Assessing macroinvertebrate diversity and temporal changes in groundwater- dependent pan wetland at Khakhea–Bray transboundary aquifer

By

Busisiwe Precious Gumede

Student no: 201728788

A research dissertation submitted in fulfilment of the requirements for the Master of Science degree, School of Biology and Environmental Sciences, University of Mpumalanga

Supervisor: Prof Tatenda Dalu, Dr Linton F Munyai

January 2026

ABSTRACT

Wetlands are productive ecosystems that provide important ecological, hydrological, andsocio–economic services. However, they are also one of the ecosystems that are most at risk around the world, especially in semi–arid areas. In southern Africa, pan wetlands primarily rely on groundwater and are becoming more susceptible to changes in land use, groundwater extraction, and climate variability. This research examined the impact of environmental gradients, elevation, and spatial positioning on physicochemical conditions and the macroinvertebrate community structure in pan wetlands located within the Khakhea–Bray Transboundary Aquifer (KBTA), a semi–arid aquifer jointly managed by South Africa and Botswana.

A total of 221 pan wetlands were sampled, which were divided into four elevation groups: <1100 m, 1100–1149 m, 1150–1199 m, and >1200 m. We used standard field and lab methods to measure the physicochemical properties of water, the concentrations of nutrients, and the types of macroinvertebrates. To find out how community composition changed across elevation classes, we used multivariate statistical tests such as permutational analysis of variance (PERMANOVA), analysis of similarities (ANOSIM), similarity percentages (SIMPER), and non–metric multidimensional scaling (nMDS). Correlation analyses and boosted regression tree (BRT) models were used to invesatigate the relationships between environmental variables, spatial gradients, and macroinvertebrate communities.

Spatial analyses demonstrated that longitude served as the most significant predictor of macroinvertebrate richness and diversity, accounting for the majority of the variation in taxa richness based on the boosted regression trees model. Diversity increased along a longitudinal gradient, suggesting that landscape–scale processes have a more significant impact on community assembly than local water chemistry or short–range elevation variations. Longitudinal gradients show differences in how well groundwater connects, how the basin is shaped, the weather, and the effects of all the land use on the aquifer system. These factors together determine how long water stays, the availabity of nutrients and how different habitats are, which has a big effect on biodiversity patterns. Local physicochemical variables only had a small effect on diversity patterns. This suggests that the water quality conditions were generally acceptable for the regional species pool.

The ecological patterns identified have significant implications for the conservation and management of groundwater–dependent pan wetlands within the Khakhea–Bray Transboundary Aquifer region. Mid–elevation pans are biodiversity hotspots because they have the most macroinvertebrates and the most diverse communities. They are also very sensitive to changes in hydroperiod, nutrient inputs, and groundwater abstraction. Low– and high–elevation pans also add to regional beta diversity by providing habitats for specialised taxa that can live in very extreme or very stable conditions. The Khakhea–Bray Transboundary Aquifer pan systems are a major water source for the people living in these areas. More studies evaluating ecosystem integrity, functionality, and service dynamics are necessary to comprehend the importance of these systems to landscape and human community dynamics.

Keywords: Groundwater–dependent wetlands, macroinvertebrate diversity, spatial connectivity, environmental variables, hydroperiod dynamics.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I would like to begin by giving heartfelt thanks to the Almighty God whose strength, grace, and guidance sustained me throughout the journey of completing this dissertation. I would also like to extend my gratitude to myself for remaining committed to this journey, even during the difficult moments when I faced emotional and personal challenges. This work was made possible through the support and contributions of many individuals.

My sincere appreciation goes to my supervisor, Prof Tatenda Dalu, and my co–supervisor, Dr Linton Munyai, for their unwavering support, constructive feedback, and invaluable mentorship during the course of my Master’s research. Their expertise and encouragement played a significant role in shaping this work.

I would also like to acknowledge and thank the NRF Thuthuka Grant (UID: TTK240409213108) awarded to Prof Tatenda Dalu, which greatly supported this research project.

I am also deeply grateful to the Aquatic Systems Research Group (ASRG) for their continuous support and for welcoming me into the group. Being part of this team has enriched both my academic and research experience.

A special thank you goes to my Mom, Dad and Siphesihle Sithole for encouragement, patience, and emotional support carried me through the most challenging stages of this journey. I am equally thankful to Sobahle Hlophe, Fannie Masina, Nombuso Themba, Ronald Mashamba, Stanford Masimini and Gugulethu Mlambo from the University of Mpumalanga for their assistance with data collection.

My appreciation further extends to Ndeka Ngwenyama and Jane Nhlane and for their dedication and help during laboratory work. Their efforts and teamwork contributed immensely to the success of this project.

DECLARATION

I, Busisiwe Precious Gumede, student number 201728788, hereby declare that the study of **“Assessing macroinvertebrates diversity and temporal changes in groundwater dependent pan wetland at khakhea–bray transboundary aquifer**” has not been submitted by anyone else or any other institution and is my own research work. I am fully aware of the University of Mpumalanga’s policy on plagiarism, and I have taken every precaution to comply with the regulations. This document has been submitted through a similarity detection software, and the report was reviewed by my supervisor(s). I declare there is no plagiarism in this dissertation.

Signature: BGumede Date: 30 January 2026

CHAPTER 1: GENERAL INTRODUCTION

Picture 1. *Phallocryptus spinosa* sampled from a salt wetland pan in the Khakhea–Bray transboundary aquifer region, South Africa. Photo by Busisiwe P Gumede.

General background

Overview and importance of wetlands

Wetlands are unique ecological systems characterised by the permanent or periodic presence of water, which has a substantial impact on their soils, vegetation, and biological processes (Yousaf, et al., 2021; Balwan et al., 2024). The National Water Act (NWA, 1998) of South Africa states that wetlands are fundamentally found where hydrology (i.e., saturation or inundation), low–oxygen soils, and hydrophytic plants converge (Marzini et al., 2021; Janardhan and Krishna., 2021). Wetlands provide important ecological purposes, but as socioeconomic development makes wetland problems more serious, wetland protection and restoration are crucial (Xu et al., 2019; Sharma and Naik, 2024). Between 35% and 50 % of wetlands in South Africa have already been lost or severely degraded, compared to an estimated 50 % of wetlands lost globally (Hu, et al, 2017; Adeeyo et al., 2022). Unsustainable social and economic factors, including mining, industry, agriculture, water abstraction, sewage waste disposal or outflow, and overgrazing, commonly impact wetlands in South Africa DWAF, 2004 (Nkosi et al., 2021; Wasserman and Dalu, 2022). This is problematic since wetlands such as pans and marshes provide important ecosystem services and are often groundwater dependent, supporting aquatic macroinvertebrates. Tehey are essencial for natural biota, the environment, and society (Gupta et al., 2019).

Wetlands are important ecologically because they are commonly recognised as hotspots for biodiversity, maintaining a remarkably diverse range of species in relation to their area (Figel, et al., 2019; Alikhani et al, 2021; Dalu and Wasserman, 2022). A diverse of emergent, and open water habitats creates different ecological niches that support a wide range of flora and fauna (Santoro et al., 2024). This biodiversity is further enhanced by seasonal variations in hydroperiod, which favour species adapted to alternating dry conditions (Catena et al., 2018; Hockaday et al., 2024). Therefore, wetlands can be considered to represent distinctive transitions between terrestrial and aquatic ecosystems (Ren and Wang, 2022; Sicking., 2025).

Wetlands perform invaluable hydrological functions and deliver a suite of ecosystem services fundamental to environmental stability and human well–being (Janse et al., 2019; Mohanty et al., 2024;). Flood attenuation and water storage are two of their most important roles (Russi et al., 2013; Quinn et al., 2024; Pedrinho et al., 2024). Wetlands work as natural sponges, absorbing floodwaters and excess rainfall, minimising erosion by slowing water flow, and reducing downstream flood peaks (Abdrabo et al., 2020; Balwan and Kour, 2021; Ahmed et al., 2024). They store 20–30 % of the world's soil carbon despite making up only 5–8 % of the land surface (Lorenz et al., 2018; Harenda et al, 2017). Because of the waterlogged conditions of wetlands, organic decomposition is slowed down, allowing carbon to build up in soils and sediments over long periods of time (Jia et al., 2020; Lázaro–Lobo and Ervin., 2021).

Wetlands decrease the need for costly engineered infrastructure, enhance the quality of drinking water, and lessen the risk of flooding (Masi et al., 2018; Stefanakis., 2019; Xu., 2020). According to Abata., (2025) wetlands provide cultural and provisioning services, help rural people by supplying clean water, food, building materials, grazing, and medicinal plants (Mandishona and Knight., 2022; Metwane., 2023; Bedo et al., 2025). They also sustain traditional customs, tourism, recreation, education, and cultural identity, all of which enhance socioeconomic resilience (Al–Amin et al 2022 Berondo, 2023; Ayassamy, 2025;). According to Sharma and Naik (2024) and Mao et al. (2025), freshwater wetlands high plant diversity plays a pivotal role in maintaining ecosystem function and stability. Diverse plant assemblages offer a variety of litter inputs and enable complementary resource usage such as variation in litter quality (e.g., carbon–to–nitrogen ratios and decomposition rates), differences in rooting depth and structure, contrasting nutrient uptake strategies **(**Chen et al., 2022; Zhang et al., 2023; Philippot, 2023).

Land–use change conversion for agriculture, forestry, aquaculture, and urban development continues to be the most direct drivers of wetland loss (Nguyen et al., 2017; Newton et al., 2018; Hoque et al., 2022). Reduced species richness and compromised ecosystem functioning result from drainage and infilling, which also decrease the water table, cut off hydrological connectivity, and simplify habitat structure (Chakraborty, 2021; Krejčová et al., 2021). Wetland degradation and carbon loss are primarily caused by land–use conversion, particularly agricultural expansion and infrastructural development according to a recent global synthesis of inland wetlands (Tan et al., 2022). This leads to feedback to the climate through carbon dioxide (CO_2) and methane (CH_4) emissions from exposed peat and organic soils (Holzknecht., 2021; Shah., 2025). Many studies (e.g., Kuenzer et al., 2019; Mao et al., 2020; Demarquet., 2023). Many aquatic systems are being modified for agricultural or urban development, altering their hydrological regimes and water chemistry (Lisetskii, and Buryak., 2023). Such changes may disrupt ecological balance, leading to reduced biodiversity and ecosystem resilience (Oliver et al., 2015; Vasiliev., 2022).

Studies have shown that wetlands particularly groundwater–dependent ecosystems such as spring–fed marshes, dune slacks, and fens rely on consistent groundwater inflows (e.g., Ghosh, 2016; Liley et al., 2021; Whiteman, 2023; Rawluk et al., 2020). Over–recharged pumping shifts plant communities to drought–tolerant species and makes peatlands more vulnerable to fire (Whitman et al., 2018). Multi–decadal satellite observations and field evaluations in Mediterranean systems provide compelling evidence that groundwater abstraction for irrigated crops (i.e., berries) has decreased the frequency and duration of pond flooding throughout the landscape (De Felipe et al., 2023; Green, 2024; Diodato et at., 2024). These findings support previous hydro–ecological reviews that found abstraction frequently degrades rivers and wetlands, albeit with site–specific sensitivity (Acreman, 2018; Palmer et al., 2019).

Climate change compounds hydrological stress through altered precipitation patterns, intensified droughts, and more frequent high–intensity rainfall events (Riedel, and Weber, 2020; Salimi and Scholz, 2022; Granata et al., 2025;). High temperatures and increased evapotranspiration rates can lead to prolonged water-level drawdowns, as shown by both process-based and empirical studies. In addition, changes in storm patterns may increase the risk of both drought and flooding within the same basin (Salimi et al., 2021; Pizzorni et al., 2024).With significant region variability and uncertainty linked to local hydrology and terrain, continental–scale modelling of inland wetlands predicts significant declines in wetland extent in the upcoming decades under mid–to–high warming scenarios (Settele et al., 2014; Xu et al., 2024;).

A diverse range of freshwater and marine environments, such as rivers, lakes, streams, ponds, springs, wetlands, lagoons, and other transitional systems, are home to aquatic macroinvertebrates, a broad class of relatively large, spineless organisms that are usually larger than 400–700 μm (Harper and Pacini., 2019; Gopal., 2020; Bonacina et al., 2023;). As bioindicators of environmental change and general water quality, macroinveretbrates are crucial to the functioning of ecosystems (Sumudumali, and Jayawardana., 2021). The health and stability of the ecosystems they live in are frequently reflected in their diversity, richness, and existence (Dalu et al., 2017;

Tecon and Or, 2017; Hauer and Resh, 2017). Aquatic invertebrates regulate primary production, decomposition, water quality, thermal stratification, and nutrient cycling in aquatic ecosystems (Dalu et al., 2017; Brown et al., 2019; Allan et al., 2021; Bonacina et al., 2023;). They are essential components of aquatic food webs since they are well recognised as a vital food source for fish, amphibians, and other invertebrates (Ruess and Müller–Navarra, 2019; Ozkan, 2024).

Dalu and Chauke (2020) highlighted that the adundance and diversity of macroiverts may be influence by macrophytes, macrophytes play a crucial role in enhancing both the abundance and diversity of macroinvertebrates within wetlands. By providing protection from predators, establishing microhabitats, and giving organic matter that can be consumed, these aquatic plants add to the habitat complexity (Cheng et al., 2017; Celewicz–Gołdyn et al., 2017; Soukup et al., 2022;). A diversity of macroinvertebrate species can flourish in an environment that is more stable and resource–rich due to their presence, (Htay et al., 2023; Shokri et al., 2024.While tolerant species, such as Chironomidae and oligochaete worms, frequently grow in abundance under deteriorated conditions, sensitive taxa, such as several Ephemeroptera, Plecoptera, and Trichoptera groups in wetlands, or some freshwater beetles and odonate nymphs in lentic wetlands, drop (Enabulele and Olomukoro., 2024; Morse., 2017).

The pan wetlands, which occur as numerous small and isolated water bodies scattered across the landscape, form naturally fragmented habitat networks. These systems provide a strong example of the spatial structure described in metacommunity theory (Bertassello, 2020; Yang et al., 2021; Jeong & Kim, 2022). Their level of connectedness is shaped by factors such as geographical barriers, distance between pans, and the presence of corridors or stepping–stone habitats, all of which influence opportunities for dispersal (Quijada–Alarcón, 2023). As species disperse, they move through a complex matrix of potential colonisation pathways created by this variable connectivity (Van Moorter, 2021). The extent of connectivity often determines whether populations in individual pans persist through demographic rescue via immigration, or whether they face a higher risk of local extinction due to isolation (Benson et al., 2016; Khan, 2021). Within this context, a metacommunity is understood as a set of local communities linked by the dispersal of multiple interacting species across a patchy landscape, where community composition is shaped by both local processes (e.g., species interactions and abiotic conditions) and regional processes (e.g., dispersal and connectivity) (Hayes and Anderson, 2018; Tonkin et al., 2018; Bergmann and Leveau, 2022; Gawecka and Bascompte, 2023; Musher, 2025). Species perseverance, and local richness arise from the interaction between local habitat conditions and regional dispersal among patches that are connected either hydrologically or overland (Heino et al., 2017; Gálvez et al., 2020), The metacommunity framework is particularly well suited to wetland systems composed of discrete, spatially separated water bodies such as pans, vernal pools, and temporary depressional wetlands (Patrick, 2021).

Macroinvertebrate communities in pan wetlands provide excellent model systems for testing metacommunity theory due to their diverse life histories, varying dispersal capabilities, and sensitivity to environmental gradients (Epele et al., 2022; Guan et al., 2024; Sicking., 2025). From slightly stable taxa for example snail mollusks to highly mobile aerial dispersers chironomid midges, these communities usually comprise representatives of several taxonomic groupings with unique ecological strategies (Frost. et al., 2024; Dole., 2024). Recent studies (e.g., Leboucher and Tison., 2024; Passy et al 2024; Fontaneto and Tao., 2025) have shown that several examples frequently function concurrently within a single metacommunity such as Species Sorting, Mass Effects, Patch Dynamics and Dispersal Limitation with the relative significance of each example varied according to the taxonomic level, environmental setting, and spatial scale (Olmo et al., 2024; Guerrero et al., 2025). Metacommunity theory represents a significant advancement in our understanding of how ecological communities are structured and maintained across fragmented landscapes (Tao et al., 2024) This show how ecological communities are organised and sustained across fragmented landscapes (Galiana et al., 2018; Pickerill et al., 2024). Metacommunity processes is crucial for creating conservation strategies that preserve the integrity of local communities and regional biodiversity patterns as these systems deal with growing anthropogenic stresses (Chase et al., 2020).

The structure of pan wetland communities is significantly influenced by species dispersal constraints (Bertassello et al., 2020). According to Liu (2021) study they used wetland metacommunity aquatic macroinvertebrates as model organisms, their research, species with poor dispersion abilities were frequently confined to a small number of closely related pans, which led to noticeable spatial clustering and an increased risk of local isolation (Coccia et al., 2021;

Walentowitz et al., 2023). Species that were better at dispersing were able to maintain wider regional distributions and colonize several wetlands (Deane et al., 2017). These species use a variety of dispersal mechanisms, such as passive movement by wind, water currents, animal vectors, and active flight by adult insects for example light–bodied larvae and eggs can be dispersed passively by wind; propagules and drifting individuals are carried between pans by surface and subsurface water flows; resting stages, like eggs or cysts, can be moved externally on the feet and feathers of water birds or internally after being consumed by animals; and many taxa with winged adult stages disperse actively through directed flight (Coughlan et al., 2017; Littlefield et al., 2019; Pires., 2021; Mason et al., 2022). Mobile species often perceive the landscape as connected, while species with limited distribution abilities experience greater isolation between pans due to differences in dispersal capacity (Vallespir Lower and Ursell, 2019; Diniz, 2020). Additionally, environmental gradients arising from variations in habitat among pans such as water chemistry, depth, vegetation structure, hydroperiod, and disturbance regimescan influence species sorting processes (Zhao et al., 2024; Ndadzungira et al., 2023).

The diversity and quantity of aquatic organisms within the systems can be influenced by anthropogenic activities as mining, urbanisation, and agriculture within and among temporary pans (Rezende et al., 2019; Ogidi, and Akpan., 2022; Bănăduc et al., 2024;). By altering the water and sediment quality, increasing pollution intake, and organising diversity patterns across different systems, such perturbation results in temporary pan degradation and loss (Khudhair et al., 2019; Chakraborty., 2021;). According to Lomnicky et al. (2019), a disturbance is any reasonably discrete occurrence in time or space that removes and creates resources or space that can be utilised by the same or different species. Macroinvertebrates react to disturbances by altering their biomass, abundances, and community structure (Phiri et al., 2012; Park et al., 2018; Datry et al., 2023;). Loss of interstitial space and shelter, increased water turbidity, which hinders photosynthesis and reduces food availability (Jacobsen and Engström–Öst., 2018). Oxygen depletion and substratum type change, physical removal of organisms through scouring, and loss of hold ability due to fine sediment coating on the substrate surface are potential causes of macroinvertebrate disturbance (McKenzie et al., 2020; Chakraborty et al., 2023). Pans with little to no human disturbance exhibit high macroinvertebrate diversity (; Burger et al.,2019; Jiang et al., 2021).

Environmental influences have a significant impact on the distribution and abundance of biological communities in aquatic ecosystems, which are dynamic and complex systems (Datry al., 2016). They are crucial for the cycling of nutrients, decomposition of organic matter, and transfer of energy to high trophic levels for example fish and amphibians (Chakraborty, 2021). Macroinvertebrates provide an accurate measure of ecosystem stability because of their extended life cycles and sedentary lifestyles, which allow them to internalise the effects of environmental conditions over time (Baker et al., 2014; Carter et al., 2017; Hamid et al., 2024;). Both natural environmental variation and man–made stresses for example pollution, eutrophication, and hydrological modification are reflected in the organisation of macroinvertebrate communities (Pilotto et al., 2015; Hamid et al., 2020; Arenas–Sánchez, et al., 2021). Even small changes in salinity can significantly alter species composition, as only certain taxa are tolerant to brackish or saline conditions (Mrozińska et al., 2021; Sarmanov, et al., 2024). Freshwater taxa such as mayflies (Ephemeroptera) and caddisflies (Trichoptera) are generally less tolerant of high salinity levels compared to dipterans for example chironomids (Perera, et al 2024). Increased salinity can also reduce macroinvertebrate richness and abundance by excluding sensitive taxa (Paradise., 2024).

Pond size influences habitat complexity, resource diversity, and the presence of predators (Arenas–Sánchez., 2021; Aranbarri, et al., 2025). Larger ponds generally support more diverse macroinvertebrate communities due to increased habitat heterogeneity, more stable environmental conditions, and greater connectivity with other water bodies (Hill et al., 2018; Cunillera–Montcusi et al., 2020; Castro, et al., 2025). In contrast, small ponds often experience greater fluctuations in temperature, dissolved oxygen, and nutrient concentrations, which can limit species survival and reproduction (Boyd et al., 2017; Meerhoff, et al., 2022). Water depth plays a significant role in regulating environmental gradients within a pond, including light penetration, temperature stratification, and oxygen distribution (Goncharov, et al., 2024). Shallow ponds often have high primary productivity due to greater light availability, which can enhance food resources for macroinvertebrates (Benvenuto et al., 2015; Rousi et al., 2018; Meyerhof et al., 2022; Burton., 2024). Changes of environmental variables influence macroinvertebrate assemblages is vital for biodiversity conservation, particularly in regions facing water scarcity, habitat fragmentation, or pollution (Thornhill, et al., 2017; Reid et al., 2019; Sowa, 2020).

Problem statement

Wetland ecosystems are essential for preserving ecological balance, controlling hydrological cycles, and preserving biodiversity (Jisha, and Puthur., 2021). However, human activity, climate change, and unsustainable water resource management are posing a growing danger to these ecosystems (Dixit et al., 2022; Edo et al., 2024). The Khakhea–Bray transboundary aquifer landscape is characterised by numerous shallow pans that provide critical but poorly understood aquatic habitats in an otherwise arid region. The Khakhea–Bray transboundary aquifer basin, shared by multiple states, faces increasing pressure due to its complex hydrological dynamics and growing human demands. This makes it particularly susceptible to overexploitation, resource conflicts, and environmental degradation, threatening both water security and the ecosystems dependent on it (Ngobe., 2022; Mishra et al., 2021).

(Mereta et al., 2012; Carter et al., 2017). There is limited understanding of how spatial and hydrological gradient's structure macroinvertebrate communities in groundwater-dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer (Masina et al., 2023). Evaluating the effects of natural and man–made changes on wetland biodiversity is difficult due to a lack of thorough baseline data and ongoing monitoring (Rebelo et al., 2018; Munging., 2023;). Effective conservation and management of these pan wetlands is further complicated by a lack of knowledge about how hydrological variability, water dependence, and spatial heterogeneity shape macroinvertebrate metacommunity patterns (Dube et al., 2019; Munyai et al., 2023). The absence of integrated ecological assessments across the broader Khakhea–Bray system inhibits the ability of policymakers to recognise early signs of ecosystem degradation (Dhyani et al., 2022; Tsopoe et al., 2025). Developing scientific information on the ecological variables impacting macroinvertebrate communities is vital for informing sustainable groundwater use, enhancing long–term monitoring systems, and promoting evidence–based transboundary wetland management (Arthington et al., 2023; Izah et al., 2024; Kant, and Wrat., 2025;). By assessing macroinvertebrate diversity and recording temporal changes in the wetland ecosystems of the Khakhea–Bray transboundary aquifer basin, this study aims to close this gap (Rampheri et al., 2023). The focus of this study fossuced on assessing macroinvertebrate diversity, metacommunity dynamics, and temporal changes in groundwater–dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer. Pans were selected to represent a range of environmental and ecological conditions relevant to the assessment of macroinvertebrate diversity, metacommunity dynamics, and temporal changes.

Aim

This study aims to quantify how biodiversity and community structure vary across the landscape, identify key environmental controls, and assess the degree to which spatial and environmental factors shape ecological patterns.

Objectives

1. Characterise, assess spatial and transboundary patterns of macroinvertebrate diversity and community composition across the pans of the Khakhea–Bray aquifer landscape.
2. Evaluate the influence of local environmental conditions on macroinvertebrate richness and assemblage structure.
1. 3 Evaluate the influence of elevation–driven environmental filters on macroinvertebrate assemblage patterns.

Hypotheses

1. Macroinvertebrate richness and community composition vary significantly among pans and are strongly influenced by local environmental conditions such as salinity and hydroperiod. Therefore, pans located on different sides of the Khakhea–Bray transboundary boundary support significantly different macroinvertebrate assemblages due to differing environmental conditions, land–use patterns, or hydrological influences.
2. Macroinvertebrate community similarity declines with increasing geographic distance between pans, indicating spatial autocorrelation and limited connectivity.
3. Macroinvertebrate taxonomic and functional diversity will decrease with increasing elevation, following a pattern of reduced species richness in colder, more variable high–elevation habitats. Therefore, harsh environmental conditions and reduced habitat

heterogeneity at high elevations are expected to limit niche availability and favour fewer, more specialised taxa.

4. Community composition will differ significantly among elevation bands, with high–elevation assemblages being distinct from low– and mid–elevation communities. Environmental filtering is expected to select for cold–adapted, resilient taxa at higher elevations, while lower elevations support more diverse and temperature–sensitive species.

Thesis structure

The thesis is comprised of one data chapter encompassed by introduction and synthesis chapters, respectively. The specifics of each chapter are as follows:

Chapter One: Introduces and outlines the study. It also includes background information, problem statement study's aims and objectives, hypotheses, and research structure.

Chapter Two: The literature review describes the theoretical literature related to the topic and looks at the empirical literature focusing on recent findings on macroinvertebrates community structure in freshwater ecosystem. he theoretical foundations of macroinvertebrate ecology are first described, including concepts such community organization, functional groups, ecological niches, and bioindicator principles. The chapter looks at regional and worldwide trends in macroinvertebrate diversity, emphasizing the ecological processes and environmental gradients that influence species abundance and composition.

Chapter Three: This chapter outlines the study’s methodological framework, including the description of the study area, sampling design, data collection procedures, and analytical approaches. Data collection included GPS–based measurement of surface area, manual depth assessments, land–use observations, and water quality measurements. Water samples were collected for laboratory analysis of key nutrients, while macroinvertebrates were sampled using a standard SASS net, preserved, and identified to genus level. Statistical analyses included descriptive statistics, PERMANOVA results that showed that the structure of the assemblage was very different between elevation categories. SIMPER analysis showed that this was mostly due to a small number of dominant taxa, not a complete turnover of species.

Chapter Four: This chapter outlines the study's the results and show revealed clear spatial and temporal variation in macroinvertebrate diversity across the groundwater–dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer. Species richness and abundance differed significantly between pans and temperature levels in each pans reflecting changes in hydroperiod, groundwater influence, and temperature conditions. Taxa were identified and classified according to functional feeding groups and tolerance levels, allowing patterns in community composition to be linked to underlying environmental drivers. Temporal shifts in metacommunity structure showed that fluctuations in groundwater availability and environmental variables played an important role in shaping assemblage dynamics each each study site. Variation among sites further indicated that connectivity, pan morphology, and surrounding land use habitat availability.

Chapter five: This chapter outlines the study's discussion about the links differences in species richness and abundance across pans and sampling periods to shifts in hydroperiod, groundwater influence, and temperature, highlighting how these drivers shape community structure. Patterns in functional feeding groups and tolerance traits are examined to explain how environmental filtering, dispersal limitations, and resource availability influence assemblage composition. The chapter further explores how temporal changes in metacommunity structure correspond to fluctuations in groundwater availability and salinity, and how site–level factors such as connectivity, pan morphology, and surrounding land use and habitat availability. Finally, the implications of these findings are considered into ecosystem resilience, groundwater dependency, and the conservation management of pan wetland biodiversity.

Chapter Six: The main focus was the summary, conclusions and recommendations. This chapter provided a synthesis of all the chapters in the study. It also provides recommendations, action plans and suggestions for future research.

CHAPTER 2: LITERATURE REVIEW

Picture 2. One of the biggest pan wetland at Morokweng (Khakhea–Bray Transboundary Aquifer region) in the North West Province of South Africa. Photo by Tatenda Dalu.

Importance and complexity of pan wetland systems

The importance and complexity of wetland pan systems are widely recognised. These ecosystems are ecologically distinctive and highly productive, enabling them to support rich and diverse biological communities (Kingsford et al., 2016; Masina et al., 2023). Wetland pan systems as unique, highly productive ecosystems with intricate ecological dynamics that sustain disproportionately high levels of biodiversity relative to their spatial extent (Wang et al., 2020). As interfaces between terrestrial and aquatic environments, wetlands in general including transient and endorheic pan systems create a mosaic of microhabitats with different water depths, hydroperiods, and water quality conditions (Schofield et al., 2018; Eckardt et al., 2022). Wetlands make a significant contribution to biodiversity worldwide; freshwater wetlands alone represent an important percentage of known species and serve as habitat for numerous endemic, rare, and migratory taxa (such as plants, vertebrates, and invertebrates) despite making up a small portion of the planet's land area (Keddy., 2009; Butt et al., 2021; Coleman et al., 2023; Richardson., 2023). Pan wetlands are biodiversity hotspots, with ephemeral pans supporting diverse macroinvertebrates and crustaceans that exploit short wet phases before entering dormancy or completing rapid life cycles (Hlophe–Ginindza et al., 2021; Leshaba., 2023; Munyai et al., 2023). When flooded, they also serve as vital breeding and foraging grounds for terrestrial fauna and waterbirds (Waliczky et al., 2019; Pan et al., 2025). Pans vary substantially according on their origin, geographic location, water composition and patterns, dominating species, and soil and sediment characteristics (Bassie et al., 2014; Twilley et al., 2019). Over centuries, wetland sediments have the capacity to trap and store significant amounts of carbon (Fennessy et al., 2018; Nag et al., 2023). This is especially crucial because wetlands stop the release of methane (CH_4) and carbon dioxide (CO_2) into the atmosphere (Gedney et al., 2019). Despite making up a very small portion of the freshwater surface of the Earth, wetlands play a huge role in climate regulation and carbon sequestration, preserving water quality, and sustaining biodiversity, hence their preservation and restoration are essential for reducing the effects of climate change (Nayak and Bhushan., 2022; Moomaw et al., 2018; Hesslerová et al., 2019).

Ecological significance of wetlands

Wetland services: hydrological and regulating functions

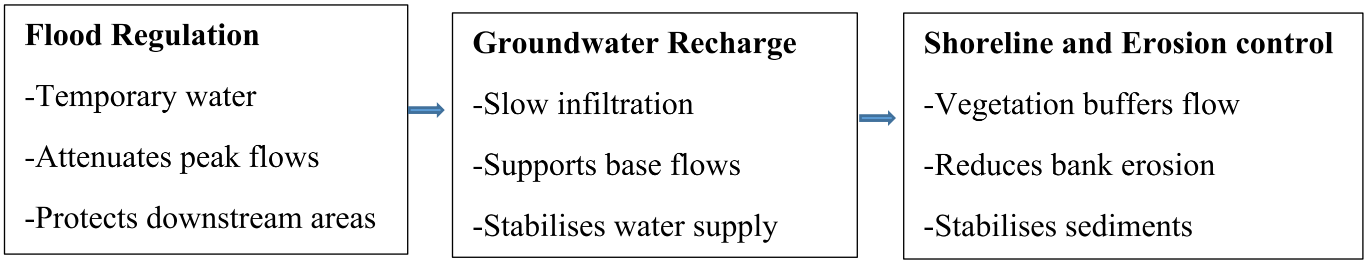

Figure 2.1: Hydrological functions of wetlands showing their role in flood regulation, groundwater recharge, and shoreline and erosion control. Adapted from general wetland ecosystem service frameworks (Sharma and Naik., 2024).

According to Mitsch and Gosselink (2015), wetlands serve as crucial components of the planet's biologically significant habitats and natural systems (Sharma and Naik, 2024). Their importance has increased as their role in environmental sustainability is better understood (Wu et al., 2023; Siraj et al., 2022). Wetlands act as natural filters that improve the quality of the water by absorbing pollutants, sediments, and nutrients before they enter larger bodies of water for exmaple rivers, lakes, and oceans (Boyd et al., 2019; Majumdar et al., 2020; Ferreira et al., 2023;). They help regulate water flow, reducing the impact of droughts and floods by acting as natural sponges that absorb excess water during times of influential rainfall and release it gradually during dry spells (Nguyen et al., 2019; Wu et al., 2023).

Wetlands and biodiversity

Several studies (Kolka et al., 2021; Poulter et al., 2021; Raturi et al., 2024) indicate that although wetlands make up only 6–8% of the Earth's freshwater surface area, they play a disproportionately important role in the global carbon cycle. (Bernal and Mitsch, 2012; Limpert et al., 2021). Although wetlands occupy only a small proportion of the global freshwater surface area, several studies demonstrate that they make a disproportionately large contribution to both ecological functioning and biodiversity conservation (Cronan et al., 2016; Were et al., 2019; Cantonati et al., 2020; Gallagher., 2022). Temporary wetland systems are increasingly recognized as biodiversity hotspots in addition to their known role in carbon storage, where wetland sediments accumulate Diverse microhabitats created by varying hydroperiods and environmental gradients support aquatic plants, macroinvertebrates, amphibians, zooplankton, and water birds adapted to cycles of inundation and drying. (Kingsford et al., 2016; Masina et al., 2023). Long–term species persistence in changeable landscapes and metacommunity dynamics depend on processes like settlement, dispersion, dormancy, and quick life–cycle completion, all of which are facilitated by these systems (Springthorpe and Penfield., 2015; Almeida–Gomes et al., 2020; Rey et al., 2021). As a result, pan wetlands are essential for preserving regional biodiversity, ecological connectedness, and ecosystem resilience to helping to regulate the global climate through carbon storage (Imran., 2025)

Role of macroinvertebrates in pan wetland ecosystem

According to Chakravarty and Gupta (2021), macroinvertebrates are important markers of aquatic ecosystem healthexamining the composition of macroinvertebrate communities. In relation to environmental and human effects, macroivertebrates are essential for effective biomonitoring and conservation efforts in temporary wetlands (De Mello et al., 2023; Mohebbi et al., 2022)). Environmentalvariables such as substrate type, dissolved oxygen, pH, and water temperature influence the diversity and composition of macroinvertebrate communities. While some species, such as leeches and certain fly larvae, can tolerate polluted environments, others including mayflies, caddisflies, and stoneflies prefer clear, well-oxygenated waters (Cabrera et al., 2021; Varadinova et al., 2022; Rai et al., 2019). (Cabrera et al., 2021; Varadinova et al., 2022; Rai et al., 2019).

