots increasingly threatened by land use changes. Among the potential consequences of the expansion and intensification of agriculture in floodplains are the toxic effects of soil leachates when they enter aquatic ecosystems. Under natural conditions, xenobiotics in leachates could interact with UV radiation (UVR) and have a significant impact on aquatic organisms, both directly by damaging DNA or indirectly by changing the potential toxicity of the leachates through photodegradation of the xenobiotics. Here, we used *Daphnia magna* cultures to assess the impact of soil leachates from various forms of floodplain land uses and natural UV radiation on zooplankton physiological endpoints (heart rate, thoracic limb activity and post-abdominal claw movement), swimming behavior and survival.

We performed two experiments. First, the effects of land use and natural UVR on *D. magna* were studied in semi-natural conditions in an outdoor experimental setup.

We included three land use types (natural forest, forage fields, corn monocultures) and three levels of UVR exposure (no UV, UV-A and UV-AB). These land use types form a gradient from natural wetlands to intensive agriculture, representative of the land use types in our focal floodplain. In the second experiment, *D. magna* individuals were exposed to soil leachates from a larger range of land uses in the absence of UVR in an indoor experimental setup. Land uses included natural maple swamp (N-MS), natural wet meadow (N-WM), forage-old cropping (F-OC), forage-recent cropping (F-RC), agriculture-environmental cropping (A-ACsoya and A-ACcorn), and agriculture-conventional cropping (A-CCsoya and A-CCcorn). This second experiment was meant to test the benefits of agro-ecological practices in reducing the impacts of intensive agriculture.

In the outdoor experiment, we found no significant impact of either land use or natural UVR on heart rate, thoracic limb movements, or reproduction. However, an interaction was observed whereby post-abdominal claw movement was faster under no UV condition when exposed to F-OC leachates. Further, a significant effect of land use only was detected on *D. magna* survival, wherein A-CCcorn had a positive impact on it. In the indoor experiment, we found a significant effect of land use on heart rate, which was lower under the A-ACsoya leachate exposure compared to the other treatments. We also found that N-MS and A-CCsoya significantly improved *D. magna* survival. The present study is the first to examine the potential interaction between soil leachates from various floodplain land uses and natural UVR on zooplankton. Although natural UVR exhibited weak effects under the experimental conditions, land use leachates influenced zooplankton, providing new insights into how agricultural practices can affect aquatic organisms and the functioning of the floodplain ecosystem.

Keywords: Agricultural intensification, agroecology, *D. magna*, ecotoxicology, mortality, sub-lethal effects, physiological endpoints, swimming speed

Introduction

Floodplains are very fertile, extremely productive and easily accessible habitats that have been used by humanity for several thousand years (Bunbury et al., 2023; Rajib et al., 2023). Floodplains are important breeding and nursery grounds for fish during seasonal flooding by supplying adequate food in the form of invertebrates to fish larvae (Farly et al., 2019; Jobin & Brodeur, 2023). Yet, global floodplains are now under enormous stress due to the rising human population (Rajib et al., 2023). Most importantly, agricultural expansion and intensification in floodplains due to increasing food demands have led to a reduction in floodplain habitat complexity and thus biodiversity (Tockner & Stanford, 2002). The conversion of natural wetlands to agricultural fields can harm biodiversity due to the physical effects of machinery during tillage and plowing that disrupt soil structure (Richard et al., 2011), but also due to contaminant usage (pesticides and other xenobiotics). Leachates from contaminated soils can reach aquatic systems (e.g., when floodplains are inundated during seasonal floods, thereby degrading water quality (Mena et al., 2022). For example, neonicotinoids, widely used in agriculture for controlling insects, are increasingly threatening aquatic systems due to their high solubility in water (Morrissey et al., 2015), and very toxic effects on non-target aquatic animals (Hébert et al., 2021; Paquet-Walsh et al., 2019; Vehovszky et al., 2015).

While the impacts of pesticides on aquatic biodiversity have been most thoroughly documented in agriculture-adjacent streams, some studies have also reported high pesticide loading in agricultural floodplain soils (e.g., Kuechle et al., 2019). Agriculture, being widely known for its negative effects on aquatic health, the intensive agriculture practices such as corn and soybean with high usage of pesticides can contaminate aquatic systems, including potable water resources and pose deleterious consequences on human health (Brown et al., 2007). They can also affect the non-target aquatic biota therein (Acayaba et al., 2021; Brown et al., 2007). Many countries have their governmental bodies to govern and monitor the water quality parameters to set limits on the pesticides or other contaminants that would otherwise have adverse effects on the drinking water or the aquatic life (Brown et al., 2007). However, to set these regulations, it is important to understand the potential impacts of land uses on the organisms at all levels of the food

chain. Ecotoxicology, by using indicators such as survival and physiological/cellular responses, can help answer these questions. However, most studies available represent the effects of either commercial formulations of the contaminants, such as fipronil and 2, 4-D (Bownik & Szabelak, 2021; Brown et al., 2007), imidacloprid (P. Wang et al., 2026), glyphosate (Romero-Alfano et al., 2026), imidacloprid (López-Valcárcel et al., 2025) or specifically cocktail or mixture of pesticides (e.g., Shahid et al., 2019), while a few addressing the landfill leachates (treated or untreated) (Makaras et al., 2026) on *D. magna*. However, in real agro-systems, wild populations are exposed to a mixture of stressors (hereafter “cocktail”) that exert a combined effect on the organisms, suggesting the need to evaluate and understand the effect of the cocktail of stressors to expand the scope of single-contaminant ecotoxicological studies.

Besides land use, natural ultraviolet radiation (UVR), which is ubiquitous, also acts as a crucial factor affecting the distribution, behavior and physiological performances of aquatic organisms such as zooplankton (Wolinski et al., 2020). UVR can severely affect zooplankton by increasing mortality (Zagarese et al., 2003), sex ratio and fecundity (Williamson et al., 2001). UVR increases water temperature, which is considered to have adverse effects on zooplankton, which cannot sustain against UVR (Hylander et al., 2025; Rautio & Tartarotti, 2010). In shallow floodplain habitats, aquatic organisms might be particularly exposed to UVR. Moreover, turbidity in such systems is highly variable, making the risk of UVR exposure spatially heterogeneous. Natural UVR can be both harmful and useful for living organisms, and both directly and indirectly (Rautio & Tartarotti, 2010; Williamson et al., 2001). Direct negative effects include DNA damage, while indirect effects could include, for example, photoactivation/photodegradation of xenobiotics, altering their toxicity in either direction. Indeed, photoactivation of organic compounds by UVR can increase the toxicity of pesticides (Bonnemoy et al., 2004), while photolysis can also degrade toxic molecules into less dangerous sub-products (Papagiannaki et al., 2020). Thus, it is likely that UVR and soil contamination have non-additive (interactive) effects on aquatic biota, a hypothesis that remains largely untested. Beketov et al. (2011) observed synergistic effects of UV and xenobiotics such as fenoxycarb and pirimicarb on *D. magna* growth and reproduction, but no effect on its survival. Moreover, most

experimental studies available used artificial UV lights (mostly UV-B), which cannot truly explain the actual potential damage that can be caused by the natural UVR, which has a specific ratio of UV-A to UV-B radiation (Fischer et al., 2006; Grad et al., 2001; Zagarese & Williamson, 2000).

In the ecotoxicological literature documenting impacts of pesticides on zooplankton, it is common to focus on individual stressors, letting aside their potential interactions among them or with other factors. Indeed, only a few studies address the combined effects of the contaminants and UVR, wherein their toxicity has been found to increase under UVR, e.g., polycyclic aromatic hydrocarbons (Jung et al., 2008) and retene (Huovinen et al., 2001). However, only rare studies presented the additive or synergistic effects of pesticides and UVR (Beketov et al., 2011) on *D. magna*. Under sublethal concentrations of pesticides such as fenoxycarb, pirimicarb, synergistic effects of both pesticides and UVR were found on the reproduction as well as growth of *D. magna*, while with tebufenpyrad, a less-than-additive effect was found, thereby suggesting that sublethal concentrations observed under standard lab tests can have adverse effects when exposed to UVR (Beketov et al., 2011).

Here, we designed a study focusing on the cumulative effects of floodplain land use and natural UVR on zooplankton. We work in a floodplain where earlier work indicated a significant impact of land use on the emergence of zooplankton from their resting stages, with natural land use types harbouring more zooplankton hatchlings compared to corn/soya croplands, while forage cropping showed intermediate responses (Badesab et al., 2026). Different factors could explain these results, including the fact that natural land use types were mostly undisturbed, had more vegetation, higher organic matter content, and lower contaminants compared to agricultural fields. To test this latter hypothesis, we exposed zooplankton to UVR and different cocktails of pesticides linked to land use. We used soil leachates prepared from different land use types (hereafter “leachates”) from the largest floodplain of the St. Lawrence River system, which has undergone dramatic changes over decades, leading to loss of habitat and biodiversity (Jobin & Brodeur, 2023). We tested the effects of leachates (both alone and in interaction with natural UVR) on *D. magna*, a widespread species in freshwater systems. This species

plays a crucial role in freshwater food webs (Ebert, 2022), and is widely used as a model organism in ecotoxicological testing (ASTM, 2004; Environment Canada 1992; USEPA 2002; OECD 1998; Zhang et al., 2016).

Besides the standard *D. magna* toxicity tests recommended by OECD that generally include immobilization (OECD TG 202), reproduction and survival (OECD TG 211), in recent years researchers have successfully incorporated other biological indicators such as their swimming behavior (e.g., speed, depth, etc.,) and physiological endpoints such as heart rate, thoracic limb activity and post-abdominal claw movement of *D. magna* (Bownik, 2017; Bownik et al., 2020; Farkas et al., 2022; Huang et al., 2017; Kwon et al., 2026; Lari et al., 2017; Makaras et al., 2026). These indicators are also suggested to be reliable indicators due to their sensitivity to different stressors and their sublethal responses, which manifest long before mortality is observed (Bownik & Szabelak, 2021). Literature suggests that contaminants, even in their low concentrations in the environment, can cause changes in behavioral as well as in respiratory physiology of *D. magna* (Duong et al., 2021; Lovern et al., 2007). Duong et al. (2021) reported a decrease in heart rate, swimming speed and survival on exposure to organochlorine pesticides. A dose-dependent decrease in heart rate, thoracic limb activity and swimming speed has been reported earlier on exposure to lambda-cyhalothrin (Bownik et al., 2019) and acetamiprid (Bownik et al., 2017). Review by Bownik (2020) on the response of thoracic limb activity revealed a decrease in the activity on exposure to pesticides, while the response of heart rate and post-abdominal claw movements observed could be in either direction depending on the pesticide. Another review on swimming behavior revealed a similar response, i.e., the change can be in either direction depending on the contaminant (Bownik, 2017). Although there exists uncertainty in the direction of effect, these indicators do respond to stressors, and therefore, in the present study, we included them along with the standard OECD tests for survival and reproduction.

In the present study, using an experimental approach, we analysed the effects of cocktails of contaminants in the form of leachates from different land use types on the physiological endpoints, swimming behavior as well as the survival of *D. magna*. In the first experiment, we examined the effects of land use and natural UVR on *D. magna*

in semi-natural conditions in an outdoor setup (natural light) and in the second experiment, we examined the effects of a larger land use range on *D. magna* in an indoor setup (without UVR). We hypothesized that there would be an interactive (either synergistic or antagonistic) effect of leachates and natural UVR on *D. magna* physiological endpoints, swimming behavior as well as their survival. More specifically, we expected that UVR would act on the contaminants in the leachate, which would then produce either a negative effect by increasing the toxicity or a positive effect by reducing the toxic power of the contaminants on the biological indicators studied. Further, we expected that natural UVR would have detrimental effects on *D. magna*. More precisely, we expected that UV-AB would have a negative effect, while UV-A can have both positive and negative effects. Furthermore, the response of *D. magna* would vary across different land use types, and the physiological endpoints, swimming behavior and survival of *D. magna* exposed to leachates from natural land uses and agri-environmental cropping practices would have a positive effect, while the agri-conventional/intensive cropping would have negative effects *on D. magna.*

Methods

Daphnia magna *culture*

We obtained *D. magna* neonate clonal cultures from a government laboratory located at the Centre d'Expertise en Analyse Environnementale du Quebec (CEAEQ, Quebec City, Quebec) on two occasions, before each experiment. Neonates were reared in the laboratory in glass aquaria filled with dechloraminated water. The *D. magna* culture medium was prepared following the CEAEQ guidelines and modified according to Qin et al. (2023). Cultures were maintained under a 16 h:8 h Light:Dark cycle. Individuals were fed dry *Spirulina* powder and baker's yeast every alternate day, and chickpea flour once a week when they reached maturity. The culture medium was renewed once or twice every week while maintaining the pH between 7.5 and 8 and hardness ~120 mg CaCO3/L. Neonates (< 24 h age) from the 3rd to 4th broods were used for the experiments.

