

**SPATIOTEMPORAL ASSEMBLAGES OF SOIL ARTHROPODS
COMMUNITIES IN A TROPICAL PALUSTRINE-ESTUARINE URBAN
COASTAL WETLAND**

By

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ABSTRACT

Caribbean coastal wetlands have undergone significant anthropogenic changes since colonial times, leading to a diverse range bio-physicochemical environments and varied vegetation. These changes have fostered complex ecosystems that support varied ecological niches for soil arthropod communities, essential to wetland food webs and biogeochemical processes. The sensitivity of soil arthropods to environmental changes makes them key bioindicators of ecological shifts.

This research aims to assess soil arthropods distribution and interactions in response to spatiotemporal bio-physicochemical dynamics within Las Cucharillas Natural Reserve, a tropical palustrine-estuarine, urban coastal wetland in Puerto Rico. We conducted sampling across two sets of 10 m² plots—one with autochthonous organic substrate and the other with allochthonous mineral soil—over a year, covering different hydroperiod conditions. In each plot, soil samples were collected from under three randomly selected plant functional types and processed using lighted Tullgren-Berlese funnels for soil arthropods extraction. Phreatic level, pH, salinity, and litter quality (C%, N% and C:N ratio) and quantity (dry weight) were measured.

Results indicated significant effects of hydroperiod conditions on soil arthropod assemblages. Optimal conditions during wet periods led to enhanced community metrics and complex assemblages. Moderate dry and moist periods resulted in decreased arthropod density, richness, and diversity, suggesting these conditions may surpass many taxa's resilience. Whereas flood periods significantly reduced arthropod richness and shifted the community composition toward water-tolerant taxa.

Vegetation type and hydroperiods influenced habitat and resource availability, impacting arthropod trophic structures and community dynamics. Soil arthropod trophic guild densities peaked in both equilibrium (C:N ratio between 20:1 and 30:1) and immobilization (C:N ratio >30:1) phases of decomposition. Fluctuations in litter mass carbon and nitrogen concentration, driven by hydroperiods and plant types, were crucial for determining soil arthropod richness and abundance.

This research highlights the combined effects of plant-hydroperiod interactions on substrate habitat and resource availability, and their influence on soil arthropod assemblages and trophic structures. It offers valuable insights for ecosystem management and conservation strategies aimed at preserving biodiversity and ecosystem functionality in wetland environments. These strategies are crucial tools for addressing global and regional climate change, sea level rise, and increased anthropogenic use of the region.

AUTHOR BIOGRAPHY

Gloria M. Ortiz Ramírez is an environmental scientist and researcher, deeply committed to understanding and appreciating our planet's natural wonders. Her academic journey began with a B.Sc. in Environmental Science from the University of Puerto Rico in 1993, where she focused her thesis on Ecotourism Management for the Piñones Natural Reserve. Expanding her expertise, Gloria earned an MBA from the University of Phoenix in 2004, specializing in Educational Management. Her master's thesis, which integrated environmental education into science curricula, highlighted her dedication to this field.

In August 2017, Gloria was admitted to the University of Puerto Rico, Rio Piedras Campus, for graduate studies in Environmental Sciences. Her research centers on the composition, structure, and dynamics of soil arthropod communities in tropical palustrine-estuarine urban coastal wetlands. Her goal is to develop effective tools for wetland management and conservation.

Gloria's scholarly work includes notable publications, such as "The Dynamics of Soil Mesofauna Communities in a Tropical Urban Coastal Wetland" in *Arthropoda* 2024, underscoring her commitment to scientific research and advancement in her field.

With a robust academic background, diverse professional experiences, and an unwavering commitment to conserving the natural world, Gloria M. Ortiz Ramírez aims to become a leading figure in environmental sciences and ecosystem management. She is driven by the hope that her research, education, and conservation efforts will continue to inspire and contribute to the sustainable management of vital ecosystems.

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DEDICATION

I dedicate this work to my beloved husband and son, my two Rafaels. It's your presence in my life that gives me the courage and strength to be my true self and find my path.

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As I approach the conclusion of my PhD journey, I am overwhelmed with gratitude for a circle of individuals whose unwavering support has been instrumental in both my academic achievements and personal development. At the forefront, I express my deepest appreciation to my family: my husband and my son. Your constant love, patience, and encouragement have been the bedrock of my resilience. I also extend my sincere thanks to my extended family and cherished friends. Your understanding and assistance provided solace and strength in times of challenge.

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CHAPTER 1: INTRODUCTION AND THESIS OVERVIEW

1.1 INTRODUCTION

Soil arthropods constitute a significant portion of global terrestrial biodiversity and compose the base for ecosystem functioning and services (Bezemer, 2019; Herrera & Cuevas 2003). They are sentinel species due to their inherent sensitivity to environmental modulations, thus facilitating the rapid detection and comprehension of the ecological alterations occurring within a given habitat (Barberena-Arias & Cuevas, 2018; Barberena-Arias & Cuevas, 2021; Havlicek, 2012; Havlicek et al., 2017; Mathieu et al., 2022). Their responsive dynamics to environmental fluctuations offer a rich repository of data, critical for interpreting the health and operational dynamics of ecosystems (Bardgett et al., 2005; Coleman et al., 2017; Pulleman et al., 2012). Despite its importance, soil biodiversity remains overlooked in global biodiversity assessments, and ecosystems management and conservation policies (Potapov et al., 2022). This oversight stems from a lack of comprehensive data on its composition and interactions, with notable deficiencies across northern latitudes, central Asia, central Africa, Latin America, and the Caribbean (Cameron et al., 2018; Guerra et al., 2020).

In the Caribbean, a region recognized as a significant biodiversity hotspot, the synergistic effects of global and regional climate variability, combined with historical and contemporary anthropogenic modifications, lead to changes in ecosystem vegetation, structure, and composition (Batzer & Sharitz, 2006; Briones, 2018; IPCC, 2022; Menta, 2020) (Figure 1; Ortiz-Ramírez et al., 2024). Given the intrinsic relationship between soil biota and vegetation as a primary energy source (Batzel & Sharitz, 2006; Nielsen et al.,

2011; Walder et al., 2004), these changes have significant impacts on soil biodiversity (Lukac, 2017). However, our understanding of the specifics of these impacts remains limited, particularly within Puerto Rican coastal ecosystems (González et al., 2021). The lack of studies addressing soil diversity in these ecosystems results in an incomplete comprehension of its community structure and the influence of environmental variables on this structure (Barberena-Arias & Cuevas, 2021; González et al., 2014). Understanding the complex patterns of this diversity, and the main factors influencing them, will elucidate the dynamics of trophic functional groups, enhancing our understanding of ecosystem resilience.