Environmental drivers of macroinvertebrate communities

Macroinvertebrate assemblages are shaped not only by water–quality variables such as temperature, conductivity, pH, salinity and dissolved oxygen (Tampo et al., 2021; Dalu et al., 2022; Brysiewicz et al., 2022). Macroinvertebrates are also influenced by biological elements such as predation pressure, competition, food availability, primary productivity, and the presence of aquatic vegetation and fish communities, as well as by physical habitat features such as hydroperiod, substrate type, water depth, vegetation structure, flow conditions, and habitat heterogeneity (Latli et al., 2019; Pille et al., 2023; Dubour et al., 2025; Gobel et al., 2025). While pollution–tolerant species such as Chironomidae and Oligochaeta dominate in degraded environments, sensitive taxa, particularly Ephemeroptera, Plecoptera, and Trichoptera (EPT), are linked to clean, oxygen–rich environments (Ratterman., 2016; Joash., 2017). Reduced oxygen levels, eutrophication, and a shift toward tolerant species are all facilitated by increased nutrient loads from agricultural runoff (O'Hare et al., 2018; Wurtsbaugh et al., 2019; Omoregie et al., 2025). Particularly in transient or shallow water bodies, temperature variations also affect metabolic and reproductive rates, changing distribution patterns (Bonacina et al., 2023). According to Dong (2021), the main factors influencing the organisation of macroinvertebrate communities are hydrological regimes, which include flow velocity, water level variations, hydroperiod, and connectedness. Food availability, sediment transport, and habitat stability are all influenced by flow variability (Worrall et al., 2014; Rolls et al., 2018). Drying and flooding cycles in transient wetlands and sporadic streams lead to repeated migration and extinction events, which drive distinctive adaptive features in macroinvertebrates, such as rapid development cycles or desiccation–resistant offspring (Stracha., 2016; Batzer and Boix., 2016; Loskotová., 2022). The promoting dispersal and recolonisation, hydrological connection support regional biodiversity through metacommunity dynamics (Sarremejane et al., 2021).

Macroinvertebrates are important biological groupings that live in freshwater, brackish and saline habitats and are essential to the preservation of ecosystem structure and function (Nieto, et al., 2017; Chakraborty et al., 2022). Insects, mollusks, crustaceans, annelids, are examples of macroinvertebrates, which are effective bioindicators of ecosystem health and water quality (López–López et al., 2017; Adesakin et al., 2023). Understanding the relationship between environmental factors and the composition of macroinvertebrate communities offers significant understanding of ecosystem processes, human impacts, and habitat quality (Juvigny–Khenafou et al., 2021; Hamid et al 2021;). Researchers can identify both natural and man–made changes in aquatic habitats because macroinvertebrates react strongly to changes in water chemistry, hydrological patterns, and habitat structure (Cantonati et al., 2017; Denis., 2019; Brooks et al., 2021).

Salinity, pond size, and water depth are some of the most important environmental factors affecting macroinvertebrate diversity and distribution in aquatic systems such ponds, wetland, and small lakes (Oertli and Parris, 2019; Labat, et al., 2024). Changes in salinity have an impact on species tolerance levels and osmotic control, while pond depth and size have an impact on thermal stratification, predator–prey relationships, and microhabitat availability (Huber et al., 2023; Dildar et al., 2025). These elements control the distribution of resources, oxygen availability, and habitat heterogeneity, which in turn control the biodiversity of these systems (Gebrekiros 2016; Moniruzzaman et al., 2021). As main consumers and decomposers, macroinvertebrates serve as the cornerstone of many aquatic food webs (Ozkan, 2024).

a). ***Habitat structure and substrate composition***

Diverse macroinvertebrate assemblages are supported by the variability of aquatic habitat, which is supplied by plants, leaf litter, stones, sand, and organic sediments (Ntloko et al., 2021; Akhtar et al., 2023; Leshaba et al., 2025). This heterogeneity provides refugia, feeding substrates, and breeding sites (Lo et al., 2024; Harrison et al., 2025; Mervyn., 2025). Species composition is influenced by the kind of substrate; for example, fine silt tends to build in habitats with slow flow or pollution, whereas coarse substrates sustain more diversified invertebrate populations (Tadesse and Lakew, 2025; Elvira et al., 2021). According to Jones (2021), the type of substrate significantly influences species composition in aquatic ecosystems. Coarse substrates such as gravel, pebbles, and cobbles generally support a greater diversity of macroinvertebrates, whereas fine sediments like silt are more likely to accumulate in areas with slow water flow or in environments affected by pollution.By regulating oxygen availability, habitat stability, and the kinds of feeding and locomotion techniques that organisms can employ (Effert–Fanta et al., 2019; Dingman., 2021; Hunt., 2022). These substrate variations change community structure, because fine particles diminish interstitial space and restrict water circulation within the substrate, they frequently create low–oxygen, unstable conditions that promote opportunistic, tolerant organisms such as deposit feeders (Natsumeda and Iguchi., 2019; Miao et al., 2024). This, communities in silt–dominated environments are usually less diversified and primarily made up of species that can withstand stress and have quick life cycles (Humphries and McCarthy, 2022). Several studies (Mathers et al., 2019; Wahl, 2020; Bustos et al., 2022) found that a greater variety of functional groups can find microhabitats on course and diverse surfaces because they offer more surface area, cracks, and stable attachment sites. Because oxygen penetration and habitat stability are better on these substrates, clingers, scrapers, filter feeders, and species that are vulnerable to disturbance and pollution are supported (Mattone, 2016; Drover et al., 2020). In addition to providing refuge from high flows and predators, interstitial spaces encourage increased species cohabitation and functional redundancy (Datry et al., 2017). The decomposition of leaf litter and the flow of energy through food webs are two ecosystem processes that are improved by coarse substrates because they are linked to higher richness, trait variety, and more balanced community composition (Richardson and Hanna., 2021; Potapov et al., 2022).

b). Biological and landscape–level influences

The distribution and diversity of macroinvertebrates in aquatic environments are also significantly influenced by competition and predation (Nieoczym et al., 2023). Predators including fish, amphibians, and big invertebrates can drastically diminish or reorganise community assemblages through direct ingestion or behavioural changes, frequently favouring species with predator–avoidance features (Buatois et al., 2022; Root., 2022; Gomo and Ngobe., 2024). Community structure is further influenced by competitive interactions, especially when species compete for scarce food supplies or habitat. Specialist feeders are more susceptible to environmental stress and resource scarcity because they are frequently more sensitive to competitive exclusion than generalists (Sponsler et al., 2023; Weideli et al., 2023; Bailey–Steinitz et al., 2024). Macroinvertebrate metacommunities are shaped by the combined effects of competition and predation, which have an impact on both local dynamics and regional biodiversity patterns (Burdon et al., 2020). According to Gebrekiros (2016), community structure is further influenced by competitive interactions, especially when species share habitat or food supplies. In situations of resource scarcity or environmental stress, specialized feeders and habitat specialists are frequently more susceptible to competitive exclusion due to exploitative and interference competition, which can limit the distribution of functionally similar taxa (Sherry et al., 2020; Leimberger et al., 2022; Bailey–Steinitz et al., 2024; Weideli et al., 2023). By changing the relative dominance of shredders, grazers, filter feeders, and detritivores, these dynamics impact not only species richness but also the functional makeup of communities, which in turn affects ecosystem processes including nutrient cycling and leaf–litter breakdown (Hines and Eisenhauer., 2021; Cereghetti., 2024).

Predation and competition outcomes are significantly affected by landscape–level processes that go beyond local interactions that affect the diversity of macroinvertebrates (Sanders and Frago., 2024). The dispersal, environmental filtration, and biotic interactions are balanced in macroinvertebrate metacommunities, the composition of local communities reflects both the strength of interactions once existent and the ability of species to colonize habitats (Burdon et al., 2020 Thuile Bistarelli., 2025; Villsen et al., 2025). Colonization opportunities following disturbance are influenced by hydrological connection, patch size, and habitat isolation. In connected systems, these factors facilitate rescue effects, whereas in isolated wetlands and pans, they promote priority effects and assembly history reliance (Buono.,2024; Thakur et al., 2025). Predator presence, resource availability, and habitat structure are further altered by land–use change, riparian degradation, and catchment–scale pollution, which can lead to changes in trait composition and patterns of regional biodiversity (Miserendino et al., 2022; Oester, R., 2024; Rumschlag et al., 2025).

c). Influence of salinity on macroinvertebrate diversity and distribution

Several studies (e.g., Botwe et al., 2018; Bray et al., 2019; Kaczmarek, 2023; Gordon., 2025) indicated that salinity is widely recognised as one of the most powerful environmental variables shaping macroinvertebrate assemblages in freshwater wetland ecosystems, largely because many taxa possess specific physiological tolerances that restrict their distribution along salinity gradients. Raising salinity levels can result in changes of the osmoregulatory demands on aquatic organisms, decreasing overall diversity and favouring halotolerant or halophilic groups (Dildar et al., 2025). This happens through natural processes, groundwater inputs, or human–induced drives such as agriculture (Narany et al., 2018). Elevated salinity has been shown to reduce sensitive species including Ephemeroptera, Plecoptera, and Trichoptera while increasing the dominance of more tolerant groups such as Chironomidae and several Coleoptera (Haggag et al., 2018; Cai et al., 2024; Golovatyuk et al., 2025;). According to Doney et al, (2020), the change in primary productivity, ionic balance, and predator–prey interactions, salinity variations have an indirect impact on macroinvertebrate ecosystems. Macroinvertebrate populations show substantial functional turnover and temporal variability in wetland systems such as pans, where salinity can vary significantly due to evaporation and groundwater recharge (O'Keefe., 2022). Furthermore, especially for species with limited ecological niches, excessive salinity occurrences might hinder colonisation success and interfere with metacommunity dispersal pathways, many ephemeral wetlands may see an increase in salinity as climate change increases evaporation rates and modifies rainfall patterns (Huynh et al., 2019; Cantonati et al., 2020; Bundschuh et al., 2023). Altering the distribution of biodiversity and ecosystem functioning and predicting species persistence, robustness, and long–term ecological dynamics in inland aquatic systems thus requires an understanding of the effect of salinity (Harvey et al., 2017; Pennekamp et al., 2018;).

d). Influence of water depth on macroinvertebrate community dynamics

Water depth is another key environmental variable that shapes macroinvertebrate diversity, distribution, and ecological functioning by regulating light penetration, temperature stability, predation pressure, and availability of oxygenated microhabitats (Pop et al.,2023; Trau et al., 2023). For taxa with longer developmental cycles in particular, deeper water basins frequently offer more stable thermal settings and less vulnerability to desiccation (Smith et al., 2019; Dahlke et al., 2020;). There is more light available in shallow places, primary productivity is usually higher (Ardyna et al., 2020; Wetzel., 2022). This leads to the establishment of macrophytes and periphyton, which provide food and shelter for macroinvertebrates (Wolters et al., 2019). Sediment properties are also influenced by water depth gradients; deeper zones tend to accumulate fine organic matter that supports burrowing species, whilst shallow zones frequently have coarser substrates that are preferred by mobile taxa (Das et al., 2017; Prentice et al., 2019; Wiesebron et al., 2021; Gnanasekaran et al., 2023;). Seasonal variations in water depth can significantly control colonisation possibilities, favouring species with quick life cycles and drought–resistant characteristics, particularly in ephemeral wetlands and pans (Brendonck et al., 2017; Mwaijengoa et al., 2020; Zinck and Montero, 2023). The depth reductions change the composition and functional variety of communities by making them more susceptible to fish and avian predation (Villéger et al., 2017; Costa et al., 2020). The variations in depth frequently reflect alterations in groundwater recharge in groundwater–dependent wetland systems, which in turn cause temporal changes in macroinvertebrate communities (Havril et al., 2018; Deane et al., 2018; Olanrewaju and Aladejana., 2025).

Dispersal and metacommunity dynamics

Several studies (e.g., Firmiano et al., 2021; Farooq et al., 2022; Sun et al., 2025) indicate that macroinvertebrate populations are influenced not only by local environmental conditions but also by regional dispersal processes operating across the broader landscape. These dispersal processes enable species to colonize new habitats and maintain connectivity between aquatic ecosystems, thereby shaping community composition and biodiversity patterns at different spatial scales. The propagules can be carried by water birds, wind, and hydrological channels, facilitating quick recolonisation after disturbances and supporting the long–term persistence of biodiversity (Johnston et al., 2017; Van der Stocken et al., 2019). By increasing communication between remote wetlands, these dispersal processes lower the danger of local extinction and encourage genetic interchange between populations (Rohde et al., 2017; Cantonati et al., 2020). The balance between environmental filtering and dispersion dynamics determines whether species successfully establish within aquatic environments, according to metacommunity theory (Heino et al., 2017; Tonkin et al., 2018; Cid et al., 2020). The predicting community composition and ecosystem resilience in wetland systems requires an understanding of both local and regional dynamics (Pelletier et al., 2020).

In macroinvertebrate communities, dispersal processes also influence temporal turnover, trait filtering, and spatial organization (Bush., 2025). Different taxa have different dispersion capacities, which result in different dynamics, while more isolated pans primarily rely on episodic dispersal events for community renewal, well–connected wetlands serve as regional species reservoirs (Lawton et al., 2016; Coelho., 2018; Naidoo et al., 2025). Limited dispersal may exacerbate historical contingency and priority effects in highly fragmented settings, indicating that the order and time of colonization have a significant impact on the community structure and functional composition of macroinvertebrates (Westveer et al., 2018; Sarremejane et al., 2022; Arias Font., 2023; Baumann et al., 2025). The mass–effects dynamics can be fostered by frequent dispersal in interconnected systems, enabling macroinvertebrates species to continue migrating into less effective habitats (Bottrell and Schoenly., 2018). Spatial patterns of biodiversity are produced by these mechanisms together with environmental filtration, where communities represent both the regional dispersion pool and local habitat limitations (Lessard et al., 2016; Heino et al., 2017; Swan et al., 2021).

Metacommunity dynamics also influence ecosystem functioning by regulating the flow of functional traits across wetland networks (Bauer et al., 2021). By increasing functional abundance and response diversity, the mobility of taxa with various feeding strategies biological traits and stress tolerances can protect ecosystems from disturbance (Raffard et al., 2022; Machado et al., 2014; Harisena., 2025). However, these dispersal channels may be disrupted by altered connection due to drainage, land–use change, or climate–driven hydrological shifts, which would decrease recolonization capacity and make isolated wetlands more susceptible to long–term biodiversity loss (Smith and Goetz., 2021; Uddin et al., 2021; Sánchez–Montoya et al., 2023). These dynamics produce strong temporal turnover, where assemblages reflect not only current environmental conditions but also the inheritance of past dispersal events and hydroperiod variability (O'Sullivan et al., 2021; Czeglédi et al., 2022). While isolated basins typically show more environmental filtering and stronger priority effects because of infrequent immigration opportunities (Lampou et al.,2025). Wetlands that are more frequently connected during flood pulses frequently serve as regional source habitats, supplying colonists to ephemeral or more isolated pans (Saros et al., 2022; Moliner Cachazo et al., 2023). Therefore, rather of being solely dependent on local habitat conditions, species–specific dispersal features, hydrogeomorphic connectivity, and dispersal pathways interact to produce spatial patterns of variety throughout the wetland network (Chen et al., 2023; Klunzinger et al., 2024).

Macroinvertebrate communities in wetlands

Impact of anthropogenic activities on macroinvertebrate diversity

Sharma (2024) argues that phosphate and nitrogen from fertilisers and pesticides are introduced via agricultural runoff those nutrients are critical drivers of eutrophication, as elevated N and P concentrations stimulate excessive algal and plant growth, which in turn reduces oxygen availability and degrades water quality. Eutrophication, which lowers the water's oxygen content and damages macroinvertebrate taxa such as Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), which require well–oxygenated conditions to survive, can be brought on by excessive nutrient loads (Jacobus et al., 2019; Serra et al., 2019; Fekadu, 2021; Kapsalis and Kalavrouziotis., 2021). Chironomid larvae (non–biting midges) and Oligochaetes (aquatic worms) are examples of pollution–tolerant organisms that tend to proliferate in contaminated environments, changing the composition of the macroinvertebrate communities (Hall et al., 2021; Kopel., 2024; Ferzoco et al., 2023). The biomonitoring of macroinvertebrates has yielded important insights into how different stressors affect biodiversity and ecological stability (Zhang et al., 2024; Ndatimana et al., 2023). By analysing the structure of macroinvertebrate communities across different locations and pollution gradients, wetlands' ecological health may be determined, and priority areas for conservation can be identified

(Cortelezzi and Paz, 2022; Byeon and Kim, 2025). According to Buçinca et al. (2024); Enabulele and Olomukoro (2024), the prevalence of pollution–sensitive species in some regions suggests generally good water quality, whereas the predominance of tolerant taxa in other regions reflect ongoing degradation.

CHAPTER 3: MATERIALS AND METHODS

Picture 3. Sampling for macroinvertebrates in the Khakhea–Bray Transboundary Aquifer region pan wetland system. Photo by Tatenda Dalu

Ethical consideration

The study was approved by the School of Biology and Environmental Sciences Research Ethics Committee. University of Mpumalanga ethics number: AS/UMP/Gumede201728788/BIO /MSc/2025/1.

Study area

The study area is situated in the Khakhea–Bray Transboundary Aquifer (KBTA) region in southern Africa. This aquifer system extends across parts of the border between Botswana and South Africa, surrounding the seasonal Molopo River (Gomo & Ngobe, 2024). South Africa and Botswana both share this aquifer, which has a low population density of 1–10 people/km² and covers an area of approximately 29,700 km² (Modie, 2022). As an essential groundwater system, the KBTA plays a critical role in providing water to both South Africa and surrounding areas (Bolivian et al., 2021). The aquifer is vital to the region's hydrology, sustaining various ecosystems, including wetlands that experience seasonal fluctuations in water levels.

The climate of the KBTA is mainly semi arid, characterized by low annual rainfall during the wet season (approximately 376 mm per year) and high rates of evapotranspiration (Murray et al., 2006). The months of November through March make up an unequal distribution of the region's rainy season. August through March are the region's summer months, with temperatures between 22 and 34 °C. In contrast, the winter season, which lasts from May to July, with average minimum temperatures of 2 degrees Celsius and maximum temperatures of 20 degrees (DWAF, 2004).

The vegetation area is covered most by thorn trees that are sparsely distributed, with clumped grass cover on relatively level ground (Chenchouni et al., 2023). In regions where Aeolian sand covers the surface, this vegetation cover is especially common. There is minimal grass cover but a preponderance of closely spaced prickly camel trees in regions with surface outcrops of dolomites or calcrete. This is because dense vegetation cannot grow because of the scant soil cover. Large trees and dense vegetation are especially evident near river channels (Mpakairi., 2022.).

The topography is characterized by very flat terrain and gradually raised portions that range from roughly 1027 to 1231 meters above mean sea level (Davies.,2013). The escarpments from the extremely resistant iron stone formation are the elevated regions to the south of the dolomite unit. There are no discernible highland regions on the Northen side of the area which is primarily flat at around 1078 meters above sea level. Mostly river channels covered in sand deposits make up the observably low–lying regions of roughly 1027m. These wetlands, particularly temporary pans and other water bodies, provide critical habitats for a range of species, including macroinvertebrates, which depend on them for survival (Voli et al., 2023).

Site selection

A total of 221 were divided into four elevation groups: <1100 m, 1100–1149 m, 1150–1199 m, and >1200 m and the wetland pans were then selected for macroinvertebrate sampling across the KBTA region. Site selection was based on key hydrological and geomorphological parameters, Size of wetland pans were classified into small, medium, and large categories to capture variability in surface area, which influences the extent of available niche space, primary productivity, and the capacity of pans to sustain diverse and functionally distinct macroinvertebrate communities. The KBTA wetland pan system is scientifically relevant because it represents a characteristic endorheic wetland landscape of semi-arid southern Africa. These pans form a network of temporary and semi-permanent wetlands that function as important biodiversity refugia and provide ideal natural gradients for studying ecological processes. The system also spans a transboundary landscape between Botswana and South Africa, allowing investigation of spatial ecological patterns across political and environmental boundaries. Consequently, the KBTA pans provide a suitable model system for examining macroinvertebrate diversity patterns, environmental filtering processes, and elevation-related ecological gradients, directly supporting the objectives of this study. Larger pans typically support greater habitat complexity and resource availability, whereas smaller pans are more disposed to to environmental fluctuations and disturbance. Pan width was recorded as a proxy for lateral habitat heterogeneity. Wider pans generally exhibit greater shoreline complexity and spatial variation in vegetation and substrate composition, which in turn promotes differentiation in refuge habitats, feeding zones, and breeding sites for macroinvertebrates. Pan depth was recorded both shallow and deep pans were included to represent variation in hydroperiod and water–retention capacity. Depth manages thermal stability, desiccation risk, and dissolved–oxygen dynamics, thereby shaping species persistence, colonisation potential, and the dominance of either opportunistic or disturbance–tolerant taxa within macroinvertebrate assemblages. (Dong et al., 2022). A one–way analysis of variance (ANOVA) was used to test for significant differences in each environmental variable across the four elevation bands: <1100 m, 1100–1149 m, 1150–1199 m, and >1200 m.

Spatial scale sampling approach

To ensure comprehensive water quality analysis across the study area, a spatially distributed sampling approach was implemented. At each of the 221 wetland pan sites, 10 water samples were drawn randomly per pan and mixed in a bucket to get an integrated sample. Thus, at each pan, two integrated water samples for nutrient analysis were collected.

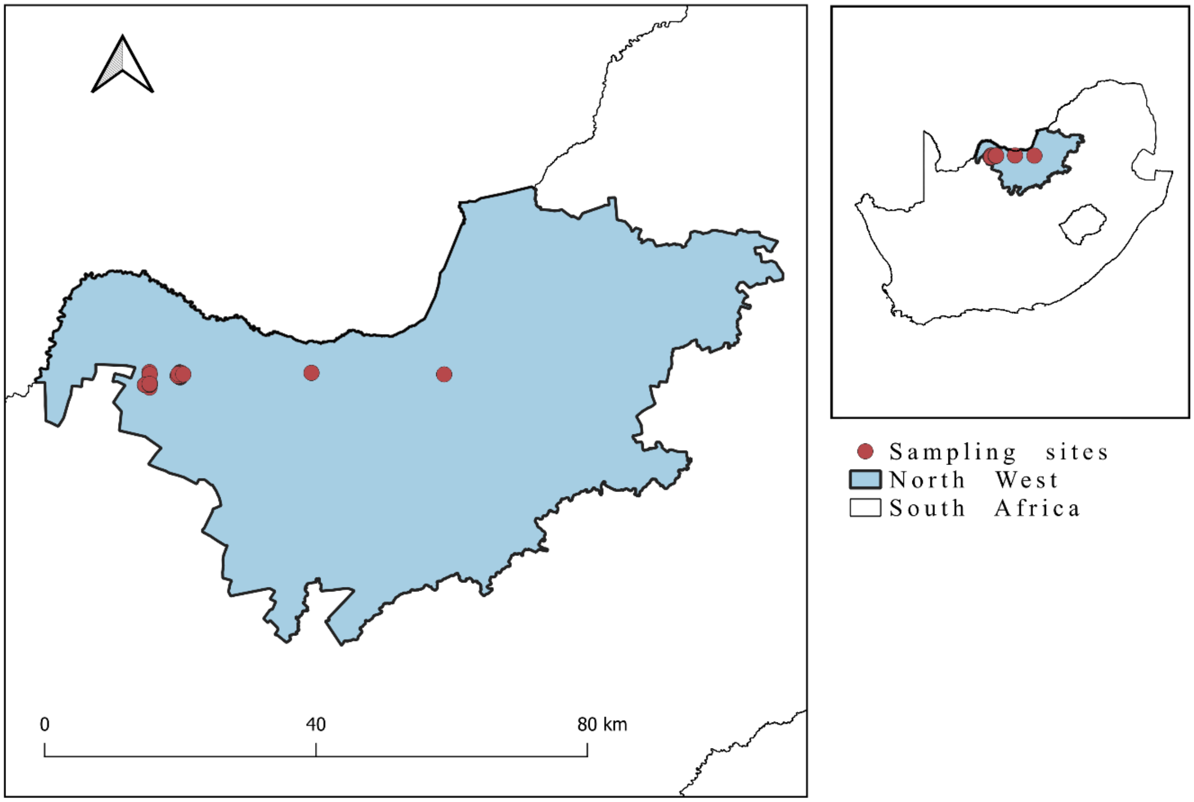

Figure 3.1. Map showing morokweng wetland pans in Khakhea–Bray Transboundary aquafer North West Province, South Africa.

Figure 3.2. Materials used during sampling at Khakhea–Bray Transboundary Aquifer. Photo by Sobahle Hlophe.

Data collection

Surface area and water depth measurement

Each wetland pan's surface area was calculated using a handheld GPS in accordance with typical field–based perimeter–mapping techniques. The GPS device was carried while walking along the edges of each pan. An estimate of the surface area for each wetland pan in the Khakhea–Bray Transboundary Aquifer system was obtained by calculating the final area using the GIS area–calculation function. Water depth was measured using a wading method, carefully moving through the wetland until the leg made contact with the silted bottom. At each selected point, the depth was determined by recording the distance from the water surface to the point on the leg where contact with the substrate occurred.

Water sampling

A portable handheld multiparameter Cyberscan Series (version HI98192, HANNA Instruments, Rhode Island) was used to measure conductivity (μS cm^{-1}), salinity (ppt), pH, water temperature (°C), dissolved oxygen (DO) (mg L^{-1}), and total dissolved solids (TDS) (mg L^{-1}) in all 221 study sites. 250 mL water bottles were then used to collect water samples and placed in cooler box for transportation.

Environmental variables

Pan wetlands were sampled across four altitudinal categories: <1100 m (n = 55), 1100–1149 m (n = 40), 1150–1199 m (n = 123), and >1200 m (n = 3). Sampling effort was highest at mid–elevations (1150–1199 m), while high–altitude pans (>1200 m) were comparatively rare, reflecting their limited spatial occurrence in the landscape and in each environmental variable across the four elevation bands: <1100 m, 1100–1149 m, 1150–1199 m, and >1200 m.Water samples were collected using pre–rinsed 250 mL polyethylene bottles and immediately stored in an ice–filled cooler box to minimize biological and chemical alteration during transport. All samples were transported to the University of Mpumalanga laboratory and for futher analysis. Nutrient analysis targeted phosphate (PO_4^{3-}), ammonium (NH_4^+), and nitrate–nitrogen (NO_3^-–N) using a HI 83203 multiparameter photometer (Hanna Instruments Inc., Rhode Island, USA). The instrument operates with an optical LED/photodiode system and uses reagent–based colorimetric methods compliant with standard wet–chemistry protocols (Jun et al., 2016). For each parameter, the instrument's working range and precision, Phosphate (PO_4^{3-}): measurement range 0.00–2.50 mg/L, Ammonium (NH_4^+–N): measurement range 0.00–5.00 mg/L; And Nitrate–nitrogen (NO_3^-–N): measurement range 0.0–30.0 mg/L. Hanna Instruments were used for each parameter, and the instrument was zeroed and calibrated prior to each batch of analyses using distilled water blanks. All measurements were conducted twice to ensure reliability, and mean values were calculated for statistical analysis.

Sampling of macroinvertebrates

Macroinvertebrates were collected at various wetlands pan at khakhea–Bray transboundary aquifer during different wetlands pans using a standardized SASS net (Dickens and Graham, 2002 This squre net (30x30 cm) has an aluminium rim and a 1 mm mesh size. It is affixed to a handle that extends to a length of 1.5 m. The squre net (30x30 cm) was fully immersed in the aquatic environment, and the collection of macroinvertebrates were conducted by systematically sweeping a designated transect measuring 10–15 meters in length. The methodology encompassed the act of traversing the water while utilizing a sampling net, as well as employing forceful movements to displace aquatic macrophytes, plants, sand, and boulders (Mondal and Pal. 2018). This method was undertaken with the purpose of removing the macroinvertebrates that had been attached. To avoid the potential escape of active organisms, the sass sample net was expeditiously retrieved from the aquatic environment. Subsequently, it was subjected to a thorough rinsing process using a coarse mesh filter, which effectively eliminated sizable detrital organic material while ensuring the retention of macroinvertebrates. Collected macroinvertebrates were then transferred into plastic containers with a volume of 500 mL and preserved using a solution of 70% ethanol to maintain sample integrity. To ensure proper preservation, all macroinvertebrate samples were stored in a cool, dark environment at approximately 4°C before laboratory processing. Samples were transported to the laboratory within 24 hours of collection and processed within a maximum of seven days to minimize degradation. In the laboratory the quantification and classification of macroinvertebrates were classified up to the Genus level using the identification guidelines provided by Thoron et al. (1995), Gerber and Gabriel (2002). Macroinvertebrate specimens were identified morphologically using both the unaided eye and a dissection microscope.

Data analysis

Environmental variables measured at each sampling pan wetland were tested for normality using Shapiro–Wilk tests and for homogeneity of variances using Levene's test. Variables that violated assumptions of normality or homoscedasticity were log–transformed prior to analysis. A one–way analysis of variance (ANOVA) was used to test for significant differences in each environmental variable across the four elevation bands: <1100 m, 1100–1149 m, 1150–1199 m, and >1200 m. Where ANOVA indicated a significant main effect ($p < 0.05$), Tukey's Honest Significant Difference (HSD) post hoc test was applied to identify which elevation pairs differed significantly (Dar, et al., 2022).

Macroinvertebrate community data were analysed using multivariate methods to test for differences in community composition across the four elevation bands (<1100 m, 1100–1149 m, 1150–1199 m, and >1200 m) (Rubio–Polania et al., 2026). All analyses were conducted in SPSS version 25. Prior to analysis, species abundance data were square–root transformed to reduce the influence of highly abundant taxa and to improve multivariate normality. A Bray–Curtis dissimilarity matrix was calculated to represent ecological distances between samples based on community composition. Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test the null hypothesis of no difference in community composition among elevation groups. The analysis was based on the Bray–Curtis matrix with 9,999 permutations. Where a significant main effect was detected, pairwise PERMANOVA tests with Bonferroni correction were performed to identify which elevation bands differed significantly (Araújo et al.,2022).

Analysis of Similarities (ANOSIM) was applied as a complementary, rank–based test to assess the degree of separation among groups. ANOSIM generates an *R*–statistic ranging from −1 to 1, where values >0 indicate greater dissimilarity between groups than within groups. An *R* close to 1 suggests strong separation. Significance was assessed using 9, 999 permutations. Similarity Percentage Analysis (SIMPER) was used to identify the taxa primarily responsible for the observed differences between elevation groups. This procedure decomposes the average Bray–Curtis dissimilarity between pairs of groups into contributions from individual species. Taxa with high contributions to dissimilarity and low within–group variability were considered important discriminators. All multivariate tests were considered significant at $p < 0.05$.

Community data were analysed using non–metric multidimensional scaling (nMDS), an ordination technique well–suited for ecological data that are non–normal or on arbitrary scales. The analysis was performed on a site–by–species matrix of macroinvertebrate relative abundance data. A Bray–Curtis dissimilarity matrix was calculated to quantify compositional differences between sites. The nMDS ordination was run with 50 random starts to ensure convergence on a stable solution, and a two–dimensional solution was selected based on stress values and interpretability. Stress values below 0.10 were considered indicative of a good ordination, while values between 0.10 and 0.20 were considered acceptable.

Univariate method was conducted to evaluate relationships between macroinvertebrate diversity indices and the measured environmental variables (Schober et al., 2018; Adino, and Mengistou., 2025). Correlation coefficients were used to describe the direction and strength of associations, while statistical significance was assessed using corresponding *p*–values (Her and Wong., 2020; Ware et al., 2019). Furthermore, relationships between macroinvertebrate richness and environmental variables were modelled using boosted regression trees (BRTs) (Theodoropoulos et al., 2018). The BRT analyses were implemented in R (R Core Team, 2022) with the gbm package (Ridgeway, 2006) following the approach of Elith et al. (2008).

CHAPTER 4: RESULTS

Picture 4. Anthropogenic stressors of wetlands in the Khakhea–Bray region, excavation currently being done on some wetlands. Photo by Tatenda Dalu.

Environmental variables

Across all altitude classes, pan wetlands were generally neutral to alkaline, with mean pH values ranging from 7.6 to 8.6. The lowest–altitude pans (<1100 m) exhibited the widest pH range (3.6–10.1), indicating substantial heterogeneity, including occasional acidic conditions. In contrast, high–altitude pans (>1200 m) were consistently alkaline (mean pH = 8.6 ± 0.4), suggesting more buffered systems at higher elevations (Table 3.1). The Oxidation–reduction potential (ORP) values showed pronounced variability across elevations. Low–altitude pans (<1100 m) had strongly oxidising conditions on average (mean = 513.7 mV), but with extremely broad ranges, indicating fluctuating redox states (Table 3.1). Mid–elevation pans (1100–1149 m and 1150–1199 m) exhibited lower and more stable ORP values, while high–altitude pans (>1200 m) included negative ORP values, suggesting periodic or persistent reducing conditions (Table 3.1).

Mean dissolved oxygen concentrations were moderate at lower and mid–elevations (~5 mg/L) but declined substantially in high–altitude pans (>1200 m; mean = 2.4 ± 0.4 mg/L). This pattern suggests increasing prevalence of hypoxic conditions with elevation, possibly linked to greater depth, and high temperatues (Table 3.1). Electrical conductivity increased from lower to mid–elevations, peaking in the 1150–1199 m category (mean = 301.0 ± 99.9 µS/cm), before declining at the highest elevations. A similar pattern was observed for TDS, with highest mean concentrations recorded at mid elevations. These results indicate solute enrichment in mid–altitude pans, potentially reflecting greater evaporative concentration or catchment inputs (Table 3.1).

Thermal regime

Water temperature varied widely across in high altitude classes, with mean temperatures ranging from 13.0 to 17.7°C. Mid– to high–altitude pans tended to exhibit slightly warmer mean temperatures, although large standard deviations suggest strong seasonal or diel variability. Temperature did not decline monotonically with altitude, indicating the influence of pan depth, surface area, and exposure (Table 3.1).

Morphometric characteristics

Pan surface area varied by several orders of magnitude across all altitude classes. The largest pans occurred at mid–elevations (1 100–1149 m and 1 150–1 199 m), with mean surface areas exceeding

7 500–10 000 m² (Table 3.1). Low–altitude pans were generally smaller, while high–altitude pans exhibited intermediate mean sizes but high variability. Mean pan depth increased with altitude. Low–altitude pans were generally shallow (mean = 7.7 ± 2.7 cm), whereas high–altitude pans (>1200 m) were substantially deeper (mean = 34.7 ± 26.6 cm). This trend suggests that higher–elevation pans may retain water for longer hydroperiods (Table 3.1).