Soil sampling and leachate preparation

Soils were collected in autumn 2020 and 2022 from different land use types from 30 sites located in four blocks (Baie-du-Febvre, Pierreville, St. Barthelemy, and île Dupas) along the Lake Saint-Pierre (LSP) floodplain (Quebec, Canada), the largest floodplain of the St. Lawrence river system (for more details see Watson et al., 2024; Badesab et al., 2026). Land use types included natural maple swamp (N-MS), natural wet meadow (N-WM), forage-old cropping (F-OC), forage-recent cropping (F-RC), agriculture-agri-environmental cropping (A-ACsoya and A-ACcorn), and agriculture-conventional cropping (A-CCsoya and A-CCcorn). We pooled and combined soils from different blocks sorted by land use to prepare the soil leachates. The first two are natural wetlands, the two types of forage cropping represent a form of non-intensive land use (perennial crops) that was dominant in the region before the 1990s (Jobin & Brodeur, 2023), and the latter two types of soy/corn fields represent a more intensive form of agriculture that expanded through the LSP floodplain in recent decades. Agri-environmental cropping (e.g., using cover crops at the end of the growing season) is an agroecological practice meant to reduce the impact of row crop (soy, corn) monocultures. F-RC, A-AC and A-CC treatments were implemented in collaboration with agricultural producers, converting a subset of A-CC fields into F-RC or A-AC between 2018 and 2022 (Watson et al., 2024).

Soil leachates were prepared using empty organic tea bags that allowed the dissolved compounds to leach into the water while holding the soil in the tea bags. For each soil type, we filled 10 tea bags with 10 g of each soil, thus incubating 100 g of soil in 2500 ml of culture water to prepare the leachate. Tea bags were hung in small 5L plastic buckets and then left for 24 hours in the dark before collecting the leachates. Empty tea bags were also hung in the culture water for the blank treatment. The leachates were prepared to mimic natural leaching during spring floods. Leachates are expected to contain pesticides, but also other contaminants, as well as microorganisms, nutrients, and small particles from the soils. Unfortunately, turbidity was not measured due to technical issues. After 24 h of incubation, the tea bags were removed, and the leachate water was gently collected to avoid resuspension of fine sediments that leached through the bags and settled at the bottom of the bucket. 50 ml of this leachate was transferred to each

glass beaker (60 ml), to which four *D. mag*na neonates (< 24 h age) were added. Fresh leachates were prepared to change the exposure water every two days during the experiment.

Exposure experiments

The first experiment was conducted in an outdoor setup with *D. magna* neonates (*n* = 720, split in 180 beakers) exposed to a combination of leachates and natural UVR, while the second experiment was conducted in an indoor controlled setup, with neonates (*n* = 280) exposed only to different soil leachates but from a broader variety of land uses (for more details, see Table 1). The duration of the experiments was based on the OECD standard of 21 days for survival and reproduction tests. More precisely, the outdoor experiment ran for 23 days, while the indoor experiment was terminated on day 22, as most individuals had died by then.

Outdoor experiment

Here, we aimed to analyse the interactive effects of land use (2020) and natural UVR on *D. magna* physiological endpoints, swimming behavior, and survival. We used a fully factorial design (4 types of leachates X 3 levels of UVR), with each of the 12 factor combinations replicated 15 times in 5 completely randomized blocks. Neonates were isolated from the culture aquaria using a 300 µm sieve (adapted from CEAEQ 2015). Then, four neonates were transferred to each of 180 glass beakers (hereafter 'incubators'). Incubators were placed in a temperature-controlled water bath containing 5 Styrofoam® coolers, which are referred to as blocks in the analyses. The water bath was laid on an outdoor table exposed to ambient sunlight. Each cooler contained 9 cells, with 3 replicates of each UVR treatment level (total = 15 cells of each UVR treatment across the 5 blocks). UVR was manipulated using light filters, as described in Paquet-Walsh et al. (2019) and Boily et al. (2011). Three types of filters were used: J-Roll® to block both UV-A and UV-B (hereafter "no UV"), Mylar-d® to block UV-B (hereafter "UV-A") and Whirlpack®, which is transparent to most visible light and UVR (hereafter "UV-A+UV-B") (see Figure S1a for light transmission data). During the experimental days, we had mostly sunshine conditions (Figure S1b). Each cell contained four incubators, one for each land use treatment.

Incubators were filled with either 50 ml of leachate from N-MS, F-OC, or A-CCcorn, with culture water only ("blanks") and were exposed to natural UVR for 8 h per day. In summary, 780 neonates were placed in 180 incubators divided into 12 treatment combinations, each replicated 15 times across 5 blocks. The individuals were fed every alternate date with Spirulina powder and baker's yeast, with feeding always done after making observations for physiological endpoints and swimming behavior (as described below). Temperature in the coolers was monitored using Onset HOBO temperature data loggers throughout the experiment (Figure S1c).

Indoor experiment

Here, we aimed to analyse the impact of a broader land use gradient on *D. magna* physiological endpoints, swimming behavior and survival, exposing neonates to all land use types described above, but in the absence of a UVR treatment. For this experiment, we used eight land use types from 2020 and five land use types from 2022, with five replicate incubators for each land use type. Each incubator again had four *D. magna* neonates ≤ 24 h age and the incubators were kept at room temperature (21 ± 2 °C) under laboratory LED lights as the light source for 8 h per day. *D. magna* feeding and leachate refreshment were done the same way as it was done in the outdoor experiment.

Daphnia magna *performance*

Various short-term and long-term physiological, behavior, and demographic outcomes were measured in both exposure experiments. Short-term endpoints included heart rate, thoracic limb activity, post-abdominal claw movement and swimming behavior, whereas long-term endpoints included survival and reproduction. After the short-term endpoint measurements, the individuals were returned to the respective beakers.

Physiological endpoints: After 48 h of exposure to treatments, *D. magna* individuals were transferred to a Petri dish and allowed to acclimatize for 3 minutes. Each individual was then placed on a microscope slide with a drop of water under a Zeiss light microscope at 40x magnification. Videos were recorded for 60 seconds using an ELP HD USB digital camera (8MP) attached to the ocular lens of the microscope. Videos were then used to

quantify heart rate, thoracic limb activity, and post-abdominal claw movement, all expressed in beats per minute. The video speed was slowed down to 25% of the original speed, and beats were counted for 15 seconds in outdoor (*n* = 58) and indoor (*n* = 69) experiments.

Swimming behavior: Swimming speed was recorded at 48 h (*n* = 170 individuals, replicate no. 1) and 72 h (*n* = 169, replicate no.2) during the outdoor experiment, and at 48 h only for the indoor experiments (*n* = 56). All individuals in any given incubator were transferred to a 5 cm Petri dish with water and left to acclimatize for 3 mins (see Table 1 for more details). Then, with a digital camera mounted on a stand, their horizontal movement was recorded for 3 minutes, before returning the individuals to their original incubators. The analysis of average swimming speed from the videos was performed using AnimalTA v2.2.1 (Chiara, 2023). 60 seconds of movement was analyzed for each video, and swimming speed was expressed as average speed (mm/sec). All individuals from the same incubator were tracked concomitantly in the analysis.

Survival: All experimental units were observed daily for any mortality until the end of the experiment. Dead individuals were counted and collected. These observations were made on a daily basis except for a day in the outdoor experiment because the meteorological conditions were unfavourable to sampling. In the case of the outdoor experiment, 710 individuals contributed to the survival analyses, as the remaining were accidentally lost during the observation period, while in the case of the indoor experiment, 280 individuals contributed to the survival analyses. In both cases, there were four individuals in each beaker at the start of the experiment.

Reproduction: The number of neonates produced was tracked and collected at each occasion we measured survival.

Pesticides in leachates and soils

Pesticide concentrations in soils from different land use types were analyzed at McGill University, Montreal, Canada. 31 compounds were measured in the soils before preparing leachates and later in the leachates extracted (in water). Toth et al. (2024)

provide the rationale behind choosing these compounds, as well as detailed methodological information including details on analyte names and relevant information. Briefly, chemical analysis was performed using a Thermo Scientific Vanquish™ UHPLC system (Waltham, MA, USA) equipped with a quaternary loading pump and a binary eluting pump, coupled to a Thermo Scientific TriPlus™ RSH EQuan™ 850 autosampler for online solid-phase extraction (SPE). The UHPLC system was interfaced with a Thermo Scientific Orbitrap Exploris™ 120 high-resolution accurate-mass (HRAM) mass spectrometer via a heated electrospray ionization (HESI) source. Instrument control, data acquisition, and processing were done using Thermo Scientific Xcalibur™ 4.3 software, while quantitative data analysis and reporting were performed using Thermo Scientific TraceFinder™ 5.1 with a general quantitative workflow.

Data analysis

All data analyses were performed using R software (v4.3.2). Linear mixed models (LMMs) with soil leachates (land use type), UVR, and their interaction as fixed factors and blocks as random factors. Separate LMMs were fit for *D. magna* heart rate, thoracic limbs activity, and post-abdominal claw movement in the outdoor experiment. For swimming behavior, generalized linear mixed models (GLMMs) were used with leachates and UVR as fixed factors, and “incubator” nested within “blocks” as random factors. To check for overdispersion and select the appropriate distribution for models, and to verify model assumptions (distribution of residuals, homoscedasticity), we used the DHARMa package (Hartig, 2016). We used a gamma distribution for swimming behavior. To test fixed effects, we fit 5 models per response variable, including a null model with a single fixed effect, an additive model with the two fixed effects but no interaction, and a full model with all 3 fixed effects, including the interaction term. The best model was selected based on the delta AICc using the MuMin package in R (Bartoń, 2022). The model with a delta AICc < 2 and the lowest number of parameters was ranked as the best model. We applied estimated marginal means (EMMs) on the best model with the emmeans package (Lenth, 2022). Multiple pairwise post hoc comparisons were performed using the ‘multcomp’ (Hothorn et al., 2016) and ‘multcompView’ packages in R (Graves et al., 2019), adjusting *p*-values with the ‘False Discovery Rate’ (FDR) method at alpha = 0.05. The analytical approach of

the indoor experiment was similar with the only difference being that models included a single fixed factor, land use type.

For survivorship, Kaplan-Meier curves of the raw survival data were plotted (Therneau, 2015). Survival analysis was then performed using the Cox proportional hazards (PH) model, using the function *coxme* () from the "Survival" package in R (Therneau, 2024). In the case of the outdoor experiment, land use, natural UVR, and their interaction were used as fixed factors, with replicates nested within blocks included as random factors. Model selection based on delta AICc (< 2) was carried out as for previous models, by comparing null, additive and interaction models. The assumption of proportionality of hazard (PH) was checked using the *cox.zph* () function and diagnostic plots from the "Survival" package (Therneau, 2015; Therneau et al., 2017). Mean daily water temperature within each block was also added as a time-varying covariate in the model if the assumption of constant proportionality of hazards was not met. Lastly, Kaplan-Meier curves were then plotted for the raw survival data (Therneau, 2015).

Survival analyses for the indoor experiment were performed in a similar way, but in this case, we ran the models separately for the two years since the number of land use types differed between them. We used a common control blank for the two years. Finally, reproductive output (i.e., the cumulative number of neonates produced per surviving female) was analysed as counts using the function *glmmTMB* () from the glmmTMB package in R using a negative binomial distribution.

Results

Outdoor experiment

Physiological endpoints: Model selection retained the interaction model as the best for each of the physiological endpoints. However, the retained models were not significant for heart rate and thoracic limb activity ($p > 0.05$, Figure 1a,b), while for the post-abdominal claw movement, the model was overall significant and showed a significant interaction. More precisely, in the absence of UVR, F-OC induced a significantly higher number of beats than BL ($p = 0.0279$; Figure 1c), while A-CCcorn and N-MS behaved intermediate.

Under UV-A and UV-AB, no significant differences were observed between the land use leachates (Figure 1c).

Swimming behavior: The results showed the null model as the best model, indicating no influence of either land use or natural UVR on the average swimming speed of *D. magna* at both 48 h and 72 h (Figure 1d-e).