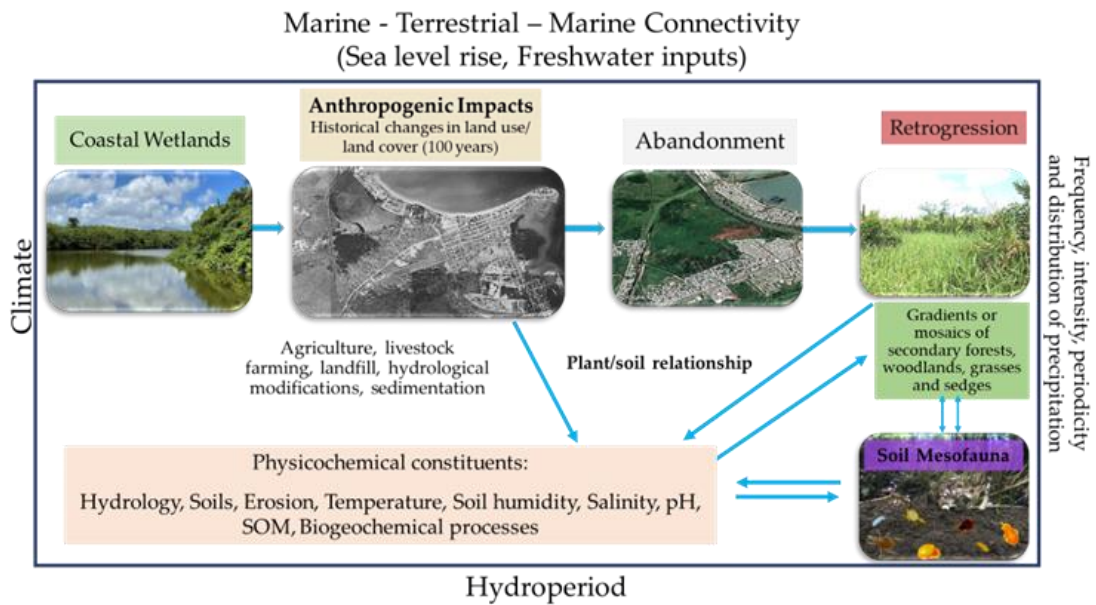


Figure 1: Historical Changes in Coastal Wetlands Land Cover. Historical changes in coastal wetlands land cover since colonial times, along with subsequent abandonment, have altered its hydrology and marine–terrestrial connectivity (upper axis). These modifications have led to shifts in the soil’s physicochemical constituents, subsequently affecting plant–soil interactions and mesofauna communities. The ongoing global and regional climate variability (left and right axes), sea-level rise (upper axis), and land use and cover changes act as additional stressors in this process. The combined effect of these anthropogenic stressors and the predominant wetland mosaic environment significantly influences the hydrological regime (lower axis), bio-physicochemical components, and soil mesofauna diversity and abundance in the ecosystem (Ortiz-Ramírez et al., 2024).

1.1.1 The Role of Soil Arthropods in the Ecosystem

Soil arthropods play an essential role as regulators in the transformation of organic matter, the mobilization of nutrients, and the formation and structural stabilization of the soil, which are important dynamics for plant growth and primary productivity (Lavelle, 1997; Lavelle et al., 2003; Brevik et al., 2015; Figure 1). In terms of species richness, arthropods comprise 85% of soil fauna (Culliney, 2013) and are grouped as macrofauna (organisms >2 mm) and mesofauna (2 mm-100 µm) (Figure 3a). These groups function at two of the three organizational levels in the decomposition food web: as plant litter transformers (mesofauna) and ecosystem engineers (macrofauna) (Figure 3b; Coleman et al., 2017; Culliney 2013; Lavelle et al., 2003, 2013; Wardle et al., 2004).

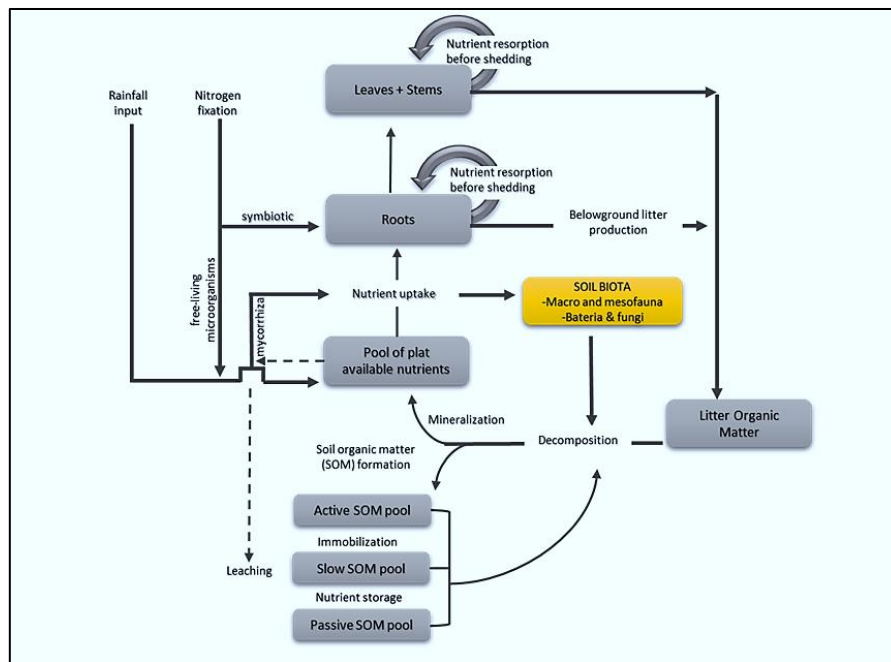


Figure 2: Conceptual model of ecosystem biological processes and interactions in nutrient cycling (Cuevas & Medina, 1998).

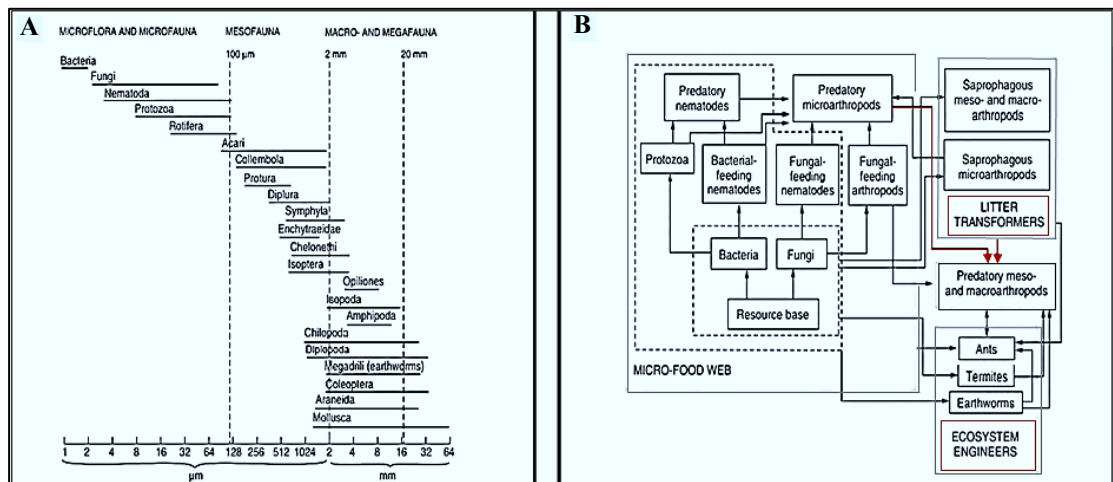


Figure 3: Soil Fauna Classification and Soil Decomposition Food Webs. A) Soil fauna classification by body width and the degree of presence in soil microhabitats 1) macrofauna (organisms larger than 2 mm), 2) mesofauna (size ranges between 100 µm to 2 mm), and 3) microfauna (organisms smaller than 100 µm). B) Organization of soil decomposition food webs in three categories: Ecosystem engineers (macrofauna), Litter transformer (mesofauna and some macrofauna), and micro-food web (microfauna and microflora) (Coleman et al., 2017; Culliney 2013; Lavelle et al. 2003 & 2013; Wardle et al. 2004).