Nutrient concentrations

Ammonium concentrations were highest in low–altitude pans (<1100 m; mean = 21.1 ± 32.4 mg/L), with values declining markedly at mid–elevations. High–altitude pans showed ammonium concentrations again (mean = 10.3 ± 11 mg/L), possibly reflecting reduced nitrification under hypoxic conditions (Table 3.1). Nitrate concentrations were highest at 1100–1149 m (mean = 71.7 ± 41.8 mg/L), with lower but still substantial concentrations across other altitude classes. Wide ranges across all categories indicate episodic nutrient inputs or strong temporal variability. Phosphate concentrations increased with altitude, peaking at mid– and high–elevations (means = 6.5 ± 1.9 mg/L and 5.3 ± 3.3 mg/L, respectively). This suggests enhanced internal loading or sediment release under reduced redox conditions at higher elevations (Table 3.1).

Table 3.1. Environmental variables and macroinvertebrate metrices recorded among pan wetlands at different elevations within the Khakhea–bray Transboundary aquifer region, South Africa. Abbreviations: ORP – oxygen reduction potential, DO – dissolved oxygen, TDS – total dissolved solids,

Taxa	**<1100 m (n = 55)**		**1100–1149 m (n = 40)**		**1150–1199 m (n = 123)**		**>1200 m (n = 3)**	
	Range	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**
Environmental								
pH	3.6 ± 10.1	7.7 ± 1.4	3.6 ± 10.1	7.6 ± 1.4	4.8 ± 10.4	7.9 ± 1.1	7.9 ± 8.9	8.6 ± 0.4
ORP (mV)	194.1 ± 2009	513.7 ± 732.6	130.1 ± 184.9	159.6 ± 19	22.8 ± 226.8	97.7 ± 75.8	–98.7 ± 161	102.1 ± 99.7
DO (mg/L)	4.8 ± 5.8	5.2 ± 0.3	4.8 ± 5.3	5.1 ± 0.1	2.4 ± 6.7	4.7 ± 1.8	2 ± 3.1	2.4 ± 0.4
Conductivity (µS/cm)	164 ± 342	242.3 ± 68.2	106 ± 402	186.5 ± 109.6	192 ± 445	301 ± 99.9	119 ± 216	167.6 ± 37.4
TDS (mg/L)	96 ± 221	133 ± 46.1	60 ± 94	81 ± 15.8	131 ± 221	157.8 ± 34.5	68 ± 108	86.1 ± 16.1
Temperature	12.4 ± 13.8	13 ± 0.5	11.5 ± 19.7	17.2 ± 3.1	12.1 ± 17.6	15 ± 2.5	16 ± 19	17.7 ± 1.1
Surface area (m^2)	50 ± 1500	550 ± 736.2	50 ± 30000	10033.3 ± 15466.1	200 ± 20000	7566.6 ± 9685.5	150 ± 5500	2883.3 ± 2394.2
Water depth (cm)	4 ± 10	7.7 ± 2.7	15 ± 34	21.3 ± 6.9	5 ± 15	8.3 ± 4	9.4 ± 61	34.7 ± 26.6
Ammonium (mg/L)	0 ± 63	21.1 ± 32.4	3.1 ± 10.7	5.7 ± 3.8	0 ± 4.6	1.6 ± 2.3	1.1 ± 24.4	10.3 ± 11
Nitrate (mg/L)	0 ± 77.6	34.3 ± 35.3	18.2 ± 104.8	71.7 ± 41.8	11.6 ± 24.4	16.2 ± 6.3	6.7 ± 29.6	16.5 ± 10.5
Phosphate (mg/L)	0 ± 5.1	1.7 ± 2.6	0 ± 5.9	2.3 ± 2.8	4.1 ± 8	6.5 ± 1.9	2.2 ± 9.4	5.3 ± 3.3
Macroinvertebrate metrices								
Taxa richness	16 ± 23	19.6 ± 3	19 ± 22	20.1 ± 1.1	16 ± 24	19.3 ± 3	13 ± 17	15.1 ± 1.4
Abundance	72 ± 118	85 ± 17.7	70 ± 595	232.8 ± 236.9	34 ± 210	106.5 ± 74	35 ± 91	60.6 ± 23.4
Simpson	0.6 ± 0.9	0.8 ± 0	0.3 ± 0.9	0.7 ± 0.2	0.7 ± 0.9	0.8 ± 0	0.6 ± 0.9	0.8 ± 0.1

Shannon–Wiener	1.8 ± 2.7	2.3 ± 0.3	0.9 ± 2.7	2.1 ± 0.7	2 ± 2.7	2.3 ± 0.2	1.5 ± 2.7	2.2 ± 0.4
Evenness	0.3 ± 0.7	0.5 ± 0.1	0.1 ± 0.7	0.5 ± 0.2	0.3 ± 0.8	0.5 ± 0.2	0.3 ± 0.8	0.6 ± 0.2
Altitude	1096.5 ± 1098.1	1097.1 ± 0.7	1128.3 ± 1129.4	1129 ± 0.5	1182.9 ± 1196.1	1187.8 ± 6.4	1210.2 ± 1327	1287.4 ± 59.7

One–way ANOVA revealed that several key physicochemical variables differed significantly among altitude classes (Table 3.2).

Table 3.2. Analysis of variance of environmental variables and macroinvertebrate metricises recorded among pan wetlands at different elevations within the Khakhea–bray Transboundary aquifer region, South Africa.

Variable	df	F	*p*
Environmental			
pH	3	1.987	0.115
Oxygen reduction potential	3	0.515	0.672
Dissolved oxygen	**3**	**12.372**	**<0.001**
Conductivity	3	0.207	0.891
Resistivity	3	1.158	0.326
Total dissolved solids	3	1.380	0.248
Temperature	**3**	**20.735**	**<0.001**
Surface area	3	0.474	0.700
Water depth	**3**	**16.345**	**<0.001**
Ammonium	**3**	**10.581**	**<0.001**
Nitrate	**3**	**18.923**	**<0.001**
Phosphate	**3**	**10.998**	**<0.001**
Macroinvertebrate metrices			
Taxa richness	**3**	**5.045**	**0.002**
Abundance	3	1.007	0.390
Simpson	3	0.195	0.900
Shannon–Wiener	3	0.829	0.478
Evenness	3	0.661	0.577

Pairwise comparisons across elevation categories revealed variable–specific patterns of change in physicochemical conditions along the elevation gradient (Table 3.3). The DO did not differ significantly between the lowest elevation (<1100 m) and 1100–1149 m sites ($p = 0.683$) or between <1100 m and 1150–1199 m ($p = 0.054$), suggesting relatively consistent oxygen levels across these lower to mid–elevation sites (Table 3.3). Significant differences were observed between <1100 m and the highest elevation (>1200 m; $p < 0.001$), as well as between 1100–1149 m and 1150–1199 m ($p = 0.003$) and 1100–1149 m and >1200 m ($p < 0.001$), indicating that higher elevations generally had distinct DO levels (Table 3.3). Similarly, 1150–1199 m and >1200 m sites differed significantly ($p < 0.001$), reflecting an elevational gradient in dissolved oxygen at higher altitudes (Table 3.3).

Temperature showed significant variation among most mid– and high–elevation comparisons. Specifically, <1100 m and 1150–1199 m ($p < 0.001$), and 1100–1149 m and 1150–1199 m ($p < 0.001$) differed significantly (Table 3.3). Water depth differed significantly between <1100 m and 1100–1149 m ($p < 0.001$) and between 1100–1149 m and 1150–1199 m ($p < 0.001$) (Table 3.3).

For nutrients, nitrates had significant differences were detected between <1100 m and 1100–1149 m ($p < 0.001$) and between 1100–1149 m and 1150–1199 m ($p < 0.001$) (Table 3.3). (Table 3.3). For ammonium, significant differences occurred between <1100 m and 1150–1199 m ($p < 0.001$) and between 1100–1149 m and 1150–1199 m ($p = 0.010$).

Table 3.3. Tukey's posthoc analysis of environmental variables and macroinvertebrate metricises recorded among pan wetlands at different elevations within the Khakhea–bray Transboundary aquifer region, South Africa.

Dependent variable	**Altitude 1**	**Altitude 2**	***p***	**Dependent variable**	**Altitude 1**	**Altitude 2**	***p***
Dissolved oxygen	<1100	1100–1499	0.683	Nitrate	<1100	1100–1149	**<0.001**
	<1100	1150–1199	0.054		<1100	1150–1199	0.786
	<1100	>1200	**<0.001**		<1100	>1200	0.955
	1100–1149	1150–1199	**0.003**		1100–1149	1150–1199	**<0.001**
	1100–1149	>1200	**<0.001**		1100–1149	>1200	0.251
	1150–1199	>1200	**<0.001**		1150–1199	>1200	0.994
Temperature	<1100	1100–1149	1.000	Phosphate	<1100	1100–1149	**<0.001**
	<1100	1150–1199	**<0.001**		<1100	1150–1199	0.624
	1100–1149	1150–1199	**<0.001**		1100–1149	1150–1199	**<0.001**
	1150–1199	>1200	0.924		1150–1199	>1200	0.978
	>1200	<1100	0.627		>1200	<1100	1.000
	>1200	1100–1149	0.634		>1200	1100–1149	0.220
Water depth	<1100	1100–1149	**<0.001**	Taxa richness	<1100	1100–1149	0.697
	<1100	1150–1199	0.472		<1100	1150–1199	0.244
	<1100	>1200	0.112		<1100	>1200	0.164
	1100–1149	1150–1199	**<0.001**		1100–1149	1150–1199	**0.020**
	>1200	1100–1149	1.000		>1200	1100–1149	0.338
	>1200	1150–1199	0.239		>1200	1150–1199	**0.045**
Ammonium	<1100	1100–1149	0.466				
	<1100	1150–1199	**<0.001**				
	<1100	>1200	0.708				

1100–1149	1150–1199	**0.010**
1150–1199	>1200	0.978
>1200	1100–1149	0.945

Macroinvertebrates

Based on PERMANOVA significant differences were observed in macroinvertebrate community structure (Pseudo–F(MC) = 1.984, p = 0.0001), with pairwise comparisons indicating significant differences for <1100 and 1100–1149 (t = 1.316, p = 0.021), <1100 and 1150–1199 (t = 1.506, p = 0.001) and 1100–1149 and 1150–1199 (t = 1.649, p = 0.0002).. Macroinvertebrate assemblages in pan wetlands were dominated by a small number of taxa in most altitude classes. However, total macroinvertebrate abundance and taxonomic composition varied along the altitudinal gradient, with higher elevations generally supporting lower overall abundances but relatively higher proportions of environmentally sensitive taxa, while lower elevations were characterised by higher abundances of tolerant taxa. These shifts in community structure suggest that altitude-related environmental factors, such as temperature, hydroperiod, and oxygen availability, act as ecological filters influencing macroinvertebrate distribution. (Table 3.4).

Low–altitude pans were strongly dominated by large branchiopods, particularly Anostraca, which exhibited the highest mean relative abundance in this altitude class (29.8± 21.8%), certain taxa dominate at low altitude especially large branchiopods. Spinicaudata (12.2 ± 8.8 %) and Notostraca (10.7 ± 7.4 %) were also prominent, together accounting for a substantial proportion of total assemblage composition. Aquatic Coleoptera and Hemiptera were present but generally occurred at low relative abundances, with most taxa contributing <5 % on average. Dipteran larvae (e.g. Ceratopogonidae, Culicidae) and molluscs were comparatively rare (Table 3.4).

Assemblages at 1100–1149 m retained a strong branchiopod signal, although mean relative abundance of Anostraca declined slightly (24.8 ± 21.5 %). Spinicaudata and Notostraca were noticeable reduced relative to low–altitude pans (Table 3.4). In contrast, aquatic insects increased in representation, particularly Coleoptera (e.g., Dytiscidae, *Cybister* sp., *Hydaticus* spp.), Hemiptera (e.g., Corixidae, *Gerris swakopensis*), and Odonata (e.g., *Anax* sp., *Sympetrum* sp.). Gastropods and dipterans (e.g., Tabanidae and *Dixella* sp.) also increased in relative abundance, indicating a more taxonomically heterogeneous community structure (Table 3.4).

At 1150–1199 m, macroinvertebrate assemblages showed the greatest compositional complexity (Table 3.4). Although Anostraca remained dominant (27.3 ± 21.8 %), relative abundances of insects and molluscs were higher and more evenly distributed than at lower elevations. Hemiptera (e.g., *Laccocoris* sp., Nepidae), Coleoptera (i.e., Elmidae, Dytiscidae), Odonata, and Diptera (i.e., Ceratopogonidae, *Dixella* sp., Oligoneuriidae) contributed substantially to overall assemblage structure. Molluscs such as *Gyraulus connollyi*, *Lamellidens* sp., and *Pila occidentalis* were more consistently represented, reflecting broader habitat use within this altitude band (Table 3.4).

High–altitude pans supported simpler assemblages, characterised by lower overall abundance but relatively high dominance by a few taxa (Table 3.4). Anostraca remained a major component (26.7 ± 21.0 %), while Notostraca increased in relative importance compared to mid–altitude pans (8.7 ± 8.0 %). Several macroinvertebrate taxa, including *Rhantus* sp., *Haliplus* sp., *Dixella* sp., *Anax* sp., and *Gyraulus connollyi*, exhibited elevated mean relative abundances, although large standard deviations reflect strong among–site variability and low sample size (Table 3.4). Many taxa were absent or occurred sporadically, resulting in comparatively even but species–poor communities.

Table 3.4. The relative abundances of macroinvertebrate taxa recorded among pan wetlands at different elevations within the Khakhea–bray Transboundary aquifer region, South Africa.

Taxa	**<1100 m**		**1100–1149 m**		**1150–1199 m**		**>1200 m**	
	Range	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**
Anostraca	0 ± 92	29.8 ± 21.8	0 ± 86.2	24.8 ± 21.5	0 ± 89.6	27.3 ± 21.8	4 ± 52.8	26.7 ± 21
Spinicaudata	0 ± 25.4	12.2 ± 8.8	0 ± 11.3	4.3 ± 5.5	0 ± 23.6	10.9 ± 9.6		
Notostraca	3.9 ± 25	10.7 ± 7.4	0 ± 4.4	2.2 ± 1.8	0 ± 4.3	1.8 ± 2	0 ± 20.6	8.7 ± 8
Rhantus sp.	0 ± 8	3 ± 3.3	0 ± 9.5	1.8 ± 3.7	0 ± 2.8	0.8 ± 1.3	0 ± 16.3	3.5 ± 6.5
Hydaticus exclamationis	0 ± 2.6	0.4 ± 1	0 ± 2.8	0.4 ± 1.1	0 ± 4.6	0.7 ± 1.8	0 ± 2.8	0.4 ± 1.1
Daphniidae	0 ± 4	0.8 ± 1.6	0 ± 2.8	0.7 ± 1.1	0 ± 4.6	1.2 ± 1.8	0 ± 5.7	0.9 ± 2.3
Loccobius sp.	0 ± 5.3	1.2 ± 2	0 ± 1.4	0.5 ± 0.6	0 ± 2.9	0.4 ± 1.2	0 ± 4.7	1.2 ± 2
Acidocerinae	0 ± 4	1 ± 1.5	0 ± 2	0.3 ± 0.8	0 ± 2.8	0.4 ± 1.1	0 ± 8.3	1.3 ± 3.4
Gryrinidae	0 ± 17.1	2.8 ± 6.9	0 ± 7.8	1.3 ± 3.1	0 ± 5.8	1.9 ± 2	0 ± 4	0.6 ± 1.6
Hydroporinae	0 ± 4.2	1.2 ± 1.6	0 ± 2.8	0.4 ± 1.1			0 ± 4.7	0.7 ± 1.9
Stenelmis sp.	0 ± 1.3	0.2 ± 0.5	0 ± 1.3	0.4 ± 0.6			0 ± 1.1	0.3 ± 0.5
Elmidae	0 ± 3.9	0.6 ± 1.6			0 ± 5.7	1.6 ± 2.4	0 ± 2.8	0.8 ± 1.2
Cybister sp.	0 ± 10.5	3.4 ± 4.1	0 ± 11.2	2.3 ± 4.4	0 ± 2.9	0.9 ± 1.2		
Hydrocanthus sp.	0 ± 6.7	1.4 ± 2.7	0 ± 5.2	2.1 ± 2.2	0 ± 1.1	0.1 ± 0.4	0 ± 5.4	2.1 ± 2.5
Dytiscidae	0 ± 7.8	1.6 ± 3			0 ± 8.8	1.9 ± 3.5	0 ± 2	0.3 ± 0.8
Haliplus sp.	0 ± 4.3	0.9 ± 1.7	0 ± 2	0.5 ± 0.9	0 ± 2.1	0.5 ± 0.9	0 ± 2.2	0.3 ± 0.9
Anisops sp.	0 ± 1.3	0.2 ± 0.5	0 ± 2.6	0.4 ± 1	0 ± 4.6	1.2 ± 1.8	0 ± 6.1	1.2 ± 2.4
Appasus sp.	0 ± 6.7	1.6 ± 2.8	0 ± 2	0.3 ± 0.8	0 ± 8.8	1.4 ± 3.6	0 ± 2.1	0.3 ± 0.8
Corixidae	0 ± 2.7	0.4 ± 1.1	0 ± 7.8	2.1 ± 3	0 ± 6	1 ± 2.4	0 ± 10	1.6 ± 4
Gerris swakopensis	0 ± 1.3	0.2 ± 0.5	0 ± 7.1	2.1 ± 3.1	0 ± 2.1	0.6 ± 0.9	0 ± 6.1	2.9 ± 2.6
Hydrometridae	0 ± 10.6	3.5 ± 4.1			0 ± 3.8	1.1 ± 1.7	0 ± 6.8	1.1 ± 2.8
Laccocoris sp.					0 ± 22.8	5.6 ± 9.1	0 ± 10	1.6 ± 4
Paraplea sp.	0 ± 3.2	0.5 ± 1.3	0 ± 6.1	1.2 ± 2.4	0 ± 0.4	0 ± 0.1	0 ± 2.8	0.4 ± 1.1
Notonectidae	0 ± 4.1	0.6 ± 1.7	0 ± 1.4	0.2 ± 0.5				
Nepidae	0 ± 1.3	0.2 ± 0.5	0 ± 0.4	0 ± 0.1	0 ± 8.5	2.8 ± 3.1	0 ± 1	0.1 ± 0.4
Sigara sp.	0 ± 1.3	0.2 ± 0.5	0 ± 2.3	0.3 ± 0.9	0 ± 0.4	0 ± 0.1	0 ± 6.1	1.8 ± 2.4
Veliidae	0 ± 1	0.1 ± 0.4	0 ± 5.1	1 ± 2	0 ± 1.1	0.1 ± 0.4		

Micronecta sp.			0 ± 2.8	0.6 ± 1.1	0 ± 4.3	0.8 ± 1.7	0 ± 10	1.6 ± 4
Hydrocanthus sp.	0 ± 5.9	2.1 ± 2.4	0 ± 7.8	1.3 ± 3.2	0 ± 5.8	0.9 ± 2.4	0 ± 8.1	3 ± 3.7
Mesovelia vittigera					0 ± 1	0.1 ± 0.4	0 ± 3.3	0.9 ± 1.4
Ranatra sp.					0 ± 1.9	0.4 ± 0.8	0 ± 0	0 ± 0
Sympetrum sp.	0 ± 3.9	1.1 ± 1.5	0 ± 8.3	2.5 ± 3.5	0 ± 5.8	0.9 ± 2.4	0 ± 2.3	0.3 ± 0.9
Chironomidae							0 ± 3.3	0.5 ± 1.3
Ceratopogonidae	0 ± 3.9	1 ± 1.7	0 ± 10	1.6 ± 4	0 ± 5.7	0.9 ± 2.3	0 ± 4.7	0.7 ± 1.9
Culicidae	0 ± 2.6	0.6 ± 1	0 ± 7.1	1.4 ± 2.8	0 ± 1.6	0.2 ± 0.6	0 ± 12.2	2 ± 4.9
Dixella sp.			0 ± 1.4	0.2 ± 0.6	0 ± 3.8	1.3 ± 1.6		
Tabanidae	0 ± 3.9	0.9 ± 1.6	0 ± 18.4	3 ± 7.5	0 ± 11.7	2.4 ± 4.7		
Tomopterna sp.	0 ± 1.3	0.2 ± 0.5	0 ± 0.8	0.1 ± 0.3	0 ± 5.8	0.9 ± 2.4	0 ± 8.1	1.3 ± 3.3
Lestes sp.	0 ± 3.9	0.9 ± 1.6	0 ± 0.5	0 ± 0.2			0 ± 1.6	0.4 ± 0.7
Anax sp.	0 ± 4.1	1.3 ± 1.7	0 ± 7.8	3 ± 3.6	0 ± 11.7	2.6 ± 4.5	0 ± 8.5	1.4 ± 3.4
Crocothemis erythraea	0 ± 2.1	0.5 ± 0.9	0 ± 4.2	0.8 ± 1.6	0 ± 2.8	0.4 ± 1.1		
Diplacodes lefebvri	0 ± 3.9	0.6 ± 1.6	0 ± 3	0.7 ± 1.2				
Orthetrum chrysostigma	0 ± 2.5	0.6 ± 1			0 ± 3.8	1.1 ± 1.7	0 ± 4.7	1.4 ± 1.8
Trithemis arteriosa			0 ± 21.4	5.5 ± 8.8	0 ± 1.1	0.3 ± 0.5	0 ± 1.1	0.1 ± 0.4
Pseudagrion sp.	0 ± 2.7	1.1 ± 1.3	0 ± 3.9	0.6 ± 1.5	0 ± 5.8	0.9 ± 2.4	0 ± 2.8	0.6 ± 1.1
Phaon iridipennis	0 ± 1.6	0.5 ± 0.7	0 ± 14.2	2.5 ± 5.7	0 ± 1	0.1 ± 0.4		
Ceratophallus natalensis	0 ± 2.7	1.1 ± 1.3	0 ± 2.6	0.4 ± 1	0 ± 5.7	1.5 ± 2	0 ± 11.4	2 ± 4.5
Corbicula fluminalis africana	0 ± 1.6	0.2 ± 0.6	0 ± 0.6	0.1 ± 0.2			0 ± 3.3	0.5 ± 1.3
Gastropoda	0 ± 1.3	0.4 ± 0.6	0 ± 15.3	3.8 ± 5.8	0 ± 4.6	1.7 ± 1.9	0 ± 4.3	0.7 ± 1.7
Gyraulus connollyi	0 ± 4.1	1.1 ± 1.6			0 ± 9.7	2.1 ± 3.9	0 ± 8.5	3 ± 3.5
Pisidium langleyanum			0 ± 1.2	0.3 ± 0.5	0 ± 2.9	0.5 ± 1.1	0 ± 2	0.3 ± 0.8
Lamellidens sp.	0 ± 1.3	0.2 ± 0.5	0 ± 5.7	1.3 ± 2.1	0 ± 5.7	1.1 ± 2.2	0 ± 2.8	1 ± 1.2
Lymnaea truncatula	0 ± 1.3	0.4 ± 0.6	0 ± 0.6	0.1 ± 0.2	0 ± 3.2	0.5 ± 1.3		
Pila occidentalis	0 ± 11.8	3.7 ± 5	0 ± 3.5	0.5 ± 1.4	0 ± 5.7	1.2 ± 2.2	0 ± 6.5	1.8 ± 2.5
Gyrinus sp.	0 ± 10.5	2.2 ± 4.1	0 ± 7.1	2.3 ± 3.3	0 ± 3.8	1.4 ± 1.6	0 ± 8.5	1.9 ± 3.4
Haliplus sp.	0 ± 2.6	0.8 ± 1.3	0 ± 11.2	3.4 ± 5	0 ± 5.8	1.7 ± 2.6	0 ± 26.1	4.9 ± 10.5
Crenigomphus sp.					0 ± 3.2	0.9 ± 1.4	0 ± 5	1 ± 2
Dixella sp.	0 ± 5.3	1.1 ± 2.1	0 ± 10	4.5 ± 4.3	0 ± 2.9	0.5 ± 1.1	0 ± 9.8	3.2 ± 4
Oligoneuriidae			0 ± 1.4	0.6 ± 0.6	0 ± 11.4	2.8 ± 4.7	0 ± 1	0.1 ± 0.4

Pinheyschna sp.	0 ± 1	0.3 ± 0.5			0 ± 5.7	1.6 ± 2.1	0 ± 7.1	1.1 ± 2.9
Ephemerellina sp.	0 ± 2.7	0.7 ± 1.2	0 ± 2.8	1 ± 1.1			0 ± 11.4	2.4 ± 4.5

Analysis of similarity (ANOSIM) revealed no significant overall differences in macroinvertebrate community composition across the four elevation categories (Global R = –0.004, *p* = 0.571; 9999 permutations), indicating that, at the scale of the entire dataset, communities were broadly similar. Pairwise comparisons between elevation groups, however, identified some significant differences. macroinvertebrate communities at low elevations are not the same as those at high elevations, and this difference is meaningful, not due to chance. A smaller but significant difference was also observed between the 1100–1149 m and >1200 m groups (R = 0.223, *p* = 0.03), and between <1100 m and 1100–1149 m sites (R = 0.042, *p* = 0.005). All other pairwise comparisons showed minimal or non–significant differences (R < 0.177, *p* > 0.05), indicating that macroinvertebrate communities were largely similar among mid–elevation sites.

The SIMPER analysis revealed that macroinvertebrate communities were moderately similar within each elevation category but exhibited substantial dissimilarity between elevations, with differences primarily driven by a few dominant taxa (Table 3.5). The within–group similarity showed that the average similarity within groups ranged from 26.1 % at the highest elevation (>1200 m) to 34.7 % at the lowest elevation (<1100 m), indicating moderate homogeneity within each elevation. Across all elevations, the fairy shrimp Anostraca consistently contributed the most to within–group similarity, accounting for 43–55 % of similarity depending on elevation (Table 3.5). Other taxa contributing to similarity varied by elevation: Notostraca, Spinicaudata, *Pila occidentalis*, and *Rhantus* sp. were consistently important in lower to mid elevations, while high–elevation sites (>1200 m) included additional contributors such as *Gerris swakopensis*, *Gyraulus connollyi*, *Dixella* sp., and *Hydrocanthus* sp. (Table 3.5).

Between–group dissimilarity, the dissimilarity between elevation pairs was substantial, ranging from 67.9 % (<1100 m and 1150–1199 m) to 73.4 % (1100–1149 m and >1200 m), reflecting marked shifts in community composition along the elevation gradient (Table 3.5). Differences were primarily driven by changes in the abundance or presence of dominant taxa such as the Anostraca which consistently contributed the largest portion to dissimilarity (16–18 %), reflecting changes in its relative abundance across elevations (Table 3.5). Spinicaudata contributed 5–8 % to dissimilarity in comparisons where it was present at one elevation but absent at another (notably absent above 1200 m) (Table 3.5), whereas Notostraca also consistently contributed 5–7 % to dissimilarity in most comparisons. Other taxa contributing to dissimilarity included *Haliplus* sp., *Rhantus* sp., *Pila occidentalis*, *Hydrocanthus* sp., and *Dixella* sp., particularly in comparisons involving the highest elevation (>1200 m), reflecting the emergence of taxa unique to or more abundant at high altitudes (Table 3.5).

The elevation–specific patterns showed that low elevations (<1100 m) were characterised by high abundances of Anostraca, Notostraca, and Spinicaudata, which together accounted for more than 78 % of within–group similarity (Table 3.5). Mid elevations (1100–1149 m and 1150–1199 m) showed similar dominant taxa, but their relative contributions shifted slightly, with Spinicaudata increasing in importance at 1100–1149 m and Anostraca remaining dominant (Table 3.5). High elevation (>1200 m) communities were more compositionally distinct, with Anostraca, Notostraca, and a suite of additional taxa (e.g., *Haliplus* sp., Dixella sp., and *Hydrocanthus* sp.) driving both within–group similarity and between–group dissimilarity (Table 3.5). The absence of certain lower–elevation taxa (e.g., Spinicaudata) at high elevations further increased dissimilarity, highlighting an elevational turnover in macroinvertebrate assemblages (Table 3.5).

Table 3.5. SIMPER analysis of macroinvertebrate communities across elevation categories.

Comparison	Average similarity / dissimilarity (%)	Top contributing taxa (%)
Within–group		
<1100 m	Avg. similarity = 34.65	Anostraca (51.56), Notostraca (14.66), Spinicaudata (12.39), *Pila occidentalis* (1.66), *Rhantus* sp. (1.51)
1100–1149 m	Avg. similarity = 29.55	Anostraca (43.82), Spinicaudata (20.19), Notostraca–T (7.73), *Pila occidentalis* (3.24), *Hydrocanthus* sp. (2.75), *Rhantus* sp. (2.01)
1150–1199 m	Avg. similarity = 30.11	Anostraca (50.34), Spinicaudata (11.11), Notostraca (9.24), *Rhantus* sp. (1.93), *Pila occidentalis* (1.24)
>1200 m	Avg. similarity = 26.07	Anostraca (54.06), Notostraca (14.72), *Gerris swakopensis* (4.99), *Gyraulus connollyi* (3.63), *Dixella* sp. (3.55), *Hydrocanthus* sp. (3.29), *Sigara* sp. (1.78)
Between–group		
<1100 m and1100–1149 m	Avg. dissimilarity = 68.52	Anostraca (17.65), Spinicaudata (8.2), Notostraca (6.91), *Pila occidentalis* (4.71), *Hydrocanthus* sp. (3.34), *Rhantus* sp. (3.08), *Sigara* sp. (1.83)
<1100 m and 1150–1199 m	Avg. dissimilarity = 67.94	Anostraca (17.8), Spinicaudata (7.2), Notostraca (7.02), *Rhantus* sp. (2.96), *Pila occidentalis* (2.92), *Hydrocanthus* sp. (2.14), *Anisops* sp. (1.73)
1100–1149 m and 1150–1199 m	Avg. dissimilarity = 70.65	Anostraca (16.97), Spinicaudata (8.44), Notostraca (5.36), *Pila occidentalis* (4.32), *Rhantus* sp. (3.31), *Hydrocanthus* sp. (3.0), *Haliplus* sp. (1.67)
<1100 m and >1200 m	Avg. dissimilarity = 70.24	Anostraca (16.62), Notostraca (6.82), Spinicaudata (6.32), *Haliplus* sp. (3.81), *Rhantus* sp. (3.27), *Pila occidentalis* (2.49), *Hydrocanthus* sp. (2.41), *Dixella* sp. (2.38)
1100–1149 m and >1200 m	Avg. dissimilarity = 73.38	Anostraca (15.68), Spinicaudata (8.41), Notostraca (5.84), *Haliplus* sp. (3.93), *Pila occidentalis* (3.87), *Rhantus* sp. (3.55), Hydrocanthus sp (2.89)
1150–1199 m and >1200 m	Avg. dissimilarity = 71.97	Anostraca (16.16), Notostraca (5.99), Spinicaudata (5.91), *Haliplus* sp. (3.79), *Rhantus* sp. (3.52), *Dixella* sp. (2.39), *Gyraulus connollyi* (2.29), *Hydrocanthus* sp. (2.23), *Pila occidentalis* (2.07)

Macroinvertebrate metrics

Mean taxa richness was remarkably consistent across altitude classes, ranging from 15.1 to 20.1 taxa. The highest richness was recorded at 1100–1149 m, while high–altitude pans (>1200 m) supported slightly fewer taxa on average (Table 3.1). Invertebrate abundance showed strong altitudinal variation. Mid–elevation pans (1100–1149 m) supported substantially higher mean abundances (232.8 ± 236.9 individuals) compared to both lower and higher elevations. High–altitude pans supported the lowest abundances (Table 3.1). Simpson and Shannon–Wiener diversity indices were consistently moderate to high across all altitude classes, with mean Simpson values around 0.7–0.8 and Shannon–Wiener values around 2.1–2.3. Evenness was also relatively stable, though slightly higher in high–altitude pans, suggesting more equitable species distributions despite lower richness and abundance (Table 3.1).

Macroinvertebrate taxa richness differed significantly among altitude classes (F = 5.045, *p* = 0.002), indicating an altitudinal influence on community composition. However, no significant differences were detected for total abundance (F = 1.007, *p* = 0.390) or for diversity indices, including Simpson's index (F = 0.195, *p* = 0.900), Shannon–Wiener diversity (F = 0.829, *p* = 0.478), and evenness (F = 0.661, *p* = 0.577) (Table 3.2). Based on the Tukey's posthoc analysis, taxa richness differed significantly between 1100–1149 m and 1150–1199 m (*p* = 0.020) and between 1150–1199 m and >1200 m (*p* = 0.045), but not for other elevation comparisons.

Relationship between macroinvertebrates, elevation and environmental variables

Non–metric multidimensional scaling (nMDS) ordination revealed no clear separation in macroinvertebrate community structure across the four altitudinal bands (<1100 m, 1100–1149 m, 1150–1199 m, >1200 m) (Figure 4). Macroinvertebrate communities from the lowest elevation (<1100 m) were not distinctly clustered in ordination space, similarly, those from middle elevations (1100–1199 m) showed partial overlap, indicating some shared taxa (Figure 4). The highest elevation band (>1200 m) showed no clear separation from the rest of the elevations, suggesting no distinct assemblage adapted to higher altitudes. Stress for the ordination was low (stress < 0.20), indicating a good representation of community dissimilarities in two–dimensional space (Figure 4).