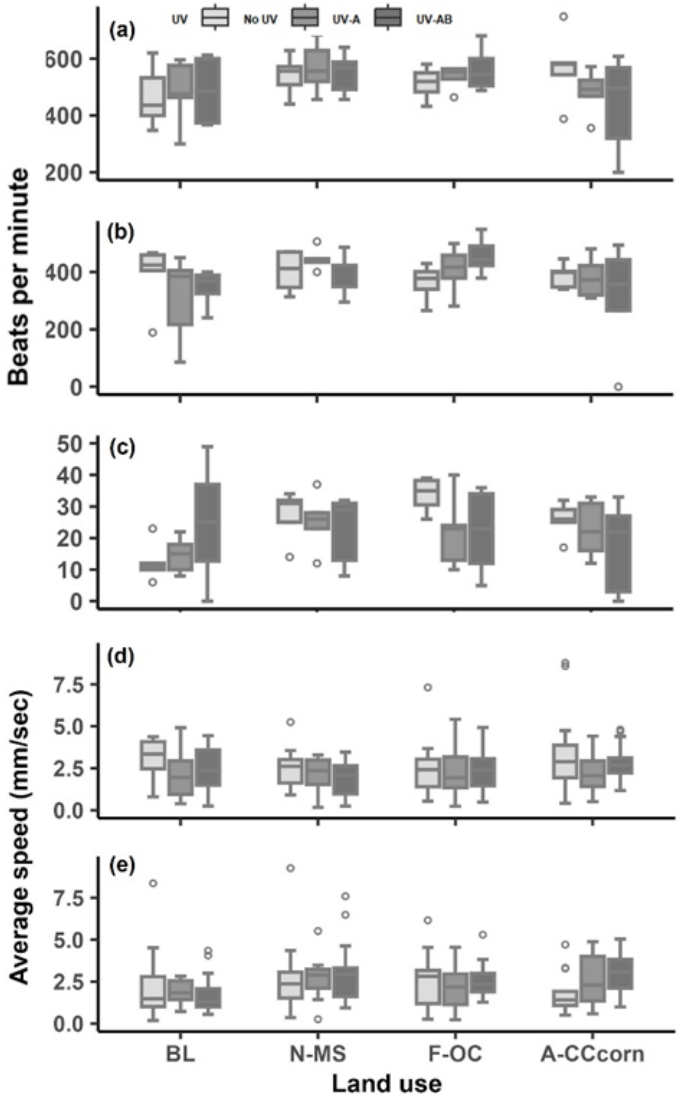


Figure 1. Effects of land use and natural UVR on *D. magna* physiological endpoints at 48 h in the outdoor experiment: (a) heart rate, (b) thoracic limbs beats, (c) post-abdominal claw beats, and swimming speed at (d) 48 h and (e) 72 h. Land use included natural maple swamp (N-MS), forage-old cropping (F-OC), agriculture-conventional cropping-corn (A-CCcorn) and a control blank (BL); While UV exposure includes: no UV, UV-A, and UV-AB. Land use nomenclature adapted from Watson et al., 2024.

Survival: Model selection indicated that the best model included land use and natural UVR as independent factors, along with an interaction between natural UVR and mean daily temperature, which helped meet the PH assumption for natural UVR. However, the model indicated significant effects of land use only, with only A-CCcorn had a significant positive impact on the survival of *D. magna* (p = 0.003; Figure 2a; Table 2). In contrast no effect of natural UVR was observed (Figure 2b; Table 2), although we see a tendency for some reduced mortality under UV-A (Figure S2).

Reproduction: No significant effects of land use nor of natural UVR exposure on *D. magna* cumulative neonates were observed (Figure 2c).

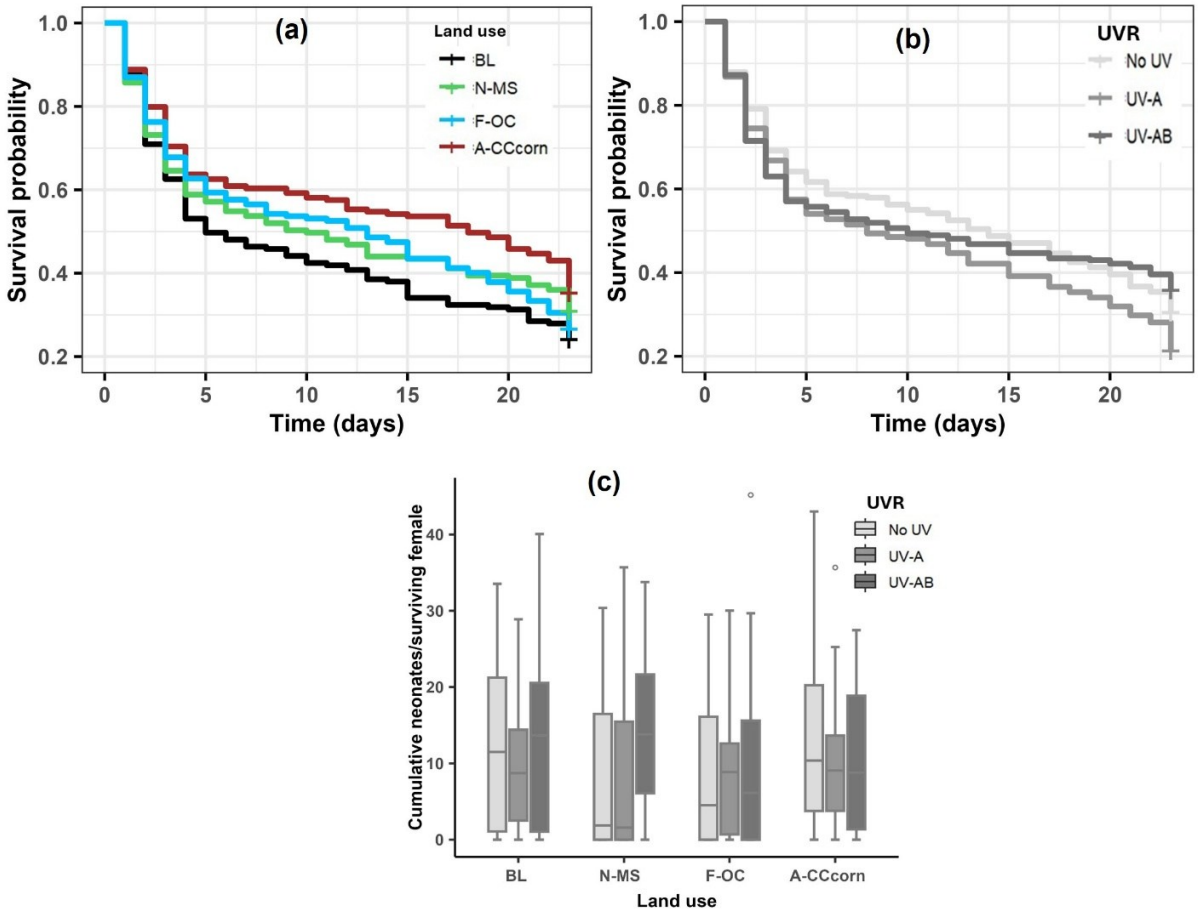


Figure 2. Effects of land use and natural UVR on *D. magna* survival and reproduction in the outdoor experiment. Survival curves for *D. magna* across land use and UVR exposure (a-b); and cumulative number of neonates produced across land use and UVR exposure (c). Land use includes natural maple swamp (N-MS), forage-old cropping (F-OC), agriculture-conventional cropping-corn (A-CCcorn) and a control blank (BL); While UV exposure includes: no UV, UV-A, and UV-AB. Land use nomenclature adapted from Watson et al., 2024.

Indoor experiment

Physiological endpoints: In the case of 2020 soil leachates, land use showed a significant impact on the heart rate. Heart rate was significantly lower in A-ACs and differed from BL (p = 0.0057), N-MS (p = 0.0013), N-WM (p = 0.0002), F-RC (p = <.0001), A-CCsoya (p = 0.0001), A-ACcorn (p = 0.0068), A-CCcorn (p = 0.0068) while no effect was observed on thoracic limbs activity and post-abdominal claw movement (Figure 3a-c). In the case of 2022 soil leachates, again, land use showed a significant impact on heart rate. Heart rate was significantly lower in A-ACsoya and differed from BL (p = 0.026), N-MS (p = 0.0013), N-WM (p = 0.0038), F-OC (p = 0.0030), A-CCsoya (p = 0.0001), while no effect was observed on thoracic limbs activity and post-abdominal claw movement (Figure 3d-f).

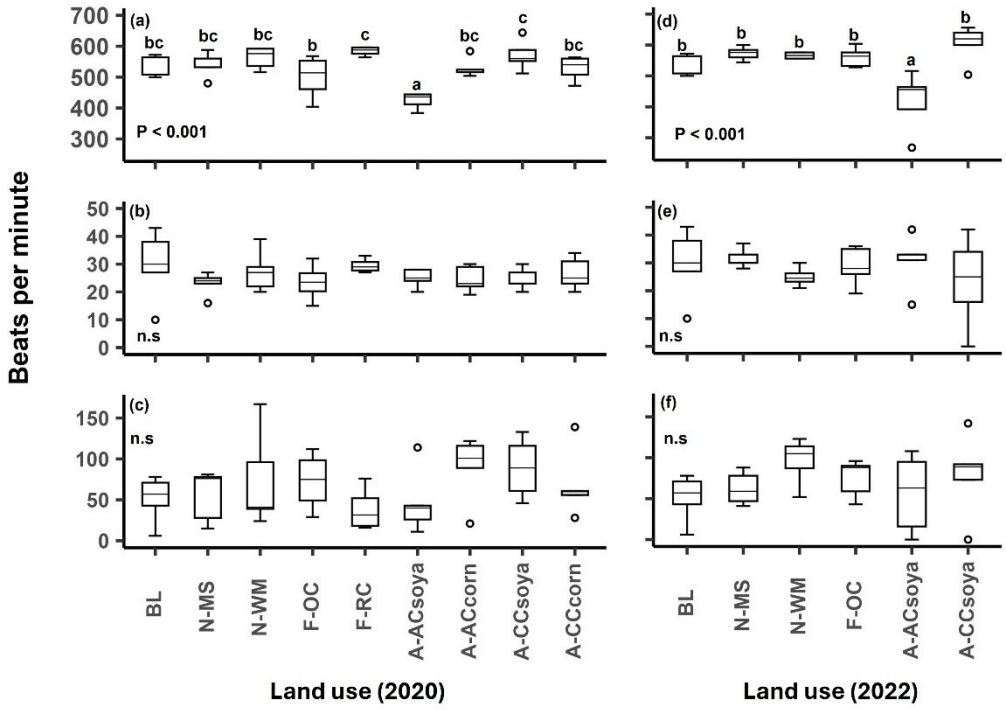


Figure 3. Effect of land use on physiological endpoints of *D. magna* in the indoor experiment: (a) heart rate, (b) thoracic limbs activity, and (c) post-abdominal claw movement for 2020; while heartbeats (d), thoracic limbs activity (e), and post-abdominal claw movement (f) for 2022. Land use included natural maple swamp (N-MS), natural wet meadow (N-WM), forage-old cropping (F-OC), forage-recent cropping (F-RC), agriculture-agri-environmental cropping-soya (A-ACsoya), agriculture-agri-environmental cropping-corn (A-ACcorn), agriculture-conventional cropping-soya (A-CCsoya), agriculture conventional cropping-corn (A-CCcorn) and control blank (BL). Land use nomenclature adapted from Watson et al., 2024. The results of post hoc tests are presented as letters in the boxplots.

Swimming speed: The null model was selected as the best model, indicating that there was no significant impact of land use on average swimming speed on exposure to leachates from both years (Figure S3). Similarly, we also explored other swimming variables, including meander and exploration value, but found no differences.

Survival: For 2020, the model with land use was selected as the best model, with N-MS and A-CCsoya showing a significant positive effect on the survival of *D. magna* (p = 0.004, p = 0.027 respectively, Figure 4a, Table 3), but for 2022, null model was selected as the best model suggesting no effect of land use on the survival (Figure 4b).

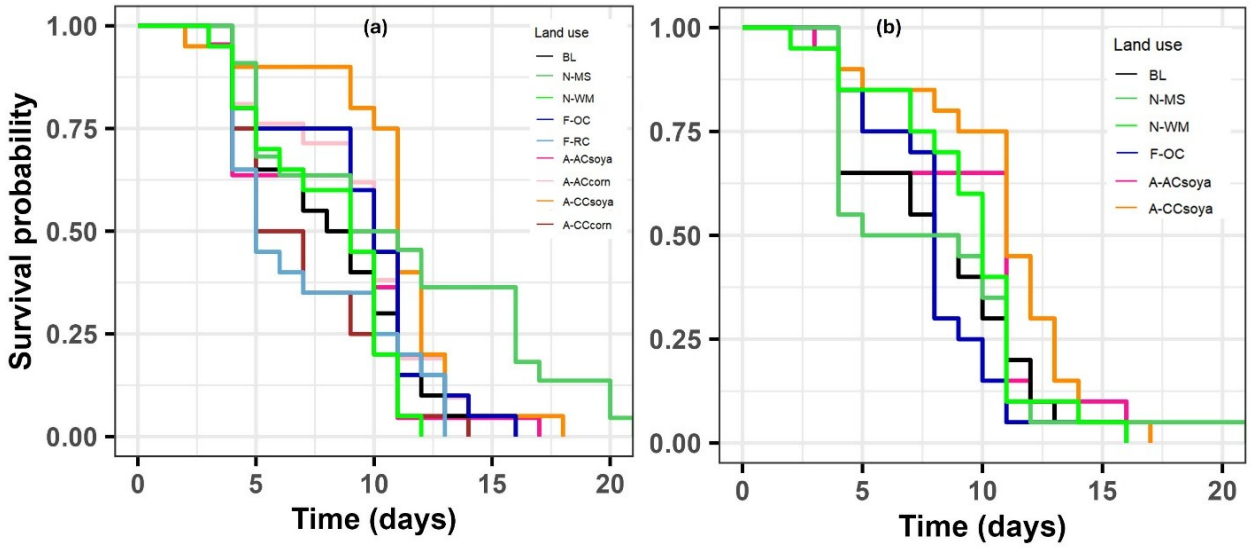


Figure 4. Effect of land use on survival of *D. magna* in an indoor experiment over 22 days of incubation: (a) 2020 and (b) 2022. Land use included natural maple swamp (N-MS), natural wet meadow (N-WM), forage-old cropping (F-OC), forage-recent cropping (F-RC), agriculture-agri-environmental cropping-soya (A-ACsoya), agriculture-agri-environmental cropping-corn (A-ACcorn), agriculture-conventional cropping-soya (A-CCsoya), agriculture conventional cropping-corn (A-CCcorn) and control blank (BL). Land use nomenclature adapted from Watson et al., 2024.