Litter transformers fragment or comminute and humidify ingested plant debris, which is deposited in feces for further mineralization by the microflora. Ecosystem engineers create biogenic structures that alter soil's physical and chemical characteristics, including its aggregate composition, and the movement of water and air, as well as the distribution of soil organic matter. Both groups foster the growth and dispersal of microbial populations and interact at different trophic levels during the litter decomposition process, as illustrated in Figure 3b (Figure 3b; Coleman et al., 2017; Culliney 2013; Lavelle et al., 2003, 2013; Wardle et al., 2004).

1.1.2 Soil Arthropods Assemblages at Ecosystem to Fine Scales

The distribution patterns and interactions of soil arthropods occur at different spatiotemporal dynamics (Coleman et al., 2017; Lavelle et al., 2003, 2013; Wardle et al., 2004), regulated by scale-dependent variables such as: climate (temperature,

precipitation), soil physicochemical properties, vegetation (resource quality and quantity), and above-belowground biologic interactions (Wardle et al., 2004). Variables operating at higher levels interact with those at lower levels, affecting a wide array of processes that operate across different scales of resolution (Table 1; Anderson et al., 1989; Culliney, 2013; Lavelle et al., 2013).

Table 1: Scales variables that regulate soil arthropods dynamics (Adapted from Anderson et al.,1989).

Scale of resolution	Operating Factors			
	Environmental controls	Resource type	Organism	Litter pool
Ecosystem	Macroclimate, edaphic conditions, and soil structure	Total leaf, root, and wood litter	Total Biota	Total Litter
Population	Microclimate Soil Structure and gradients	Composition of litter by plant species	Functional groups and key arthropods species	Patch variation in total Litter
Organism	Microclimate soil structure and soil minerals	Cellulose, lignin, microbial products as energy sources	Arthropod species	Litter fractions

At ecosystem scale, the distribution and assemblage of soil arthropods are regulated by the environmental factors that influence litter¹decomposition and soil nutrient cycling: macroclimate (temperature and precipitation/humidity), vegetation composition, edaphic properties, microtopography, and bioturbation (Lavelle et al., 2013; Anderson et al., 1989; Culliney, 2013). For example, in temperate ecosystems, arthropod species that are active during winter exhibit optimal temperature ranges between 5 °C and 10 °C, while those active in summer prefer temperatures between 10 °C and 18 °C. Prostigmata mites and Psocoptera (commonly known as barklice or booklice) are prevalent in soils

¹ Detritus or a mixture of dead organic matter intermixed with soil.

characterized by low nutrient content and humidity. Conversely, Oribatid mites, Collembola (springtails), and Diplura (two-pronged bristletails) are typically found in humid, nutrient-rich environments, with the latter group showing limited tolerance to desiccation (Ghiglieno et al., 2020; Socarrás, 2013; Coleman et al., 2017). Moreover, litter quality has also influenced the abundance and diversity of soil fauna as seen in a secondary tropical forest in the Lesser Antilles (Loranger-Merciris et al., 2007). In a tropical dry forest (located in Guánica, Puerto Rico), Barberena-Arias (2018) found higher arthropod diversity under deciduous plant species when compared to evergreen plant species. It has been shown that microtopography influence earthworm population densities, with variations correlated to an increasing gradient from wet to dry areas (Lavelle, 1997; Lavelle et al., 2006; Lavelle & Spain, 2001).

At the fine-scale resolution of soil, patterns of biodiversity over ranges of centimeters to meters are likely linked to habitat heterogeneity (Bardgett, 2005). This includes both the structural complexity, or patchiness, of the soil environment and the chemical complexity of resources. At this level, biological processes (like reproduction and mortality) and biotic interactions (such as predation, competition, and facilitation), along with microscale variations in edaphic factors, plant species litter, soil structure, and bioturbation, influence the assembly of arthropods (Anderson et al., 1989; Culliney 2013; Lavelle et al., 2013). This is a two-way interaction between soil arthropods and the substrate's bio-physicochemical properties² (Barberena-Arias & Cuevas, 2018). Bio-physicochemical properties influence soil arthropods' composition, dynamics, and

² The bio-physicochemical properties include litter quality (CNS) and quantity, substrate pH, water content, and salinity.

distribution patterns (Barberena-Arias & Cuevas 2021; Lavelle et al., 2013; Wardle et al., 2004). In turn, soil arthropods shape ecosystem bio-physicochemical properties by regulating the organic matter decomposition process, nutrient circulation, plant growth, plant litter quality and quantity, and food web interactions.

Soil arthropods are found in resource patches, or 'hot spot' zones, including the detritosphere, rhizosphere, drilosphere, and porosphere (Lavelle et al., 2003). Most arthropod assemblages are concentrated in the detritosphere, or the litter system, which comprises the loose litter layer and the upper 1-5 cm of soil. This system comprises above-ground leaf litter, which serves as the primary nutritional resource, and an intermittent mat³ of fine roots that acts as a nutrient sink for decomposing litter, accompanied by epigeic arthropods and microbial communities, predominantly fungi. Within this system, soil arthropods are pivotal regulators, primarily through their priming

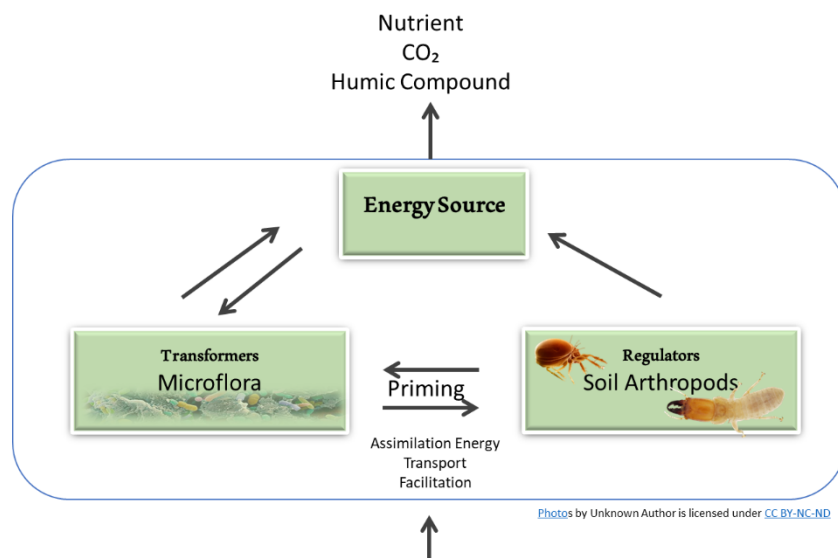


Figure 4: General organization of biological systems of regulations in soils (Adapted from Lavelle, 1997).

³ An intermittent mat refers to a sporadically occurring layer of fine roots within the litter system.

effects, which augment microbial activity (see Figure 4; Lavelle et al., 2003; Mulder et al., 2009; Nielsen, 2019; Swift et al., 1979).

In the litter system, the synchronization and synlocation⁴ between litter inputs and arthropods responses are moderated by the spatial and temporal dynamics between the availability and quality of detrital resources (plant litter) and the diversity and abundance of arthropods communities of different functional groups (micro predators, litter transformers, and ecosystem engineers) (Anderson et al., 1989; Culliney, 2013; Lavelle et al., 2003, 2006, 2013). Plant litter availability appears to be related to the distribution, complexity, and heterogeneity of litter layers, which are influenced by litter quality and quantity⁵. The quantity and quality of litter inputs are determined by vegetation diversity and spatial structure (Barberena-Arias & Cuevas, 2018; Wardle et al., 2004).