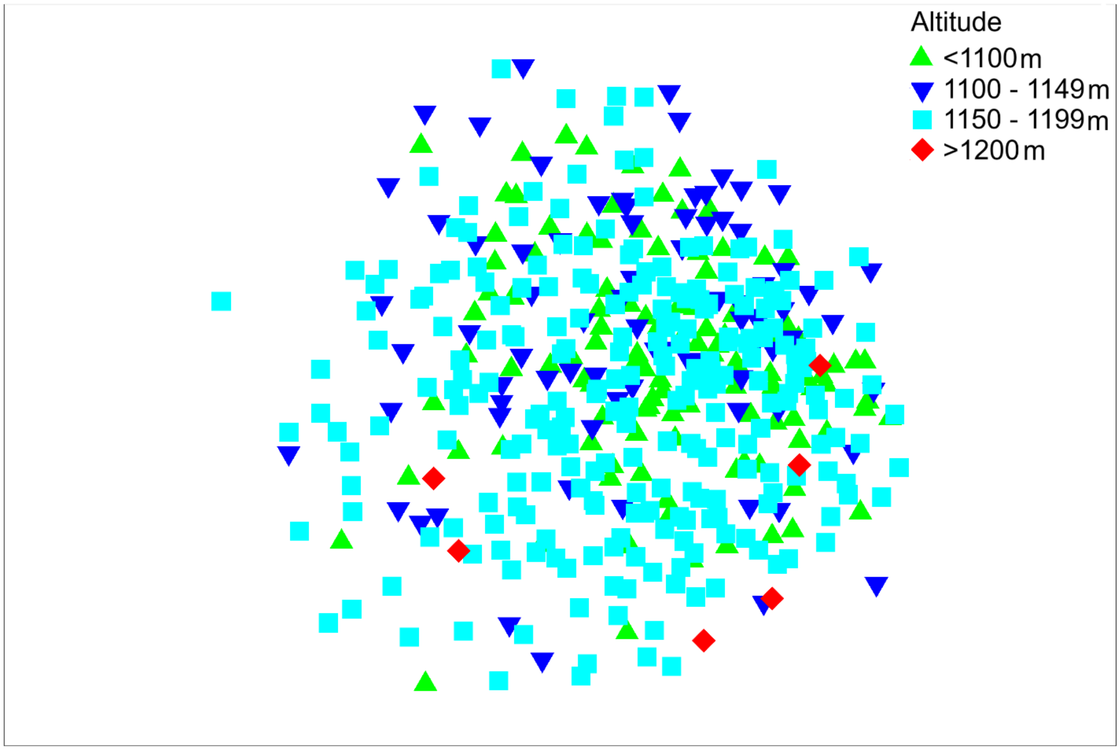

Figure 4. Non–metric multidimensional scaling (nMDS) ordination of macroinvertebrate community composition across four altitudinal bands in Khakhea–Bray Transboundary Aquifer region pan wetlands. Points represent sample sites, with symbols and colours corresponding to elevation categories. Stress = 0.19 indicate a reliable ordination.

Spatial patterns of macroinvertebrate diversity

Analysis of macroinvertebrate communities across the sampled transect revealed clear spatial structuring in both species' richness and Shannon–Wiener diversity. The most pronounced gradient was latitude, and the degree of confidence is high compared to longitude. Communities at the westernmost sites exhibited substantially higher diversity values compared to the depauperate eastern sites (Figure 4). In contrast, patterns related to altitude were negligible within the studied range (1–3 meters above sea level). Statistical analysis confirmed no significant relationship between either richness or Shannon H′ and the minimal elevational gradient captured in this dataset. Given the study design, which sampled a narrow latitudinal band (approximately –25.0° to –25.1° S), latitude was effectively held constant. Consequently, no latitudinal diversity gradient could be assessed, and the observed variation is attributed primarily to longitudinal position. Thus, macroinvertebrate diversity in the study region was strongly and positively correlated with longitude, while showing no relationship with the subtle altitudinal variation present across the sampling sites (Figure 3.2).

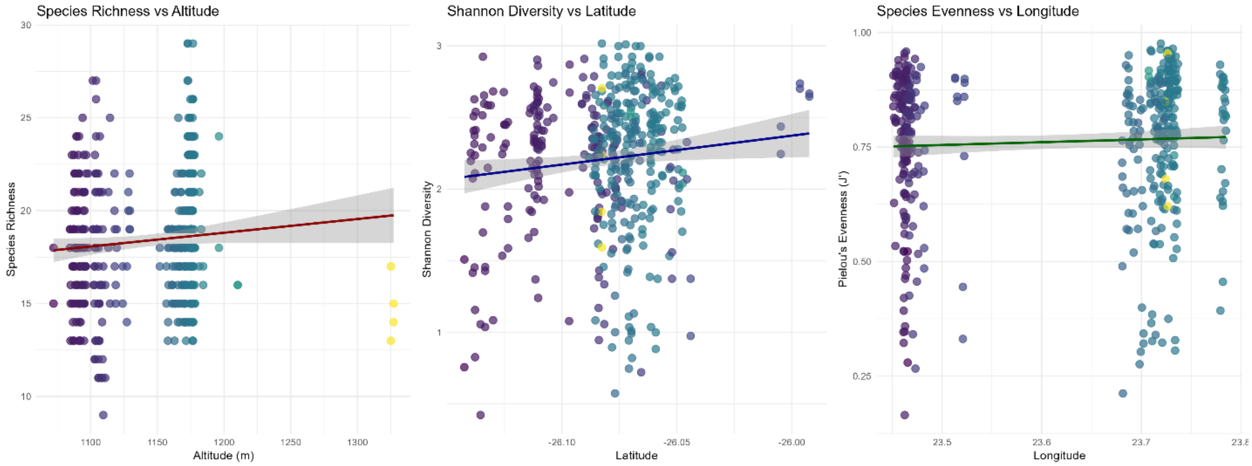

Figure 3.4. Spatial variation in macroinvertebrate community diversity across the study transect. plots show (a) species richness and (b) Shannon–Wiener diversity index plotted against longitude, latitude, and altitude/elevation.

Correlation analysis revealed no significant relationships between altitude and any of the macroinvertebrate diversity indices. correlations were observed between altitude and taxa richness (*r* = 0.09, *p* = 0.063) and between altitude and Shannon–Wiener diversity (*r* = 0.09, *p* = 0.063), although these relationships were not statistically significant. Similarly, altitude showed weak and non–significant correlations with Simpson's diversity index (*r* = 0.054, *p* = 0.255) no relationship and Pielou's evenness (*r* = 0.07, *p* = 0.159), indicating minimal influence of altitudinal variation on macroinvertebrate community structure within the study area.

Latitude exhibited modest but statistically significant weak relationships with Shannon diversity (*r* = 0.107, *p* = 0.024) and evenness (*r* = 0.101, *p* = 0.034). These results suggest a slight increase in overall diversity and a more even distribution of taxa along the latitudinal gradient. In contrast, the correlation between latitude and taxa richness was weak and non–significant (*r* = 0.049, *p* = 0.3035), as was the relationship with Simpson's diversity index (*r* = 0.091, *p* = 0.056), indicating that changes in diversity were driven primarily by relative abundance patterns rather than by an increase in the number of taxa in (Figure 3.4).

Longitude showed the strongest spatial association with macroinvertebrate assemblages, exhibiting a significant weak correlation with taxa richness ($r = 0.147$, $p = 0.002$) in (figure 3.4). This finding indicates an increase in macroinvertebrate taxa richness along the longitudinal gradient of the reservoir shoreline. However, correlations between longitude and Shannon diversity ($r = 0.091$, $p = 0.056$), Simpson's diversity index ($r = 0.043$, $p = 0.369$), and evenness ($r = 0.050$, $p = 0.299$) were weak and not statistically significant, suggesting that while the number of taxa varied spatially, overall community dominance and evenness remained relatively consistent.

The BRT results demonstrate that macroinvertebrate richness in pan wetlands is structured predominantly by broad–scale spatial driverrather than by local physicochemical conditions. The dominance of longitude and the secondary influence of altitude and latitude imply that regional landscape position, historical connectivity, and dispersal processes are likely more important drivers of macroinvertebrate richness than instantaneous water quality parameters Figure 3.5. The predictive performance of boosted regression trees (BRT) models relating macroinvertebrate taxa richness to environment variables was as follows: 4 000 number of trees fitted (boosted models), with a mean total and residual deviance of 0.589 and 0.001, respectively. The estimated cross–validated deviance ± standard error was 0.001 ± 0.001 and the cross–validated correlation of 0.99 (with a training data correlation of 0.98). 99.99% of variation was explained, retained as significant terms in the BRT model relating macroinvertebrate species richness to environmental variables, with the first 6 variables accounting for ~99.98 % of macroinvertebrate taxa richness variation, with high predictor contributor to model fit being observed for longitude (76.8 %), latitude (8.6 %) and altitude (14.5 %).

Boosted regression tree analysis indicated that macroinvertebrate richness in pan wetlands was primarily influenced by spatial variables, with longitude emerging as the dominant predictor. Longitude accounted for 76.8 % of the total relative influence in the model, indicating a strong longitudinal gradient in macroinvertebrate richness across the study area (Figure 3.3). The fitted response showed an abrupt increase in richness within a narrow longitudinal range, followed by a plateau, suggesting the presence of a threshold beyond which additional longitudinal change did not result in further increases in richness. Altitude contributed 14.5 % to the model and exhibited a moderate positive effect on macroinvertebrate richness (Figure 3.3). The fitted function indicated stepwise increases in richness with increasing altitude, implying that elevation–related factors such as hydrology, basin morphology, or climatic gradients may influence habitat suitability in pan wetlands. Latitude accounted for a smaller but still measurable proportion of the explained variation (8.6 %), with richness showing a modest increase across the latitudinal gradient before stabilising, suggesting secondary spatial structuring of communities (Figure 3.3). In contrast, water quality variables made a negligible contribution to explaining macroinvertebrate richness. The pH, dissolved oxygen, and electrical conductivity each contributed less than 0.1 % to the model (0.04 %, 0.04 %, and 0.01 %, respectively). The fitted response curves for these variables were effectively flat across their observed ranges, indicating no discernible influence on richness within the conditions sampled. This suggests that water quality across the pan wetlands was relatively homogeneous or within tolerance limits for most macroinvertebrate taxa.

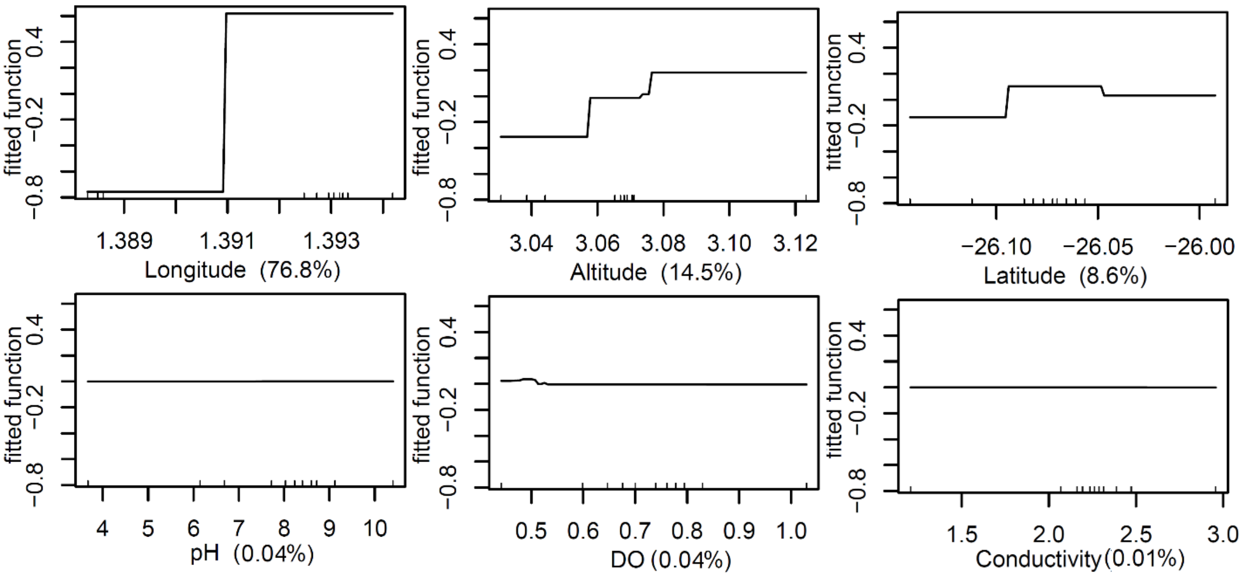

Figure 3.5. Variation in macroinvertebrate taxa richness predicted by a boosted regression trees (BRT) model for the first 6 environmental variables and using environmental characteristics as predictors.

CHAPTER 5: DISCUSSION

Picture 5. Some of the most common birds feeding on the diverse macroinvertebrate taxa in the pan wetlands, brown bird – glossy ibis *Plegadis falcinellus* and white bird – cattle egret *Bubulcus ibis*. Photo by Tatenda Dalu.

Environmental variables

Pan wetlands were primarily neutral to alkaline across all elevation classes, a pattern consistent with the carbonate-rich geology of the region and the strong influence of groundwater inputs. However, the wider pH range observed in low-altitude pans indicates greater environmental variability within these systems. This variability likely results from episodic surface runoff, fluctuating hydroperiods, and evaporative concentration during dry periods, which can alter the chemical composition of wetland waters (Jacobsen and Dangles, 2017; Ge et al., 2025). Such processes introduce pulses of dissolved ions and nutrients, contributing to short-term shifts in water chemistry. In contrast, pans located at higher elevations exhibited more stable and consistently alkaline conditions. This trend may reflect stronger groundwater control, reduced influence of surface runoff, and longer water residence times, which together promote greater buffering capacity and chemical stability within these systems, the observed patterns suggest that elevation influences the degree of hydrological connectivity and water balance processes, which in turn shape the physico-chemical characteristics of pan wetlands.

The findings of the study are in with findings from Masina et al. (2023), who found that the indication of macroinvertebrate contrast diversity in Khakhea–Bray pan wetlands is maximized under intermediate environmental conditions, where hydroperiod stability, oxygen availability, nutrient enrichment, and habitat complexity intersect. Their study results highlighted the ecological importance of mid–elevation pans and emphasise the sensitivity of macroinvertebrate communities to changes in groundwater–surface water interactions (Fair et al., 2017). Given increasing pressures from groundwater abstraction and climate variability, protecting the hydrological integrity of these pan wetlands is essential for maintaining biodiversity and ecosystem functioning across the transboundary aquifer (Jeethu, 2025; Moomaw et al., 2018).

We observed that significant changes in water temperature were found between lower and mid–elevation sites, especially between <1100 m and 1150–1199 m. The results show that the higher elevations, shows that differences were less pronounced. This finding is consistent with the study by Pandey et al. (2021), which also reported minimal temperature variation among high-elevation pans, suggesting that the influence of altitude may be overridden by local factors such as pan depth, surface area, and shading.

Significant variations in water depth were found mostly between adjacent elevation groups, especially between <1100 m and 1100–1149 m and between 1100–1149 m and 1150–1199 m. It also indicates that rather than throughout the entire elevation gradient, hydrological variation is most visible during lower to mid–elevation transitions. The findings of the study are consistent with findings from Adams (2016) who reported that the longer hydroperiods are probably encouraged by increased depth at mid–elevations, improving habitat stability and enabling a greater variety of species to finish their life cycles. According to Shrestha et al. (2021) research, they reported that depth and hydroperiod length are among the best indicators of macroinvertebrate abundance and richness in pan wetlands, frequently surpassing the direct impacts of elevation.

The study results show that strong elevation–specific patterns were seen in the dynamics of nutrients, especially phosphate and nitrate. This is in contrast to a study by Martin et al (2018), which highlighted that significant variations in nitrate concentrations between low and mid–elevation locations point to increased nitrification or external inputs at these altitudes, which may be related to oxygen availability and watershed processes in contrast, the present study demonstrates that macroinvertebrate assemblage patterns vary significantly across the altitudinal gradient, with shifts in dominant taxa and community composition occurring between elevation classes. By explicitly examining spatial patterns across multiple elevation categories, this study provides new insights into how elevation-driven environmental filters structure macroinvertebrate assemblages within the Khakhea–Bray aquifer landscapeWe observed that phosphate displayed a similar pattern, with variations focused in the elevation area between 1100 and 1149 meters. Johnson et al. (1997) findings are consistent with those of other groundwater–dependent wetlands, where a combination of surface runoff, groundwater inflow, and internal recycling frequently results in the highest nutrient concentrations at intermediate altitudes. Higher macroinvertebrate abundance can be indirectly supported by increased primary productivity brought about by elevated nutrients, but if enrichment becomes excessive, it may also favor tolerant taxa (Wagenhoff, et al., 2012; Davis et al., 2018; Kendrick et al., 2019;)

Specific deposition at mid–elevations is suggested by the considerable differences in ammonium concentrations between low and mid–elevation locations, especially in the 1150–1199 m category (Taylor et al., 2021). According to Whitby (2025), specific deposition could be the result of higher organic matter decomposition in pans with longer hydroperiods or decreased nitrification under varying oxygen conditions.

Macroinvertebrates

This study shows that significant differences in macroinvertebrate community structure across elevation categories, as indicated by PERMANOVA results, demonstrate that elevation–related environmental gradients play a key role in shaping assemblage composition in groundwater–dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer region. These findings were consistent with those by Cukusic (2025): Mungenge et al. (2023) They also found that the Variations in relative abundance and dominance patterns indicate that community organization responds sensitively to changes in hydrology, water chemistry, and habitat stability, even though pan wetlands across elevations share a core group of organisms. Bird et al. (2019) reported that elevation-related differences in macroinvertebrate assemblages are common worldwide, where elevation acts indirectly by reflecting variations in hydroperiod, oxygen availability, and nutrient dynamics.

Largebranchiopods, especially Anostraca, Spinicaudata, and Notostraca, dominated low–altitude pans and made up a significant portion of the assemblage composition. These taxa predominate in shallow, short–hydroperiod wetlands that undergo frequent drying and abrupt environmental changes (Demeter et al., 2008; Van den Broeck et al., 2015). According to Moyo (2023), Anostraca, Spinicaudata, and Notostraca have quick life cycles and ability to produce drought–resistant resting eggs. Large branchiopods are well suited to these circumstances and can take advantage of transient habitats before they dry out. Mataba (2023), found that ephemeral pan wetlands in southern Africa and other arid and semi–arid regions, where branchiopods frequently outcompete aquatic insects under extremely variable conditions.

Increased taxonomic heterogeneity was observed in macroinvertebrate assemblages at 1100m–1149 m, as evidenced by a decrease in branchiopod dominance and an increase in aquatic insects, such as Coleoptera, Hemiptera, and Odonata These findings are consistent with those of Gerstle et al. (2023), who reported that lower-elevation wetlands are often associated with longer hydroperiods and greater habitat stability. Such conditions support the establishment of taxa with longer developmental cycles and more specific habitat requirements. Similar transitions from assemblages dominated by branchiopods to communities rich in insects have been documented by Boix and Batzer. (2016) in wetlands undergoing moderate hydroperiods, where more diverse functional groups are favored by improved oxygen conditions and increased structural complexity.

The study showed a trend most compositionally complex macroinvertebrate communities, with comparatively high and uniformly distributed abundances of insects, mollusks, and branchiopods, were found in mid–elevation pans (1150–1199 m). The resulst show that the increased habitat heterogeneity and ecological stability within this elevation band are suggested by the persistent presence of Coleoptera, Hemiptera, Odonata, Diptera, and molluscs such as *Gyraulus connollyi* and *Pila occidentalis*.Wetlands influenced by groundwater have also been shown to support higher macroinvertebrate diversity when hydroperiods are intermediate, as these conditions balance environmental disturbance with habitat persistence (Orsholm and Elenius, 2022). . A greater variety of ecological niches, such as benthic, littoral, and vegetated microhabitats, are probably offered by these pans (Gleason., 2017).

Macroinvertebrate diversity were found to be significantly influenced by dissolved oxygen conditions. Strongly oxidising but highly variable ORP values at low elevations indicate fluctuating aerobic conditions, whereas negative ORP values and low dissolved oxygen concentrations at high elevations indicate persistent or intermittent hypoxia (Niu et al., 2015; Lipson et al., 2012). These reduced conditions are likely linked to longer hydroperiods, deeper water, and less mixing in high–altitude pans (Tianzhu et al.,2017). According to Harrison et al. (2018) hypoxic environments typically favor taxa to adapt to low oxygen availability, for example Diptera, while restricting oxygen–sensitive groups may account for the decreased abundance and taxonomic richness seen at >1200 m. Despite lower richness, relatively high evenness and diversity indices at higher elevations point to more stable community structures dominated by fewer, well–adapted taxa (Lalbiaknunga et al., 2025).

This study results show that the highest macroinvertebrate abundance and consistently high diversity metrics were found in mid–elevation pans (1100–1199 m). The increased surface area and intermediate depths at these elevations likely enhance habitat heterogeneity by maintaining a mosaic of littoral and benthic microhabitats, which are known to support macroinvertebrate diversity. At mid–elevations, higher phosphate and nitrate concentrations boosted primary productivity, which in turn supported higher secondary production and macroinvertebrate abundance (Everall et al., 2019). The findings of the study are in contrast with findings from Weyer et al. (2018) who reported that nutrient patterns highlight the connection between hydrology and biogeochemistry, their results show that high ammonium concentrations in low–altitude pans suggest strong external inputs or rapid mineralization under different redox conditions, whereas lower ammonium but higher nitrate at mid–elevations indicate active nitrification under more oxic conditions. The return of raised ammonium and increasing phosphate concentrations at high elevations could be due to reduced nitrification and internal nutrient loading from sediments under reducing conditions (Ma et al., 2023; Ding et al., 2022). These nutrient regimes can influence the makeup of macroinvertebrate communities by altering food availability and favoring taxa that can thrive in enriched or oxygen–deprived conditions (Dangles., 2023). These results show that the constant change of these groundwater–dependent wetlands is highlighted by temporal variability, which is inferred from wide ranges and significant variances across most variables. According Fornaroli et al., (2020) study shows that the temporal changes in macroinvertebrate assemblages are probably caused by seasonal variations in temperature, water depth, and nutrient concentrations, especially in shallow low–altitude pans with brief hydroperiods. Which align with this study because deeper high–altitude pans, they operate as chemically limited but more temporally stable systems.

Macroinvertebrate community similarity declines with increasing geographic distance between pans, indicating spatial autocorrelation and limited connectivity, with regards to second hypothesis. We found that across low to mid–elevation pans, dissolved oxygen (DO) conditions were comparatively consistent, with no discernible variations between sites below 1100 m and those between 1100–1149 m or 1150–1199 m. This indicates that the oxygen availability in these elevation bands is generally similar, which is probably due to the shallow depths and frequent mixing linked to shorter hydroperiods (Dodds et al., 2019; Herbst et al., 2019). This results show that was significant variations in the highest elevation category (>1200 m), there was a significtly higer DO in the highest elevation category (>1200 m) however, show a definite shift toward different oxygen conditions at higher elevations. According to Nyman et al. (2008), longer water retention, and less mixing are frequently linked to lower oxygen levels at higher elevations, which favor oxygen–tolerant macroinvertebrate species and may restrict the occurrence of sensitive groups. Which align with this study because from the results, there study show that groundwater–fed wetlands, are steady but low–oxygen conditions result in simpler but more uniform macroinvertebrate groups, are consistent with this pattern.

The results show that macroinvertebrate metabolism and development rates are all significantly influenced by temperature and increased thermal variability at low and mid elevations probably leads to larger temporal turnover in species composition. Similar results by Gutierrez. (2024) have been documented in transient wetlands, where seasonal macroinvertebrate succession is shaped by temperature variations and hydroperiod. Mccormick (2004) in their study they found that wetland systems, ammonium enrichment has been linked to changes toward opportunistic and detritivorous macroinvertebrate taxa, which may account for observed variations in community composition rather than significant alterations in total taxonomic richness. In this study we observed that macroinvertebrate metrics indicated significant but comparatively small elevation–related variations. This is in contrast to a study by Amundrud and Srivastava. (2020) which highlighted that some mid– and high–elevation comparisons showed considerable differences in taxonomic richness, suggesting that communities may be structured by environmental thresholds rather than progressive gradients. According to Ferrari et al. (2016) the changes in abundance and community composition are more sensitive indicators of environmental change, the lack of widespread substantial alterations in richness shows that many macroinvertebrate taxa in pan wetlands are generally tolerant. This pattern align with our study is in line because we found that groundwater–fed wetlands, where assemblage structure and dominance patterns change in response to oxygen, nutrients, and hydroperiod, but richness stays constant across gradients.

Simpler assemblages with lower overall abundance but comparatively high dominance by a few taxa were found in high–altitude pans (>1200 m). Increases in Notostraca and certain insect taxa such as *Rhantus*, *Haliplus, Dixella*, and *Anax*. indicate adaptation to deeper, longer–lasting, and frequently lower–oxygen conditions, even though Anostraca remained predominant. Other wetland studies by (Schriever et al., 2014; Birrell et al., 2020; Obertegger et al., 2021) have documented decreased species richness at higher elevations, which is typically explained by lower temperatures, less oxygen availability, and longer hydroperiods that exclude taxa adapted to ephemeral conditions.

The results show that Anostraca's were persistence across all elevation categories emphasizes the critical role that groundwater–dependent hydrology plays in preserving pan–wetland biodiversity this was because both transient and semi–permanent taxa can coexist throughout the landscape. These findings were consistent with those of Yihdego et al. (2017) who also found that wetlands, where groundwater connectivity increases resilience but also increases sensitivity to hydrological alteration. According to Deane (2018) study shows that the elevation–related shifts in macroinvertebrates community, changes in overall richness that provide a sensitive indicator of ecological change in groundwater–dependent wetlands. These findings align with this study because we also found that the importance of protecting natural groundwater regimes to maintain biodiversity and ecosystem functioning in transboundary pan wetland systems.

The ANOSIM results show that the macroinvertebrate communities in the Khakhea–Bray groundwater–dependent pan wetlands were mostly the same when looked at across the whole elevation gradient. We found that pans are strongly connected ecologically and share species pools. These findings were consistent with those of Leshaba (2023) their study found similarity in line with the fact that many generalists and disturbance–tolerant taxa are found in temporary wetland systems. According to Mpakairi. (2022) documented that pairwise disparities between the lowest and highest elevation sites, as well as between high and certain mid–elevation sites, found that community composition varies at elevational extremes. The finding aligns with Ramírez (2024), study because the found differences due to changes in hydroperiod, water depth, oxygen availability, and habitat stability, all of which are known to affect macroinvertebrate assemblages in pan and ephemeral wetlands. Similar study by Arts (2022) observed that other groundwater–influenced wetlands, where general compositional similarity conceals nuanced yet ecologically significant turnover along environmental gradients.

The SIMPER analysis revealed that both within–group similarity and between–group dissimilarity was predominantly influenced by a limited number of dominant taxa, especially Anostraca, which consistently represented the largest proportion of similarity and dissimilarity across all elevations.

The result of this study shows that high relative abundances of large branchiopods such as Anostraca, Spinicaudata, and Notostraca were found in low– and mid–elevation pans. According to Chertoprud (2024) study shows that these organisms have adapted to changing hydroperiods and in drying periods. The results show that high–elevation pans had more compositionally distinct communities. I also observed that they also had more aquatic insects and mollusks, such as *Haliplu, Dixella, Hydrocanthus* and *Gyraulus connollyi.* Some low–elevation taxa were missing. According to McDaniel. (2022) turnover in elevation suggests that while groundwater inputs make regions more similar, environmental factors at higher elevations create simpler but different groups of macroinvertebrates. The study results show that changes in dominance and relative abundance, rather than complete species replacement, are what cause macroinvertebrates to respond to changes in elevation in groundwater–dependent pan wetlands.

Macroinvertebrate metrices

Patterns of macroinvertebrate metrics across altitude classes show that elevation had a subtle rather than dominant effect on the community structure in the Khakhea–Bray Transboundary Aquifer pan wetlands. Although taxa richness differed significantly among altitude classes, the overall ordination pattern indicated that elevation explained only a small proportion of the variation in macroinvertebrate community structure. The considerable overlap among elevation groups in the nMDS ordination suggests that a large proportion of community variation remained unexplained by altitude alone, likely reflecting the influence of other environmental variables such as hydroperiod stability, substrate composition, and water quality. Mean taxa richness remained relatively stable across elevations, exhibiting only a slight decrease at the highest altitudes (>1200 m). This indicates that regional species pools and dispersal mechanisms significantly influence assemblages throughout the landscape (Onditi et al., 2024; Leberg et al., 2024). The findings of the study are in contrast with findings from Rubin et al., (2024) they reported similar patterns that have been observed in other temporary and groundwater–dependent wetlands, where extensive environmental tolerances and significant dispersal capabilities of numerous taxa diminish pronounced richness gradients along elevation. This study uniquely demonstrates that in the Khakhea–Bray Transboundary Aquifer pan wetlands, macroinvertebrate richness peaks at mid–elevations (1100–1149 m) where hydroperiod conditions allow coexistence of early-colonizing branchiopods and later-successional insect taxa. This suggests that hydroperiod dynamics rather than elevation structure macroinvertebrate assemblages in these groundwater-dependent pan wetlands.We observed that there was a slightly higher richness at mid–elevations (1100m–1149m) this may be due to the harsh hydroperiod conditions, where pans hold water long enough to support both early–colonizing branchiopods and later–successional insect taxa without drying out or being stressed by the weather for too long (Keith et al., 2022; Dalu et a., 2025).

The foundings of this study is that abundance of macroinvertebrates showed significant changes with altitude, reaching its highest point at mid–elevations and dropping off at both lower and higher altitudes. Increased abundances at 1100m–1149 m probably indicate good combinations of water permanence, productivity, and habitat stability. The findings of the study are in contrast with findings from Dolmans et al. (2025) who find that those conditions that are known to help ephemeral wetland invertebrates grow in number. Similar mid–elevation abundance peaks have been observed in African and semi–arid wetland ecosystems, where intermediate disturbance regimes optimize population size while accommodating disturbance–adapted taxa (Culp et al., 2022; Dorji., 2024; Granath et al., 2024). The lower numbers seen at higher elevations may be because of cooler temperatures, shorter hydroperiods, and lower primary productivity, which all make it harder for new plants to grow and survive (Dolabela et al., 2022). We also observed that the abundance of species varied, diversity indices and evenness stayed stable across all the elevations.

The notable disparities in taxa richness across elevation classes, especially between mid– and high–elevation bands, indicate nuanced environmental filtering along the elevational gradient. The findings of the study are in contrast with findings from Che et al. (2025), who reported that the lack of substantial differences in abundance, Simpson’s diversity, Shannon–Wiener diversity, and evenness suggests that the overall organisation of the community remains largely consistent across elevations. Many studies (Lechêne et al., 2018; Coccia et al., 2021; Keith et al., 2025) have found that separation of richness from diversity metrics in temporary wetlands, where functional redundancy and shared life–history traits protect communities from changes in the environment. The results from Tukey posthoc analysis show that elevational thresholds between 1150m and 1200 m may be transitional zones where some taxa become less common or disappear altogether, rather than clear ecological boundaries.

The boosted regression tree (BRT) analysis from this study shows that spatial gradients, not local physicochemical variables, are what mostly shape the richness of macroinvertebrates in pan wetlands of the Khakhea–Bray Transboundary Aquifer. I found that longitude was the most important factor, explaining (76.8%) of the variation in taxa richness. This pattern indicates that extensive landscape factors, including historical connectivity, dispersal mechanisms, or basin morphology, significantly affect community composition (Rampheri et al., 2023; Uroy et al.,2019). We observed that Altitude had a moderate effect (14.5 %) on richness, with higher elevations leading to more richness. This suggests that factors related to elevation, like hydrology or microclimate, are not the main factor that determine habitat suitability (Stark et al., 2022). The result shows that latitude had a smaller effect (8.6 %), with richness going up a little along the gradient. This suggests that communities are not very structured by latitude (Ren et al., 2018). The findings of this study do not strongly support those of Olmedo et al., (2021) who reported that water quality parameters such as pH, dissolved oxygen, and conductivity had minimal influence on macroinvertebrate communities (<0.1%), with fitted response curves remaining largely flat. In contrast, the present study suggests that environmental gradients may still contribute to shaping macroinvertebrate assemblages within the Khakhea–Bray Transboundary Aquifer pan wetlands. From our results we observed that the water chemistry was either fairly uniform or within acceptable ranges for the macroinvertebrate taxa that were sampled. Correlation analyses corroborated these results, revealing weak and predominantly non–significant relationships among altitude, latitude, and diversity indices, with the exception of minor positive correlations between latitude and Shannon diversity and evenness (Burger., 2017; Alavaisha et al., 2019; Munyai et al., 2023b). This study results show that the diversity of macroinvertebrates in these pan wetlands is mostly affected by where they are in the landscape, with water quality having little effect these patterns show how important it is to think about factors on a regional scale when measuring biodiversity.

The nMDS ordination analysis shows that macroinvertebrate communities are not significantly differentiated by altitude in the study area. The significant overlap among elevation categories in ordination space indicates that the majority of taxa inhabit various altitudinal bands, underscoring the significance of regional connectivity, dispersal, and groundwater influence in shaping pan wetland communities. The findings of the study are in contrast with findings from Jacobsen et al. (2020) and Devi et al (2020), because the found similar ordination patterns that have been documented in other groundwater–fed and temporary wetland systems, where localized environmental variability surpasses extensive topographic gradients. The absence of a distinct high–altitude assemblage suggests that elevation alone does not impose sufficiently robust environmental constraints to foster unique macroinvertebrate communities (Chaves et al., 2008). According to Fu et al. (2018) found that patterns we see are probably caused by small changes in relative abundance, hydroperiod length, and habitat conditions. Our results show that macroinvertebrate communities in the Khakhea–Bray pan wetlands are organized along a continuum rather than separate elevation zones because the elevation is one of the secondary factors that interacts with hydrology and local habitat conditions.

According to Nsor et al. (2020) who reported that spatial pattern indicates that spatial coordinate, serving as a proxy for underlying environmental gradients, significantly influences the composition of macroinvertebrate assemblages along the study transect. Similar longitudinal structuring has been observed in aquatic ecosystems where alterations in climatic conditions, hydrology, substrate composition, or land–use intensity manifest along east–west gradients (Shah et al., 2018; Mayfield., 2020; Valente–Neto et al., 2025). In many areas, longitudinal variation signifies alterations in moisture availability, productivity, or water permanence, all of which are essential determinants of macroinvertebrate diversity (Smith et al., 2017). We found that the diversity at the western sites may signify more stable or heterogeneous habitats that accommodate a broader range of ecological niches in contrast to the more environmentally restricted eastern sites.

Ecological mechanisms to longitudinal diversity gradients, the positive correlation between longitude and macroinvertebrate diversity identified in this study corresponds with the species habitat heterogeneity (Frainer et al., 2018; Dézerald et al., 2023; Scott et al., 2025). More complex habitats, better water quality, or less disturbance in the western part of the transect could make it easier for species to settle in and less likely for them to be excluded by competition, this would lead to more species richness and evenness (Brown et al., 2011; Tolonen, 2018). Similar research by Starr (2014) and Van Looy (2017), has shown that macroinvertebrate communities exhibit significant responses to spatial gradients associated with hydrological connectivity and nutrient availability, which frequently fluctuate longitudinally across landscapes. The significant gradient observed from our study corroborates the perspective that spatial position, rather than plain geographic distance, is a principal factor influencing community assembly in freshwater invertebrates.

Absence of altitudinal impact on community structure, unlike longitude, altitude did not have a noticeable effect on species richness or Shannon diversity in this study. We observed that the was very small range of elevations that were sampled (1–3 m level). Similar research by Hou et al. (2025) shown that altitude affects the diversity of macroinvertebrates mostly over wide elevation gradients where temperature, oxygen levels, and flow patterns change. According to Zaharescu et al. (2016) found that restricted altitudinal range, environmental conditions are probably quite uniform, leaving little room for altitudinal variation in community structure. We observed that the lack of an altitudinal signal in this study indicates methodological and geographical limitations rather than the ecological irrelevance of elevation itself.