Reproduction: The null model was selected as the best model, thus suggesting no effect of land use on cumulative neonates from 2020 (Figure S3).

Pesticide measurements

Pesticide analysis in soil leachates obtained from different land uses showed an overall relatively low level of contamination. More precisely, in soil leachates used for the

outdoor experiment, 2, 4-D was detected in N-MS (0.539 µg/L) and A-CCcorn (0.389 µg/L). While in the 2020 soil leachates from the indoor experiment 2, 4-D was found in N-MS (1.159 µg/L), N-WM (0.945 µg/L), F-OC (1.267 µg/L), A-ACsoya (0.0767 µg/L), A-CCsoya (0.0717 µg/L), while desisopropylatrazine was found only in N-MS (0.0630 µg/L) (Table S2). Lastly, in 2022, soil leachates from the indoor experiment, metolachlor was found only in A-CCsoya (0.327 µg/L), while 2,4-D was found in N-MS (1.182 µg/L), N-WM (0.837 µg/L), A-ACsoya (0.967 µg/L) and A-CCsoya (0.268 µg/L) (Table S2). Besides this, pesticides detected in different land use types before leachate preparation are presented in Table S3 for 2020 and Table S4 for 2022 in the case of the indoor experiment and were not measured for the outdoor experiment (in this case, soil samples were a sub-sample of the 2020 soils used indoors).

Discussion

Despite our previous work on the same system, which revealed a clear negative effect of conventional agriculture on zooplankton emergence success from the same soils used here (Badesab et al., 2026), our experimental approach failed to clearly link these effects to the variation in toxicity of the leachates related to different land uses. The low levels of contamination detected in the leachates used in our experiments are a likely explanation for these results, with only three molecules detected and with relatively low concentrations. In addition, we did not observe a clear higher concentration of contaminants in the agricultural sites, as expected. This might eventually contribute to explaining the unexpected positive effects of conventional agriculture (A-CCorn, outdoor experiment; A-CCsoya, indoor experiment) on survival, but at the same time, we found a less surprising positive effect of N-MS (indoor experiment). The low level of contamination probably explains also the fact that we did not detect clear interactive effects between land use and UVR. However, we detected some interactive effects on one of the physiological endpoints.

In contrast to our expectations, although the interaction model including land use and natural UVR was selected as the best model for all physiological endpoints in our outdoor experiment, it was statistically significant only for post-abdominal claw movement,

with differences in response to land use being observed only in the absence of UVR. This result is in accordance to what we found for heart rate in the indoor experiment, which did not include UVR. No effect of land use and/or natural UVR was observed on the average swimming speed of *D. magna*. Lastly, no effect on *D. magna* reproductive output was found in the two experiments.

Physiological endpoints

No significant effects of land use or natural UVR were found on the heart rate and thoracic limb activity of *D. magna* in the semi-natural conditions. These results partially echo those from another study wherein no impact of UVR was observed on the heart rate, while the fungicide azoxystrobin was found to increase the heart rate in comparison to the control, but the interaction was not significant (Lari et al., 2024). In another study on the effects of landfill leachate toxicity from multiple sites (both treated and untreated), a reduction in heart rate was found to be dose dependent for most leachates, except the non-operational landfill leachates, wherein an increase in heart rate was observed (Makaras et al., 2026). On the other hand, when *D. magna* was exposed only to leachates in the indoor experiment, we found a significant impact of land use on one of the physiological endpoints, i.e., heart rate, which was lower when exposed to leachate from agri-environmental cropping (A-ACsoya) soils and differed significantly from others for both years. This result on heart rate, a sensitive indicator of physiological stress (Bownik & Szabelak, 2021), its low values under A-ACsoya leachate compared to others could be due to the lower 2,4-D concentration (0.0767 µg/L) found in this soil type compared to others. Accordingly, relatively lower heart rates have been reported earlier for *D. magna* exposed to the insecticide fipronil (Bownik & Szabelak, 2021), suggesting that a reduction in heart rate might not be unequivocally a proxy of good health status. Post-abdominal claw movement is important in removing excess particles from the feeding groove, and we thus expected to see some differences in its activity. Accordingly, we observed some effects on this variable in the case of the outdoor experiment under no UV with higher beats in F-OC leachate than the control. This finding is in accordance with other studies reporting a significant impact of pesticides such as fipronil at different concentrations on the post-abdominal claw, with lower concentrations increasing the beats, while higher

concentrations decreasing them (e.g., Bownik & Szabelak, 2021). Furthermore, no significant effect of land use and/or UVR was observed on the thoracic limbs activity in both experiments, and a similar observation has been made in the case of *D. magna* when exposed to Azoxystrobin and UVR (Lari et al., 2024). While Bownik & Szabelak (2021) found an increase in activity when exposed to lower concentrations of fipronil and a decrease with increasing concentrations.

Swimming speed

Our outdoor experiment demonstrated no variations in the swimming speed when exposed to leachates under no UV, UV-A and UV-AB filters. This contrasts with Makaras et al., (2026), who reported a significant increase in velocity when exposed to some untreated landfill leachates, while a decrease was observed in more contaminated leachates. Some other studies reported that exposure to UVR increased the swimming speed of *D. magna* (Lee & Hansson, 2021; Zheng, 2018), and moved to greater depths. However, while doing so, there could also be trade-offs, for e.g., in the presence of patchy food availability, wherein they can compromise with the UVR exposure risk as well (Lee & Hansson, 2021).

Survival and reproduction

Soil leachates from different land use types were found to influence the survival, but with a significant positive effect of A-CCcorn overall in the case of the outdoor experiment. These results are in contrast to what has been observed in another study, wherein the interaction between sublethal concentrations of pesticides and UVR exhibited no effects on the *D. magna* survival (Beketov et al., 2011). The pesticide concentrations found in our study in leachates were far below water quality guidelines for our study region (Giroux, 2018), which could partially explain the lack of significant interaction in our results. Furthermore, when *D. magna* was exposed only to the land use leachates in the indoor experiment, again a significant impact of land use was observed on the survival of *D. magna*, with leachates from N-MS and A-CCsoya were found to improve their survival significantly, but only for the 2020 soil leachates. We currently do not have an explanation

for why conventional agriculture improved survival in both the indoor and outdoor experiments.

The detrimental effects of UVR on the fitness and survival of *Daphnia* species have been reported earlier in laboratory conditions (Eshun-Wilson et al., 2020). Another study suggested that UV-B exposure can lead to higher mortality in *Daphnia* sp., but further exposure to UV-A could increase survival in the presence of natural visible light, owing to photorepair stimulation (Huebner et al., 2006; Williamson et al., 2001), but it depends on the duration of exposure (Huebner et al., 2006). So, we expected that UV-A would have either a negative or positive effect, but with UV-AB, we would see some worse effects than with UV-A only. Unexpectedly, this was not the case, and we found no significant effect of either of them. Our results are well supported by a study on *D. catawba,* wherein no significant differences in survival across different UV treatments were observed (Fischer et al., 2006), suggesting that the impact of UVR could be dose dependent. Unfortunately, our UV sensor did not work properly during the experiment, and it is not possible to test this hypothesis with the data in hand. Further, the ratio between the damaging effect of UV-B and repair by UV-A changes with day as well as season, altitude, latitude and total ozone thickness, wherein low solar radiation or lower altitude or increased clouds can favor UV-A (Weihs et al., 2013). Hence, depending on the UV environment, adaptations and/or resistance by organisms to UV have been reported earlier (Weihs et al., 2013).

Reproduction measured in terms of cumulative neonates was not affected by either of the factors manipulated in our experiment, suggesting that, despite some effects on mortality, there was some sort of compensation in terms of newborns. This finding is partially in accordance with a study on the impact of azoxystrobin and UVR, which found no impact of UVR on fecundity, but at the same time, azoxystrobin reduced fecundity significantly when compared to the control (Lari et al., 2024). However, contrary to our results, some other studies have reported significant impacts of UVR on the reproductive output, e.g., it was found to increase with exposure to photorepair radiation in *D. pulicaria* (Grad et al., 2001), while a decrease has also been reported in the case of *D. magna* when exposed to UV-B radiation (Huebner et al., 2006). Beketov et al. (2011) reported a

synergistic effect of pesticides (fenoxycarb and pirimicarb) and UVR on the reproduction of *D. magna,* which was found to be lower than the control. Similar to the outdoor experiment, no effect of land use was found on the cumulative neonates when exposed only to the soil leachates in the indoor experiment; however, given the high mortality, the results from the indoor experiment need to be interpreted carefully, as they came from a bit weaker culture, as it can be seen from survival curves, showing a relatively high mortality compared to the outdoor experiment.

In the present study, the outdoor experiment allowed us to highlight the effects of land use and UVR on, e.g., survival, whereas the indoor experiment allowed us to expand the land use gradient and see some effects on physiological endpoints. However, the lower survival and the near-zero reproductive output observed in the indoor experiment show that this batch of individuals was not thriving well compared to those used for the outdoor experiment, suggesting that care should be taken when interpreting these results. A relatively short period of rearing or acclimation in our lab before the indoor experiment might partially explain this result.

Amongst pesticides, 2,4-D, metolachlor and desisopropylatrazine were detected in the land use leachates, albeit at relatively low concentrations (< 1.5, 0.5, 0.1 µg/L, respectively), which are far below the values established as toxic for aquatic life after chronic exposure (e.g., 220 µg/L for 2, 4-D, 7.8 µg/L for metolachlor and 1.8 µg/L for atrazine) (Giroux, 2018). So, observing the positive effects on survival of *D. magna* under agricultural croppings could be attributed to these relatively lower concentrations of pesticides found.

Conclusions

To our knowledge, the present study is the first to explicitly analyze the potential interaction between different floodplain land uses and natural UVR, with most ecotoxicological studies analyzing them separately and/or under artificial UV sources (mostly UV-B). In addition, a comparison of ecotoxicological effects between a wider range of land uses has been performed for the first time, by testing the effects of soil

leachates along a land use gradient representative of the conditions found in the Lake St. Pierre floodplain. This study includes novel approaches such as the use of physiological endpoints and swimming behavior that are finding an important place in toxicity impact assessments in recent years, as they serve as early indicators of effects in ecotoxicological studies when using *D. magna*. The results of the present study reveal independent effects of natural UVR and land use leachates on *D. magna* survival. Results from Badesab et al. (2026) suggested a significant effect of land use, with natural wetlands favouring resilience of zooplankton through dormancy and hatching, while conventional croppings lowered hatching; however, the present study using the same soils failed to find potential mechanisms for our past results. Instead, conventional croppings were found to improve survival, and further, the agri-environmental cropping was found to reduce the heart rate. We suggest that it is now necessary to test the effects of these leachates on other indicators such as biochemical or genetic changes, which could be behind the observed effects on hatching of zooplankton in this study. Furthermore, because to our knowledge, no study is available revealing the combined effects of land use and natural UVR on zooplankton, it becomes necessary to incorporate such studies while addressing the ecotoxicological impacts on the aquatic systems and on the organisms under a cocktail of stressors due to both climate change and anthropogenic alterations to the natural habitats with the increasing human populations and need to meet the demands.

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Author contribution

Conceptualisation: SB, AB, VF. Developing methods: SB, AB, VF, VY, JT, MP. Conducting research: SB, LC, AS, JT, MP. Data analysis: SB, AB, VF. Data interpretation: SB, AB, VF. Preparation of figures and tables: SB, AB, VF. Writing: SB, AB, VF.

Data availability statement

The data will be made available on the Borealis repository upon acceptance of the manuscript for publication.

Conflict of interest

The authors declare no conflict of interest.