The horizontal and vertical distribution, quality, and quantity of plant litter change over time, and these changes are attributed to different stages of the decomposition processes (Barberena-Arias & Cuevas, 2021). The different decomposition stages and distribution of litter are strong drivers of soil arthropods vertical and horizontal assemblage (Culliney, 2013; Lavelle et al., 2003) since specific groups of arthropods are associated with the stratum containing most resources (Barberena-Arias & Cuevas, 2021; Lavelle et al., 2003; Mulder et al., 2009; Swift et al., 1979). For example, the horizontal distribution of

⁴ Synchronization (time correlation) refers to variation in organism abundance in response to resource availability over time. Synlocation (spatial correlation) refers to variations in organism abundance in response to resource availability over space. Both are considerable importance since interactions between consumers will depend on the timing and location of available resources, and the capacities of consumers to respond to it by increasing their populations (Myers et al., 1994; Lavelle et al., 2003).

⁵ The quality of resources is defined by its chemical composition (which determines its ease of digestion) where C/N ratio and the content of nitrogen and lignin govern its susceptibility to ingestion by consumers (Swift et al., 1979). Resources may be of high, medium, or low quality, depending on the degree of adaptation required for their exploitation (Lavelle et al., 2003).

Collembola is often highly aggregated at small spatial scales, because of variations in litter quality and abundance, and the microclimate conditions. There is some evidence that this aggregation may be caused by pheromones which attract the animals to the most suitable micro-environments with the most resources (Lavelle et al., 2006). In black pine plantation soil, Oribatids' vertical abundance was higher in the upper 3 cm due to the greater concentrations of suitable food in this region (Pande & Berthet, 1975).

The response of soil fauna to changes in litter quality promotes the formation of two interactive energetic channels for decomposition: the bacteria channel and the fungi channel. These channels moderate the soil arthropods trophic assemblages. Low C:N litter is predominantly dominated by bacteria (Culliney, 2013) where a rapid cycle of carbon transformation develops, and bacteria, protozoa, nematodes and earthworms predominate. The fungi channel predominates in High C:N litter because fungi can break down complex compounds (lignin, humic or phenolic acids and cellulose). The transformation of these compounds occurs slowly and fungi and mesofauna (mites, springtails) are involved (Barberena-Arias & Cuevas 2021; Bardgett et al., 2005; Culliney 2013; Moore et al., 1991). For example, in Australia, the mesofauna assemblages of two contrasting semi-arid ecosystems reveal a positive relationship between High C:N ratios, and the richness and abundance of mites (Culliney, 2013; Nielsen, 2019).

1.1.3 Wetlands Arthropods Assemblages

Soil arthropods comprise most of freshwater wetland's biodiversity, playing important roles in food webs and as key bioindicators of wetland ecological health. In a paper review, Batzer et.al. (2020), established that wetlands have a unique arthropod diversity

associated with the litter system, where five groups of soil arthropods are primarily represented: Isopoda, Myriapoda, Insect, Acari, and Collembola, being the latter two, the

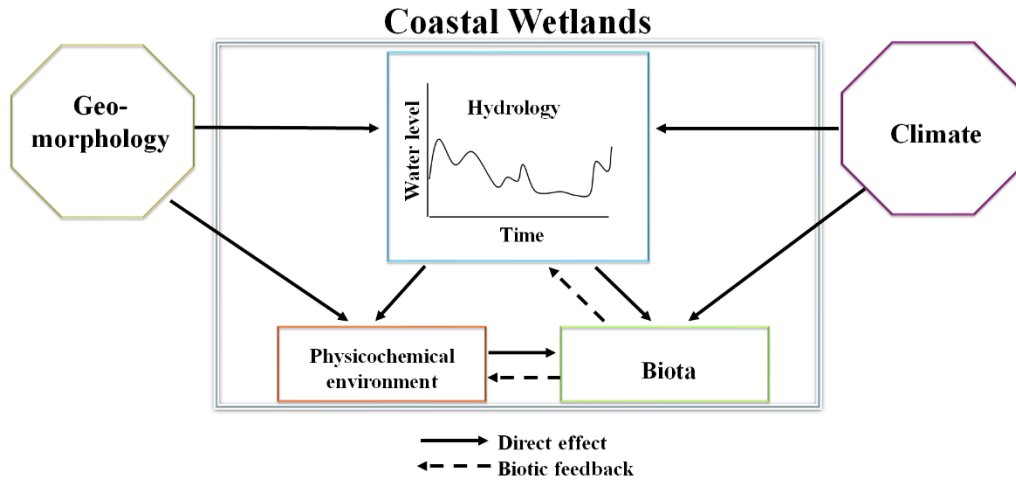


Figure 5: Schematic indicating the important factors influencing wetland biota (adapted from NRC 1995 at Batzer et al., 2006).

most abundant and diverse. In temporarily flooded coastal wetlands, the spatiotemporal variations in the abundance of these organisms are also influenced by drying and wetting cycles or hydro-patterns effects on soil bio- physicochemical conditions (Batzer et al., 2006) (Figure 5).

Waterlogging and flooding time, frequency, duration, rate of water rises, and depth are affected by different water sources that enter via *in-situ* precipitation, freshwater inputs, and seawater flows (Figure 6; Hernández et al., 2022). The hydro-pattern regime determines the degree of salinity, pH, and water content in the wetland soil and influences the spatiotemporal vegetation cover, litter quality and quantity, and arthropods composition (Batzer et al., 2006 & 2016; Hernández et al., 2022). For example, distinct soil arthropods assemblages represented by Acari, Collembola, and Insecta, occur across different wetlands sites in Canada, China, and southeast Florida. The hydro patterns variations at these wetlands, in conjunction with spatial and temporal bio-

physicochemical factors fluctuations influence soil invertebrates faunistic diversity and abundance (Batzer et.al. 2016; Li et al., 2020; Wharton, 1982).

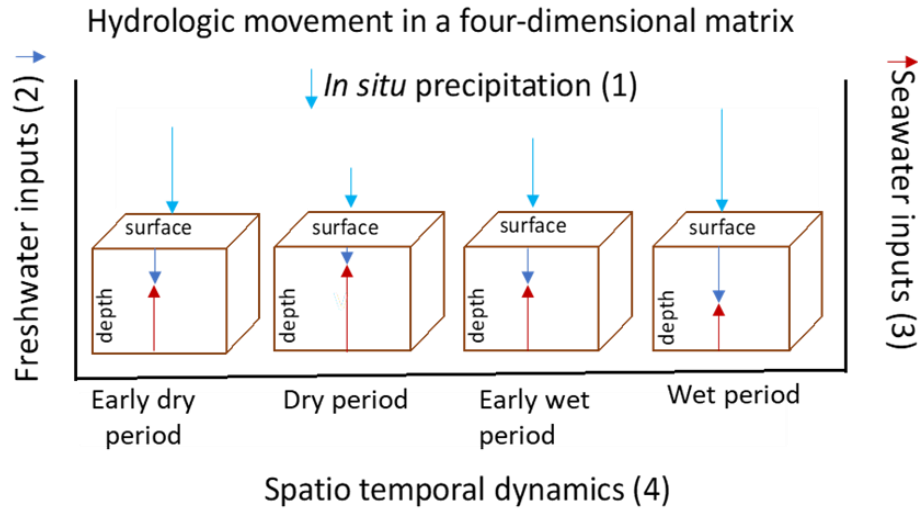


Figure 6: Coastal wetlands hydrologic movement (Hernandez et al., 2022).