We found that the latitude is often linked to extensive biodiversity patterns, such as the well–established latitudinal diversity gradient, this study was not intended to evaluate these effects. The sampling was confined to a limited latitudinal range (approximately −25.0° to −25.1° S), thereby maintaining latitude at a constant level, no significant latitudinal trends in macroinvertebrate diversity were detected. This result aligns with Milner et al. (2023) and Heino et al. (2013) study because they reported that other fine–scale investigations that indicate minimal or non–existent latitudinal effects when geographic extent is constrained. The results from the study show that the absence of a latitudinal signal substantiates has led us to conclusion that the observed variation in diversity is predominantly influenced by longitudinal differences rather than extensive biogeographic gradients.

We found that the pronounced longitudinal structuring of macroinvertebrate diversity identified in this study emphasizes the necessity of incorporating spatial gradients in the evaluation of freshwater biodiversity (Schmera et al., 2017). Macroinvertebrates are extensively utilized as bioindicators of ecosystem health, and the findings indicate that longitudinal position must be explicitly integrated into monitoring and conservation strategies (Assie et al., 2014; Heino et al., 2015). The findings of the study differ with findings from Yirigui et al. (2019) because tthey reportedthat regional and global assessments of freshwater biodiversity have made similar suggestions, stressing how the spatial context affects biological communities.

CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS

Picture 6. Some fairy shrimp swimming and feeding the pan wetland. Photo by Busisiwe Gumede.

The aim of the study is to quantify how biodiversity and community structure vary across the landscape, identify key environmental controls, and assess the degree to which spatial and transboundary factors shape ecological patterns. These insights are essential for informing conservation planning and long–term monitoring of groundwater–linked surface ecosystems in this shared aquifer system. In this study, I evaluated water nutrients, environmental variables and diversity of macroinvertebrates in relation to anthropogenic wetlands activities that may be taking place in the Khakhea–Bray TBA in South Africa. This study shows that macroinvertebrate diversity and community structure in groundwater–dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer are strongly influenced by altitudinal gradients through their effects on physicochemical conditions, morphometry, and nutrient dynamics. In line with the first hypothesis, therefore hypothesis one was supported, the study results indicated that altitude is not a direct ecological driver, it integrates multiple interacting environmental variables that collectively shape habitat suitability and temporal variability in these systems. The study results show that the macroinvertebrate community similarity declines with increasing geographic distance between pans, indicating spatial autocorrelation and limited connectivity Therefore second hypothesis was supported, Harsh environmental conditions and reduced habitat heterogeneity at high elevations and they were limited niche availability and favour fewer, more specialised taxa, thefore hypothesis three is rejected. This study shows that community composition from the results differ significantly among elevation bands, with high–elevation assemblages being distinct from low– and mid–elevation communitie and environmental filtering seleced for cold–adapted, resilient taxa at higher elevations, while lower elevations support more diverse and temperature–sensitive species, thefore. hypothesis four was supported.

Overall synthesis of findings

This study was to assess macroinvertebrate diversity, community structure, and temporal variability in groundwater-dependent pan wetlands within the Khakhea–Bray Transboundary Aquifer (TBA), with particular emphasis on environmental controls, spatial drivers, and transboundary ecological dynamics. The findings demonstrate that macroinvertebrate assemblages in these wetlands are shaped by a complex interplay of hydrological stability, physicochemical conditions, and landscape scale spatial gradients rather than by altitude as a single, direct ecological driver. Across the study area, pan wetlands supported diverse macroinvertebrate communities dominated by taxa adapted to hydroperiod variability and groundwater influence. Elevation emerged as an integrative variable that reflects changes in hydroperiod length, water depth, oxygen availability, and nutrient dynamics, rather than acting as an independent determinant of biodiversity (Sgarzi et al., 2025; Taurozzi and Scalici, 2026). This supports the view that groundwater-linked surface ecosystems operate as coupled systems in which biological responses are governed by indirect environmental filtering processes (Bjerring et al., 2013; Barba et al., 2019). The study further revealed that spatial structuring, particularly along a longitudinal gradient, played a more influential role in shaping macroinvertebrate diversity than local water chemistry alone. Community similarity declined with increasing geographic distance, highlighting limited connectivity among pans and reinforcing the importance of dispersal constraints and spatial autocorrelation in this semi-arid landscape. These findings underscore the need to interpret biodiversity patterns in groundwater-dependent wetlands within a multi-scale framework that integrates local habitat conditions with broader landscape processes.

Environmental drivers of macroinvertebrate communities

Physicochemical conditions across the Khakhea–Bray pan wetlands were generally consistent with groundwater influence, particularly neutral to alkaline pH conditions associated with respective to carbonate-rich geology. However, variability in dissolved oxygen, redox conditions, nutrient concentrations, and water depth exerted strong indirect controls on macroinvertebrate assemblages (Majdi et al., 2016; Michael, 2024). Mid-elevation pans consistently supported higher macroinvertebrate abundance and more balanced community structures, reflecting optimal combinations of hydroperiod stability, nutrient availability, and habitat heterogeneity. These systems appear to function as ecological transition zones where both disturbance-tolerant taxa and species with longer developmental requirements can coexist (Jentsch et al., 2022). In contrast, low-elevation pans were characterised by high environmental variability and episodic disturbance, favouring opportunistic and fast-colonising taxa, while high-elevation pans supported simpler but more stable assemblages dominated by taxa adapted to deeper, longer-lasting, and frequently low-oxygen conditions (Chong et al., 2013; Villarreal and Coronato, 2017). Importantly, the relative stability of diversity indices across elevation classes indicates that changes in community structure were driven primarily by shifts in dominance and relative abundance rather than wholesale species loss. This suggests a degree of functional redundancy within macroinvertebrate communities, which may confer resilience to moderate environmental fluctuations but also masks early ecological degradation if assessments rely solely on richness-based metrics (Brandl et al., 2016; Worischka et al., 2023).

Macroinvertebrate community structure and functional patterns

Macroinvertebrate assemblages across the Khakhea–Bray pan wetlands exhibited clear compositional difference along elevation-linked and hydrological gradients, despite sharing a common regional species pool. Large branchiopods were a defining feature across all elevation classes, reflecting the ecological importance of temporary and semi-permanent hydroperiods in shaping wetland biodiversity within the TBA (Mabidi and Perissinotto, 2017). Their persistence across the landscape highlights the buffering role of groundwater inputs, which allow both transient and longer-lived taxa to coexist within these systems (Alfonso et al., 2016; McLean et al., 2020). At lower elevations, communities were dominated by taxa adapted to frequent drying and rapid environmental change, whereas mid-elevation pans supported the highest compositional complexity, with a diverse mix of aquatic insects, molluscs, and branchiopods (MacLeod, 2013; Sarkar, 2023). High-elevation pans, although less taxonomically rich, supported distinct assemblages characterised by oxygen-tolerant and cold-adapted taxa, indicating strong environmental filtering under more stable but restrictive conditions (Schaefer et al., 2016) Multivariate analyses confirmed that while elevation alone did not create discrete ecological zones, subtle but ecologically meaningful shifts in community organisation occurred along environmental continua (Cordeiro et al., 2023; Niculita-Hirzel et al., 2024) . These shifts were primarily reflected in dominance patterns rather than in overall richness or diversity indices, reinforcing the importance of abundance-based and compositional metrics in the assessment of groundwater-dependent wetlands (Salazar Flórez et al., 2025).

Spatial and transboundary patterns

One of the most significant findings of this study is the pronounced longitudinal structuring of macroinvertebrate diversity across the Khakhea–Bray TBA. Species richness and Shannon–Wiener diversity increased from east to west, indicating that spatial position within the landscape exerts a stronger influence on community assembly than altitude or latitude within the limited gradients sampled (Derartu, 2023; Gabriel et al., 2025). The decline in community similarity with increasing geographic distance between pans provides clear evidence of spatial autocorrelation and limited connectivity, particularly relevant in a transboundary context (Peng et al., 2024). Although groundwater connectivity enhances hydrological stability, it does not necessarily translate into biological connectivity for macroinvertebrates, many of which rely on passive dispersal mechanisms (Sarremejane et al., 2022; Land and Peters., 2023) These findings emphasise that pan wetlands within the Khakhea–Bray TBA should not be viewed as ecologically uniform units, but rather as spatially structured systems requiring coordinated management across national boundaries. The absence of strong latitudinal and altitudinal signals further indicates that biodiversity patterns in this system are driven more by landscape-scale spatial organisation than by classical biogeographic gradients (Stevens et al., 2019; Mikryukov et al., 2023; García-Beltrán, et al., 2025). This highlights the importance of incorporating spatial context into monitoring programmes and conservation planning for transboundary aquifer-dependent ecosystems (Msesane et al., 2025).

Implications for conservation and management

The results of this study have important implications for the conservation of groundwater-dependent pan wetlands in semi-arid regions. The sensitivity of macroinvertebrate communities to changes in hydroperiod stability, oxygen availability, and nutrient dynamics underscores the vulnerability of these systems to groundwater abstraction, land-use change, and climate variability (Chiloane et al., 2022; Rampheri et al., 2023). Mid-elevation pans, in particular, emerge as biodiversity hotspots that warrant priority protection due to their high abundance, compositional complexity, and functional importance (Kidane et al., 2022). Given that biodiversity responses were more strongly linked to spatial gradients than to local water chemistry, conservation strategies should move beyond site-specific assessments and adopt landscape-scale approaches (Morris et al., 2019; Graziano et al., 2022). Protecting hydrological connectivity, maintaining natural groundwater regimes, and limiting cumulative impacts across the transboundary aquifer are essential for sustaining ecosystem functioning and resilience (Maass-Morales et al., 2024; Sabzevari and Eslamian, 2026).

The finding highlights the need for coordinated conservation and management strategies for groundwater-dependent pan wetasland in the Khakhea-Bray Tranboundary Aqufer. To keep hydroperiod stability, coordinated transboundary governance should enforce limits on sustainable groundwater abstraction (Loucks and Van Beek, 2017; Golovina et al., 2021). Mid-elevation pans should be prioritized for protection because they are home to a lot of different species and are important for the environment (Kafle et al., 2020; Jaiswal and Jayakumar, 2024). Biodiversity monitoring programs ought to integrate spatial gradients, especially longitudinal patterns, and prioritize macroinvertebrate community composition and abundance as sensitive indicators of environmental change (Van Looy et al., 2017; Mureithi et al., 2025). Future research should focus on long-term, multi-seasonal monitoring, functional and trait-based assessments, and integrated hydrological-ecological studies. Such approaches will improve understanding of landscape connectivity, ecosystem resilience, and biodiversity dynamics within groundwater-dependent pan wetland systems.

Conclusion

In conclusion, this study demonstrates that macroinvertebrate diversity and community structure in groundwater-dependent pan wetlands of the Khakhea–Bray Transboundary Aquifer are shaped by interacting environmental and spatial covariance operating across multiple scales. Elevation functions as an indirect integrator of hydrological and physicochemical conditions, while spatial position within the landscape exerts a dominant influence on biodiversity patterns. These findings highlight the ecological significance of pan wetlands as dynamic, groundwater-linked ecosystems and reinforce the urgent need for integrated, transboundary management to safeguard their biodiversity and ecosystem services under increasing environmental pressure.

REFERENCES

Picture 7. Illegal dumping of bottles in the pan wetland. Photo by Busisiwe Gumede

Abata, O.E., Adesorioye, K.C., Babaniyi, E.E. & Adebomi, J.I., 2025. Constructed wetlands for wastewater treatment and role of wetlands in water quality improvement and filtration. In: *Wetland Ecosystems: Conservation Strategies, Policy Management and Applications*, pp. 297–323. Cham: Springer Nature Switzerland.

Adams, R., 2016. Water–table elevation and depth to water table. Minnesota Department of Natural Resources, Ecological and Water Resources Division, County Geologic Atlas Program.

Adeeyo, A.O., Ndlovu, S.S., Ngwagwe, L.M., Mudau, M., Alabi, M.A. & Edokpayi, J.N., 2022. Wetland resources in South Africa: threats and metadata study. *Resources*, 11(6), p.54.

Adesakin, T.A., Erhomosele, E.I., Ogunrinola, O.F., Oloyede, O.O., Adedeji, A.A., Odufuwa, P.T., Aimienoho, A., Aduwo, A.I. & Adewumi, E.A., 2023. Using benthic macroinvertebrates as bioindicators to evaluate the impact of anthropogenic stressors on water quality and sediment properties of a West African lagoon. *Heliyon*, 9(9).

Ahmed, H.G., Aziz, S.Q., Wu, B., Ahmed, M.S., Jha, K., Wang, Z., Nie, Y. & Huang, T., 2024. Application of sponge city for controlling surface runoff pollution. *Asian Journal of Environment & Ecology*, 23(9), pp.1–23.

Al–Amin, A.K.M., Alam, K., Shrestha, U.B., Prodhan, M.H., Hossain, M.A., Sattar, N., Hossain, M.J. & Akhter, T., 2021. Ecosystems, livelihood assets and willingness to pay for wetland conservation in Bangladesh. *Environment, Development and Sustainability*, 23(12), pp.17503–17534.

Alavaisha, E., Lyon, S.W. & Lindborg, R., 2019. Assessment of water quality across irrigation schemes: A case study of wetland agriculture impacts in Kilombero Valley, Tanzania. *Water*, 11(4), p.671.

Alfonso, G., Beccarisi, L., Pieri, V., Frassanito, A. and Belmonte, G., 2016. Using crustaceans to identify different pond types. A case study from the Alta Murgia National Park, Apulia (South-eastern Italy). *Hydrobiologia*, *782*(1), pp.53-69.

Alikhani, S., Nummi, P. & Ojala, A., 2021. Urban wetlands: A review on ecological and cultural values. *Water*, 13(22), p.3301.

Allan, J.D., Castillo, M.M. & Capps, K.A., 2021. Energy flow and nutrient cycling in aquatic communities. In: *Stream Ecology: Structure and Function of Running Waters*, pp. 357–381. Cham: Springer International Publishing.

Almeida–Gomes, M., Valente–Neto, F., Pacheco, E.O., Ganci, C.C., Leibold, M.A., Melo, A.S. & Provete, D.B., 2020. How does the landscape affect metacommunity structure? A quantitative review for lentic environments. *Current Landscape Ecology Reports*, 5(3), pp.68–75.

Amundrud, S.L. & Srivastava, D.S., 2020. Thermal tolerances and species interactions determine the elevational distributions of insects. *Global Ecology and Biogeography*, 29(8), pp.1315–1327.

Appiah, R., Zhou, L., Boadi, E.B., Nsiah, T.K., Ayamba, E.C., Minkah, A.Y. & Asante, H.K., 2023. The causal link between anthropogenic activities, water pollution and health–related quality of life from residents' perspective: a review. *International Journal of Scientific Research in Science and Technology*, 10, pp.211–226.

Ardyna, M., Mundy, C.J., Mayot, N., Matthes, L.C., Oziel, L., Horvat, C., Leu, E., Assmy, P., Hill, V., Matrai, P.A. & Gale, M., 2020. Under–ice phytoplankton blooms: shedding light on the "invisible" part of Arctic primary production. *Frontiers in Marine Science*, 7, p.608032.

Arias Font, R., 2023. *Impacts of flow alteration on stream ecosystems* (Doctoral dissertation, University of Birmingham).

Arthington, A.H., Tickner, D., McClain, M.E., Acreman, M.C., Anderson, E.P., Babu, S., Dickens, C.W., Horne, A.C., Kaushal, N., Monk, W.A. & O'Brien, G.C., 2023. Accelerating environmental flow implementation to bend the curve of global freshwater biodiversity loss. *Environmental Reviews*, 32(3), pp.387–413.

Arts, G.H.P., Watson, M., Solheim, A.L., Schaminee, J.H.J., Evans, D., Lund, M.P. & Tryfon, E., 2022. Revision of the EUNIS inland surface water habitat group: finalisation of level 3 and outlook to level 4. ETC/BD Report to the EEA.

Assie, A.F., Arimoro, F.O., Ndatimana, G., Keke, U.N., Ayanwale, A.V., Edia, E.O. & Edegbene, A.O., 2024. Development of a macroinvertebrate–based biotic index to assess water quality of rivers in Niger State, North Central Ecoregion of Nigeria. *Environmental Monitoring and Assessment*, 196(3), p.230.

Aubeneau, A.F., Botter, G., Jawitz, J.W. & Rao, P.S.C., 2020. Emergent dispersal networks in dynamic wetlandscapes. *Scientific Reports*, 10(1), p.14696.

Ayassamy, P., 2025. Mangroves as a nature–based solution and a tool for coastal resilience. *Ballut–Dajud, Wetlands*, 45(6), pp.1–18.

Bailey–Steinitz, R., 2024. *The tall price of being small: the energetic and fitness costs of interspecific feeding competition in wild primates* (Doctoral dissertation, University of California, Santa Barbara).

Baker, T.J., Tyler, C.R. & Galloway, T.S., 2014. Impacts of metal and metal oxide nanoparticles on marine organisms. *Environmental Pollution*, 186, pp.257–271.

Ballut–Dajud, G.A., Sandoval Herazo, L.C., Fernández–Lambert, G., Marín–Muñiz, J.L., López Méndez, M.C. & Betanzo–Torres, E.A., 2022. Factors affecting wetland loss: a review. *Land*, 11(3), p.434.

Balwan, W.K. & Kour, S., 2021. Wetland–an ecological boon for the environment. *East African Scholars Journal of Agriculture and Life Sciences*, 4(3), pp.38–48.

Bănăduc, D., Curtean–Bănăduc, A., Barinova, S., Lozano, V.L., Afanasyev, S., Leite, T., Branco, P., Gomez Isaza, D.F., Geist, J., Tegos, A. & Simić, S.B., 2024. Multi–interacting natural and anthropogenic stressors on freshwater ecosystems: their current status and future prospects for 21st century. *Water*, 16(11), p.1483.

Barba, C., Folch, A., Gaju, N., Sanchez-Vila, X., Carrasquilla, M., Grau-Martínez, A. and Martínez-Alonso, M., 2019. Microbial community changes induced by Managed Aquifer Recharge activities: linking hydrogeological and biological processes. *Hydrology and Earth system sciences*, *23*(1), pp.139-154.

Batzer, D. & Boix, D., 2016. An introduction to freshwater wetlands and their invertebrates. In: *Invertebrates in freshwater wetlands: an international perspective on their ecology*, pp.1–23. Cham: Springer International Publishing.

Bauer, B., Kleyer, M., Albach, D.C., Blasius, B., Brose, U., Ferreira-Arruda, T., Feudel, U., Gerlach, G., Hof, C., Kreft, H. & Kuczynski, L., 2021. Functional trait dimensions of trophic metacommunities. *Ecography*, 44(10), pp.1486–1500.

Baumann, K.A., Scholl, E.A., Rantala, H.M. & Whiles, M.R., 2025. Macroinvertebrate community responses to disturbance in a fragmented river with contrasting legacies of alteration. *River Research and Applications*, 41(3), pp.638–651.

Bedo, D., Mekuriaw, A. & Bantider, A., 2025. Climate change impacts on ecosystem services in the wetlands of Abijata Shala Lakes National Park, Ethiopia. *International Journal of Environmental Studies*, 82(2), pp.807–824.

Benbow, M.E., Receveur, J.P. & Lamberti, G.A., 2020. Death and decomposition in aquatic ecosystems. *Frontiers in Ecology and Evolution*, 8, p.17.

Benson, J.F., Mahoney, P.J., Sikich, J.A., Serieys, L.E., Pollinger, J.P., Ernest, H.B. & Riley, S.P., 2016. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. *Proceedings of the Royal Society B: Biological Sciences*, 283(1837), p.20160957.

Benvenuto, C., Knott, B. & Weeks, S., 2015. Crustaceans of extreme environments. In: *The natural history of the Crustacea*, vol. 2, pp.379–417.

Berde, V.B., Chari, P.V.B. and Berde, C.V., 2022. Wetland and biodiversity hotspot conservation. In *Research anthology on ecosystem conservation and preserving biodiversity* (pp. 775–784). IGI Global Scientific Publishing.

Bergmann, G.E. and Leveau, J.H., 2022. A metacommunity ecology approach to understanding microbial community assembly in developing plant seeds. *Frontiers in Microbiology*, *13*, p.877519.

Berondo, R.G., 2023. The impact of socio–economic and traditional practices of the local folks in the tourism industry. *Cultural Landscape Insights*, *1*(2), pp.57–63.

Bertassello, L.E., Aubeneau, A.F., Botter, G., Jawitz, J.W. and Rao, P.S.C., 2020. Emergent dispersal networks in dynamic wetlandscapes. *Scientific reports*, *10*(1), p.14696.

Bird, M.S., Mlambo, M.C., Wasserman, R.J., Dalu, T., Holland, A.J., Day, J.A., Villet, M.H., Bilton, D.T., Barber–James, H.M. and Brendonck, L., 2019. Deeper knowledge of shallow waters: reviewing the invertebrate fauna of southern African temporary wetlands. *Hydrobiologia*, *827*(1), pp.89–121.

Birrell, J.H., Shah, A.A., Hotaling, S., Giersch, J.J., Williamson, C.E., Jacobsen, D. and Woods, H.A., 2020. Insects in high-elevation streams: Life in extreme environments imperiled by climate change. *Global Change Biology*, *26*(12), pp.6667–6684.

Bjerring, R., Olsen, J., Jeppesen, E., Buchardt, B., Heinemeier, J., McGowan, S., Leavitt, P.R., Enevold, R. and Odgaard, B.V., 2013. Climate-driven changes in water level: a decadal scale multi-proxy study recording the 8.2-ka event and ecosystem responses in Lake Sarup (Denmark). *Journal of Paleolimnology*, *49*(2), pp.267-285.

Bogan, M.T., Chester, E.T., Datry, T., Murphy, A.L., Robson, B.J., Ruhi, A., Stubbington, R. and Whitney, J.E., 2017. Resistance, resilience, and community recovery in intermittent rivers and ephemeral streams. In *Intermittent rivers and ephemeral streams* (pp. 349–376). Academic Press.

Boggs, C.L., 2024. Changes in insect population dynamics due to climate change. *Effects of Climate Change on Insects: Physiological, Evolutionary, and Ecological Responses*, p.157.

Boix, D. and Batzer, D., 2016. Invertebrate assemblages and their ecological controls across the world's freshwater wetlands. In *Invertebrates in freshwater wetlands: An international perspective on their ecology* (pp. 601–639). Cham: Springer International Publishing.

Bonacina, L., Fasano, F., Mezzanotte, V. and Fornaroli, R., 2023. Effects of water temperature on freshwater macroinvertebrates: a systematic review. Biological Reviews, 98(1), pp.191–221.

Bottrell, D.G. and Schoenly, K.G., 2018. Integrated pest management for resource–limited farmers: challenges for achieving ecological, social and economic sustainability. *The Journal of Agricultural Science*, *156*(3), pp.408–426.

Botwe, P.K., Carver, S., Magierowski, R., McEvoy, P., Goonan, P., Madden, C. and Barmuta, L.A., 2018. Effects of salinity and flow interactions on macroinvertebrate traits in temporary streams. *Ecological Indicators*, *89*, pp.74–83.

Boyd, C.E., 2017. General relationship between water quality and aquaculture performance in ponds. In *Fish diseases* (pp. 147–166). Academic Press.

Boyd, C.E., 2019. Water quality protection. In *Water quality: an introduction* (pp. 379–409). Cham: Springer International Publishing.

Brandl, S.J., Emslie, M.J., Ceccarelli, D.M. and T. Richards, Z., 2016. Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere*, *7*(11), p.e01557.

Brannen, P., 2017. *The Ends of the World: Volcanic Apocalypses, Lethal Oceans and Our Quest to Understand Earth's Past Mass Extinctions*. Simon and Schuster.

Bray, J.P., Reich, J., Nichols, S.J., Kon Kam King, G., Mac Nally, R., Thompson, R., O'Reilly–Nugent, A. and Kefford, B.J., 2019. Biological interactions mediate context and species–specific sensitivities to salinity. *Philosophical Transactions of the Royal Society B*, *374*(1764), p.20180020.

Brendonck, L., Pinceel, T. and Ortells, R., 2017. Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. *Hydrobiologia*, *796*(1), pp.201–222.

Brown, B.L., Swan, C.M., Auerbach, D.A., Campbell Grant, E.H., Hitt, N.P., Maloney, K.O. and Patrick, C., 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society*, *30*(1), pp.310–327.

Brown, L.E., Pitts, C.S., Dunn, A.M. and Hassall, C., 2019. Aquatic ecosystems. In Water Resources (pp. 195–240). Routledge.

Brysiewicz, A., Czerniejewski, P., Dąbrowski, J. and Formicki, K., 2022. Characterisation of benthic macroinvertebrate communities in small watercourses of the european central plains ecoregion and the effect of different environmental factors. *Animals*, *12*(5), p.606.

Buatois, L.A., Davies, N.S., Gibling, M.R., Krapovickas, V., Labandeira, C.C., MacNaughton, R.B., Mángano, M.G., Minter, N.J. and Shillito, A.P., 2022. The invasion of the land in deep time: integrating Paleozoic records of paleobiology, ichnology, sedimentology, and geomorphology. *Integrative and Comparative Biology*, *62*(2), pp.297–331.

Bundschuh, M., Mesquita-Joanes, F., Rico, A. and Camacho, A., 2023. Understanding ecological complexity in a chemical stress context: A reflection on recolonization, recovery, and adaptation of aquatic populations and communities. *Environmental Toxicology and Chemistry*, *42*(9), pp.1857–1866.

Buono, C.M., 2024. *Are Ecological Systems Resilient to Anthropogenic Change? Understanding the Potential for Recovery of Ecological Systems From Invasive Species and Land Use Impacts* (Doctoral dissertation, State University of New York at Binghamton).

Burdon, F.J., McIntosh, A.R. and Harding, J.S., 2020. Mechanisms of trophic niche compression: Evidence from landscape disturbance. *Journal of Animal Ecology*, *89*(3), pp.730–744.

Burger, M., 2017. *A Comparison of Water Quality, Macro–Invertebrate Community Structure and Sediment Sharacteristics in Endorheic Depression Wetlands and a Salt Pan in the Gauteng Province, South Africa*. University of Johannesburg (South Africa).

Burger, M., Van Vuren, J.H.J., De Wet, L. and Nel, A., 2019. A comparison of water quality and macroinvertebrate community structure in endorheic depression wetlands and a salt pan in the Gauteng province, South Africa. *Environmental monitoring and assessment*, *191*(1), p.14.

Bush, B., 2025. *Spatiotemporal Variation in Dispersal as a Driver of Macroinvertebrate Metacommunity Dynamics* (Doctoral dissertation, Virginia Tech).

Bustos, M.J., Garibotti, I.A., Cech, N., Navarro, M.C., Gonzalez Polo, M. and Satti, P., 2022. Microhabitat–specific differences on the composition and function of biological soil crust communities. *Plant and Soil*, *479*(1), pp.663–677.

Butt, M.A., Zafar, M., Ahmed, M., Shaheen, S. and Sultana, S., 2021. *Wetland plants: a source of nutrition and ethno–medicines*. Springer Nature.

Byeon, J.S. and Kim, D.G., 2025. Development of a Wetland Ecosystem Health Assessment Method Using Benthic Macroinvertebrate Community. *Wetlands*, *45*(1), p.4.

Cai, S., Zhang, Y., Pan, M., Zhang, Z., Lu, B., Tian, C., Wang, C., Fang, T. and Wu, X., 2024. Combined effect of freshwater salinization and harmful algae on the benthic invertebrate Chironomus pallidivittatus. *Chemosphere*, *359*, p.142149.

Cantonati, M., Poikane, S., Pringle, C.M., Stevens, L.E., Turak, E., Heino, J., Richardson, J.S., Bolpagni, R., Borrini, A., Cid, N. and Čtvrtlíková, M., 2020. Characteristics, main impacts, and stewardship of natural and artificial freshwater environments: consequences for biodiversity conservation. *Water*, *12*(1), p.260.

Carter, J.L., Resh, V.H. and Hannaford, M.J., 2017. Macroinvertebrates as biotic indicators of environmental quality. In *Methods in stream ecology* (pp. 293–318). Academic Press.

Catena, G., Da Silva, D.M., Suarez, Y.R. and Scremin–Dias, E., 2018. Effects of flood pulse dynamics on functional diversity of macrophyte communities in the Pantanal Wetland. *Wetlands*, *38*(5), pp.975–991.

Celewicz–Gołdyn, S. and Kuczyńska–Kippen, N., 2017. Ecological value of macrophyte cover in creating habitat for microalgae (diatoms) and zooplankton (rotifers and crustaceans) in small field and forest water bodies. PLoS One, 12(5), p. e0177317.

Cereghetti, E., 2024. *Stream ecosystems and terrestrial resources: a temporal perspective on detritus cycling and keystone shredders* (Doctoral dissertation, University of Zurich).

Chakraborty, A., Saha, G.K. and Aditya, G., 2022. Macroinvertebrates as engineers for bioturbation in freshwater ecosystem. *Environmental Science and Pollution Research*, *29*(43), pp.64447–64468.

Chakraborty, S.K., 2021. Land–use changes: floodplains, dams, and reservoirs–integrated river basins management. In *Riverine Ecology Volume 2: Biodiversity Conservation, Conflicts and Resolution* (pp. 531–607). Cham: Springer International Publishing.

Chakraborty, S.K., 2021. River pollution and perturbation: Perspectives and processes. In Riverine Ecology Volume 2: Biodiversity Conservation, Conflicts and Resolution (pp. 443–530). Cham: Springer International Publishing.

Chakraborty, S.K., Sanyal, P. and Ray, R., 2023. Biodiversity and Its Functional Significance: Case Studies from East Kolkata Wetlands. In *Wetlands Ecology: Eco–biological uniqueness of a Ramsar site (East Kolkata Wetlands, India)* (pp. 379–520). Cham: Springer International Publishing.

Chase, J.M., Jeliazkov, A., Ladouceur, E. and Viana, D.S., 2020. Biodiversity conservation through the lens of metacommunity ecology. *Annals of the New York Academy of Sciences*, *1469*(1), pp.86–104.

Chaves, M.L., Rieradevall, M., Chainho, P., Costa, J.L., Costa, M.J. and Prat, N., 2008. Macroinvertebrate communities of non-glacial high altitude intermittent streams. *Freshwater Biology*, *53*(1), pp.55–76.

Che, J., Ye, M., He, Q., Zeng, G., Li, M., Chen, W., Pan, X., Qian, J. and Lv, Y., 2025. Elevation gradient effects on grassland species diversity and phylogenetic in the two–river source forest region of the Altai Mountains, Xinjiang, China. *Frontiers in Plant Science*, *16*, p.1487582.

Chen, X., Chen, H.Y. and Chang, S.X., 2022. Meta–analysis shows that plant mixtures increase soil phosphorus availability and plant productivity in diverse ecosystems. *Nature Ecology & Evolution*, *6*(8), pp.1112–1121.

Cheng, S., Tan, S.Y. and Li, Z., 2017. Ecological interaction between submerged macrophytes and zoobenthos. J. Earth Sci. Environ. Studies, 2, pp.173–182.

Chertoprud, E.S., Novichkova, A.A., Novikov, A.A., Garibian, P.G. and Dadykin, I.A., 2024. Patterns of diversity and driving factors in microcrustacean assemblages in the lowland and mountain Arctic: comparison of the Anabar Plateau and the adjacent regions of Middle Siberia. *Acta Biologica Sibirica*, *10*, pp.997–1024.

Chiloane, C., Dube, T. and Shoko, C., 2022. Impacts of groundwater and climate variability on terrestrial groundwater dependent ecosystems: A review of geospatial assessment approaches and challenges and possible future research directions. *Geocarto International*, *37*(23), pp.6755-6779.

Chimento, M., Alarcón–Nieto, G. and Aplin, L.M., 2021. Population turnover facilitates cultural selection for efficiency in birds. *Current biology*, *31*(11), pp.2477–2483.

Chong, C., Edwards, W., Pearson, R. and Waycott, M., 2013. Sprouting and genetic structure vary with flood disturbance in the tropical riverine paperbark tree, Melaleuca leucadendra (Myrtaceae). *American Journal of Botany*, *100*(11), pp.2250-2260.

Chukwuma Sr, C., 2025. Invariance of Extreme Hydrologic Events and Climate Change in the Risk Reduction on Environment and Health. *Grn Int J Apl Med Sci*, *3*(2), pp.92–102.

Cid, N., Bonada, N., Heino, J., Cañedo–Argüelles, M., Crabot, J., Sarremejane, R., Soininen, J., Stubbington, R. and Datry, T., 2020. A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *BioScience*, *70*(5), pp.427–438.

Coccia, C., Almeida, B.A., Green, A.J., Gutiérrez, A.B. and Carbonell, J.A., 2021. Functional diversity of macroinvertebrates as a tool to evaluate wetland restoration. *Journal of Applied Ecology*, *58*(12), pp.2999–3011.

Coelho, M.A., 2018. *Life history traits of Caribbean octocorals of the genus Antillogorgia and their implications for larval dispersal* (Doctoral dissertation, State University of New York at Buffalo).

Coleman, H.T., Matthews, T.G., Sherman, C.D., Holland, O.J., Clark, Z.S., Farrington, L., Prentice, G. and Miller, A.D., 2023. Contrasting patterns of biodiversity across wetland habitats using single-time-point environmental DNA surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *33*(12), pp.1401–1412.

Cordeiro, A.D.A.C., Klanderud, K., Villa, P.M. and Neri, A.V., 2023. Patterns of species richness and beta diversity of vascular plants along elevation gradient in Brazilian páramo. *Journal of Mountain Science*, *20*(7), pp.1911-1920.

Costa, F.R.C., Zuanon, J.A.S., Baccaro, F.B., de Almeida, J.S., Menger, J.D.S. and Souza, J.L.P., 2020. Effects of climate change on central amazonian forests: a two decades' synthesis of monitoring tropical biodiversity. *Oecologia Australis*, *24*(2), pp.317–335.

Cronan, C.S., 2023. Wetland ecosystems. In *Ecology and Ecosystems Analysis* (pp. 161–176). Cham: Springer Nature Switzerland.

Cukusic, A., Karwautz, C., Murhammer, C., Pjevac, P., Rasch, G., Stumpp, C. and Griebler, C., 2025. Dynamic changes of protist community composition along a surface water–groundwater transect in the Danube wetland Lobau, Vienna, Austria. *bioRxiv*, pp.2025–07.

Culp, J.M., Goedkoop, W., Christensen, T., Christoffersen, K.S., Fefilova, E., Liljaniemi, P., Novichkova, A.A., Ólafsson, J.S., Sandøy, S., Zimmerman, C.E. and Lento, J., 2022. Arctic freshwater biodiversity: Establishing baselines, trends, and drivers of ecological change. *Freshwater Biology*, *67*(1), pp.1–13.