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Supplementary material

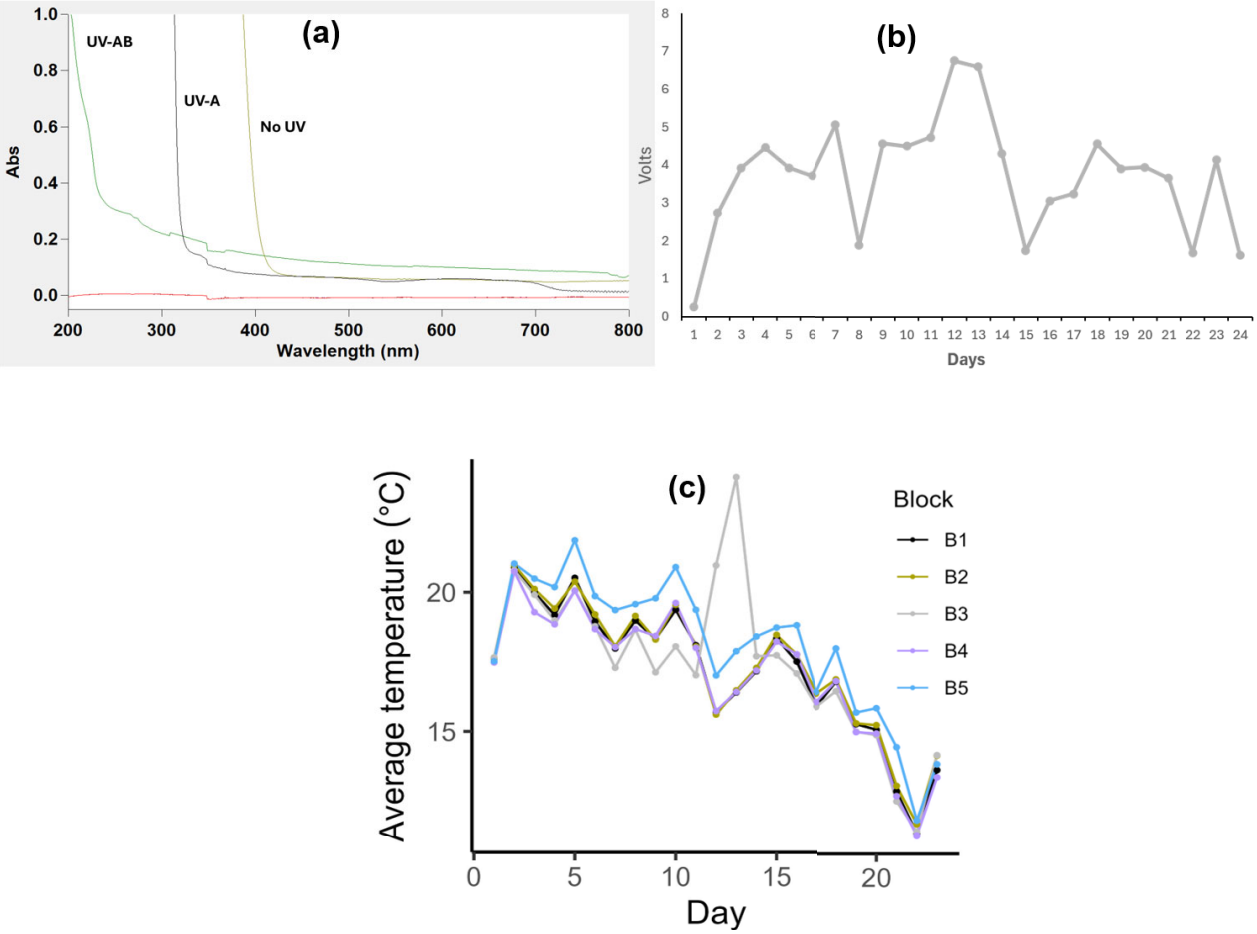


Figure S1. Variations in the absorbance by different UV filters (a), daily integrated sensor output (b) and temperature in the blocks (c) in the outdoor experimental setup.

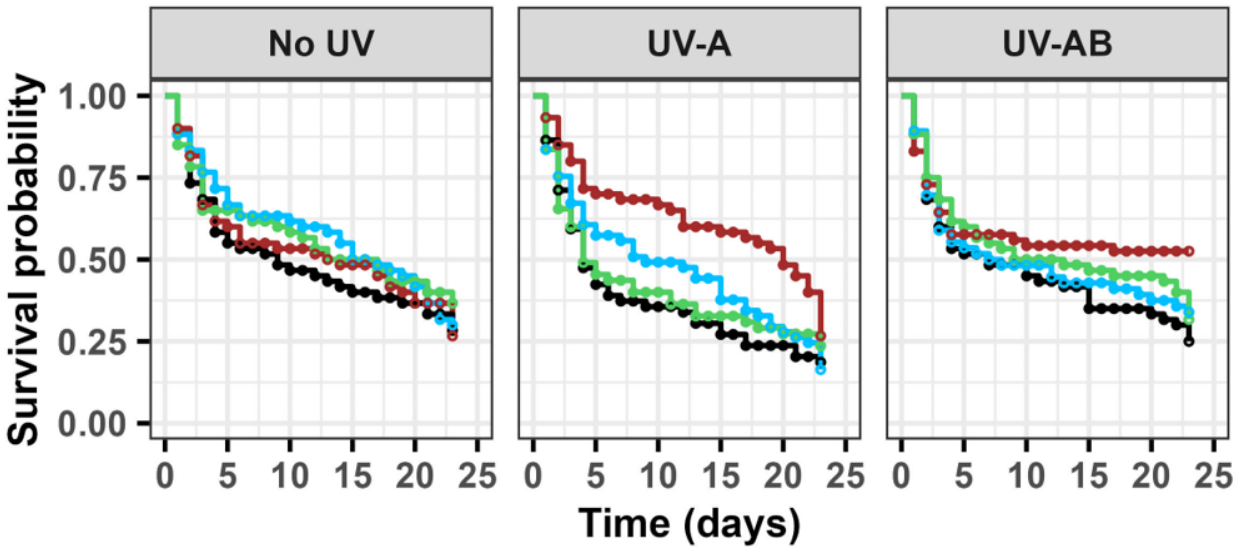


Figure S2. Effects of soil leachates from different land use types and natural UVR on *D. magna* survival in the outdoor experiment. Survival curves for *D. magna* across land use and UV exposure. Land use includes natural maple swamp (N-MS), forage-old cropping (F-OC), agriculture-conventional cropping-corn (A-CCcorn) and a control blank (BL); While UV exposure includes: no UV, UV-A, and UV-AB. Land use nomenclature adapted from Watson et al., 2024.

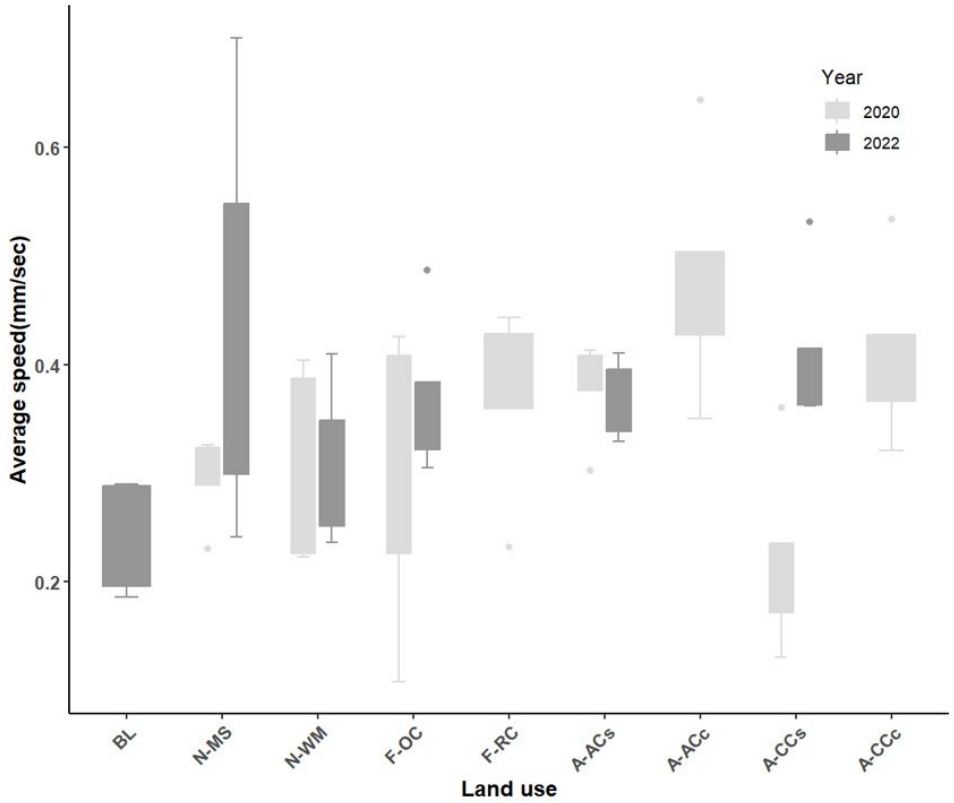


Figure S3. Effect of land use in an indoor experiment on the average swimming speed of *D. magna*.

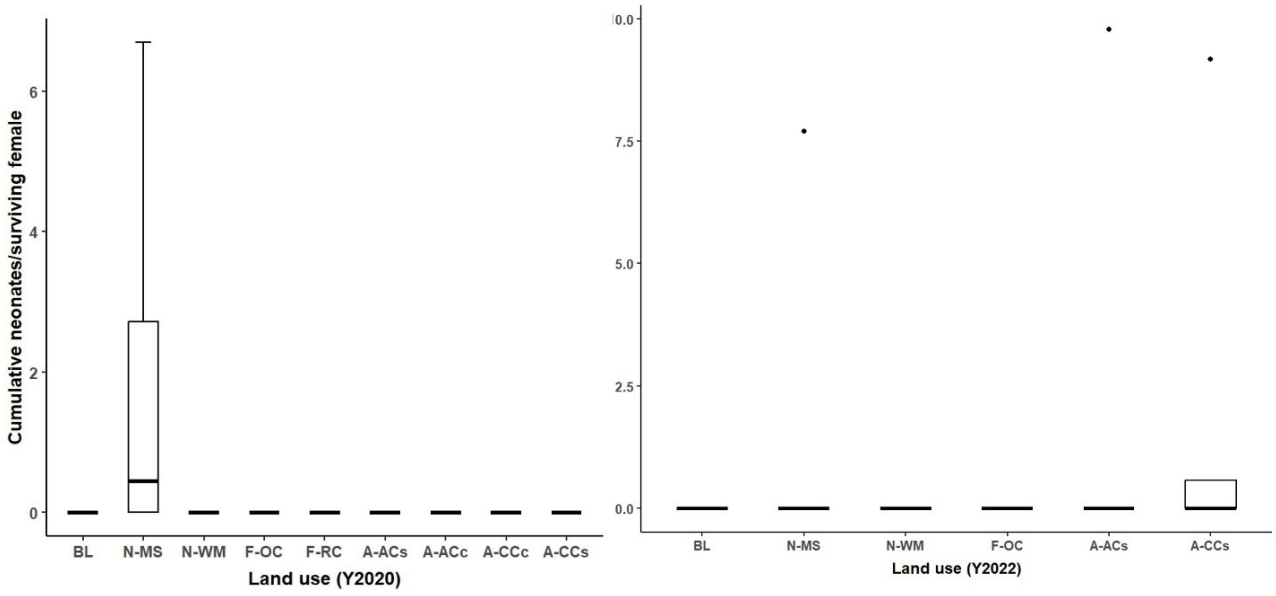


Figure S4. Effect of land use in an indoor experiment on cumulative neonates of *D. magna*.

Table S1. Pesticide concentrations in soil leachates (µg/L) for 2020 land use. Natural Maple Swamp (N-MS), Natural Wet Meadow (N-MW), Forage Old Cropping (F-OC), Forage Recent Cropping (F-RC), agriculture-agri-environmental cropping (A-ACcorn and A-ACsoya), agriculture-conventional cropping (A-CCcorn, A-CCsoya). ND = Not detected; < LOD = below detection limit; < LOQ = below quantitation limit.