Wetland soil arthropods will differ in their response to changes in the litter system biophysicochemical factors via adaptive avoidance or tolerance behavior of the prevailing environmental conditions. Inter- and intra-specific responses to these variations will determine their spatial and temporal distribution (Barbera-Arias & Cuevas, 2018; Batzer et al., 2020). For example, in a lowland peat area in The Netherlands, moderate to high gradients of substrate wetness from elevated groundwater levels influence collembolans distribution (van Dijk et al., 2009). Most myriapods are full-time wetland residences, and their distribution can be influenced by flooding, substrate nutrient concentration, pH, and water content (Sterzynska et al., 2015). Furthermore, in the wetland litter system, plant species, wind, hydro-patterns, and microtopography contribute to the creation of areas with specific physicochemical conditions, and accumulations or deficits of litter resources. That induces changes in soil arthropods horizontal and vertical assemblages (Batzer et al., 2020; Lavelle et al., 2006).

1.1.4 Soil Arthropods and Anthropogenic stressors

Climate projections for the Caribbean anticipate more extreme precipitation events, rising temperatures, and increased sea levels due to shifts in global and regional climate patterns, which are expected to have significant impacts on the region's coastal wetlands ecosystems (IPCC, 2022). Because Caribbean coastal wetlands were anthropogenically modified since colonial times, a mosaic of physicochemical conditions, habitats, and vegetation cover characterizes these ecosystems. Global and regional climate variability, sea-level rise, land use and land cover changes act as additional stressors, further shaping these environments (Figure 1).

The combined effect between these anthropogenic stressors and the predominant wetland mosaic environment influences the hydrological regime, bio-physicochemical components, and soil fauna diversity, abundance, and functional relationships among taxa (Barberena-Arias & Cuevas, 2018; Bardgett et al., 2005; Filho et al., 2023; IPCC, 2022). Sea-level rise, for example, impacts coastal soil processes by altering ecosystems' net primary production through salinity variations, which in turn affects the diversity and functionality of soil mesofauna both directly and indirectly, as evidenced by Mazhar et al. (2022). This relationship is further illustrated by a laboratory study conducted by Pereira et al. (2015), which demonstrated that increased salinity had differential impacts on the reproductive cycles of soil taxa such as Acari (mites), Collembola (springtails), and Enchytraeidae (pot worms); mites exhibited the least sensitivity and maintained their reproductive cycles, while springtails and pot worms, more sensitive to salinity changes, experienced significant declines in reproduction. The impact of phreatic level fluctuations on soil arthropod assemblages is evidenced by a field experiment in the Zhanjiang Plain

wetland, which simulated phreatic level fluctuations in response to precipitation changes. This study revealed significant impacts on soil arthropod communities due to variations in substrate water levels. The experiment documented slight increases in total abundance under natural water level dynamics, while significant reductions were observed under conditions of constant water levels (Wu et al., 2015). Significant reductions in soil fauna abundance are often linked to their responses to cold and dry conditions. This is supported by a meta-analysis focusing on soil biota reactions to climate change, revealing that soil fauna tend to exhibit reduced abundance in colder or drier habitats. Within such environments, specific taxa adjust their vertical positioning in response to variations in moisture levels and experience increased mortality rates under higher temperatures (Culliney, 2013). Lastly, Wardle (1995) determined that the diversity of different macrofaunal groups could either be substantially elevated or reduced by land use and land cover changes depending on soil type and climate variability.

1.2 STUDY AREA

The study took place in 2.2 ha (research area) within the Ciénaga Las Cucharillas Natural Reserve, a palustrine-estuarine coastal urban wetland on the northern coast of the Caribbean Island of Puerto Rico. The reserve is in the municipality of Cataño (18°26'25.27" N, 66°08'08.39" W). The wetland comprises the western side of the San Juan Bay (Figure 7A).



Figure 7: Study area and plots location. (A) Ciénaga las Cucharillas located on the northern coast of the Caribbean Island of Puerto Rico, at the western side of the San Juan Bay, (B) study area (2.2 ha), and (C) study plots 3, 5, 10, and 6.

Average monthly temperature ranges from 31°C to 25°C from May to October, and 22°C to 28°C from December to March. The area has a humid climate with an average annual precipitation of 1920 millimeters. The rainfall distribution is bimodal, with lower precipitation occurring from December to April-May and two peak periods from May to June, and September to November (Torres-Valcarcel et al., 2014). The study was carried out from 2020 to 2021 (Figure 8). In 2020, the wettest month was July, with monthly mean precipitation of 9.64 millimeters and 24 rainy days. The driest month was May, with monthly mean precipitation of 0.51 millimeters and 6 rainy days. In 2021, the wettest month was September, with monthly mean precipitation of 8.63 millimeters and 18 rainy days. The driest month was May, with monthly mean precipitation of 1.78 millimeters and 13 rainy days.

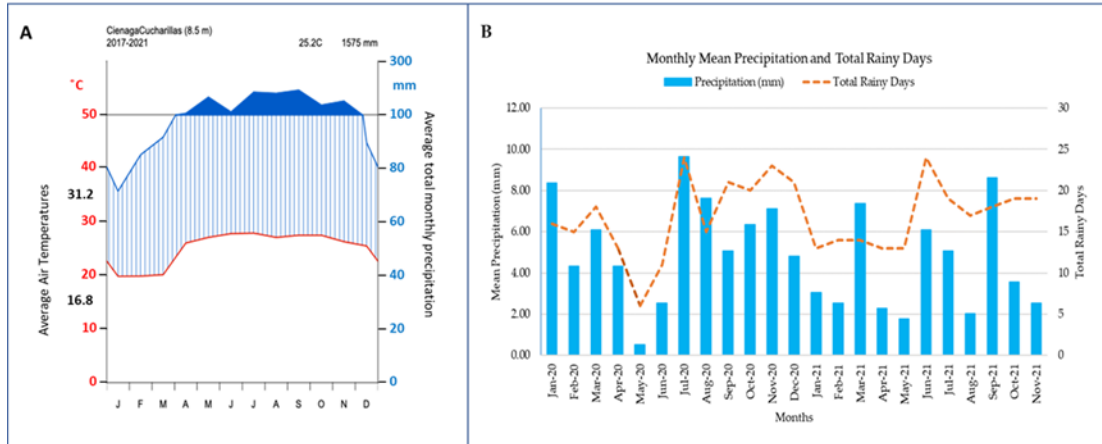


Figure 8: Climate diagram. (A) The climate diagram illustrates monthly average air temperatures in C (left y axis, in red) and average total monthly precipitation in mm (right y axis, in blue) from January 2017 to December 2021 (months are represented by letters) at Ciénaga Las Cucharillas Natural Reserve (Hernández, 2022) (B) The graph presents the mean monthly precipitation and the total number of rainy days, using climatological data from January 2020 to November 2021, sourced from the Toa Baja Levittown, PR Meteorological Station (National Weather Service, 2023).