Cunillera–Montcusi, D., Boix, D., Sala, J., Compte, J., Tornero, I., Quintana, X.D. and Gascon, S., 2020. Large–and small–regional–scale variables interact in the dispersal patterns of aquatic macroinvertebrates from temporary ponds. *Aquatic Ecology*, *54*(4), pp.1041–1058.

Dahlke, F.T., Wohlrab, S., Butzin, M. and Pörtner, H.O., 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*(6499), pp.65–70.

Dalu, T. and Chauke, R., 2020. Assessing macroinvertebrate communities in relation to environmental variables: the case of Sambandou wetlands, Vhembe Biosphere Reserve. Applied Water Science, 10(1), pp.1–11.

Dalu, T. and Tavengwa, N. eds., 2022. *Emerging freshwater pollutants: Analysis, fate and regulations*. Elsevier.

Dalu, T., Cuthbert, R.N., Methi, M.J., Dondofema, F., Chari, L.D. and Wasserman, R.J., 2022. Drivers of aquatic macroinvertebrate communities in a Ramsar declared wetland system. Science of The Total Environment, 818, p.151683.

Dalu, T., Mwedzi, T., Wasserman, R.J., Madzivanzira, T.C., Nhiwatiwa, T. and Cuthbert, R.N., 2022. Land use effects on water quality, habitat, and macroinvertebrate and diatom communities in African highland streams. *Science of the Total Environment*, *846*, p.157346.

Dalu, T., Wasserman, R.J., Tonkin, J.D., Alexander, M.E., Dalu, M.T., Motitsoe, S.N., Manungo, K.I., Bepe, O. and Dube, T., 2017. Assessing drivers of benthic macroinvertebrate community structure in African highland streams: an exploration using multivariate analysis. Science of the Total Environment, 601, pp.1340–1348.

Dalu, T., Zantsi, B.P., Wu, N. and Cuthbert, R.N., 2025. Effects of water and sediment chemistry variables on aquatic macroinvertebrate community structuring in a subtropical Austral river system. *Environmental Science and Pollution Research*, *32*(4), pp.1830–1845.

Dangles, O., 2023. Underwater Flies. In *Climate Change on Mountains: Reviving Humboldt's Approach to Science* (pp. 101–183). Cham: Springer Nature Switzerland.

Dániel Ferreira, J., 2021. Linear infrastructure habitats for the conservation of plants and pollinators–The value of road verges and power–line corridors for landscape–scale diversity and connectivity. *Acta Universitatis Agriculturae Sueciae*, (2021: 63).

Das, S., Tseng, L.C., Wang, L. and Hwang, J.S., 2017. Burrow characteristics of the mud shrimp Austinogebia edulis, an ecological engineer causing sediment modification of a tidal flat. *PLoS One*, *12*(12), p. e0187647.

Datry, T., Bonada, N. and Heino, J., 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos*, *125*(2), pp.149–159.

Datry, T., Boulton, A.J., Fritz, K., Stubbington, R., Cid, N., Crabot, J. and Tockner, K., 2023. Non–perennial segments in river networks. *Nature Reviews Earth & Environment*, *4*(12), pp.815–830.

Datry, T., Corti, R., Heino, J., Hugueny, B., Rolls, R.J. and Ruhí, A., 2017. Habitat fragmentation and metapopulation, metacommunity, and metaecosystem dynamics in intermittent rivers and ephemeral streams. In *Intermittent rivers and ephemeral streams* (pp. 377–403). Academic Press.

Davidson, N.C., Van Dam, A.A., Finlayson, C.M. and McInnes, R.J., 2019. Worth of wetlands: revised global monetary values of coastal and inland wetland ecosystem services. *Marine and Freshwater Research*, *70*(8), pp.1189–1194.

Davis, S.J., Mellander, P.E., Kelly, A.M., Matthaei, C.D., Piggott, J.J. and Kelly–Quinn, M., 2018. Multiple–stressor effects of sediment, phosphorus and nitrogen on stream macroinvertebrate communities. *Science of the Total Environment*, *637*, pp.577–587.

De Mello, K., Taniwaki, R.H., Macedo, D.R., Leal, C.G. and Randhir, T.O., 2023. Biomonitoring for watershed protection from a multiscale land–use perspective. *Diversity*, *15*(5), p.636.

Deane, D.C., Harding, C., Aldridge, K.T., Goodman, A.M., Gehrig, S.L., Nicol, J.M. and Brookes, J.D., 2018. Predicted risks of groundwater decline in seasonal wetland plant communities depend on basin morphology. *Wetlands Ecology and Management*, *26*(3), pp.359–372.

Demarquet, Q., Rapinel, S., Dufour, S. and Hubert–Moy, L., 2023. Long–term wetland monitoring using the landsat archive: A review. *Remote Sensing*, *15*(3), p.820.

Demeter, L. and Stoicescu, A., 2008. A review of the distribution of large branchiopods (Branchiopoda: Anostraca, Notostraca, Spinicaudata, Laevicaudata) in Romania. *North–Western Journal of Zoology*, *4*(2), pp.203–223.

Denis, S., 2019. Effect of Human Activities On the Benthic-Macroinverbrate Assembles in Insooba Stream, Lubigi Catchment, Kampala.

Derartu, T., 2023. *oody plant Species Composition and Structural Analysis of Mura Forest, Ambo District, West Shewa Zone, Oromia, Ethiopia* (Doctoral dissertation, Ambo University).

Devi Tachamo Shah, R., Sharma, S., Narayan Shah, D. and Rijal, D., 2020. Structure of benthic macroinvertebrate communities in the rivers of Western Himalaya, Nepal. *Geosciences*, *10*(4), p.150.

Dézerald, O., Roussel, J.M., Lanoë, E., Beauverger, T., Bazin, A., Rodríguez–Pérez, H., Dufour, S., Bernez, I. and Piscart, C., 2023. Fast but transient recovery of aquatic and terrestrial communities after a large dam removal. *Frontiers in Ecology and Evolution*, *11*, p.1254462.

Dhyani, S., Sivadas, D., Basu, O. and Karki, M., 2022. Ecosystem health and risk assessments for high conservation value mountain ecosystems of South Asia: a necessity to guide conservation policies. *Anthropocene Science*, *1*(1), pp.211–225.

Di Pietro, S., Mantoni, C. and Fattorini, S., 2021. Influence of urbanization on the avian species–area relationship: insights from the breeding birds of Rome. *Urban Ecosystems*, *24*(4), pp.779–788.

Diana, J.S., Szyper, J.P., Batterson, T.R., Boyd, C.E. and Piedrahita, R.H., 2017. Water quality in ponds. *Dynamics of pond aquaculture*, pp.53–71.

Dildar, T., Cui, W., Ikhwanuddin, M. and Ma, H., 2025. Aquatic Organisms in Response to Salinity Stress: Ecological Impacts, Adaptive Mechanisms, and Resilience Strategies. *Biology*, *14*(6), p.667.

Ding, S., Dan, S.F., Liu, Y., He, J., Zhu, D. and Jiao, L., 2022. Importance of ammonia nitrogen potentially released from sediments to the development of eutrophication in a plateau lake. *Environmental pollution*, *305*, p.119275.

Dingman, P.D., 2021. Comparing Macroinvertebrate Total Abundance and Total Biomass on Five Substrate Types from Upstream to Downstream on the North Branch of the Au Sable River.

Diniz, M.F., Cushman, S.A., Machado, R.B. and De Marco Júnior, P., 2020. Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecology*, *35*(1), pp.41–58.

Diodato, N., Seim, A., Ljungqvist, F.C. and Bellocchi, G., 2024. A millennium–long perspective on recent groundwater changes in the Iberian Peninsula. *Communications Earth & Environment*, *5*(1), p.257.

Dixit, A., Madhav, S., Mishra, R., Srivastav, A.L. and Garg, P., 2022. Impact of climate change on water resources, challenges and mitigation strategies to achieve sustainable development goals. *Arabian Journal of Geosciences*, *15*(14), p.1296.

Dodds, W.K., Bruckerhoff, L., Batzer, D., Schechner, A., Pennock, C., Renner, E., Tromboni, F., Bigham, K. and Grieger, S., 2019. The freshwater biome gradient framework: predicting macroscale properties based on latitude, altitude, and precipitation. *Ecosphere*, *10*(7), p. e02786.

Dolabela, B.M., Costa, F.V.D., Pinto, V.D., Lopes, I., Bezerra-Neto, J.F., Barbosa, F.A.R. and Ribeiro, S.P., 2022. Forest–lake ecotones in a tropical forest: Terrestrial invertebrate inputs to lakes decrease with forest distance. *Freshwater Biology*, *67*(6), pp.1079–1090.

Dole, M., 2024. *Ecological drivers of macroinvertebrate communities in ponds* (Doctoral dissertation, University of Sussex).

Dolmans, V., Partoens, L., Deboelpaep, E., Horváth, Z. and Vanschoenwinkel, B., 2025. Dietary data suggest large branchiopods may be an underrecognised food resource for a wide range of waterbirds. *Hydrobiologia*, pp.1–17.

Doney, S.C., Busch, D.S., Cooley, S.R. and Kroeker, K.J., 2020. The impacts of ocean acidification on marine ecosystems and reliant human communities. *Annual Review of Environment and Resources*, *45*(1), pp.83–112.

Dong, R., Wang, Y., Lu, C., Lei, G. and Wen, L., 2021. The seasonality of macroinvertebrate β diversity along the gradient of hydrological connectivity in a dynamic river–floodplain system. *Ecological Indicators*, *121*, p.107112.

Doretto, A., Bona, F., Falasco, E., Morandini, D., Piano, E. and Fenoglio, S., 2020. Stay with the flow: How macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought. *River Research and Applications*, *36*(1), pp.91–101.

Dorji, K., 2024. Macroinvertebrates Diversity and Seasonal Dynamics in the Streams of Southwest Bhutan: Preliminary Findings and Implications for Future Research. *Bhutan Journal of Natural Resources and Development*, *11*(2), pp.88–102.

Drover, D.R., Schoenholtz, S.H., Soucek, D.J. and Zipper, C.E., 2020. Multiple stressors influence benthic macroinvertebrate communities in central Appalachian coalfield streams. *Hydrobiologia*, *847*(1), pp.191–205.

Dube, T., Pinceel, T., De Necker, L., Wepener, V., Lemmens, P. and Brendonck, L., 2019. Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa. *Freshwater Biology*, *64*(12), pp.2189–2203.

Dubour, A.J., Lewis, T.L., Lindberg, M.S. and Gurney, K.E., 2025. Factors affecting intraspecific diet variation of ducklings: Niche partitioning in a heterogeneous landscape? *Ecosphere*, *16*(12), p. e70513.

Eckardt, F.D., Maggs–Kölling, G., Marais, E. and de Jager, P.C., 2022. A brief introduction to hot desert environments: climate, geomorphology, habitats, and soils. In *Microbiology of Hot Deserts* (pp. 1–36). Cham: Springer International Publishing.

Effert–Fanta, E.L., Fischer, R.U. and Wahl, D.H., 2019. Effects of riparian forest buffers and agricultural land use on macroinvertebrate and fish community structure. *Hydrobiologia*, *841*(1), pp.45–64.

Eichelmann, E., Naber, N., Battamo, A.Y., O'Sullivan, J.J., Salauddin, M. and Kelly–Quinn, M., 2025. A review of the impact of extreme weather events on freshwater, terrestrial and marine ecosystems. In *Biology and Environment: Proceedings of the Royal Irish Academy* (Vol. 125, No. 1, pp. 101–134). Royal Irish Academy.

Elvira, B., Nicola, G.G., Ayllon, D. and Almodovar, A., 2021. Determinants of large-scale spatial distribution and seasonal microhabitat selection patterns of the endangered freshwater blenny Salaria fluviatilis in the Ebro River basin, Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(11), pp.3261–3275.

Emery-Butcher, H.E., Beatty, S.J. and Robson, B.J., 2020. The impacts of invasive ecosystem engineers in freshwaters: A review. Freshwater Biology, 65(5), pp.999-1015.

Enabulele, C. and Olomukoro, J., 2024. Benthic macroinvertebrates as indicators of water quality and ecological health in a tropical lake, Southern Nigeria. Limnology and Freshwater Biology, pp.1276-1283.Epele, L.B., Grech, M.G., Williams–Subiza, E.A., Stenert, C., McLean, K., Greig, H.S., Maltchik, L., Pires, M.M., Bird, M.S., Boissezon, A. and Boix, D., 2022. Perils of life on the edge: climatic threats to global diversity patterns of wetland macroinvertebrates. *Science of the Total Environment*, *820*, p.153052.

Evans, A., Jacquemyn, H. and Brys, R., 2023. Drivers of ecological niche breadth in partially mycoheterotrophic orchids and implications for future distributions.

Everall, N.C., Johnson, M.F., Wood, P., Paisley, M.F., Trigg, D.J. and Farmer, A., 2019. Macroinvertebrate community structure as an indicator of phosphorus enrichment in rivers. *Ecological Indicators*, *107*, p.105619.

Fair, H.L., 2017. *Ecology of aquatic insects in monsoonal temperate glacier streams of Southeast Tibet: A departure from the conceptual model*. The Ohio State University.

Farley, E.B., Schummer, M.L., Leopold, D.J., Coluccy, J.M. and Tozer, D.C., 2022. Influence of water level management on vegetation and bird use of restored wetlands in the Montezuma Wetlands Complex. *Wildlife Biology*, *2022*(2), p. e01016.

Farooq, M., Li, X., Li, Z., Yang, R., Tian, Z., Tan, L., Fornacca, D., Li, Y., Cili, N., Ciren, Z. and Liu, S., 2022. The joint contributions of environmental filtering and spatial processes to macroinvertebrate metacommunity dynamics in the alpine stream environment of Baima Snow Mountain, Southwest China. *Diversity*, *14*(1), p.28.

Fekadu, M.B., 2021. *Impact of land use change in water qualities, habitat qualities and benthic macroinvertebrates assembleges in Kipsinende River, Lake Victoria basin, Kenya* (Doctoral dissertation, University of Eldoret).

Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S.B., Byrne, M. and Figueira, W., 2016. Quantifying the response of structural complexity and community composition to environmental change in marine communities. Global change biology, 22(5), pp.1965-1975.Ferreira, V., Elosegi, A., D. Tiegs, S., von Schiller, D. and Young, R., 2020. Organic matter decomposition and ecosystem metabolism as tools to assess the functional integrity of streams and rivers–a systematic review. *Water*, *12*(12), p.3523.

Ferzoco, I.M.C., Murray–Stoker, K.M., Hasan, L.S., Javier, C.M., Modi, V., Singh, R., Tjan, G., Toth, O. and McCauley, S.J., 2023. Freshwater insect communities in urban environments around the globe: a review of the state of the field. *Frontiers in Ecology and Evolution*, *11*, p.1174166.

Figel, J.J., Botero–Cañola, S., Forero–Medina, G., Sánchez–Londoño, J.D., Valenzuela, L. and Noss, R.F., 2019. Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot. *PLoS One*, *14*(9), p. e0221705.

Firmiano, K.R., Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Macedo, D.R., Linares, M.S., Bonada, N. and Callisto, M., 2021. Land use and local environment affect macroinvertebrate metacommunity organization in Neotropical stream networks. *Journal of Biogeography*, *48*(3), pp.479–491.

Fontaneto, D., 2025. Fundamental questions in meiofauna research highlight how small but ubiquitous animals can improve our understanding of Nature.

Fornaroli, R., White, J.C., Boggero, A. and Laini, A., 2020. Spatial and temporal patterns of macroinvertebrate assemblages in the River Po Catchment (Northern Italy). *Water*, *12*(9), p.2452.

Frainer, A., Polvi, L.E., Jansson, R. and McKie, B.G., 2018. Enhanced ecosystem functioning following stream restoration: The roles of habitat heterogeneity and invertebrate species traits. *Journal of Applied Ecology*, *55*(1), pp.377–385.

Frolking, S., Roulet, N. and Fuglestvedt, J., 2006. How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research: Biogeosciences*, *111*(G1).

Frost, L.K., Mika, S.J., Thompson, R.M. and Growns, I., 2023. Influence of hydroperiod on aquatic food–web structure and energy production in a floodplain wetland: implications for environmental flow management. *Marine and Freshwater Research*, *75*(1), pp. NULL–NULL.

Fu, L., Jiang, Y., Ding, J., Liu, Q., Peng, Q.Z., Kang, M.Y. and Wang, L.Z., 2015. Spatial variation of macroinvertebrate community structure and associated environmental conditions in a subtropical river system of southeastern China. *Knowledge and Management of Aquatic Ecosystems*, (416), p.17.

Gabriel, R., Morgado, L.N., Poponessi, S., Henriques, D.S., Coelho, M.C., Silveira, G.M. and Borges, P.A., 2025. Diversity and Distribution of Bryophytes Along an Altitudinal Gradient on Flores Island (Azores, Portugal). *Plants*, *14*(24), p.3766.

Galiana, N., Lurgi, M., Claramunt–López, B., Fortin, M.J., Leroux, S., Cazelles, K., Gravel, D. and Montoya, J.M., 2018. The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, *2*(5), pp.782–790.

Gálvez, Á., Aguilar–Alberola, J.A., Armengol, X., Bonilla, F., Iepure, S., Monrós, J.S., Olmo, C., Rojo, C., Rueda, J., Rueda, R. and Sasa, M., 2020. Environment and space rule, but time also matters for the organization of tropical pond metacommunities. *Frontiers in Ecology and Evolution*, *8*, p.558833.

Gamito, S., Quental–Ferreira, H., Parejo, A., Aubin, J., Christensen, V. and Cunha, M.E., 2020. Integrated multi–trophic aquaculture systems: energy transfers and food web organization in coastal earthen ponds. *Aquaculture Environment Interactions*, *12*, pp.457–470.

García-Beltrán, J.A., Toledo, S., Melo-Gaymer, M.P., Rosas, M.R., Cisternas-Fuentes, A. and Guerrero, P.C., 2025. Geographic distance and landscape ruggedness shape genome-wide divergence and admixture in Leucostele cacti across the Atacama–central Chile biodiversity hotspot. *Annals of Botany*, p.mcaf323.

Gavrilaș, S., Burescu, F.L., Chereji, B.D. and Munteanu, F.D., 2025. The Impact of Anthropogenic Activities on the Catchment's Water Quality Parameters. *Water*, *17*(12), p.1791.

Gawecka, K.A. and Bascompte, J., 2023. Habitat restoration and the recovery of metacommunities. *Journal of Applied Ecology*, *60*(8), pp.1622–1636.

Ge, J., Chen, J., Zi, F., Song, T., Hu, L., He, Z., Wu, L., Ding, Y. and Li, H., 2025. Seasonal Variations in Macrobenthos Communities and Their Relationship with Environmental Factors in the Alpine Yuqu River. *Biology*, *14*(2), p.120.

Gebrekiros, S.T., 2016. Factors affecting stream fish community composition and habitat suitability. *Journal of Aquaculture and Marine Biology*, *4*(2), p.00076.

Gedney, N., Huntingford, C., Comyn–Platt, E. and Wiltshire, A., 2019. Significant feedbacks of wetland methane release on climate change and the causes of their uncertainty. *Environmental Research Letters*, *14*(8), p.084027.

Gerstle, V., Manfrin, A., Kolbenschlag, S., Gerken, M., Islam, A.M.U., Entling, M.H., Bundschuh, M. and Bruehl, C.A., 2023. Benthic macroinvertebrate community shifts based on Bti–induced chironomid reduction also decrease Odonata emergence. *Environmental Pollution*, *316*, p.120488.

GHOSH, P., 2016. Hydrological, Morphological, Ecological and Economical important and Threats of Wetland (A Case Study of Sandhya Wetland in Jadupur–2). Lulu. com.

Girona, M.M., Aakala, T., Aquilué, N., Bélisle, A.C., Chaste, E., Danneyrolles, V., Díaz–Yáñez, O., D'Orangeville, L., Grosbois, G., Hester, A. and Kim, S., 2023. Challenges for the sustainable management of the boreal forest under climate change. In *Boreal forests in the face of climate change: Sustainable management* (pp. 773–837). Cham: Springer International Publishing.

Gleason, J.E., 2017. Aquatic macroinvertebrate communities and diversity patterns in the Northern Prairie Pothole Region.

Gnanasekaran, S. and Raj, S.A., 2023. Heavy metal bioaccumulation in sediment and benthic biota. In *Heavy Metals–Recent Advances*. IntechOpen.

Gobel, N., Laufer, G., Kacevas, N., Cortizas, S., Pais, J., Arim, M. and González–Bergonzoni, I., 2025. Fish modulate how connectivity and local factors shape food webs of permanent ponds. *Oikos*, *2025*(5), p. e11062.

Golovatyuk, L.V., Zinchenko, T.D., Kanapatskiy, T.A., Umanskaya, M.V., Gorbunov, M.Y., Gorokhova, O.G., Lobus, N.V. and Gusakov, V.A., 2025. Benthic communities of saline rivers in the arid zone of south Russia: saliny tolerance, production, trophic conditions. *Aquatic Sciences*, *87*(2), p.32.

Golovina, E., Pasternak, S., Tsiglianu, P. and Tselischev, N., 2021. Sustainable management of transboundary groundwater resources: Past and future. *Sustainability*, *13*(21), p.12102.

Gomo, M. and Ngobe, T., 2024. Interaction of pans and groundwater: A case study in the Khakhea–Bray Transboundary aquifer portion in South Africa. *Physics and Chemistry of the Earth, Parts A/B/C*, *136*, p.103753.

Gopal, B., 2020. Freshwater ecosystems: Ecological characteristics and ecosystem services. In Ecosystems and integrated water resources management in South Asia (pp. 13–48). Routledge India.

Gordon, Z., 2025. Community and decomposition dynamics along a saltwater intrusion gradient on Sapelo Island, Georgia.

Granata, F., Zhu, S. and Di Nunno, F., 2025. Hydrological extremes in the Mediterranean basin: interactions, impacts, and adaptation in the face of climate change. *Regional Environmental Change*, *25*(3), p.100.

Granath, G., Hyseni, C., Bini, L.M., Heino, J., Ortega, J.C. and Johansson, F., 2024. Disentangling drivers of temporal changes in urban pond macroinvertebrate diversity. *Urban Ecosystems*, *27*(4), pp.1027–1039.

Graziano, M.P., Deguire, A.K. and Surasinghe, T.D., 2022. Riparian buffers as a critical landscape feature: insights for riverscape conservation and policy renovations. *Diversity*, *14*(3), p.172.

Greider, M.L., Lim, J.P. and Studinski, J.M., 2025. The persistent adaptability of aquatic macroinvertebrate communities: assessing responses to anthropogenic stressors in central Wisconsin's restored wetlands. *Hydrobiologia*, pp.1–15.

. Gross, C.P., 2023. Trait-based and phylogenetic approaches to understanding community assembly processes in eelgrass beds (Doctoral dissertation, University of California, Davis).

Guan, Q., He, F., Li, Z., Cai, Y., Kang, Y., Zhang, Z. and Wu, H., 2024. Contrasting diversity patterns and drivers of aquatic macroinvertebrates in floodplain and non–floodplain wetlands. *Science of The Total Environment*, *945*, p.174045.

Guerrero, F., Ortega, F., García–Rodríguez, G. and Gilbert, J.D., 2025. Diversity and Metacommunity Structure of Aquatic Macrophytes: A Study in Mediterranean Mountain Wetlands. *Sustainability*, *17*(13), p.6103.

Guo, X., Liu, Y., Xie, T., Li, Y., Liu, H. and Wang, Q., 2025. Impact of Ecological Restoration on Carbon Sink Function in Coastal Wetlands: A Review. *Water*, *17*(4), p.488.

Gupta, G., Khan, J., Upadhyay, A.K. and Singh, N.K., 2019. Wetland as a sustainable reservoir of ecosystem services: prospects of threat and conservation. In *Restoration of wetland ecosystem: A trajectory towards a sustainable environment* (pp. 31–43). Singapore: Springer Singapore.

Gutierrez, C., 2024. *Changes in Functional Structure of Aquatic Insect Communities Across Environmental Gradients in Mountain Streams* (Doctoral dissertation, Colorado State University).

Haggag, A.A., Mahmoud, M.A., Bream, A.S. and Amer, M.S., 2018. Family variation of aquatic insects and water properties to assess freshwater quality in El–Mansouriya stream, Egypt. *African Entomology*, *26*(1), pp.162–173.

Hall, O., 2021. *The impacts of stormwater runoff on the littoral–benthic macroinvertebrate communities along the shoreline of Lake Wanaka & Lake Wakatipu* (Doctoral dissertation, University of Otago).

Hamid, A., Bhat, S.U. and Jehangir, A., 2020. Local determinants influencing stream water quality. *Applied Water Science*, *10*(1), pp.1–16.

Hamid, A., Bhat, S.U. and Jehangir, A., 2021. Assessment of ecological characteristics of macroinvertebrate communities and their relationship with environmental factors in a stream ecosystem. *Chemistry and Ecology*, *37*(9–10), pp.746–766.

Hanisch, J.R., Connor, S.J., Scrimgeour, G.J. and Cobbaert, D., 2020. Bioassessment of benthic macroinvertebrates in wetlands: a paired comparison of two standardized sampling protocols. *Wetlands Ecology and Management*, *28*(2), pp.199–216.

Harenda, K.M., Lamentowicz, M., Samson, M. and Chojnicki, B.H., 2017. The role of peatlands and their carbon storage function in the context of climate change. In *Interdisciplinary approaches for sustainable development goals: Economic growth, social inclusion and environmental protection* (pp. 169–187). Cham: Springer International Publishing.

Harisena, N.V., 2025. *Investigating the legacies of the past: Influences of spatio–temporal landscape dynamics on current biodiversity patterns* (Doctoral dissertation, ETH Zurich).

Harper, D.M. and Pacini, N., 2019. Freshwater populations, interactions and networks. Freshwater ecology and conservation: Approaches and techniques, pp.257–282.

Harrison, A.B., Slack, W.T. and Ochs, C., 2025. Hydrologic Connectivity and Secondary Channel Habitat Properties of the Lower Mississippi River, a Large, Meandering River in the Southern USA. *River Research and Applications*, *41*(9), pp.1864–1873.

Harrison, J.F., Greenlee, K.J. and Verberk, W.C., 2018. Functional hypoxia in insects: definition, assessment, and consequences for physiology, ecology, and evolution. *Annual Review of Entomology*, *63*(1), pp.303–325.

Harvey, E., Gounand, I., Ward, C.L. and Altermatt, F., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. *Journal of Applied Ecology*, *54*(2), pp.371–379.

Havril, T., Tóth, Á., Molson, J.W., Galsa, A. and Mádl–Szőnyi, J., 2018. Impacts of predicted climate change on groundwater flow systems: can wetlands disappear due to recharge reduction? *Journal of hydrology*, *563*, pp.1169–1180.

Hayes, S.M. and Anderson, K.E., 2018. Beyond connectivity: how the structure of dispersal influences metacommunity dynamics. *Theoretical Ecology*, *11*(2), pp.151–159.Beyond connectivity: how the structure of dispersal influences metacommunity dynamics. *Theoretical Ecology*, *11*(2), pp.151–159.

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J. and Virtanen, R., 2017. Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia*, *183*(1), pp.121–137.

Herbst, D.B., Cooper, S.D., Medhurst, R.B., Wiseman, S.W. and Hunsaker, C.T., 2019. Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshwater Biology*, *64*(5), pp.886–902.

Hesslerová, P., Pokorný, J., Huryna, H. and Harper, D., 2019. Wetlands and forests regulate climate via evapotranspiration. In *Wetlands: Ecosystem services, restoration and wise use* (pp. 63–93). Cham: Springer International Publishing.

Hill, M.J., Biggs, J., Thornhill, I., Briers, R.A., Ledger, M., Gledhill, D.G., Wood, P.J. and Hassall, C., 2018. Community heterogeneity of aquatic macroinvertebrates in urban ponds at a multi–city scale. *Landscape Ecology*, *33*(3), pp.389–405.

Hill, M.J., Death, R.G., Mathers, K.L., Ryves, D.B., White, J.C. and Wood, P.J., 2017. Macroinvertebrate community composition and diversity in ephemeral and perennial ponds on unregulated floodplain meadows in the UK. *Hydrobiologia*, *793*(1), pp.95–108.

Hill, M.J., Heino, J., White, J.C., Ryves, D.B. and Wood, P.J., 2019. Environmental factors are primary determinants of different facets of pond macroinvertebrate alpha and beta diversity in a human–modified landscape. *Biological Conservation*, *237*, pp.348–357.

Hilty, J.A., Keeley, A.T., Lidicker Jr, W.Z. and Merenlender, A.M., 2019. *Corridor ecology: linking landscapes for biodiversity conservation and climate adaptation*. Island Press.

Hines, J. and Eisenhauer, N., 2021. Species identity and the functioning of ecosystems: the role of detritivore traits and trophic interactions in connecting of multiple ecosystem responses. *Oikos*, *130*(10), pp.1692–1703.

Hlophe–Ginindza, S., Chimonyo, V.G., Nhamo, L., Mpandeli, S., Liphadzi, S., Naidoo, D., Modi, A.T. and Mabhaudhi, T., 2021. Enhancing food and water security through innovations in South Africa: 50 years of research.

Hockaday, A.C., Leon, A.S., Patterson, K. and Pennings, S.C., 2024. Freshwater wetlands for flood control: How manipulating the hydroperiod affects plant and invertebrate communities. *Plos one*, *19*(7), p. e0306578.

Holzknecht, A., Land, M., Dessureault–Rompré, J., Elsgaard, L., Lång, K. and Berglund, Ö., 2025. Effects of converting cropland to grassland on greenhouse gas emissions from peat and organic–rich soils in temperate and boreal climates: a systematic review. *Environmental Evidence*, *14*(1), p.1.

Hoque, M.Z., Ahmed, M., Islam, I., Cui, S., Xu, L., Prodhan, F.A., Ahmed, S., Rahman, M.A. and Hasan, J., 2022. Monitoring changes in land use land cover and ecosystem service values of dynamic saltwater and freshwater systems in coastal Bangladesh by geospatial techniques. *Water*, *14*(15), p.2293.

Hou, Y., Pan, B., Feng, Z., Li, G., Huang, Z., Xie, H. and Zhao, G., 2025. Flooding enhances species–patch network stability of macroinvertebrate community in low–connectivity oxbow lakes. *Journal of Hydrology*, p.134585.

Htay, T., Røskaft, E., Ringsby, T.H. and Ranke, P.S., 2023. Spatio–temporal variation in avian taxonomic, functional, and phylogenetic diversity and its relevance for conservation in a wetland ecosystem in Myanmar. Biodiversity and Conservation, 32(8), pp.2841–2867.

Hu, S., Niu, Z., Chen, Y., Li, L. and Zhang, H., 2017. Global wetlands: Potential distribution, wetland loss, and status. *Science of the total environment*, *586*, pp.319–327.

Huber, E.D., Wilmoth, B., Hintz, L.L., Horvath, A.D., McKenna, J.R. and Hintz, W.D., 2023. Freshwater salinization reduces vertical movement rate and abundance of Daphnia: interactions with predatory stress. *Environmental Pollution*, *330*, p.121767.

Humphries, M. and McCarthy, T., 2022. Chemical sedimentation as a driver of habitat diversity in dryland wetlands. *Wetlands Ecology and Management*, *30*(4), pp.675–694.

Hunt, D.S., 2022. *Impacts and Dispersal of Invasive Bivalves, Dreissena and Corbicula Spp., On Stream Benthic Communities* (Doctoral dissertation, Wayne State University).

Huynh, M., 2019. Dispersal as a Buffer Against Zooplankton Community Change in Response to Fluctuating Salinity Levels on the Great Plains.

Imran, 2025. Carbon cultivation for sustainable agriculture, ecosystem resilience, and climate change mitigation. *Communications in Soil Science and Plant Analysis*, *56*(9), pp.1430–1456.

Iqbal, A. and Shang, Z., 2019. Wetlands as a carbon sink: Insight into the Himalayan Region. In *Carbon management for promoting local livelihood in the Hindu Kush Himalayan (HKH) Region* (pp. 125–144). Cham: Springer International Publishing.

Isaac, G.O., Hamzat, A.B. and Daramola, O.O., 2025. Ecological Importance and Functions of Wetlands. In *Wetland Ecosystems: Conservation Strategies, Policy Management and Applications* (pp. 23–42). Cham: Springer Nature Switzerland.

Izah, S.C., Abdelkhalek, S.T., Ogwu, M.C. and Hamidifar, H., 2024. Overview and perspectives of biomonitoring in the global south. In *Biomonitoring of Pollutants in the Global South* (pp. 3–36). Singapore: Springer Nature Singapore.

Jacobsen, D. and Dangles, O., 2017. *Ecology of high altitude waters*. Oxford University Press.

Jacobsen, D., Wiberg–Larsen, P., Brodersen, K.P., Hansen, S.B., Lindegaard, C., Friberg, N., Dall, P.C., Kirkegaard, J., Skriver, J. and Toman, M., 2020. Macroinvertebrate communities along the main stem and tributaries of a pre–Alpine river: Composition responds to altitude, richness does not. *Limnologica*, *84*, p.125816.

Jacobsen, L. and Engström–Öst, J., 2018. Coping with environments; vegetation, turbidity and abiotics. In *Biology and ecology of pike* (pp. 32–61). CRC press.

Jacobus, L.M., Macadam, C.R. and Sartori, M., 2019. Mayflies (Ephemeroptera) and their contributions to ecosystem services. *Insects*, *10*(6), p.170.

Jaiswal, N. and Jayakumar, S., 2024. Elevation gradients and environmental variables shaping tree diversity and composition in Srivilliputhur Wildlife Sanctuary, Western Ghats. *Geology, Ecology, and Landscapes*, pp.1-21.

Janardhan, S. and Krishna, G.S., 2021. Role of biochar in agriculture–its implications and perspectives. Agriculture & Food: E–Newsletter.

Janse, J.H., Van Dam, A.A., Hes, E.M., De Klein, J.J., Finlayson, C.M., Janssen, A.B., Van Wijk, D., Mooij, W.M. and Verhoeven, J.T., 2019. Towards a global model for wetlands ecosystem services. *Current opinion in environmental sustainability*, *36*, pp.11–19.

Jeethu, J.C., 2025. Wetlands and Climate Change Resilience, an Enhancing Ecosystem Services for a Sustainable Future: A Review. *Journal of Climate Change*, *11*(3), pp.13–13.

Jentsch, A., Seidl, R., Wohlgemuth, T., Jentsch, A., Jentsch, A., Burton, P.J., Walker, L.R., Senf, C., von Heßberg, A., Jentsch, A. and White, P.S., 2022. Disturbances and disturbance regimes. In *Disturbance ecology* (pp. 11-40). Cham: Springer International Publishing.