Treatment	N-MS	N-WM	F-OC	F-RC	A-AC corn	A-AC soya	A-CC corn	A-CC soya
Bentazone	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Thiamethoxam*	ND	ND	<LOQ	ND	<LOQ	ND	ND	ND
Imidacloprid*	<LOQ	<LOQ	<LOQ	ND	ND	ND	ND	<LOQ
Clothianidin*	ND	ND	ND	ND	ND	ND	ND	ND
Chlorantraniliprole*	ND	ND	ND	ND	ND	ND	ND	ND
Desethyl_Atrazine	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Azoxystrobin⁺	ND	ND	ND	ND	ND	ND	ND	ND
Atrazine	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Boscalid⁺	ND	ND	ND	ND	ND	ND	ND	ND
Dimethenamid	ND	ND	ND	ND	ND	ND	ND	ND
Pyrimethanil⁺	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Metolachlor	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Chlorpyrifos*	ND	ND	ND	ND	ND	ND	ND	ND
Metribuzin	<LOD	<LOD	ND	<LOD	ND	ND	ND	ND
Bromoxynil	ND	ND	ND	ND	ND	ND	ND	ND
MCPA	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Carbaryl*	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
MCPP.Mecoprop	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
2,4.D	1.159	0.945	1.267	<LOD	<LOD	0.0767	<LOD	0.0717
Nicosulfuron	ND	ND	ND	ND	ND	ND	ND	<LOD
Imazethapyr	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Flumetsulam	ND	ND	ND	ND	ND	ND	ND	ND
Rimsulfuron	<LOD	ND	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Thiacloprid*	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Mesotrione	ND	ND	ND	ND	<LOQ	ND	ND	ND
Dicamba	<LOD	<LOD	<LOD	ND	<LOD	<LOD	ND	<LOD
Linuron	ND	ND	ND	ND	ND	ND	ND	ND
Fenamidone⁺	ND	ND	ND	ND	<LOD	ND	ND	ND
Dimethoate*	ND	ND	ND	ND	ND	ND	ND	ND
Desisopropylatrazine	0.0630	<LOQ	<LOQ	<LOD	<LOQ	<LOD	<LOD	<LOD
Cyantraniliprole*	ND	ND	ND	ND	ND	ND	ND	ND

Note: *insecticides; ⁺fungicides

Table S2. Pesticide concentrations in soil leachates (µg/L) for 2022 land use. Natural Maple Swamp (N-MS), Natural Wet Meadow (N-MW), Forage Old Cropping (F-OC), agriculture-agri-environmental cropping (A-ACsoya), agriculture-conventional Cropping (A-CCsoya), and control Blank (BL). Note that the blank here is the same for Table S1 and Table S2 but is represented in only Table S2 for aesthetic reasons. ND = Not detected; < LOD = below detection limit; <LOQ = below quantitation limit.

Treatment	BL	N-MS	N-WM	F-OC	A-AC soya	A-CC soya
Bentazone	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Thiamethoxam*	<LOQ	<LOQ	ND	ND	ND	ND
Imidacloprid*	ND	<LOQ	ND	<LOQ	ND	ND
Clothianidin*	<LOD	<LOD	<LOD	<LOD	ND	ND
Chlorantraniliprole*	<LOD	ND	ND	ND	<LOD	<LOQ
Desethyl_Atrazine	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Azoxystrobin⁺	<LOD	<LOD	ND	<LOQ	ND	ND
Atrazine	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Boscalid⁺	ND	<LOD	ND	ND	ND	ND
Dimethenamid	<LOD	ND	ND	ND	ND	ND
Pyrimethanil⁺	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Metolachlor	<LOD	<LOD	<LOD	<LOD	<LOD	0.327
Chlorpyrifos*	ND	ND	ND	ND	ND	<LOD
Metribuzin	<LOD	ND	ND	ND	ND	ND
Bromoxynil	ND	ND	ND	ND	ND	ND
MCPA	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Carbaryl*	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
MCPP.Mecoprop	ND	<LOD	<LOD	<LOD	<LOD	<LOD
2,4.D	<LOQ	1.182	0.837	<LOD	0.967	0.268
Nicosulfuron	ND	ND	ND	ND	<LOD	ND
Imazethapyr	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Flumetsulam	ND	ND	ND	ND	<LOD	ND
Rimsulfuron	<LOD	<LOD	ND	<LOD	<LOD	<LOD
Thiacloprid*	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Mesotrione	ND	ND	ND	ND	ND	<LOQ
Dicamba	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Linuron	ND	ND	ND	<LOQ	ND	ND
Fenamidone⁺	ND	<LOD	ND	<LOQ	ND	ND
Dimethoate*	ND	<LOQ	ND	ND	ND	ND
Desisopropylatrazine	<LOQ	<LOD	<LOQ	<LOQ	<LOQ	<LOD
Cyantraniliprole*	ND	ND	ND	ND	ND	ND

Note: *insecticides; ⁺fungicides

Table S3. Pesticide concentrations in soil (ng/g) for 2020 land use. Natural Maple Swamp (N-MS), Natural Wet Meadow (N-MW), Forage Old Cropping (F-OC), Forage Recent Cropping (F-RC), agriculture-agri-environmental cropping (A-ACcorn and A-ACsoya), agriculture-conventional cropping (A-CCcorn, A-CCsoya). ND = Not detected; < LOD = below detection limit; <LOQ = below quantitation limit.

Treatment/Y2020	N-MS	N-MS	N-WM	N-WM	F-OC	F-OC	F-RC	F-RC	A-AC soya	A-AC soya	A-AC corn	A-AC corn	A-CC soya	A-CC soya	A-CC corn	A-CCcorn
Replicate	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Bentazone	<LOD	<LOD	<LOD	<LOQ	0.176	0.203	0.391	0.341	ND	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOQ	<LOQ
Thiamethoxam	<LOD	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND
Imidacloprid	ND	ND	ND	<LOD	ND	ND	<LOD	ND	ND	ND	ND	ND	<LOD	ND	ND	ND
Clothianidin	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND
Chlorantraniliprole	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	<LOD	ND	ND
Desethyl_Atrazine	<LOQ	<LOQ	<LOQ	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOQ	<LOQ	<LOQ	<LOQ	<LOD	<LOD
Azoxystrobin	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	<LOD	ND	ND	ND	ND
Atrazine	0.105	0.099	0.119	0.127	0.077	0.061	0.050	0.074	0.159	0.167	0.182	0.184	0.049	0.075	0.139	0.181
Boscalid	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	<LOD	<LOQ	ND	ND	ND
Dimethenamid	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	<LOD	<LOD	ND	<LOD	<LOD
Pyrimethanil	<LOD	<LOD	<LOD	ND	<LOD	<LOD	<LOD	ND	ND	<LOD	<LOD	ND	ND	ND	ND	ND
Metolachlor	<LOQ	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOQ	<LOQ	0.016	<LOQ	0.351	0.529	<LOQ	<LOQ	0.359	0.2518
Chlorpyrifos	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Metribuzin	<LOQ	0.018	<LOQ	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Bromoxynil	<LOD	<LOD	<LOQ	0.018	<LOD	<LOQ	<LOQ	0.010	<LOQ	<LOD	<LOD	<LOD	<LOQ	<LOQ	<LOD	<LOD
MCPA	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	ND	<LOD	<LOD
Carbaryl	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
MCPP-Mecoprop	0.466	0.467	0.018	<LOQ	<LOD	0.019	<LOD	<LOD	<LOD	<LOD	<LOQ	<LOQ	<LOQ	<LOQ	<LOD	<LOD
2,4-D	0.013	<LOQ	0.323	0.311	0.288	0.281	ND	ND	ND	ND	<LOQ	0.017	ND	<LOQ	ND	<LOD
Nicosulfuron	ND	ND	ND	<LOD	ND	ND	ND	<LOD	ND	ND	ND	<LOD	ND	ND	<LOD	ND
Imazethapyr	<LOD	<LOD	<LOD	<LOD	<LOD	ND	ND	ND	ND	ND	<LOD	<LOD	ND	ND	<LOD	<LOD
Flumetsulam	ND	ND	ND	<LOQ	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Rimsulfuron	<LOQ	ND	0.028	<LOQ	<LOQ	<LOQ	ND	ND	<LOD	<LOD	<LOQ	<LOQ	<LOQ	0.031	<LOD	<LOD
Thiacloprid	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND	ND
Mesotrione	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND	<LOQ	ND	ND	ND	ND	ND
Dicamba	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	ND	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Linuron	ND	ND	ND	<LOD	ND	ND	ND	<LOD	ND	<LOD	ND	ND	ND	<LOD	ND	ND
Fenamidone	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	<LOD	ND	ND	ND	ND
Dimethoate	ND	ND	ND	<LOD	ND	<LOD	0.044	0.069	<LOQ	<LOD	ND	ND	ND	<LOD	<LOD	ND
Desisopropylatrazine	ND	ND	ND	<LOD	ND	ND	ND	<LOD	ND	ND	ND	ND	ND	ND	ND	<LOD
Cyantraniliprole	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND

Table S4. Pesticide concentrations in soil (ng/g) for 2022 land use. Natural Maple Swamp (N-MS), Natural Wet Meadow (N-MW), Forage Old Cropping (F-OC), agriculture-agri-environmental cropping (A-ACsoya), agriculture-conventional cropping (A-CCsoya), and control Blank (BL). Note that the blank here is the same for Table 2 and Table 3, but is represented in only Table 3 for aesthetic reasons. ND = Not detected; < LOD = below detection limit; < LOQ = below quantitation limit.

Treatment/Y2022	BL	BL	BL	N-MS	N-MS	N-WM	N-WM	F-OC	F-OC	A-AC soya	A-AC soya	A-CC soya	A-CC soya
Replicate	1	2	3	1	2	1	2	1	2	1	2	1	2
Bentazone	<LOD	ND	<LOD	0.128	0.135	<LOD	<LOD	<LOD	<LOD	0.156	0.163	<LOD	<LOD
Thiamethoxam	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND	ND	ND	ND
Imidacloprid	ND	ND	ND	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	ND	<LOD
Clothianidin	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND
Chlorantraniliprole	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	1.05	1.00
Desethyl_Atrazine	<LOD	<LOD	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ	<LOQ
Azoxystrobin	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND
Atrazine	<LOQ	<LOQ	<LOQ	0.226	0.278	0.069	0.068	0.059	0.055	0.101	0.124	0.240	0.215
Boscalid	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND
Dimethenamid	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Pyrimethanil	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	ND	ND	ND	<LOD	ND	ND	ND
Metolachlor	<LOD	<LOD	ND	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	0.206	0.184	2.639	2.656
Chlorpyrifos	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Metribuzin	ND	ND	ND	0.018	ND	0.395	0.460	<LOQ	<LOQ	ND	ND	<LOQ	<LOQ
Bromoxynil	<LOD	<LOD	<LOD	<LOD	<LOQ	<LOD	<LOD	<LOD	<LOD	0.018	<LOQ	0.127	0.111
MCPA	<LOQ	<LOQ	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Carbaryl	ND	<LOD	<LOD	<LOD	<LOQ	<LOD	<LOD	<LOQ	<LOQ	<LOD	<LOD	<LOD	<LOD
MCPP-Mecoprop	<LOD	<LOD	<LOD	<LOQ	<LOQ	0.463	0.447	<LOQ	<LOQ	0.168	0.155	<LOQ	<LOQ
2,4-D	ND	ND	ND	0.276	0.274	<LOQ	<LOQ	ND	ND	<LOQ	ND	<LOQ	<LOQ
Nicosulfuron	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND	ND	ND	ND
Imazethapyr	<LOD	ND	ND	<LOD	ND	<LOD	ND	<LOD	<LOD	ND	ND	ND	ND
Flumetsulam	ND	ND	ND	ND	<LOD	ND	ND	ND	ND	ND	<LOD	ND	ND
Rimsulfuron	ND	ND	ND	ND	<LOD	ND	ND	<LOD	<LOD	ND	<LOD	<LOQ	<LOQ
Thiacloprid	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Mesotrione	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Dicamba	<LOQ	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
Linuron	ND	ND	ND	ND	<LOD	ND	<LOD	ND	ND	ND	ND	ND	ND
Fenamidone	ND	ND	ND	ND	ND	ND	ND	ND	ND	<LOD	ND	ND	ND
Dimethoate	<LOQ	ND	ND	<LOD	<LOD	<LOD	ND	<LOD	<LOD	<LOD	ND	ND	ND
Desisopropylatrazine	<LOD	ND	<LOD	ND	<LOD	ND	<LOD	<LOD	ND	ND	ND	ND	ND
Cyantraniliprole	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

GENERAL DISCUSSION AND CONCLUDING REMARKS

This thesis evaluated the impacts of land use on zooplankton communities in a large temperate river floodplain using a unique ecosystem-scale experiment wherein land use was directly manipulated. This work was carried out and funded as part of the "Multidisciplinary Hub of Expertise on the Sustainable Management of the Littoral Zone of Lake Saint-Pierre" (in French: *Pôle d'expertise en gestion durable du littoral du lac Saint-Pierre*) established in 2018 by Québec Ministries (Agriculture, Fisheries and Food; Forests, Fauna and Parks; and Environment and Fight against Climate Change). It aimed to evaluate, identify and propose a sustainable land use management strategy in the floodplain. By evaluating i) water column zooplankton communities during spring flooding, ii) emergence of zooplankton from resting egg banks in soils and iii) survival and physiological performance of a zooplankter, *Daphnia magna*, we provide a broad portrait of the impact of land use at different biological levels (individuals, community, and their resilience through resting egg banks) by coupling different approaches. To recall, land use impact comparisons were made using three major land use types, each with two sub-types: natural wetland (maple swamps and wet meadows), forage cropping (old and recently sown), and agricultural croppings (agri-environmental and agri-conventional). Here, agri-environmental practices (e.g., cover crops, intercropping, perennial grass strips) were included upon the willingness and permission of the farmers and landowners to implement them (Clermont et al., 2023; Watson et al., 2024) and were expected to have a beneficial impact on zooplankton over conventional agriculture.

Chapter I of this thesis assessed the active water column zooplankton community in Lake Saint-Pierre (LSP) floodplain during spring flooding across different land use types. The results of this chapter highlight the importance of considering land use at a larger spatial (regional) scale to understand its effects on water column zooplankton communities.