Ciénaga Las Cucharillas Natural Reserve is representative of how coastal wetlands in the Tropics, especially in the Caribbean, have been hydrologically modified from colonial times to the present. The hydrological modifications include (a) drainage channels for agricultural use from the 17th century until the mid-20th century (Kennaway et.al., 2007; Pumarada-O’Neill, 1991); (b) the construction of a flood control channel (La Malaria channel) in the late 1940s, bringing a direct flow of fresh water to the wetland from the upper and middle parts of the basin; and (c) restricted seawater exchange due to the dike effect of an outflow water pump structure at the mouth of the channel (Webb et.al., 1998) (Figure 9). As a result, tidal interaction in this wetland occurs via deep subsurface flow (Cuevas, 2020). Historical and present hydrological modifications bring about a mosaic of physicochemical conditions, habitats, and vegetation cover.



Figure 9: La Malaria flood control channel (represented by blue lines). This channel is positioned northwest of the delineated research area (highlighted with a yellow line) at Ciénaga Las Cucharillas Natural Reserve (outlined with a red line). The location of the outflow water pump structure is indicated by a yellow square at the channel's downstream point of discharge.

The 2018 USGS Lidar Digital Elevation Model (Office for Coastal Management Partners, 2018) reveals that the study area is a lowland, characterized by ground elevation fluctuations ranging from -1.0 meter (below sea level) to 1.0 meter (above sea level). These variations in micro-elevation dictate the direction of runoff flow and lead to the formation of a system of micro-basins or catchment areas within the Natural Reserve (Figure 10; Ortiz Ramírez, 2019).

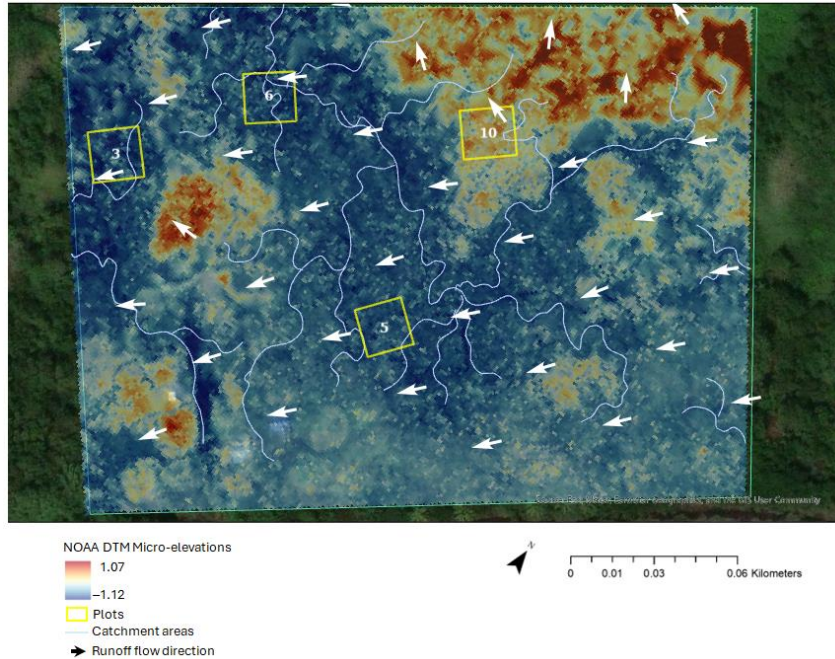


Figure 10: Variations in Micro-Elevation at the Study Area. This figure illustrates how micro-elevation variations influence the movement and direction of precipitation runoff (indicated by white arrows) and delineate catchment areas (depicted by light blue lines) in the study plots (marked as yellow squares) (Ortiz Ramírez, 2019).

The study area is characterized by two soil types: Saladar muck (Sm) series and Martin Peña (Mp) series (Figure 11; USDA, 2023). Saladar muck (Sm) series consists of black, highly decomposed (peat) autochthonous vegetation materials, that reach down to bedrock depth in the soil (Table 1). Martin Peña (Mp) series contains deposits of organic material close to surface (0- 20 cm), over mineral sediments, which includes silty clay loam embedded in the peat down to bedrock depth (20-45 cm). At the study site, the layers of mineral sediments found in the soil are the result of anthropogenic allochthonous infills from upper terrestrial sources, which were deposited during land preparation for shanty town establishment.

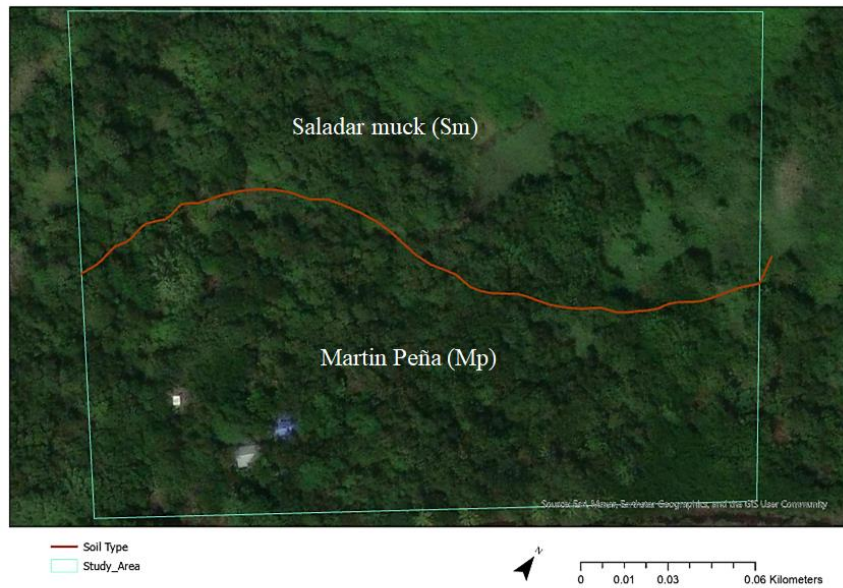


Figure 11: Soil Types at the Study Site. This figure illustrates the distribution of soil types within the study area, characterized by two distinct series: Saladar muck (Sm) and Martin Peña (Mp). Data sourced from the United States Department of Agriculture (USDA, 2023).

1.2.1 Research Area

Four study plots (3, 5, 6, and 10), each encompassing 100 square meters, were established in a research area within the Natural Reserve, with each plot featuring distinct physicochemical factors and habitat types. The plots, labeled as 3, 5, 6, and 10, correspond to their respective pre-established monitoring wells (Figure 12), of which there are ten in total, in place since 2017. This approach was chosen to maintain consistency with the long-term phreatic level and salinity monitoring data available from these wells.



Figure 12: Aerial view of the study plots (yellow squares) in las Cucharillas Wetland Research Area. The naming of the plots as 3, 5, 6, and 10 refers to their corresponding pre-established monitoring wells (white circles), which have been in place since 2017.

Plot locations were chosen based on geospatial analysis to determine micro-elevations and the presence of predominant plant functional types, along with onsite measurements of soil abiotic factors (Hernández, 2021, 2022). Their distance from the Malaria Channel (indicating freshwater influence) and the coast (indicating seawater influence) varies. Each plot is characterized by a dominant plant assemblage and displays variations in micro-elevations, vegetation cover, and soil type (Table 3).

Table 2: Physicochemical factors and plots/habitats characteristics at the study site. Source (Hernandez et. al., 2021; Hernández, 2022).