Jeong, S.Y. and Kim, T.G., 2021. Effects of plants on metacommunities and correlation networks of soil microbial groups in an ecologically restored wetland. *Microbial ecology*, *81*(3), pp.657–672. Effects of plants on metacommunities and correlation networks of soil microbial groups in an ecologically restored wetland. *Microbial ecology*, *81*(3), pp.657–672.

Jia, B., Niu, Z., Wu, Y., Kuzyakov, Y. and Li, X.G., 2020. Waterlogging increases organic carbon decomposition in grassland soils. *Soil Biology and Biochemistry*, *148*, p.107927.

Jiang, W., Pan, B., Jiang, X., Shi, P., Zhu, P., Zhang, L., Chen, J. and Wu, N., 2021. A comparative study on the indicative function of species and traits structure of stream macroinvertebrates to human disturbances. *Ecological Indicators*, *129*, p.107939.

Jisha, K.C. and Puthur, J.T., 2021. Ecological importance of wetland systems. *Wetlands conservation: Current challenges and future strategies*, pp.40–54.

JOASH, O.N., 2017. Influence of Planted Riparian Buffer Vegetation Cover and Water Quality on The Benthic Macroinvertebrate Assemblages in Kuywa River, Bungoma County, Kenya.Johnson, L., Richards, C., Host, G. and Arthur, J., 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. *Freshwater biology*, *37*(1), pp.193–208.

Johnston, E.L., Dafforn, K.A., Clark, G.F., Rius, M. and Floerl, O., 2017. Anthropogenic activities promoting the establishment and spread of marine non–indigenous species post–arrival.

Jones, T.R., Henderson, C.J., Olds, A.D., Connolly, R.M., Schlacher, T.A., Hourigan, B.J., Goodridge Gaines, L.A. and Gilby, B.L., 2021. The mouths of estuaries are key transition zones that concentrate the ecological effects of predators. *Estuaries and Coasts*, *44*(6), pp.1557–1567.

Juma, H., 2023. *Degradation of Msimbazi Wetland and Its Impact on the Livelihoods of the Urban Poor in Dar es Salaam Tanzania* (Doctoral dissertation, The Open University of Tanzania).

Juvigny-Khenafou, N.P., Piggott, J.J., Atkinson, D., Zhang, Y., Macaulay, S.J., Wu, N. and Matthaei, C.D., 2021. Impacts of multiple anthropogenic stressors on stream macroinvertebrate community composition and functional diversity. *Ecology and Evolution*, *11*(1), pp.133–152.

Kaczmarek, N., 2023. *Macroinvertebrate community composition and ecosystem health in response to salinity and environmental change in the Draa River basin, Morocco* (Doctoral dissertation, Rheinland–Pfälzische Technische Universität Kaiserslautern–Landau).

Kafle, A., Jha, S. and Huettmann, F., 2020. The relevance and significant role of mid-elevation for the watersheds and biodiversity conservation in the Hindu Kush-Himalaya: The Case of Nepal in the Anthropocene. In *Hindu Kush-Himalaya Watersheds Downhill: Landscape Ecology and Conservation Perspectives* (pp. 331-343). Cham: Springer International Publishing.

Kant, N. and Wrat, G., 2025. A review of integrated groundwater and surface water management for environmental sustainability. *Acta Geochimica*, pp.1–22.

Keddy, P.A., Fraser, L.H., Solomeshch, A.I., Junk, W.J., Campbell, D.R., Arroyo, M.T. and Alho, C.J., 2009. Wet and wonderful: the world's largest wetlands are conservation priorities. *BioScience*, *59*(1), pp.39–51.

Keith, B.R., Carleen, J.D., Larson, D.M., Anteau, M.J. and Fitzpatrick, M.J., 2022. *Protocols for collecting and processing macroinvertebrates from the benthos and water column in depressional wetlands* (No. 2022–1029). US Geological Survey.

Keith, K.M., Potvin, M.K., Saad, S.R. and Surasinghe, T.D., 2025. Temporal Shifts in Biological Community Structure in Response to Wetland Restoration: Implications for Wetland Biodiversity Conservation and Management. *Diversity*, *17*(3), p.198.

Kendrick, M.R., Hershey, A.E. and Huryn, A.D., 2019. Disturbance, nutrients, and antecedent flow conditions affect macroinvertebrate community structure and productivity in an Arctic river. *Limnology and Oceanography*, *64*(S1), pp. S93–S104.

Khan, A., Patel, K., Shukla, H., Viswanathan, A., van der Valk, T., Borthakur, U., Nigam, P., Zachariah, A., Jhala, Y.V., Kardos, M. and Ramakrishnan, U., 2021. Genomic evidence for inbreeding depression and purging of deleterious genetic variation in Indian tigers. *Proceedings of the National Academy of Sciences*, *118*(49), p. e2023018118.

Khudhair, N., Yan, C., Liu, M. and Yu, H., 2019. Effects of habitat types on macroinvertebrates assemblages structure: case study of sun island bund wetland. *Biomed research international*, *2019*(1), p.2650678.

Kidane, Y., 2022. *Vegetation diversity and distribution along the Bale mountains Afroalpine hotspot of biodiversity in the face of a fast-changing world* (Doctoral dissertation).

Kingsford, R.T., Basset, A. and Jackson, L., 2016. Wetlands: conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), pp.892–916.

Kolka, R., Trettin, C. and Windham-Myers, L., 2021. The importance of wetland carbon dynamics to society: Insight from the second state of the carbon cycle science report. *Wetland carbon and environmental management*, pp.421–436.

Kolka, R.K., D’Amato, A.W., Wagenbrenner, J.W., Slesak, R.A., Pypker, T.G., Youngquist, M.B., Grinde, A.R. and Palik, B.J., 2018. Review of ecosystem level impacts of emerald ash borer on black ash wetlands: what does the future hold? *Forests*, *9*(4), p.179.

Krejčová, J., Vicentini, F., Flynn, T., Mudrák, O. and Frouz, J., 2021. Biodiversity loss caused by subsurface pipe drainage is difficult to restore. *Ecological Engineering*, *170*, p.106336.

Kroll, S.A., Horwitz, R.J., Keller, D.H., Sweeney, B.W., Jackson, J.K. and Perez, L.B., 2019. Large–scale protection and restoration programs aimed at protecting stream ecosystem integrity: the role of science–based goal–setting, monitoring, and data management. *Freshwater Science*, *38*(1), pp.23–39.

Kuenzer, C., Heimhuber, V., Huth, J. and Dech, S., 2019. Remote sensing for the quantification of land surface dynamics in large river delta regions-A review. *Remote Sensing*, *11*(17), p.1985.

Lalbiaknunga, J. and Lalbiaknii, P.C., 2025. Influence of altitude on tree species diversity, structure and composition in a protected area of the Eastern Himalayas, Mizoram, India. *Flora*, p.152741.

Land, E. and Peters, C.N., 2023. Groundwater impacts on stream biodiversity and communities: a review. *Journal of freshwater ecology*, *38*(1), p.2260801.

Latli, A., Michel, L.N., Lepoint, G. and Kestemont, P., 2019. River habitat homogenisation enhances trophic competition and promotes individual specialisation among young of the year fish. *Freshwater Biology*, *64*(3), pp.520–531.

Lawton, R.O., Lawton, M.F., Lawton, R.M. and Daniels, J.D., 2016. The montane cloud forests of the volcanic cordilleras. *Costa Rican Ecosystems*, pp.415–450.

Lázaro–Lobo, A. and Ervin, G.N., 2021. Wetland invasion: a multi–faceted challenge during a time of rapid global change. *Wetlands*, *41*(5), p.64.

Leberg, S.S., Osterhaus, D.M., Pierce, C.L. and Stewart, T.W., 2024. Restored oxbow wetlands within an agricultural landscape: using physical and biological characteristics to evaluate impacts of tile drainage input. *Wetlands*, *44*(3), p.27.

Leboucher, T., Tison-Rosebery, J., Budnick, W.R., Jamoneau, A., Vyverman, W., Soininen, J., Boutry, S. and Passy, S.I., 2020. A metacommunity approach for detecting species influenced by mass effect. *Journal of Applied Ecology*, *57*(10), pp.2031–2040.

Lechêne, A., Lobry, J., Boët, P. and Laffaille, P., 2018. Change in fish functional diversity and assembly rules in the course of tidal marsh restoration. *PLoS One*, *13*(12), p. e0209025.

Leimberger, K.G., Dalsgaard, B., Tobias, J.A., Wolf, C. and Betts, M.G., 2022. The evolution, ecology, and conservation of hummingbirds and their interactions with flowering plants. *Biological Reviews*, *97*(3), pp.923–959.

Leshaba, E.N., 2023. *Assessment of metals, carbon dynamics and macroinvertebrates diversity in pan wetlands across geological areas of central Kruger National Park, South Africa* (Master's thesis).

Leshaba, E.N., Dube, T., Dondofema, F., Munyai, L.F., Keates, C., Riddell, E., Khosa, D. and Dalu, T., 2025. Macroinvertebrate diversity within pan wetlands in relation to geological type and hydroperiod in a protected subtropical Austral national park. *Chemistry and Ecology*, *41*(5), pp.587–609.

Lessard, J.P., Weinstein, B.G., Borregaard, M.K., Marske, K.A., Martin, D.R., McGuire, J.A., Parra, J.L., Rahbek, C. and Graham, C.H., 2016. Process–based species pools reveal the hidden signature of biotic interactions amid the influence of temperature filtering. *The American Naturalist*, *187*(1), pp.75–88.

Liao, L., Wang, X., Wang, J., Liu, G. and Zhang, C., 2021. Nitrogen fertilization increases fungal diversity and abundance of saprotrophs while reducing nitrogen fixation potential in a semiarid grassland. *Plant and Soil*, *465*(1), pp.515–532.

Liley, D., Saunders, P. and Caals, Z., 2021. Habitats Regulations Assessment of Local Plan Review pre–submission.

Lim, S.H. and Do, Y., 2023. Macroinvertebrate conservation in river ecosystems: Challenges, restoration strategies, and integrated management approaches. *Entomological Research*, *53*(8), pp.271–290.

Lipson, D.A., Zona, D., Raab, T.K., Bozzolo, F., Mauritz, M. and Oechel, W.C., 2012. Water–table height and microtopography control biogeochemical cycling in an Arctic coastal tundra ecosystem. *Biogeosciences*, *9*(1), pp.577–591.

Littlefield, C.E., Krosby, M., Michalak, J.L. and Lawler, J.J., 2019. Connectivity for species on the move: supporting climate-driven range shifts. *Frontiers in Ecology and the Environment*, *17*(5), pp.270–278.

Liu, D., Yu, H., Lu, K., Guan, Q. and Wu, H., 2021. Freshwater releases into estuarine wetlands change the determinants of benthic invertebrate metacommunity structure. *Frontiers in Ecology and Evolution*, *9*, p.721628.

Liu, Y., Ren, Y., Zhang, H., Qiu, D. and Zhu, Y., 2025. Characteristics of invasive alien plants in different urban areas: the case of Kunshan City, Jiangsu Province, China. *Frontiers in Plant Science*, *16*, p.1539457.

Livinus, M.U., Bala, S.Z., Abdulsalam, M., Innocent, M.O., Hassan, M., Elelu, S.A. and Kini, P., 2024. Role of microbes in soil food webs and vegetation development. In *Soil Microbiome in Green Technology Sustainability* (pp. 107–132). Cham: Springer Nature Switzerland.

Lo, H.W., Klaar, M., Smith, M. and Woulds, C., 2024. Effects of natural flood management woody dams on benthic macroinvertebrates and benthic metabolism in upland streams: Importance of wood-induced geomorphic changes. *Ecohydrology*, *17*(5), p. e2654.

López–López, E. and Sedeño–Díaz, J.E., 2014. Biological indicators of water quality: The role of fish and macroinvertebrates as indicators of water quality. In *Environmental indicators* (pp. 643–661). Dordrecht: Springer Netherlands.

Lorenz, K. and Lal, R., 2018. Carbon sequestration in wetland soils. In *Carbon sequestration in agricultural ecosystems* (pp. 211–234). Cham: Springer International Publishing.

Loskotová, B., 2022. *Aquatic macroinvertebrate persistence in intermittent streams* (Doctoral dissertation, Doctoral Dissertation]. Masaryk University, Czech Republic).

Loucks, D.P. and Van Beek, E., 2017. Water resources planning and management: An overview. *Water resource systems planning and management: an introduction to methods, models, and applications*, pp.1-49.

Ma, S.N., Xu, Y.F., Wang, H.J., Wang, H.Z., Li, Y., Dong, X.M., Xu, J.L., Yu, Q., Søndergaard, M. and Jeppesen, E., 2023. Mechanisms of high ammonium loading promoted phosphorus release from shallow lake sediments: A five–year large–scale experiment. *Water Research*, *245*, p.120580.

Maass-Morales, C., Stigter, T., Fraser, C., Van Breukelen, B.M. and Jewitt, G., 2024. Management zones in transboundary aquifers: A review of delineation methods under a new framework of cross-border groundwater impacts. *Journal of Environmental Management*, *357*, p.120677.

Mabidi, A., Bird, M.S. and Perissinotto, R., 2017. Distribution and diversity of aquatic macroinvertebrate assemblages in a semi-arid region earmarked for shale gas exploration (Eastern Cape Karoo, South Africa). *PLoS one*, *12*(6), p.e0178559.

Machado, K.B., de Oliveira, P.H.F., Ferragut, C., Teresa, F.B. and Nabout, J.C., 2024. Environmental gradients and anthropogenic landscape modification determine composition of functional traits of periphyton community in Brazilian Cerrado streams. *Hydrobiologia*, *851*(20), pp.4995–5009.

MacLeod, A., 2013. Patterns of diversity in high elevation grassland Diptera.

Majdi, N., Kreuzinger-Janik, B. and Traunspurger, W., 2016. Effects of flatworm predators on sediment communities and ecosystem functions: a microcosm approach. *Hydrobiologia*, *776*(1), pp.193-207.

Majumdar, A., Shrivastava, A., Sarkar, S.R., Sathyavelu, S., Barla, A. and Bose, S., 2020. Hydrology, sedimentation and mineralisation: A wetland ecology perspective. *Climate Change and Environmental Sustainability*, *8*(2), pp.134–151.

Manu, M.K., Ashiagbor, G., Seidu, I., Groen, T., Gyimah, T. and Toxopeus, B., 2023. Odonata as bioindicator for monitoring anthropogenic disturbance of Owabi wetland sanctuary, Ghana. *Aquatic Insects*, *44*(2), pp.151–169.

Mao C, Li X, Dunthorn M, Xu W, Luo X, Xiong X, Al–Farraj SA, Huang J. Diversity and assembly mechanisms of zooplankton communities in freshwater aquaculture ponds. Marine Life Science & Technology. 2025 Aug 20:1–6.

Mao, L., Li, M. and Shen, W., 2020. Remote sensing applications for monitoring terrestrial protected areas: Progress in the last decade. *Sustainability*, *12*(12), p.5016.

Martin, R.M., Wigand, C., Elmstrom, E., Lloret, J. and Valiela, I., 2018. Long-term nutrient addition increases respiration and nitrous oxide emissions in a New England salt marsh. *Ecology and Evolution*, *8*(10), pp.4958–4966.

Marzini, L., Amaddii, M., Papasidero, M.P., D'Addario, E., Disperati, L. and Chianucci, F., 2021. Relationships between vegetation characters and saturated hydraulic conductivity at catchment scale. In *BeGEO Scientists 2021–ABSTRACT BOOK* (pp. 146–146). Società Geologica Italiana.

Masi, F., Rizzo, A. and Regelsberger, M., 2018. The role of constructed wetlands in a new circular economy, resource oriented, and ecosystem services paradigm. *Journal of environmental management*, *216*, pp.275–284.

Masina, F.M., Wasserman, R.J., Wu, N., Mungenge, C.P., Dondofema, F., Keates, C., Shikwambana, P. and Dalu, T., 2023. Macroinvertebrate diversity in relation to limnochemistry in an Austral semi–arid transboundary aquifer region pan system. *Science of The Total Environment*, *878*, p.163161.

Mataba, G., 2023. Exploring integrated strategies to control oviposition and larval development in mosquitoes in Northern Tanzania.

Mathers, K.L., Rice, S.P. and Wood, P.J., 2019. Predator, prey, and substrate interactions: The role of faunal activity and substrate characteristics. *Ecosphere*, *10*(1), p. e02545.

Mattone, C., 2016. *Benthic infauna of mangrove forests: dissolved oxygen and environmental settings determine their community composition and function* (Doctoral dissertation, James Cook University).

Mayfield, R.J., 2020. *Analysing structural ecosystem change in high latitude lakes* (Doctoral dissertation, University of Southampton).

Mbulaheni, L., 2022. *Assessment of Water Quality Status of the Woestalleen Wetland Before and After Rehabilitation* (Master's thesis, University of the Witwatersrand, Johannesburg (South Africa).

Mccormick, P.V., Shuford III, R.B. and Rawlik, P.S., 2004. Changes in macroinvertebrate community structure and function along a. *Hydrobiologia*, *529*(1), pp.113–132.

McDaniel, J.L., 2022. *Chihuahuan desert rock pool community assemblages: Patterns of taxonomic diversity* (Master's thesis, The University of Texas at El Paso).

McKenzie, M., Mathers, K.L., Wood, P.J., England, J., Foster, I., Lawler, D. and Wilkes, M., 2020. Potential physical effects of suspended fine sediment on lotic macroinvertebrates. *Hydrobiologia*, *847*(3), pp.697–711.

McLean, K.I., Mushet, D.M., Sweetman, J.N., Anteau, M.J. and Wiltermuth, M.T., 2020. Invertebrate communities of Prairie-Pothole wetlands in the age of the aquatic Homogenocene. *Hydrobiologia*, *847*(18), pp.3773-3793.

Mervyn, M.K., 2025. Macroinvertebrate Communities and Food Web Structure in Tundra Streams are Shaped by Substrate Size and Beaver Impoundments.

Miao, L., Zhang, J., Luo, D., Adyel, T.M., Ao, Y., Li, C., Yao, Y., Wu, J., You, G. and Hou, J., 2024. Distinct effects of flow intermittency on the benthic microbial diversity and their denitrification on different substrates. *Science of The Total Environment*, *957*, p.177394.

Michael, T., 2024. *Direct and indirect animal-mediated biogeochemical effects on nutrient dynamics in coastal Lake Erie ecosystems*. Kent State University.

Mikryukov, V., Dulya, O., Zizka, A., Bahram, M., Hagh-Doust, N., Anslan, S., Prylutskyi, O., Delgado-Baquerizo, M., Maestre, F.T., Nilsson, H. and Pärn, J., 2023. Connecting the multiple dimensions of global soil fungal diversity. *Science advances*, *9*(48), p.eadj8016.

Milner, A.M., Loza Vega, E.M., Matthews, T.J., Conn, S.C. and Windsor, F.M., 2023. Long-term changes in macroinvertebrate communities across high-latitude streams. *Global Change Biology*, *29*(9), pp.2466–2477.

Minot, M., Aubert, M. and Husté, A., 2021. Pond creation and restoration: patterns of odonate colonization and community dynamics. *Biodiversity and Conservation*, *30*(14), pp.4379–4399.

Miserendino, M.L., Brand, C., Assef, Y.A., Horak, C.N., Manzo, L.M., Epele, L.B. and Williams–Subiza, E., 2022. Land–use effects on aquatic and wetland ecosystems: an overview of environmental impacts and tools for ecological assessment. *Freshwaters and Wetlands of Patagonia: Ecosystems and Socioecological Aspects*, pp.295–321.

Mishra, B.K., Kumar, P., Saraswat, C., Chakraborty, S. and Gautam, A., 2021. Water security in a changing environment: Concept, challenges and solutions. *Water*, *13*(4), p.490.

Mohanty, S., Pandey, P.C., Pandey, M., Srivastava, P.K. and Dwivedi, C.S., 2024. Wetlands contribution and linkage to support SDGs, its indicators and targets-A critical review. *Sustainable Development*, *32*(5), pp.5348–5392.

Mohebbi, N., Nouri, J., Khorasani, N. and Riazi, B., 2022. Environmental management for human communities around wetlands adjacent urban region by ecological risk approach. *International Journal of Human Capital in Urban Management*, *7*(1), pp.1–16.

Moomaw, W.R., Chmura, G.L., Davies, G.T., Finlayson, C.M., Middleton, B.A., Natali, S.M., Perry, J.E., Roulet, N. and Sutton–Grier, A.E., 2018. Wetlands in a changing climate: science, policy and management. *Wetlands*, *38*(2), pp.183–205.

Morris, R.L., Heery, E.C., Loke, L.H., Lau, E., Strain, E., Airoldi, L., Alexander, K.A., Bishop, M.J., Coleman, R.A., Cordell, J.R. and Dong, Y.W., 2019. Design options, implementation issues and evaluating success of ecologically engineered shorelines. *Oceanography and marine biology*.

Morse, J.C., 2017. Biodiversity of aquatic insects. *Insect biodiversity: science and society*, pp.205–227.

Moyo, S 2023. High–Altitude Temporary Systems and Macroinvertebreats Composition in La Nina Cycle, Maloti Drakenserg. Animals, 44 (32), p.2631.

Mpakairi, K.S., 2022. *Spatial Characterization of Vegetation Diversity with Satellite Remote Sensing in the Khakea–Bray Transboundary Aquifer* (Doctoral dissertation, University of the Western Cape).

Mramba, R.P. and Kahindi, E.J., 2023. Pond water quality and its relation to fish yield and disease occurrence in small–scale aquaculture in arid areas. *Heliyon*, *9*(6).

Mrozińska, N., Glińska–Lewczuk, K. and Obolewski, K., 2021. Salinity as a key factor on the benthic fauna diversity in the coastal lakes. Animals, 11(11), p.3039.

Msesane, Q., 2025. *Spatial modelling of the hydrogeological connection between groundwater-dependent ecosystems and aquifers in the Kruger National Park, South Africa* (Doctoral dissertation, University of the Western Cape).

Munyai, L.F., Gumede, B.P., Dondofema, F. and Dalu, T., 2025. Environmental characteristics shape macroinvertebrate community structure across spatiotemporal scales in a subtropical African river system. *Scientific Reports*, *15*(1), p.6595.

Munyai, L.F., Mugwedi, L., Wasserman, R.J., Dondofema, F. and Dalu, T., 2023. Assessing fish and macroinvertebrates assemblages in relation to environmental variables in Makuleke floodplain pans: implications for biodiversity conservation. *Wetlands*, *43*(7), p.93.

Munyai, L.F., Mugwedi, L., Wasserman, R.J., Dondofema, F. and Dalu, T., 2023. Assessing fish and macroinvertebrates assemblages in relation to environmental variables in Makuleke floodplain pans: implications for biodiversity conservation. *Wetlands*, *43*(7), p.93.

Mureithi, P.W., Aine, A., Basooma, R., Namumbya, J., Nansumbi, F., Yegon, M.J., Meimberg, H. and Graf, W., 2025. Advancements in macroinvertebrate-based river bioassessment research in the Afrotropical region: review and steps towards a regional framework. *Environmental Monitoring and Assessment*, *197*(8), p.935.

Musher, L.J., 2025. The biogeographic and genomic signatures of dynamic river networks for terrestrial species in Amazonia. *Biological Reviews*.

Mwaijengoa, G.N., Njau, K.N., Vanschoenwinkel, B. and Brendoncka, L., 2020. Seasonal river connections modulate community structure in tropical temporary pools. *Towards sustainable management of inland waters in Tanzania assessing the ecological integrity of river ecosystems in the upper Pangani river basin (Tanzania)*, p.167.

Mykrä, H. and Heino, J., 2017. Decreased habitat specialization in macroinvertebrate assemblages in anthropogenically disturbed streams. *Ecological Complexity*, *31*, pp.181–188.

Nag, S.K., Ghosh, B.D. and Sarkar, U.K., 2020. Wetlands are important carbon sink in the context of global warming and climate change. *Indian Farming*, *70*(11).

Naidoo, R., Aylward, C., Elliott, W., Keeley, A., Kinnaird, M., Knight, M., Papp, C.R., Thapa, K. and Antelo, R., 2025. From science to impact: Conserving ecological connectivity in large conservation landscapes. *Proceedings of the National Academy of Sciences*, *122*(31), p. e2410937122.

Narany, T.S., Sefie, A. and Aris, A.Z., 2018. The long–term impacts of anthropogenic and natural processes on groundwater deterioration in a multilayered aquifer. *Science of the total environment*, *630*, pp.931–942.

Natsumeda, T. and Iguchi, K.I., 2019. Habitat–specific effects of interstitial space between stream substrate particles on the colonization of aquatic organisms. *International Aquatic Research*, *11*(4), pp.347–358.

Ndadzungira, E., Kupika, O.L., Muposhi, V.K., Muboko, N., Chanyandura, A. and Mbikiyana, M., 2023. Structure and composition of woody vegetation along the Zambezi river floodplain and seasonal water pans in Mana Pools National Park, Zimbabwe. *Tropical Ecology*, *64*(1), pp.105–113.

Ndatimana, G., Nantege, D. and Arimoro, F.O., 2023. A review of the application of the macroinvertebrate–based multimetric indices (MMIs) for water quality monitoring in lakes. Environmental Science and Pollution Research, 30(29), pp.73098–73115.

Newton, A., Icely, J., Cristina, S., Perillo, G.M., Turner, R.E., Ashan, D., Cragg, S., Luo, Y., Tu, C., Li, Y. and Zhang, H., 2020. Anthropogenic, direct pressures on coastal wetlands. *Frontiers in Ecology and Evolution*, *8*, p.144.

Ngobe, T.F., 2022. *Geophysical investigations in the Khakhea–Bray Transboundary Aquifer* (Doctoral dissertation, University of the Free State).

Nguyen, H.H., Dargusch, P., Moss, P. and Aziz, A.A., 2017. Land–use change and socio–ecological drivers of wetland conversion in Ha Tien Plain, Mekong Delta, Vietnam. *Land Use Policy*, *64*, pp.101–113.

Nguyen, T.T., Ngo, H.H., Guo, W., Wang, X.C., Ren, N., Li, G., Ding, J. and Liang, H., 2019. Implementation of a specific urban water Management–Sponge City. *Science of the Total Environment*, *652*, pp.147–162.

Niculita-Hirzel, H., Hirzel, A.H. and Wild, P., 2024. A GIS-based approach to assess the influence of the urban built environment on cardiac and respiratory outcomes in older adults. *Building and Environment*, *253*, p.111362.

Nieland, M.A., Moley, P., Hanschu, J. and Zeglin, L.H., 2021. Differential resilience of soil microbes and ecosystem functions following cessation of long–term fertilization. *Ecosystems*, *24*(8), pp.2042–2060.

Nieoczym, M., Stryjecki, R., Buczyński, P., Płaska, W. and Kloskowski, J., 2023. Differential abundance, composition and mesohabitat use by aquatic macroinvertebrate taxa in ponds with and without fish. *Aquatic Sciences*, *85*(1), p.25.

Nieto, C., Ovando, X.M., Loyola, R., Izquierdo, A., Romero, F., Molineri, C., Rodríguez, J., Rueda Martín, P., Fernández, H., Manzo, V. and Miranda, M.J., 2017. The role of macroinvertebrates for conservation of freshwater systems. Ecology and evolution, 7(14), pp.5502–5513.

Niu, L., Li, Y., Wang, P., Zhang, W., Wang, C. and Wang, Q., 2015. Understanding the linkage between elevation and the activated–sludge bacterial community along a 3,600–meter elevation gradient in China. *Applied and environmental microbiology*, *81*(19), pp.6567–6576.

Nkosi, M., Mathivha, F.I. and Odiyo, J.O., 2021. Impact of land management on water resources, a South African context. *Sustainability*, *13*(2), p.701.

Nsor, C.A., Oppong, S.K., Danquah, E., Ochem, M. and Antobre, O.O., 2020. Spatiotemporal dynamics of terrestrial invertebrate assemblages in the riparian zone of the Wewe river, Ashanti region, Ghana. *Open Life Sciences*, *15*(1), pp.331–345.

Ntloko, P., Palmer, C.G., Akamagwuna, F.C. and Odume, O.N., 2021. Exploring macroinvertebrates ecological preferences and trait–based indicators of suspended fine sediment effects in the Tsitsa River and its tributaries, Eastern Cape, South Africa. *Water*, *13*(6), p.798.

Nyman, M., Weckström, J. and Korhola, A., 2008. Chironomid response to environmental drivers during the Holocene in a shallow treeline lake in northwestern Fennoscandia. *The Holocene*, *18*(2), pp.215–227.

O'Hare, M.T., Baattrup–Pedersen, A., Baumgarte, I., Freeman, A., Gunn, I.D., Lázár, A.N., Sinclair, R., Wade, A.J. and Bowes, M.J., 2018. Responses of aquatic plants to eutrophication in rivers: a revised conceptual model. *Frontiers in plant science*, *9*, p.451.

Obertegger, U., Andreis, D., Piccolroaz, S. and Flaim, G., 2021. Extreme events and ice cover determine dissolved oxygen in a mountain lake. In *SEFS12: Symposium for European freshwater sciences, online, 25–30 July, 2021* (p. 358).

Oertli, B. and Parris, K.M., 2019. Toward management of urban ponds for freshwater biodiversity. *Ecosphere*, *10*(7), p. e02810.

Oester, R., 2024. *The Role of Riparian Forests for Aquatic–Terrestrial Linkages, Ecosystem Functions, and Biodiversity in Stream Food Webs* (Doctoral dissertation, University of Zurich).

Ogidi, O.I. and Akpan, U.M., 2022. Aquatic biodiversity loss: impacts of pollution and anthropogenic activities and strategies for conservation. In *Biodiversity in Africa: potentials, threats and conservation* (pp. 421-448). Singapore: Springer Nature Singapore.

O'Keefe, J., 2022. *Property Planning: AgGuide–A Practical Handbook*. Department of Regional NSW.

Olanrewaju, M.T. and Aladejana, O.O., 2025. Mapping groundwater dependent ecosystems in a semi–arid environment: a case study from the Nigerian Sudan Savannah. *Earth Science Informatics*, *18*(1), p.143.

Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L. and Proença, V., 2015. Biodiversity and resilience of ecosystem functions. *Trends in ecology & evolution*, *30*(11), pp.673–684.

Olmedo, E. and Smith, M., 2021, March. Development of an IoT water quality monitoring system for data–based aquaculture siting. In *SoutheastCon 2021* (pp. 1–8). IEEE.

Olmo, C., Ramos–Jiliberto, R., Boix, D., López, C. and Barbosa, L.G., 2024. Temporary lentic waterbodies of Latin America and the Caribbean: a scientometric study. *Inland Waters*, pp.1–16.

Omoregie, A.I., Silini, M.O.E., Wong, L.S. and Rajasekar, A., 2025. Nitrogen eutrophication in Chinese aquatic ecosystems: drivers, impacts, and mitigation strategies. *Nitrogen*, *6*(4), p.92.

Onditi, K.O., de la Sancha, N.U., Musila, S., Kioko, E. and Jiang, X., 2024. Unravelling spatial scale effects on elevational diversity gradients: insights from montane small mammals in Kenya. *BMC ecology and evolution*, *24*(1), p.139.

Orsholm, J. and Elenius, M., 2022. Effects of hydrology on wetlandbiodiversity: A literature study and development of hydrological indicators.

Ozkan, N., 2024, September. Roles of benthic macroinvertebrates in the food web. In Proceedings of VI. International Agricultural, Biological & Life Science Conference, Edirne, Turkey (pp. 184–193).

Palmer, M. and Ruhi, A., 2019. Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. *Science*, *365*(6459), p. eaaw2087.

Pan, C., Xu, S., Qian, Z., Liao, Q., Wu, T. and Wang, G., 2025. How Do Waterbird Communities Respond to Multi–Scale Environmental Variables in the Satellite Wetlands Surrounding a Ramsar Site, Shengjin Lake in China? *Diversity*, *17*(3), p.176.

Pandey, B., Pan, K., Dakhil, M.A., Liao, Z., Timilsina, A., Khanal, M. and Zhang, L., 2021. Contrasting gymnosperm diversity across an elevation gradient in the ecoregion of China: The role of temperature and productivity. *Frontiers in Ecology and Evolution*, *9*, p.679439.

Park, J.H., Nayna, O.K., Begum, M.S., Chea, E., Hartmann, J., Keil, R.G., Kumar, S., Lu, X., Ran, L., Richey, J.E. and Sarma, V.V., 2018. Reviews and syntheses: Anthropogenic perturbations to carbon fluxes in Asian river systems–concepts, emerging trends, and research challenges. *Biogeosciences*, *15*(9), pp.3049–3069.

Passy, S.I., Larson, C.A., Mruzek, J.L., Budnick, W.R. and Leboucher, T., 2024. A new perspective on the spatial, environmental, and metacommunity controls of local biodiversity. *Science of the Total Environment*, *926*, p.171618.

Patrick, C.J., Anderson, K.E., Brown, B.L., Hawkins, C.P., Metcalfe, A., Saffarinia, P., Siqueira, T., Swan, C.M., Tonkin, J.D. and Yuan, L.L., 2021. The application of metacommunity theory to the management of riverine ecosystems. *Wiley Interdisciplinary Reviews: Water*, *8*(6), p. e1557.

Pedrinho, A., Mendes, L.W., de Araujo Pereira, A.P., Araujo, A.S.F., Vaishnav, A., Karpouzas, D.G. and Singh, B.K., 2024. Soil microbial diversity plays an important role in resisting and restoring degraded ecosystems. *Plant and Soil*, *500*(1), pp.325–349.

Pelletier, M.C., Ebersole, J., Mulvaney, K., Rashleigh, B., Gutierrez, M.N., Chintala, M., Kuhn, A., Molina, M., Bagley, M. and Lane, C., 2020. Resilience of aquatic systems: review and management implications. *Aquatic sciences*, *82*(2), p.44.

Peng, Y., Xin, J., Peng, N., Li, Y., Huang, J., Zhang, R., Li, C., Wu, Y., Gong, B. and Wang, R., 2024. Global patterns and drivers of spatial autocorrelation in plant communities in protected areas. *Diversity and Distributions*, *30*(1), pp.119-133.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E.A., Ganesanandamoorthy, P., Garnier, A., Griffiths, J.I. and Greene, S., 2018. Biodiversity increases and decreases ecosystem stability. *Nature*, *563*(7729), pp.109–112.

Philippot, L., Griffiths, B.S. and Langenheder, S., 2021. Microbial community resilience across ecosystems and multiple disturbances. *Microbiology and Molecular Biology Reviews*, *85*(2), pp.10–1128.

Phiri, C., Chakona, A. and Day, J.A., 2012. Macroinvertebrates associated with two submerged macrophytes, Lagarosiphon ilicifolius and Vallisneria aethiopica, in the Sanyati Basin, Lake Kariba, Zimbabwe: effect of plant morphological complexity. *African Journal of Aquatic Science*, *37*(3), pp.277–288.