Chapter II explored the effect of land use on the zooplankton egg bank in soils. Through a series of emergence experiments, our results highlight how natural wetlands favour zooplankton resilience (emergence from egg bank), and how flood regime (duration

and frequency) affects the distribution of resting stages as well as the emergence of individuals from the egg bank.

Chapter III presented an ecotoxicological approach that helped dissect some of the mechanisms through which floodplain zooplankton survival and performance respond to both land use gradient and natural ultraviolet radiation (UVR). This chapter presented some puzzling results on the impact of land use; wherein agricultural soils favoured the survival of the model organism *Daphnia magna* in contrast to natural soils. Otherwise, no major effects of land use were detected with this approach.

In the following section, “synthesis and scientific contribution”, the findings of the chapters are revisited as a whole to signify their outcome and contribution in achieving the main aim of the thesis, which is to assess the impact of land use on zooplankton in a large river floodplain. Towards the end, the limitations of this work are also listed, which will help derive future research perspectives. Lastly, the general conclusions of the thesis are presented.

Synthesis and scientific contribution

Impact of land use on zooplankton at all three biological levels, i.e., active water column zooplankton communities, recruitment from their dormant egg banks and individual performance

Water column zooplankton communities studied during spring flooding indicated no clear effects of land use at the local scale. However, the regional sampling design revealed clear spatial effects of water quality on zooplankton. This was reflected in the observed effects of water quality variables such as DOC, turbidity, Chl *a*, and pH, which had a relatively strong influence on the zooplankton community. The water entering these sites was potentially influenced by land uses at larger spatial (regional) scales, i.e., land use in the neighbouring watershed influenced the streams that drained into these floodplains, thus affecting the water quality. These results align well with a methodological study that used eDNA for monitoring fish communities in the same study area, i.e., LSP floodplain, which also revealed a weaker influence of land use at the local scale, but the sectors or regions of the floodplain were strongly associated with the fish

community composition (Astorg et al., 2025). The results of Chapter I of the thesis are also supported by a study on water turbidity at the same sites, wherein land use at the local scale explained only ≤ 5% of the spatiotemporal variations in water turbidity in the floodplains, and the sediment load from the watersheds upstream that entered the floodplains contributed majorly to the turbidity of the study area (Clermont et al., 2023; Ziyad et al., 2025).

Following this, Chapter II investigated the recruitment of zooplankton through egg banks and showed that the distribution of resting stages did not vary across land use types at the local scale. These findings aligned well with what was observed for water column zooplankton communities in Chapter I. This suggests that since all sites were located at the same elevation, they received similar water during flooding, thus homogenising the water column communities and ultimately leading to similar distribution of eggs across different land use types (Agostinho et al., 2004). However, the analysis of zooplankton emergence from resting stages showed clear differences across land use types, with natural wetlands supporting higher emergence compared to the agriculture sites, while the forage croplands behaved intermediate. Interestingly, copepods emerged mainly from the natural sites, while ostracods and rotifers hatched from all sites, but with differences between the land use types. Although laboratory conditions were selected to maximize emergence, the cladocerans did not emerge as expected. These differences in the abundances of emerged zooplankton groups across land use types indicate that eggs deposited in the soils could either be affected by water quality during flooding, or once deposited, their viability is affected by the contaminants (e.g., pesticides) and physical treatments (such as use of machinery) of the soil, depending on the land use types. Pesticides such as glyphosate and fenoxycarb present in the soil have been reported to enter the resting eggs, thereby disrupting their hatching (Gutierrez et al., 2017; Portinho et al., 2018). High concentrations of herbicides such as glyphosate and its derivative aminomethylphosphonic acid (AMPA) and insecticides such as clothianidin and thiamethoxam have been reported in the LSP agricultural soils compared to other land use types, but with clothianidin and glyphosate being below detection limits in natural wetlands (Prashar et al., 2023). However, there were no significant differences in

concentrations of clothianidin, glyphosate and AMPA between agri-environmental and agri-conventional croppings (Prashar et al., 2023). Aligning with the results of this chapter, soil moisture content has been reported to be significantly higher in natural forests and meadows compared to agricultural cropping in the top 10 cm (Lieberman et al., 2026), which might have favoured more emergence. Besides this, significant differences in soil carbon pools across the same land use types have been reported, with natural wetlands (forest swamps, wet meadows) and forage (old cropping) having higher stable organic carbon compared to both agriculture croppings (agri-environmental and conventional) (Rabearison et al., 2025). Furthermore, natural forests harbored the highest vegetation and soil microbial biomass, followed by natural wet meadows and old forage croppings (Rabearison et al., 2025), which aligns with the emergence results of Chapter II. Other studies conducted within the same experimental framework, but focusing on organisms other than zooplankton, reported findings consistent with ours. For example, the soil microbial extracellular enzyme activity (EEA) mediated through carbon and nutrient cycling was found to decrease with increasing land use intensity (Harman-Denhoed et al., 2025). Natural wetlands had higher soil moisture content and also increased microbial populations, while perennial agriculture exhibited an intermediate position between natural wetland and conventional agriculture, suggesting it to be possibly a good compromise between intensive agricultural practices and natural habitats (Harman-Denhoed et al., 2025).

Having realised that the abundance of hatchlings varied across the land use types and that the water column zooplankton were affected by water quality, the question was then what causes these variations. In natural environments, aquatic organisms are exposed to multiple stressors, including both pollutants and the UVR that act together (and potentially interact) on these organisms (Beketov et al., 2011). Hence, Chapter III addresses the combined effects of land use leachates and natural UVR on a model zooplankter, *Daphnia magna.* Neonates of *D. magna* (< 24 h age) were exposed to a cocktail of contaminants obtained by preparing leachates from soils of different land use types in both outdoor as well as indoor experiments. In the case of the outdoor experiment, the potential interactive effects of land use types and natural UVR were tested (which also

included no UV treatment as well), while in the indoor experiment, only land use impact was tested. For UVR exposure, the *D. magna* neonates were exposed to natural UVR using three light treatments (no UV, only UV-A, and both UV-AB) in an outdoor experimental setup, while most studies in the literature used artificial UV lamps under laboratory conditions. The leachates prepared were expected to represent maximum contaminants/stressors that could leach from soils and influence survival as well as performance (swimming and physiological) of *D. magna*. The uniqueness of this study was, firstly, the use of empty organic tea bags for preparing soil leachates, then exposing *D. magna* to natural UV radiation (no artificial lamps), and novelty in the use of AnimatTA software (Chiara & Kim, 2023) for tracking *D. magna* swimming behavior (e.g., average speed). Most ecotoxicological studies in the literature have used artificial UVR lights in laboratory-controlled conditions. We expected interactive effects of natural UVR and land use types, as the land use types are expected to cause a disproportionate shift in the light entering the aquatic systems, and also could potentially cause photodegradation or photoactivation of the xenobiotics present and thus affect the organisms. We found no interactive effects of land use and natural UVR on *D. magna* (see below for full discussion on the effects of UVR). Surprisingly, both in the presence as well as in the absence of UVR, survival of *D. magna* was higher in the agri-conventional soils compared to the other soils, while there was no effect on either the reproduction output or swimming speed reported. This could be due to increased nutrients (nitrogen and phosphorus) from use of fertilizers (Khadra et al., 2018) that might cause an increase in cyanobacteria (although low quality), or nutritious green algae (but reported to be low in both cropland as well as natural forest compared to forage-old cropping) (Guillemette et al., 2023) serving as additional source of food besides the dry spirulina provided to *D. magna*. Despite the fact that the analysis of nitrogen and phosphorus in the leachates was not carried out, their variations in waters across land use gradient are presented by Guillemette et al. (2023) and have been reported to be in high concentration in agriculture and forage-recently sown cropping fields. Terrestrial-dissolved organic matter (t-DOM) and the t-DOM supported heterotrophic bacteria have been found to serve as a supplementary food source for *Daphnia,* thereby supporting their growth and reproduction rates even when algae become limiting, and on the contrary, when only algae were provided, it caused high

mortality in *Daphnia magna* (Mcmeans et al., 2015). Furthermore, humic and aromatic DOM from natural wetlands is more difficult to degrade and thus does not easily support bacterial growth (Guillemette et al., 2023). However, there are other studies which suggest that natural DOM (with humic component) at low concentrations could also help mitigate impacts of contaminants (e.g., heavy metals, organic pollutants) on *D. magna* by binding and reducing the bioavailability of the harmful substances, but could have an inverse effect at high concentrations (Meems et al., 2004). However, some other study showed that red maple-derived DOM had negative effects on *Daphnia* sp. wherein their survival and growth rates were significantly lower, irrespective of the presence or absence of algae, compared to those exposed to an invasive shrub-derived DOM (Wilkins et al., 2020). The other possible explanations for better survival in agricultural soils could be the leaching of dissolved calcium and carbonate ions from the soils serving as a buffer and hard water supplement. Agricultural liming ($CaCO_3$) routinely applied by farmers to increase pH and crop growth optimization (Goulding, 2016) can contribute to the availability of calcium, thus supporting the exoskeletal growth at every molt. However, as reported by Bolduc et al. (2026), calcium was apparently not limiting in LSP, just close to our sampling sites.

On the other hand, among the physiological endpoints (heart rate, thoracic limb movement, post-abdominal claw movement) and swimming behavior studied (average speed), the effect of land use was visible only on the heartbeats of *D. magna*, but only in the absence of natural UVR. Specifically, agri-environmental land use type lowered the heart rate, although this lower value was within the expected normal heartbeat range for *D. magna*, but lower than the other land uses. Partially supporting the results of the present study, another ecotoxicological experiment using soils from LSP floodplain found that agricultural soils affected zebrafish (*Danio rerio*), resulting in early hatching and increased mortality (Head et al., 2023). Similarly, exposure of yellow perch (*Perca flavescens*) larvae to such agricultural soils and natural UV radiation produced a relatively low toxicity effect with only a few genes associated with protein digestion and absorption being dysregulated by agricultural soils and some others by UVR (Head et al., 2023). In the case of swimming behavior, we presented here average speed only;

other parameters, such as exploration value (includes areas explored), meander (incorporates turning angle), also did not yield any significant results.

Effects of natural UV radiation on Daphnia magna

To test the effect of natural UVR, *D. magna* neonates were exposed to UV-A, UV-AB and unselective filters described in the third chapter in combination with leachates from three soil types (natural maple swamp, forage-old cropping, and agri-conventional cropping). Contrary to the well-established norm about the negative effects of UVR on zooplankton in the literature, our analysis did not identify any effects of UVR either independently or interactively with land use on *D. magna*. These results might sound puzzling and necessitate further studies. The extent of impact of UV on zooplankton is suggested to vary depending on the physiological state of the organism, its environment, and its ability to protect itself from UVR (Rautio & Tartarotti, 2010). Most experimental studies that present effects of UV radiation mainly used artificial UV lights (e.g., Hessen & Rukke, 2000; Ribeiro et al., 2011; Stábile et al., 2021), while in this experiment, *D. magna* were exposed to natural UV radiation (outdoor experiment). For example, Ribeiro et al. (2011) investigated the combined effects of the fungicide of carbendazim (a pure chemical formulation) and artificial UV light. They found that while UVR was the dominant stressor, the combined exposure to UVR and carbendazim produced an antagonistic effect on feeding inhibition but a synergistic effect on reproduction (Ribeiro et al., 2011). Furthermore, another study revealed that low calcium in the environment could lead to increased UV susceptibility in *D. magna* (Hessen & Rukke, 2000); however, this might not be the case there, as calcium has not been a limiting factor in areas closer to soil sampling sites in LSP (Bolduc et al., 2026). Furthermore, a study comparing the effects of constant and fluctuating UV-A in laboratory conditions on *D. magna* found no difference in survival across exposures, a similar reproductive output between individuals exposed to control (no UV) and constant UV, a lower number of changes in position under constant exposure, while reproduction success decreased when exposed to fluctuating UVR (Stábile et al., 2021). Here, the leached contaminants from the soils could have acted as a protective shield against UVR. Although DOC concentrations were found to vary across land use types in the LSP floodplain (Guillemette et al., 2023), their mere presence,

in addition to that contributed from the organic tea bags used (for preparing leachates) might have interfered with UVR providing protection to *Daphnia* against UVR. It is also possible that the nutrients in agricultural soils supported high bacterial growth, which might have had an impact on UVR penetration. Besides this, turbidity across land use might have a mitigating impact on UVR stress by increasing scattering and thus lowering its penetration. Lastly, in the experimental setup, the beakers used contained only 50 ml of exposure medium, which might have been too shallow for the light to be attenuated enough, owing to the presence of the contaminants in the leachates that caused scattering instead.