Plot	3	5	6	10
Micro-elevation(m)	-0.79	-0.72	-0.86	0.1
Distance from the coast (m)	985	910	920	785
Distance from Malaria Channel	335	445	390	457
Habitat Type	Mangrove woodland	Rehabilitated Mangrove woodland	Mangrove woodland	> 50 years Shrub & 6 years grass & ferns

Plot	3	5	6	10
Stage	Mature	Rehabilitated, damaged in Hurricane Maria	Natural Recolonization Damaged in Hurricane Maria	Mature & Early successional
% Cover	92.6 %	59.9 %	46.0 %	40.4 %
Plants Species	<i>L. racemosa</i>	young and seedlings <i>L. racemosa</i> , 33.8 % Herbs and vines	young and seedlings <i>L. racemosa</i> , 7.9 % <i>Acrostichum</i> sp.,	40.4 % <i>D. ecastaphyllum</i> 2.2 % <i>L. racemosa</i> (young trees), 0.4 % <i>Acrostichum</i> sp.,
	3.2 % <i>Acrostichum</i> sp.	4.2% grasses of Poaceae family	13.3 % <i>D. ecastaphyllum</i> ,	56.9 % <i>Echinochloa</i> sp
	4.2% grasses of Poaceae family	2.0 % <i>Acrostichum</i> sp.	32.8 % grasses of Poaceae family	
Plant Type	Tree, Fern and Grass	Tree, Fern, Herbs and Grass	Tree, Fern, Shrub and Grass	Shrub Tree, Fern and Grass
Soil Type	Mineral allochthonous embedded in an organic matrix (Martín Peña)		Organic (peat) Autochthonous (Saladar muck)	

Plot 3 represents a mature mangrove woodland habitat, predominantly populated by *Laguncularia racemosa* C.F.Gaertn. In contrast, Plot 5 is a 25-year-old restoration mangrove woodland with a primary cover of *L. racemosa*, interspersed with herbaceous species from the Cyperaceae, Vitaceae, and Polygonaceae families, as well as grassy patches from the Poaceae family. Both are located on mineral allochthonous soil embedded in an organic matrix, specifically the Martin Peña (Mp) soil series (refer to Table 3). Plot 6 features a transitioning mangrove woodland characterized by natural recolonization with young *L. racemosa* trees and seedlings, along with Poaceae grasses. Meanwhile, Plot 10 comprises a mature 50-year-old shrub habitat dominated by *Dalbergia ecastaphyllum* (L.) Taub and an adjacent 6-year-old grassland succession area

primarily consisting of *Echinochloa polystachya* (Kunth) Hitchc. These plots are situated on organic (peat) autochthonous soil, belonging to the Saladar muck (Sm) soil series.

The research area is influenced by the interplay of marine-terrestrial subsurface connectivity, local weather conditions, and regional climate variability. This interplay impacts water source inputs, which include *in-situ* precipitation, freshwater inputs from the Malaria Channel, and deep subsurface seawater flow (refer to Figure 13; Pinto-Pacheco, 2023). These factors significantly influence the spatial and temporal patterns of

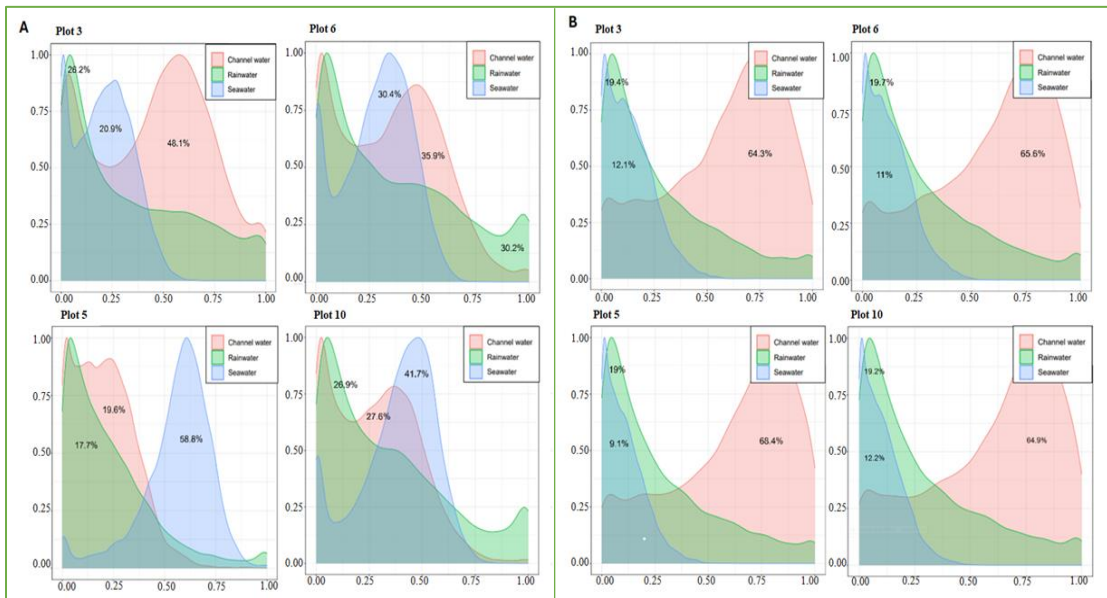


Figure 13: Posterior scaled densities and proportion of water source (channel, rain, seawater) contribution for phreatic water in the study area during (A) dry and (B) wet periods. Percentages represent the median CI 95% interval contribution for each source. Medians in graph are proportions multiplied by 100 (adapted from Pinto Pacheco 2023).

wetting and drying periods, ultimately resulting in a distinct regime. This regime is characterized by variations in the phreatic level, as well as the frequency, duration, and timing of inundation among plots. The dominant sources of water also affect soil salinity. Predominance of *in-situ* precipitation and freshwater inputs from the Malaria Channel leads to salinity levels oscillating from fresh (0.0 to 0.5 ppt) to oligohaline conditions (>0.5 to 5.0 ppt). Conversely, when deep subsurface seawater flow is the primary

influence, soil salinity ranges from mesohaline (>5.0 to 18.0 ppt) to polyhaline conditions (>18.0 to 33.0 ppt).

In the study plots, variations in micro-elevations play a crucial role in determining the movement, direction, and catchment areas of precipitation runoff (Figure 10; Ortiz Ramírez, 2019). The combined effects of regional and local precipitation, tidal fluctuations, and microtopography will determine above surface water levels or surface water film conditions during flood disturbances. Higher micro-elevations, such as those found in Plots 5 and 10 (Table 3), act as buffers against inundation. During flood disturbances, these plots experience a surface water film⁶. In contrast, Plots 3 and 6, which have lower micro-elevations, exhibit water levels rising above the soil surface during flooding events. The duration of these conditions varies, persisting for several months, just a few days or hours, depending on the interplay of climate dynamics.

1.3 CHAPTERS OVERVIEW & RESEARCH AIMS

Soil arthropods communities play an essential role in wetlands biological processes. However, understanding of their spatiotemporal dynamics in coastal wetlands, especially in the Caribbean region, remains limited. This lack of knowledge is further highlighted in the study area by the absence of prior research on the spatiotemporal effects of plant functional types on its distribution and assemblages. Further research is imperative to comprehend how marine-terrestrial-marine connectivity, soil bio-physicochemical components, and future climate change scenarios impact soil arthropods assemblages.

⁶ A shallow, film-like layer of water covering the soil surface.