Pickerill, J., Chitewere, T., Cornea, N., Lockyer, J., Macrorie, R., Blažek, J.M. and Nelson, A., 2024. URBAN ECOLOGICAL FUTURES: Five Eco‐Community Strategies for more Sustainable and Equitable Cities. *International Journal of Urban and Regional Research*, *48*(1), pp.161–176.

Pille, F., Pinto, L. and Denoël, M., 2023. Functional and temporal facets of predation by marsh frogs across the aquatic–terrestrial ecotone of ponds and implications in the context of biological invasions. *Freshwater Biology*, *68*(12), pp.2184–2196.

Pilotto, F., Bazzanti, M., Di Vito, V., Frosali, D., Livretti, F., Mastrantuono, L., Pusch, M.T., Sena, F. and Solimini, A.G., 2015. Relative impacts of morphological alteration to shorelines and eutrophication on littoral macroinvertebrates in Mediterranean lakes. *Freshwater Science*, *34*(2), pp.410–422.

Pires, M.M., Bieger, L., Boelter, T., Stenert, C. and Maltchik, L., 2021. Spatiotemporal assembly patterns of macroinvertebrate metacommunity structure in subtropical wetlands with different hydroperiods. *International Review of Hydrobiology*, *106*(5–6), pp.239–248.

Pop, M.M., Di Lorenzo, T. and Iepure, S., 2023. Living on the edge–An overview of invertebrates from groundwater habitats prone to extreme environmental conditions. *Frontiers in Ecology and Evolution*, *10*, p.1054841.

Potapov, A.M., Beaulieu, F., Birkhofer, K., Bluhm, S.L., Degtyarev, M.I., Devetter, M., Goncharov, A.A., Gongalsky, K.B., Klarner, B., Korobushkin, D.I. and Liebke, D.F., 2022. Feeding habits and multifunctional classification of soil‐associated consumers from protists to vertebrates. *Biological Reviews*, *97*(3), pp.1057–1117.

Poulter, B., Fluet-Chouinard, E., Hugelius, G., Koven, C., Fatoyinbo, L., Page, S.E., Rosentreter, J.A., Smart, L.S., Taillie, P.J., Thomas, N. and Zhang, Z., 2021. A review of global wetland carbon stocks and management challenges. *Wetland carbon and environmental management*, pp.1–20.

Prentice, C., Hessing-Lewis, M., Sanders-Smith, R. and Salomon, A.K., 2019. Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows. *Limnology and Oceanography*, *64*(6), pp.2389–2404.

Puche, E., Rodrigo, M.A., Segura, M. and Rojo, C., 2021. Habitat coupling mediated by the multi–interaction network linked to macrophyte meadows: ponds versus lakes. *Aquatic Sciences*, *83*(3), p.55.

Quijada–Alarcón, J., Rodríguez–Rodríguez, R., González–Cancelas, N. and Bethancourt–Lasso, G., 2023. Spatial Analysis of Territorial Connectivity and Accessibility in the Province of Coclé in Panama. *Sustainability*, *15*(15), p.11500.

Quinn, P.F., Hewett, C.J., Wilkinson, M.E. and Adams, R., 2022. The role of runoff attenuation features (RAFs) in natural flood management. *Water*, *14*(23), p.3807.

Raffard, A., Bestion, E., Cote, J., Haegeman, B., Schtickzelle, N. and Jacob, S., 2022. Dispersal syndromes can link intraspecific trait variability and meta–ecosystem functioning. *Trends in Ecology & Evolution*, *37*(4), pp.322–331.

Rai, A., Shah, D.N., Shah, R.D.T. and Milner, C., 2019. Influence of environmental parameters on benthic macroinvertebrate assemblages in the headwaters of Bagmati river, Kathmandu valley, Nepal. *Banko Janakari*, *29*(1), pp.53–61.

Ramírez, G.M.O., 2024. *Spatiotemporal Assemblages of Soil Arthropods Communities in a Tropical Palustrine–Estuarine Urban Coastal Wetland* (Doctoral dissertation, University of Puerto Rico, Rio Piedras (Puerto Rico)).

Rampheri, M.B., Dube, T., Dondofema, F. and Dalu, T., 2023. Identification and delineation of groundwater–dependent ecosystems (GDEs) in the Khakea–Bray transboundary aquifer region using geospatial techniques. *Geocarto International*, *38*(1), p.2172217.

Rampheri, M.B., Dube, T., Dondofema, F. and Dalu, T., 2023. Progress in the remote sensing of groundwater-dependent ecosystems in semi-arid environments. *Physics and Chemistry of the Earth, Parts A/B/C*, *130*, p.103359.

Ratterman, D.J., 2016. *Biotic assessment of two central Kentucky streams: Examining the effects of wastewater treatment and anthropogenic disturbance* (Master's thesis, Eastern Kentucky University).

Raturi, A., Raturi, A. and Singh, H., 2024. Climate change impacts on wetland ecosystem functioning with special reference to greenhouse gas emissions. In *Forests and Climate Change: Biological Perspectives on Impact, Adaptation, and Mitigation Strategies* (pp. 345–364). Singapore: Springer Nature Singapore.

Rawluk, A., Beilin, R., Bender, H. and Ford, R., 2020. *Practices in social ecological research*. Springer International Publishing.

Rebelo, L.M., Finlayson, C.M., Strauch, A., Rosenqvist, A., Perennou, C., Tottrup, C., Hilarides, L., Paganini, M., Wielaard, N., Siegert, F. and Ballhorn, U., 2018. The use of Earth Observation for wetland inventory, assessment and monitoring.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J. and Smol, J.P., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological reviews, 94(3), pp.849–873.

Ren, B., Hu, Y., Chen, B., Zhang, Y., Thiele, J., Shi, R., Liu, M. and Bu, R., 2018. Soil pH and plant diversity shape soil bacterial community structure in the active layer across the latitudinal gradients in continuous permafrost region of Northeastern China. *Scientific Reports*, *8*(1), p.5619.

Ren, M. and Wang, J., 2022. Phylogenetic divergence and adaptation of Nitrososphaeria across lake depths and freshwater ecosystems. *The ISME Journal*, *16*(6), pp.1491–1501.

Rey, P.J., Camacho, F.M., Tarifa, R., Martínez–Núñez, C., Salido, T., Pérez, A.J. and García, D., 2021. Persistence of seed dispersal in agroecosystems: effects of landscape modification and intensive soil management practices in avian frugivores, frugivory and seed deposition in olive croplands. *Frontiers in Ecology and Evolution*, *9*, p.782462.

Rezende, R.D.S., Biasi, C., Hepp, L.U., Pretrucio, M.M. and Júnior, J.F.G., 2019. Effects of leaf litter traits on alpha and beta diversities of invertebrate assemblages in a tropical watershed. *Ecología Austral*, *29*(3), pp.365–379.

Richardson, J.S. and Hanna, D.E., 2021. Leaf litter decomposition as a contributor to ecosystem service provision. In *The Ecology of Plant Litter Decomposition in Stream Ecosystems* (pp. 511–523). Cham: Springer International Publishing.

Richardson, M., 2023. *Threatened and Recently Extinct Vertebrates of the World: A Biogeographic Approach*. Cambridge University Press.

Riedel, T. and Weber, T.K., 2020. The influence of global change on Europe's water cycle and groundwater recharge. Hydrogeology Journal, 28(6), pp.1939–1959.

Rohde, K., Hau, Y., Kranz, N., Weinberger, J., Elle, O. and Hochkirch, A., 2017. Climatic effects on population declines of a rare wetland species and the role of spatial and temporal isolation as barriers to hybridization. *Functional Ecology*, *31*(6), pp.1262–1274.

Rolls, R.J., Heino, J., Ryder, D.S., Chessman, B.C., Growns, I.O., Thompson, R.M. and Gido, K.B., 2018. Scaling biodiversity responses to hydrological regimes. *Biological Reviews*, *93*(2), pp.971–995.

Root, L., 2022. *Molecular Physiology of Tilapia Salinity Tolerance: comparative proteome dynamics of Oreochromis species under high osmoregulatory stress* (Doctoral dissertation, University of California, Davis).

Rousi, H., Korpinen, S. and Bonsdorff, E., 2019. Brackish–water benthic fauna under fluctuating environmental conditions: the role of eutrophication, hypoxia, and global change. *Frontiers in Marine Science*, *6*, p.464.

Rubin, S.P., Davis, M.J., Grossman, E.E., Woo, I., De La Cruz, S.E., Nakai, G. and Takekawa, J.Y., 2024. Benthic macroinvertebrate response to estuarine emergent marsh restoration across a delta–wide environmental gradient. *Frontiers in Ecology and Evolution*, *12*, p.1356679.

Ruess, L. and Müller–Navarra, D.C., 2019. Essential biomolecules in food webs. Frontiers in Ecology and Evolution, 7, p.269.

Rumschlag, S.L., Gallagher, B., Hill, R., Schäfer, R.B., Schmidt, T.S., Woods, T., Kopp, D., Dumelle, M., Rohr, J.R., De Laender, F. and Hoffman, J., 2025. Diverging fish biodiversity trends in cold and warm rivers and streams. *Nature*, pp.1–7.

Sabina, R., Paul, J., Sharma, S. and Hussain, N., 2025. Synthetic Nitrogen Fertilizer Pollution: Global Concerns and Sustainable Mitigating Approaches. In *Agricultural Nutrient Pollution and Climate Change: Challenges and Opportunities* (pp. 57–101). Cham: Springer Nature Switzerland.

Sabzevari, Y. and Eslamian, S., 2026. Hydropower and Ecohydrology Nexus Sustainable Solutions for Balancing Energy and Ecosystems. *Global Nexus Handbook*, *2*, pp.717-747.

Salazar Flórez, J.E., Restrepo, B.N., Freitas, L.P., Carabali, M., Jaramillo Ramírez, G.I., Balaguera, C.G., Monsalve, B.S.A. and Zinszer, K., 2025. Spatio-temporal analysis of the distribution and co-circulation of dengue, chikungunya, and Zika in Medellín, Colombia, from 2013 to 2021. *PLoS Neglected Tropical Diseases*, *19*(9), p.e0013470.

Salimi, S. and Scholz, M., 2022. Importance of water level management for peatland outflow water quality in the face of climate change and drought. *Environmental Science and Pollution Research*, *29*(50), pp.75455–75470.

Sample, V.A., Bixler, R.P. and Miller, C. eds., 2016. *Forest conservation in the Anthropocene: science, policy, and practice*. University Press of Colorado.

Samways, M.J., Gaigher, R., Deacon, C. and Pryke, J.S., 2025. Heterogeneous conservation corridors of remnant vegetation protect biodiversity in South African timber mosaics. *Biodiversity and Conservation*, *34*(2), pp.357–379.

Sánchez–Montoya, M.M., Datry, T., Ruhi, A., Carlson, S.M., Corti, R. and Tockner, K., 2023. Intermittent rivers and ephemeral streams are pivotal corridors for aquatic and terrestrial animals. *BioScience*, *73*(4), pp.291–301.

Sanders, D. and Frago, E., 2024. Ecosystem engineers shape ecological network structure and stability: A framework and literature review. *Functional Ecology*, *38*(8), pp.1683–1696.

Santoro, A., Beatty, S.J., Chambers, J.M. and Ebner, B.C., 2024. Implications of Climatic Drying on the Aquatic Habitat and Aestivation Sites of an Endemic Freshwater Turtle. *Wetlands*, *44*(8), p.127.

Sarkar, I.D., 2023. *Diversity, assemblage, and functional trait patterns of spiders (Araneae: Araneomorphae) along an elevational gradient in Himachal Pradesh, India* (Doctoral dissertation, Ph. D. Thesis. Wildlife Institute of India, Dehradun, India and Saurashtra University, RajKot5 India).

Sarremejane, R., Messager, M.L. and Datry, T., 2022. Drought in intermittent river and ephemeral stream networks. *Ecohydrology*, *15*(5), p.e2390.

Sarremejane, R., Messager, M.L. and Datry, T., 2022. Drought in intermittent river and ephemeral stream networks. *Ecohydrology*, *15*(5), p. e2390.

Sarremejane, R., Stubbington, R., England, J., Sefton, C.E., Eastman, M., Parry, S. and Ruhi, A., 2021. Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. *Global Change Biology*, *27*(17), pp.4024–4039.

Schaefer, C.E., Corrêa, G.R., Candido, H.G., Arruda, D.M., Nunes, J.A., Araujo, R.W., Rodrigues, P.M., Fernandes Filho, E.I., Pereira, A.F., Brandão, P.C. and Neri, A.V., 2016. The physical environment of rupestrian grasslands (Campos Rupestres) in Brazil: geological, geomorphological and pedological characteristics, and interplays. In *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 15-53). Cham: Springer International Publishing.

Schmera, D., Heino, J., Podani, J., Erős, T. and Dolédec, S., 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia*, *787*(1), pp.27–44.

Schofield, K.A., Alexander, L.C., Ridley, C.E., Vanderhoof, M.K., Fritz, K.M., Autrey, B.C., DeMeester, J.E., Kepner, W.G., Lane, C.R., Leibowitz, S.G. and Pollard, A.I., 2018. Biota connect aquatic habitats throughout freshwater ecosystem mosaics. *JAWRA Journal of the American Water Resources Association*, *54*(2), pp.372–399.

Schriever, T.A., Cadotte, M.W. and Williams, D.D., 2014. How hydroperiod and species richness affect the balance of resource flows across aquatic–terrestrial habitats. *Aquatic Sciences*, *76*(1), pp.131–143.

Scott, R.W., Sharma, S., Wang, X. and Quinlan, R., 2025. Hydrological connectivity influences the aquatic metacommunity structure of an Arctic delta floodplain. *Arctic Science*, *11*, pp.1–14.

Serra, S.R., Calapez, A.R., Simões, N.E., Sa Marques, J.A., Laranjo, M. and Feio, M.J., 2019. Effects of variations in water quantity and quality in the structure and functions of invertebrates' community of a Mediterranean urban stream. *Urban Ecosystems*, *22*(6), pp.1173–1186.

Settele, J., Scholes, R., Betts, R.A., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Angel Taboada, M., Adrian, R., Allen, C. and Anderegg, W., 2014. Terrestrial and inland water systems. Cambridge University Press.

Sgarzi, S., Badosa, A., Compte, J., Leiva-Presa, À., Ersoy, Z., López, E. and Brucet, S., 2025. Longer hydroperiods intensify predation effects on planktonic size spectra in Mediterranean temporary ponds. *Hydrobiologia*, pp.1-17.

Shah, R.D.T., 2018. *Monitoring river degradation and climate change impacts in the central Himalaya: Assessment tools and management approaches* (Doctoral dissertation).

Shah, S.A., 2025. Nexus of household livelihood dependence and conservation approach to wetlands: a study of North Himalayan wetland in India. *Environment, Development and Sustainability*, *27*(1), pp.1071–1095.

Sharma, L.K. and Naik, R., 2024. Wetland ecosystems. In *Conservation of saline wetland ecosystems: an initiative towards UN decade of ecological restoration* (pp. 3–32). Singapore: Springer Nature Singapore.

Sherren, K., Ellis, K., Guimond, J.A., Kurylyk, B., LeRoux, N., Lundholm, J., Mallory, M.L., Van Proosdij, D., Walker, A.K., Bowron, T.M. and Brazner, J., 2021. Understanding multifunctional Bay of Fundy dykelands and tidal wetlands using ecosystem services—a baseline. *Facets*, *6*(1), pp.1446–1473.

Sherry, T.W., Kent, C.M., Sánchez, N.V. and Şekercioğlu, Ç.H., 2020. Insectivorous birds in the Neotropics: Ecological radiations, specialization, and coexistence in species–rich communities. *The Auk*, *137*(4), p. ukaa049.

Shokri, M., Marrocco, V., Cozzoli, F., Vignes, F. and Basset, A., 2024. The relative importance of metabolic rate and body size to space use behavior in aquatic invertebrates. Ecology and Evolution, 14(5), p. e11253.

Shrestha, S., Tachamo–Shah, R.D., Doody, T., Cuddy, S. and Shah, D.N., 2021. Establishing the relationship between benthic macroinvertebrates and water level fluctuation in subtropical shallow wetlands. *Environmental Monitoring and Assessment*, *193*(8), p.534.

Sicking, E.A., 2025. *The influences of hydrology and vegetation on emergent insect and benthic macroinvertebrate communities across space and time in seasonally inundated, geographically isolated wetlands* (Doctoral dissertation, Virginia Tech).

Singh, P.K., Kumar, U., Kumar, I., Dwivedi, A., Singh, P., Mishra, S., Seth, C.S. and Sharma, R.K., 2024. Critical review on toxic contaminants in surface water ecosystem: sources, monitoring, and its impact on human health. *Environmental Science and Pollution Research*, *31*(45), pp.56428–56462.

Siraj, A., Taneja, S., Zhu, Y., Jiang, H., Luthra, S. and Kumar, A., 2022. Hey, did you see that label? It's sustainable! Understanding the role of sustainable labelling in shaping sustainable purchase behaviour for sustainable development. *Business Strategy and the Environment*, *31*(7), pp.2820–2838.

Smith, A.J. and Goetz, E.M., 2021. Climate change drives increased directional movement of landscape ecotones. *Landscape Ecology*, *36*(11), pp.3105–3116.

Smith, C.R., McCormick, P.V., Covich, A.P. and Golladay, S.W., 2017. Comparison of macroinvertebrate assemblages across a gradient of flow permanence in an agricultural watershed. *River Research and Applications*, *33*(9), pp.1428–1438.

Smith, L.L., Subalusky, A.L., Atkinson, C.L., Earl, J.E., Mushet, D.M., Scott, D.E., Lance, S.L. and Johnson, S.A., 2019. Biological connectivity of seasonally ponded wetlands across spatial and temporal scales. *JAWRA Journal of the American Water Resources Association*, *55*(2), pp.334–353.

Song, A., Liang, S., Li, H. and Yan, B., 2024. Effects of biodiversity on functional stability of freshwater wetlands: a systematic review. *Frontiers in Microbiology*, *15*, p.1397683.

Soukup, P.R., Näslund, J., Höjesjö, J. and Boukal, D.S., 2022. From individuals to communities: Habitat complexity affects all levels of organization in aquatic environments. Wiley Interdisciplinary Reviews: Water, 9(1), p. e1575.

Sponsler, D., Iverson, A. and Steffan-Dewenter, I., 2023. Pollinator competition and the structure of floral resources. *Ecography*, *2023*(9), p. e06651.

Springthorpe, V. and Penfield, S., 2015. Flowering time and seed dormancy control use external coincidence to generate life history strategy. *elife*, *4*, p. e05557.

Stamenković, O., Stojković Piperac, M., Milošević, D., Čerba, D., Cvijanović, D., Gronau, A., Vlaičević, B. and Buzhdygan, O., 2024. Multiple anthropogenic pressures and local environmental gradients in ponds governing the taxonomic and functional diversity of epiphyticmacroinvertebrates. *Hydrobiologia*, *851*(1), pp.45–65.

Stark, J.R. and Fridley, J.D., 2022. Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography*, *31*(3), pp.562–575.

Starr, S.M., Benstead, J.P. and Sponseller, R.A., 2014. Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem. *Landscape Ecology*, *29*(6), pp.1017–1031.

Stefanakis, A.I., 2019. The role of constructed wetlands as green infrastructure for sustainable urban water management. *Sustainability*, *11*(24), p.6981.

Stevens, R.D., Rowe, R.J. and Badgley, C., 2019. Gradients of mammalian biodiversity through space and time. *Journal of Mammalogy*, *100*(3), pp.1069-1086.

. Sumudumali, R.G.I. and Jayawardana, J.M.C.K., 2021. A review of biological monitoring of aquatic ecosystems approaches: with special reference to macroinvertebrates and pesticide pollution. Environmental management, 67(2), pp.263-276.

Sun, J., Chen, Y., Lv, X., Li, W. and Zhang, H., 2025. Enhancing pond connectivity: impacts on common and rare species of macrophyte in an agricultural multi–pond system. *Hydrobiologia*, pp.1–23.

Swan, C.M., Brown, B., Borowy, D., Cavender-Bares, J., Jeliazkov, A., Knapp, S., Lososová, Z., Padullés Cubino, J., Pavoine, S., Ricotta, C. and Sol, D., 2021. A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems. *Ecosphere*, *12*(7), p. e03650.

Tadesse, H. and Lakew, A., 2025. Fish composition and their habitat preferences in human impacted tributaries of the upper Awash River, Ethiopia. *Fisheries and Aquatic Sciences*, *28*(6), pp.396–405.

Tampo, L., Kaboré, I., Alhassan, E.H., Ouéda, A., Bawa, L.M. and Djaneye–Boundjou, G., 2021. Benthic macroinvertebrates as ecological indicators: their sensitivity to the water quality and human disturbances in a tropical river. *Frontiers in Water*, *3*, p.662765.

Tan, L., Ge, Z., Ji, Y., Lai, D.Y., Temmerman, S., Li, S., Li, X. and Tang, J., 2022. Land use and land cover changes in coastal and inland wetlands cause soil carbon and nitrogen loss. *Global Ecology and Biogeography*, *31*(12), pp.2541–2563.

Tao, Y., Hastings, A., Lafferty, K.D., Hanski, I. and Ovaskainen, O., 2024. Landscape fragmentation overturns classical metapopulation thinking. *Proceedings of the National Academy of Sciences*, *121*(20), p. e2303846121.

Taurozzi, D. and Scalici, M., 2026. Environmental and elevational drivers of diatom diversity in alpine temporary ponds. *Ecohydrology & Hydrobiology*, p.100726.

Taylor, L.L., Driscoll, C.T., Groffman, P.M., Rau, G.H., Blum, J.D. and Beerling, D.J., 2021. Increased carbon capture by a silicate–treated forested watershed affected by acid deposition. *Biogeosciences*, *18*(1), pp.169–188.

Tecon, R. and or, D., 2017. Biophysical processes supporting the diversity of microbial life in soil. FEMS microbiology reviews, 41(5), pp.599–623.

Thakur, P., Mehla, S., Raghuram, P., Kumar, R., Kumar, V., Sharma, R. and Rana, A., 2025. Ecological and Evolutionary Responses of Insects to Climate Change: A Review. *International Journal of Environment and Climate Change*, *15*(12), pp.163–179.

Thuile Bistarelli, L., 2025. *Biofilms in river ecosystems–mechanisms governing biofilm structure and function from local to regional scales* (Doctoral dissertation, Universität Potsdam).

Tianzhu, L., Guicai, S., Jian, W. and Gengxin, Z., 2017. Microbial communities and associated enzyme activities in alpine wetlands with increasing altitude on the Tibetan Plateau. Wetlands, 37(3), pp.401-412.

Tolonen, K., 2018. Taxonomic and functional organization of macroinvertebrate communities in subarctic streams.

Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U. and Lytle, D.A., 2018. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology*, *63*(1), pp.141–163.

Tornero Pinilla, I., 2020. Metacommunities and biodiversity patterns in Mediterranean temporary ponds: the role of pond size, network connectivity and dispersal mode.

Trau, F.N., Fisch, K. and Lorenz, S., 2023. Habitat type strongly influences the structural benthic invertebrate community composition in a landscape characterized by ubiquitous, long–term agricultural stress. *Inland Waters*, *13*(4), pp.473–485.

Tsopoe, M., Chakrabarty, A., Meetei, K.B., Giri, K., Mishra, G. and Kumar, S., 2025. Ecosystem Restoration: Success Stories and Best Practices. In *Biodiversity Conservation and Land Degradation Neutrality: From Loss to Restoration* (pp. 263–287). Singapore: Springer Nature Singapore.

Twilley, R.R., 2019. Mangrove wetlands. In *Southern forested wetlands* (pp. 445–473). Routledge.

Uddin, S.Z., 2021. Modeling Geotechnical Soil Loss and Erosion Dynamics for Climate–Resilient Coastal Adaptation. *American Journal of Interdisciplinary Studies*, *2*(04), pp.01–38.

Uroy, L., Ernoult, A. and Mony, C., 2019. Effect of landscape connectivity on plant communities: a review of response patterns. *Landscape ecology*, *34*(2), pp.203–225.

Valente–Neto, F., Mello, J.L., Pestana, G.C., Shimabukuro, E.M., de Siqueira, A.S., Covich, A.P. and Saito, V.S., 2025. Ecological perspectives on the organization of biodiversity in Neotropical streams. *Hydrobiologia*, *852*(12), pp.3025–3047.

Vallespir Lowery, N. and Ursell, T., 2019. Structured environments fundamentally alter dynamics and stability of ecological communities. *Proceedings of the National Academy of Sciences*, *116*(2), pp.379–388.

Van den Broeck, M., Waterkeyn, A., Rhazi, L. and Brendonck, L., 2015. Distribution, coexistence, and decline of Moroccan large branchiopods. *Journal of crustacean biology*, *35*(3), pp.355–365.

Van der Stocken, T., Wee, A.K., De Ryck, D.J., Vanschoenwinkel, B., Friess, D.A., Dahdouh-Guebas, F., Simard, M., Koedam, N. and Webb, E.L., 2019. A general framework for propagule dispersal in mangroves. *Biological Reviews*, *94*(4), pp.1547–1575.

Van Looy, K., Piffady, J. and Floury, M., 2017. At what scale and extent environmental gradients and climatic changes influence stream invertebrate communities?. *Science of the Total Environment*, *580*, pp.34-42.

Van Looy, K., Piffady, J. and Floury, M., 2017. At what scale and extent environmental gradients and climatic changes influence stream invertebrate communities? *Science of the Total Environment*, *580*, pp.34-42.

Van Moorter, B., Kivimäki, I., Panzacchi, M. and Saerens, M., 2021. Defining and quantifying effective connectivity of landscapes for species' movements. *Ecography*, *44*(6), pp.870–884.

Varadinova, E., Sakelarieva, L., Park, J., Ivanov, M. and Tyufekchieva, V., 2022. Characterisation of Macroinvertebrate Communities in Maritsa River (South Bulgaria)-Relation to Different Environmental Factors and Ecological Status Assessment. *Diversity*, *14*(10), p.833.

Villarreal, M.L. and Coronato, A., 2017, May. Characteristics and nature of pans in the semi-arid temperate/cold steppe of Tierra del Fuego. In *Advances in Geomorphology and Quaternary Studies in Argentina: Proceedings of the Sixth Argentine Geomorphology and Quaternary Studies Congress* (pp. 203-224). Cham: Springer International Publishing.

Villéger, S., Brosse, S., Mouchet, M., Mouillot, D. and Vanni, M.J., 2017. Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences*, *79*(4), pp.783–801.

Villsen, K., Bêche, L., Archambaud–Suard, G. and Daufresne, M., 2025. Community size and disturbance history jointly explain the interplay between stochastic and deterministic community variation in benthic invertebrates. *Oikos*, *2025*(4), p. e10968.

Wagenhoff, A., Townsend, C.R. and Matthaei, C.D., 2012. Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology*, *49*(4), pp.892–902.

Wahl, M., 2020. Living attached: aufwuchs, fouling, epibiosis. In *Fouling organisms of the Indian Ocean* (pp. 31–83).

Waliczky, Z., Fishpool, L.D., Butchart, S.H., Thomas, D., Heath, M.F., Hazin, C., Donald, P.F., Kowalska, A., Dias, M.P. and Allinson, T.S., 2019. Important Bird and Biodiversity Areas (IBAs): their impact on conservation policy, advocacy and action. *Bird Conservation International*, *29*(2), pp.199–215.

Wang, H.W., Kuo, P.H. and Dodd, A.E., 2020. Gate operation for habitat–oriented water management at Budai Salt Pan Wetland in Taiwan. *Ecological Engineering*, *148*, p.105761.

Weideli, O.C., Daly, R., Peel, L.R., Heithaus, M.R., Shivji, M.S., Planes, S. and Papastamatiou, Y.P., 2023. Elucidating the role of competition in driving spatial and trophic niche patterns in sympatric juvenile sharks. *Oecologia*, *201*(3), pp.673–688.

Weldeslassie, T., Naz, H., Singh, B. and Oves, M., 2017. Chemical contaminants for soil, air and aquatic ecosystem. In *Modern age environmental problems and their remediation* (pp. 1–22). Cham: Springer International Publishing.

Were, D., Kansiime, F., Fetahi, T., Cooper, A. and Jjuuko, C., 2019. Carbon Sequestration by Wetlands: A Critical Review of Enhancement Measures for Climate Change Mitigation: D. Were et al. *Earth Systems and Environment*, *3*(2), pp.327–340.

Westveer, J.J., van der Geest, H.G., van Loon, E.E. and Verdonschot, P.F., 2018. Connectivity and seasonality cause rapid taxonomic and functional trait succession within an invertebrate community after stream restoration. *PloS one*, *13*(5), p. e0197182.

Wetzel, R.G., 2022, May. Techniques and problems of primary productivity measurements in higher aquatic plants and periphyton. In *Primary Productivity in Aquatic Environments: Proceedings of an IBP PF Symposium, Pallanza, Italy, April 26–May 1, 1965* (p. 249). Univ of California Press.

Weyer, C., Peiffer, S. and Lischeid, G., 2018. Stream water quality affected by interacting hydrological and biogeochemical processes in a riparian wetland. *Journal of Hydrology*, *563*, pp.260–272.

Whitby, T.G., 2025. *Increased Rates of Soil Respiration and Microbial Enzyme Activity Under Two Complementary Experimental Warming Methods: Implications for Carbon–Climate Feedbacks* (Doctoral dissertation, Appalachian State University).

Whiteman, M., Farr, G., Haslam, A., Train, C., Kieboom, N., Farrell, R., Davison, P., Williams, H., Tang, S., Hall, J. and Jones, L., 2023. Source apportionment of nitrogen pressures at a Chalk–fed groundwater–dependent wetland.

Whitman, E., Parisien, M.A., Thompson, D.K. and Flannigan, M.D., 2018. Topoedaphic and forest controls on post–fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest. Forests, 9(3), p.151.

Wiesebron, L.E., Steiner, N., Morys, C., Ysebaert, T. and Bouma, T.J., 2021. Sediment bulk density effects on benthic macrofauna burrowing and bioturbation behavior. *Frontiers in marine science*, *8*, p.707785.

Wolters, J.W., Reitsema, R.E., Verdonschot, R.C., Schoelynck, J., Verdonschot, P.F. and Meire, P., 2019. Macrophyte-specific effects on epiphyton quality and quantity and resulting effects on grazing macroinvertebrates. *Freshwater Biology*, *64*(6), pp.1131–1142.

Worischka, S., Schöll, F., Winkelmann, C. and Petzoldt, T., 2023. Twenty-eight years of ecosystem recovery and destabilisation: Impacts of biological invasions and climate change on a temperate river. *Science of the Total Environment*, *875*, p.162678.

Worrall, T.P., Dunbar, M.J., Extence, C.A., Laize, C.L., Monk, W.A. and Wood, P.J., 2014. The identification of hydrological indices for the characterization of macroinvertebrate community response to flow regime variability. *Hydrological Sciences Journal*, *59*(3–4), pp.645–658.

Wurtsbaugh, W.A., Paerl, H.W. and Dodds, W.K., 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *Wiley Interdisciplinary Reviews: Water*, *6*(5), p. e1373.

Xu, T., Weng, B., Yan, D., Wang, K., Li, X., Bi, W., Li, M., Cheng, X. and Liu, Y., 2019. Wetlands of international importance: Status, threats, and future protection. *International journal of environmental research and public health*, *16*(10), p.1818.

Xu, X., Chen, M., Yang, G., Jiang, B. and Zhang, J., 2020. Wetland ecosystem services research: A critical review. *Global Ecology and Conservation*, *22*, p. e01027.

Yadav, N.K., Patel, A.B., Singh, S.K., Mehta, N.K., Anand, V., Lal, J., Dekari, D. and Devi, N.C., 2024. Climate change effects on aquaculture production and its sustainable management through climate–resilient adaptation strategies: a review. *Environmental Science and Pollution Research*, *31*(22), pp.31731–31751.

Yan, Y., Jarvie, S., Zhang, Q., Han, P., Liu, Q., Zhang, S. and Liu, P., 2023. Habitat heterogeneity determines species richness on small habitat islands in a fragmented landscape. *Journal of Biogeography*, *50*(5), pp.976–986.

Yang, S., Wan, R., Yang, G. and Li, B., 2024. A novel framework to assess the hydrological connectivity of lake wetlands in plain river networks with dense hydraulic facilities: Comparing natural and disturbed states over a century. *Journal of Hydrology*, *630*, p.130787.

Ye, S., Pei, L., He, L., Xie, L., Zhao, G., Yuan, H., Ding, X., Pei, S., Yang, S., Li, X. and Laws, E.A., 2022. Wetlands in China: Evolution, carbon sequestrations and services, threats, and preservation/restoration. *Water*, *14*(7), p.1152.

Yihdego, Y., Webb, J.A. and Vaheddoost, B., 2017. Highlighting the role of groundwater in lake–aquifer interaction to reduce vulnerability and enhance resilience to climate change. *Hydrology*, *4*(1), p.10.

Yirigui, Y., Lee, S.W. and Nejadhashemi, A.P., 2019. Multi–scale assessment of relationships between fragmentation of riparian forests and biological conditions in streams. *Sustainability*, *11*(18), p.5060.

Yousaf, A., Khalid, N., Aqeel, M., Noman, A., Naeem, N., Sarfraz, W., Ejaz, U., Qaiser, Z. and Khalid, A., 2021. Nitrogen dynamics in wetland systems and its impact on biodiversity. Nitrogen, 2(2), pp.196–217.

Zaharescu, D.G., Burghelea, C.I., Hooda, P.S., Lester, R.N. and Palanca–Soler, A., 2016. Small lakes in big landscape: Multi–scale drivers of littoral ecosystem in alpine lakes. *Science of the Total Environment*, *551*, pp.496–505.

Zhang, W.P., Fornara, D., Yang, H., Yu, R.P., Callaway, R.M. and Li, L., 2023. Plant litter strengthens positive biodiversity–ecosystem functioning relationships over time. *Trends in Ecology & Evolution*, *38*(5), pp.473–484.

Zhao, X., Ma, Y., Xie, H., Du, C., Zhan, A., Xu, J., Giesy, J.P., Wu, F. and Jin, X., 2024. Spatial distribution of benthic taxonomic and functional diversity in the Yellow River Basin: From ecological processes to associated determinant factors. *Environment International*, *188*, p.108745.

Zinck, J.A. and Montero, P.G., 2023. Sand Dynamics and Distribution in Meadow Environment: A Geo–Pedological Approach. In *Psammic Peinobiomes: Nutrient–Limited Ecosystems of the Upper Orinoco and Rio Negro Basins* pp. 325–394.