Impact of flood regime on zooplankton egg bank

The comparison of egg banks between low elevation sites that are frequently flooded and high elevation sites that are less frequently flooded allowed us to evaluate the effect of flood regime on the distribution of eggs across the land use gradient. Interestingly, at high elevation sites, which are less frequently flooded and for shorter durations only, the abundance of resting stages differed across the land use gradient. Higher elevation forage-old cropping had higher abundance of resting stages (rotifer and cladoceran eggs) compared to agricultural cropping. In contrast, there were no significant differences in their abundances across land use types at low elevations. This could be due to the homogenization effect as all sites sampled here were exposed to a similar degree of inundation (Agostinho et al., 2004). However, in the case of emergence from resting stages, the abundance of hatchlings varied across land use types at low elevation sites (i.e., those that are more frequently flooded) than at high elevation sites. Furthermore, when the effects of inundation duration on the emergence of zooplankton from resting egg banks were tested for 5 weeks, only ostracod emergence appeared to be significantly influenced by inundation period. Ostracod emergence was higher in the first two weeks, which later decreased. This could be attributed to the first flooding as an important hatching cue for the incubators of 1st two weeks, while for the incubators thereafter, there might have been either crowding, competition for food resources, or cannibalistic behavior (Rossi et al., 2012) that might have caused a drop in the emergence of ostracods, although inundation duration was extended. Savignac et al. (1982) have reported changes

in invertebrate biomass in accordance with flooding phases wherein insects and crustaceans contributed to ~ 90% of the biomass during the initial flooding, while from the 3rd week of flooding molluscs took over by contributing to 50-90% of their biomass. Flood regime (duration and frequency) and connectivity with the main river channel significantly influence invertebrate production and biodiversity on the floodplains (Wooden et al., 2026) and it plays an important role in subsidizing the littoral fish communities (Farly et al., 2021). Cabana et al. (2023) reported that the growth rate of yellow perch in LSP correlated well with longer flooding duration and was also associated with abundant zooplankton in the floodplain.

Implications for floodplain ecology and management

Overall, the work carried out in this thesis using a unique ecosystem-scale experiment helps us understand how changes in land use could shape zooplankton communities in a large river floodplain. Changes in water quality variables can influence active zooplankton, while the physical and chemical properties of soil (details can be found in PôleLSP, 2024) can affect the resting egg banks (quantity and viability) and the survival and physiological performance of zooplankton through their leachates (albeit weak effects). All these effects together can thereby alter their contribution in rebuilding zooplankton communities in the water column following drying. In floodplains, any alterations to land use such as construction, switch to agricultural land that includes tilling, mowing, usage of various pesticides, associated agricultural drainage, runoff containing pesticides, and fertilizers could alter biogeochemical properties of the sites and thus significantly degrade the habitats around it in the wetlands (Baker et al., 2016), thus making them unsuitable for aquatic and other organisms, including zooplankton. The contaminants, such as pesticides, can affect the viability of the resting eggs by causing mortality of the embryos within, and also by affecting the hatching process (Navis et al., 2013).

This thesis filled a large temporal gap in studies of zooplankton communities in the Lake Saint-Pierre floodplain (after Savignac et al., 1982). It demonstrates the significant role of changes in land use and flood regime on zooplankton egg bank and provides

insights into some of the mechanisms through which these zooplankton communities function. This work highlights the importance of incorporating land use at a larger spatial scale, as the water column zooplankton were mainly associated with regional rather than local land use, being affected by water quality influenced by neighbouring watersheds as well. These are important observations that could help us understand how aquatic communities respond to anthropogenic stressors at different spatial scales in the context of global change. Furthermore, this study helps identifying potential land use practices that could aid in the sustainable management of floodplains, thereby serving as an important tool in the protection of the natural habitat and conservation of biodiversity. The results of the present study on zooplankton emergence from resting egg banks indicated that forage-cropping exhibited an intermediate response between natural wetlands and agricultural croppings, thus suggesting a realistic compromise for implementation in the floodplains, which is also in agreement with Rabearison et al. (2025), who suggested conservation of forage-old cropping and less disturbed land use, as it supports higher stable organic carbon storage. However, Harman-Denhoed et al. (2025), studying microbial enzyme activity in the same floodplains, suggested using managed perennial forage (agri-environmental agriculture) practices to be a better compromise. Integrating community ecology, egg bank dynamics, and individual response to changes in environmental conditions in the study helped in understanding the zooplankton community dynamics in a large river floodplain. Such an approach can be very promising in understanding the ecological consequences of ongoing changes in land use in floodplains.

Limitations and future perspectives

This work involved comparing the impacts of different land use types on zooplankton dynamics in a large river floodplain, including agri-environmental cropping practices, some of which were implemented only recently. Hence, there were rarely any differences observed in impacts between agri-environmental and agri-conventional cropping in this study. This might be indicative of the need for monitoring over a longer period, which could potentially help to concretely decode the impact of agri-environmental practices on

zooplankton communities in the floodplain by allowing communities to adapt to the new conditions.

Sampling of water column zooplankton was carried out only once during each flooding year, but Savignac et al. (1982) suggested that the zooplankton community varies with flooding phases. In the present thesis, sampling during different phases was not carried out. It would therefore be interesting to extend sampling efforts to see the combined effects of flooding sampling and land use at the local scale by sampling during different phases of inundation (initial, peak and receding). Also, evaluating the impact of land use on different functional traits (e.g., size fraction, feeding types) and biomarkers such as lipids, fatty acid profiling, stable isotopes of zooplankton and DNA metabarcoding will add further value to the observational approach and contribute significantly in monitoring the effects of changes in land use and associated environmental variables at both local and larger spatial scale on zooplankton communities in floodplains.

For the emergence of zooplankton from resting stages, cladoceran hatching was not effective despite we targeted the best possible hatching conditions based on the literature. Previous studies suggested that temperature, photoperiod and incubation duration strongly influenced cladoceran hatching, but the optimal conditions varied between species and populations of a given species found in different geographical locations (Vandekerkhove et al., 2005). For example, for European and other temperate regions, incubation of soils at a lower temperature (~15 °C) has been found to be a optimal one to yield maximum hatching (Vandekerkhove et al., 2005). Thus, the low cladoceran hatching observed in the present study could either be due to effects on their viability or the lack of sufficient hatching cues required by some species. Hence, to disentangle the potential mechanisms behind this result, we suggest that a combination of hatching cues should be used. Firstly, isolation of resting stages from soils before incubation could be complemented in parallel to direct soil incubation, as some studies report better hatching from the isolated resting stages (Vandekerkhove et al., 2004b). Secondly, the resting eggs could be isolated and tested for possible chemical stressors (e.g., pesticides) to compare different land use types. Also, as the literature suggests that some resting eggs might take longer time for hatching (Pancella & Stross, 1963; Vandekerkhove et al., 2005),

longer incubation periods could also be considered. Preparing a catalogue of resting stages using microscopy or scanning electron microscopy from floodplains would be a great initiative for researchers working in floodplain ecology/freshwater ecosystems and can help improve our understanding of zooplankton biodiversity and community dynamics. This would also aid in understanding if non-native zooplankton species transported through ballast waters contribute to the egg bank and thus find their way to flourish in the region.

Concerning the ecotoxicological study, tea bags were used to provide a cocktail of contaminants in leachates, but it is possible that some contaminants might not have leached into the water, or the time used for extraction (24 h) might not have been sufficient to extract maximum contaminants from the soils. Also, the possibility of tea bag material adding any additional stress, as they were of organic origin, cannot be ignored. Hence, either switching to some other extraction method (e.g., centrifugation) or increasing the extraction time or collecting the fresh water during flooding might be a few other alternatives. However, most pesticides detected in the soils collected were well below the toxic levels established for aquatic life on chronic exposure in Quebec waters and therefore possibly did not reveal any effects on the physiological endpoints or swimming behavior. Finding no effect of UV radiation could be due to multiple reasons mentioned earlier; however, since the leachate contents were not fully analysed (including those contributed from the tea bag material, if any), it would be highly interesting to look at the overall chemistry of the leachates to investigate how this might mitigate the impacts of UVR. Future research plans could include studying more response variables of *D. magna* such as body size, survival of neonates produced, and features such as turning angle in the case of swimming behavior.

Lastly, experiments conducted in this thesis (such as emergence and ecotoxicology) were carried out in semi-natural experimental settings, which did yield significant results in understanding the zooplankton dynamics in the floodplain to a great extent. Nonetheless, it would be interesting, but moving one step further, it would be interesting (although complex) to run experiments using natural mesocosms to get clarity on the effects of the cocktail of multiple stressors that exist in natural environments.

Conclusions

Through a unique ecosystem-scale experiment, this thesis analyses the impact of changes in land use on zooplankton communities in a large river floodplain. Water column zooplankton communities studied during spring inundation indicated no clear effect of land use at the local scale but showed association with regions of the floodplain and were influenced by water quality, suggesting inclusion of land use at a larger spatial scale in studying floodplain zooplankton dynamics. Further, zooplankton resilience studied via egg bank revealed a significant impact of land use on their emergence from resting stages and flood regime on some groups. Natural wetlands favoured higher emergence from resting stages, while agricultural soils hampered their resilience, indicating impairment of soil properties affecting the viability of resting stages due to agricultural practices (e.g., use of pesticides, tillage process, lower organic matter content), while flooding duration influenced ostracods only. Lastly, using an ecotoxicological approach to study the interactive effects of soil leachates from different land use types and natural UVR on *Daphnia magna* revealed independent but mixed results. We found that the agri-conventional soils supported higher survival of *D. magna* over other soil types, while the heart rate of the organism was lower in agri-environmental soils compared to others. We do not have a clear explanation to it. While this thesis comes up with some clear conclusions about the impact of agriculture on the ecology of the floodplains, it also raises some key questions. Because water quality was apparently not at stake here, and zooplankton dispersal does not seem to be a limiting factor, we cannot explain the observed land use effects on hatching with the data at hand (Figure 1). Future studies should thus address the mechanisms behind our results on zooplankton hatching potential, thus helping in better understanding the ecology of these exploited temporary bodies of water. We hope that advances in this avenue will ultimately contribute to refining agricultural management policies compatible with the long-term preservation of diverse and healthy floodplain ecosystems.

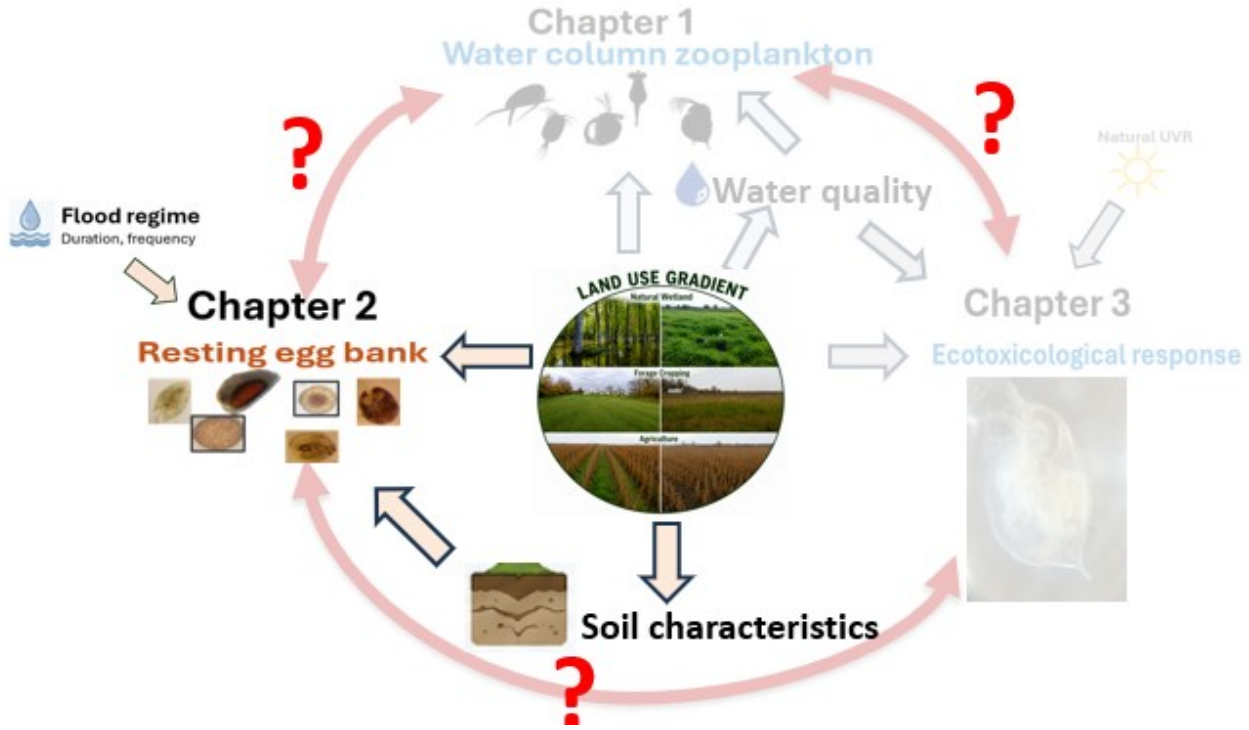


Figure 1. Conceptual framework illustrating links between response variables of the thesis chapters. We were able to highlight the land use impact only on hatching, while the mechanisms behind these results need further study.

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