This study seeks to bridge a gap in current knowledge regarding soil arthropods in urban wetland ecosystems. The **aim** is to assess the distribution patterns and interactions of soil arthropods under the influence of spatiotemporal bio-physicochemical dynamics within the litter system of a tropical, palustrine-estuarine, urban coastal wetland. This research addresses two fundamental questions: **1) How do variations in phreatic level, pH, and salinity during different hydroperiods impact the composition and vertical distribution of soil arthropod assemblages within and across study plots? 2) In what manner does the presence of plant litter cover affect the abundance and diversity of functional soil arthropods groups?** It was hypothesized that changes in phreatic level conditions, litter system salinity, and pH will significantly influence the spatiotemporal composition of soil arthropods communities, with phreatic level being the strongest predictors. Furthermore, we posit that the synchrony and synlocation of the arthropod food web structure and distribution will depend on the specific plant functional type, litter quality, and accumulation.

This document is structured to address research questions and hypotheses. In Chapter 2, the study evaluates the spatiotemporal effects of phreatic level fluctuations and litter system physicochemical variations on soil meso and macrofauna. By considering the specific environmental dependencies of these organisms, the study aims to assess how shifts in hydrological regimes and variations in soil physicochemical components affect their composition. This knowledge is crucial for understanding ecosystem responses to global and regional climate changes, sea-level rise, and increasing human activity in the region. Chapter 3 discusses the role of plant litter, quantity and quality, in shaping the spatial distribution and assemblages of soil arthropods. The chapter offers insights into

how arthropod assemblages and the soil food web structure respond to changes in plant litter characteristics, advancing our understanding of wetland litter system functioning and its broader ecological implications. Chapter 4 presents a comprehensive discussion of overall research findings to offer a cohesive understanding of the dynamics at play, linking arthropod assemblages to broader ecosystem processes. Finally, Chapter 5 summarizes the key findings and proposes recommendations for future research and management strategies.

This research is essential for understanding how arthropod communities respond to and interact with their habitat, providing insights into ecological processes at both micro and macro levels. The in-depth analysis of arthropod biodiversity conducted in this study serves a dual purpose. Firstly, elucidates the current ecological state of the wetland ecosystem. Secondly, it provides a solid foundation for developing adaptive management strategies based on a robust understanding of ecosystem dynamics.

1.4 REFERENCES

- Anderson, J. M., & Ingram, J. S. I. (Eds.). (1989). *Tropical soil biology and fertility* (p. 171). Wallingford: CAB International. [DOI: 10.2307/2261129](https://doi.org/10.2307/2261129)
- Barberena-Arias, F. M., Cuevas, E. (2018). Physicochemical Foliar Traits Predict Assemblages of Litter / Humus Detritivore Arthropods, 1–20. [DOI:10.5772/intechopen.59971](https://doi.org/10.5772/intechopen.59971)
- Barberena-Arias, F. M., & Cuevas, E. (2021). Vertical Arthropod Dynamics across Organic Matter Fractions in Relation to Microclimate and Plant Phenology. IntechOpen. doi: 10.5772/intechopen.94747
- Bardgett, R. D., Yeates, G. W., & Anderson, J. M. (2005). Patterns and determinants of soil biological diversity. *Biological diversity and function in soils*, 100-118.
- Batzer, P. D, Sharitz, R.R. (2006). *Ecology of Freshwater and Estuarine Wetlands*. The University of California.
- Batzer, D., Wu, H., Wheeler, T., & Eggert, S. (2016). Peatland invertebrates. In: Batzer, D.P., Boix, D. (Eds.), *Invertebrates in Freshwater Wetlands*. pp. 219–250.

Springer International Publishing, Cham, Switzerland.
https://doi.org/10.1007/978-3-319-24978-0_7.

- Batzer, D. P., & Wu, H. (2020). Ecology of terrestrial arthropods in freshwater wetlands. *Annual Review of Entomology*, 65, 101-119.
<https://doi.org/10.1146/annurev-ento-011019-024902>
- Bezemer, T. M., Fountain, M. T., Barea, J. M., Christensen, S., Dekker, S. C., Duyts, H., Van Hal, R., Harvey, J. A., Hedlund, K., Maraun, M., Mikola, J., Mladehov, A. G., Robin, C., De Ruiter, P. C., Scheu, S., Setälä, H., Šmilauer, P., & van der Putten, W. H. (2010). Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. *Ecology*, 91(10), 3027-3036. <https://doi.org/10.1890/09-2198.1>
- Briones, M. J. (2018). The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. *Frontiers in Environmental Science*, 6, 149.
<https://doi.org/10.3389/fenvs.2018.00149>
- Cameron, E. K., Martins, I. S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., & Gottschall, F. (2018). Global gaps in soil biodiversity data. *Nature Ecology & Evolution*, 2(6), 1042-1043. <https://doi.org/10.1038/s41559-018-0573-8>
- Coleman, D. C., Callahan, M., & Crossley Jr, D. A. (2017). *Fundamentals of soil ecology*. Academic press. Cambridge, MA, USA.
- Cuevas E. (March, 2020). Personal communication Ecolab. University of Puerto Rico. Rio Piedras.
- Cuevas E., Medina E. (1998). The Role of Nutrient Cycling in the Conservation of Soil Fertility in Tropical Forested Ecosystems. In Gopal, B., Pathak, P.S. and Saxena, K.G. (Editors) *Ecology Today: An Anthology of Contemporary Ecological Research*: 263-278
- Culliney, T.W. (2013). Role of Arthropods In Maintaining Soil Fertility. Plant Epidemiology and Risk Analysis Laboratory, Plant Protection, and Quarantine, Center for Plant Health Science and Technology, USDA-APHIS. *Agriculture* 2013, 3, 629-659; doi:10.3390/agriculture3040629
- Culliney, T. W. (2013). Role of arthropods in maintaining soil fertility. *Agriculture*, 3(4), 629-659. <https://doi.org/10.3390/agriculture3040629>
- González, G., Barberena-Arias, M.F., Huang, W., Ospina-Sánchez, C.M. (2021). Sampling Methods for Soil and Litter Fauna. In: Santos, J.C., Fernandes, G.W. (eds) *Measuring Arthropod Biodiversity*. Springer, Cham.
https://doi.org/10.1007/978-3-030-53226-0_19
- González, G., Lodge, D. J., Richardson, B. A., & Richardson, M. J. (2014). A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. *Forest Ecology and Management*, 332, 32-46.
<https://doi.org/10.1016/j.foreco.2014.06.024>

- Guerra, C. A., Heintz-Buschart, A., Sikorski, J., Chatzinotas, A., Guerrero-Ramírez, N., Cesarz, S., ... & Eisenhauer, N. (2020). Blind spots in global soil biodiversity and ecosystem function research. *Nature communications*, *11*(1), 3870. <https://doi.org/10.1038/s41467-020-17688-2>
- Ghiglieno, I., Simonetto, A., Orlando, F., Donna, P., Tonni, M., Valenti, L., & Gilioli, G. (2020). Response of the arthropod community to soil characteristics and management in the Franciacorta viticultural area (Lombardy, Italy). *Agronomy*, *10*(5), 740. <https://doi.org/10.3390/agronomy10050740>
- Havlicek, E. (2012). Soil biodiversity and bioindication: from complex thinking to simple acting. *European Journal of Soil Biology*, *49*, 80-84. https://link.springer.com/chapter/10.1007/978-94-017-8890-8_2
- Haynert, K., Kiggen, M., Klarner, B., Maraun, M., & Scheu, S. (2017). The structure of salt marsh soil mesofauna food webs—The prevalence of disturbance. *PLoS One*, *12*(12), e0189645. <https://doi.org/10.1371/journal.pone.0189645>
- Hernández, E., Cuevas, E., Pinto-Pacheco, S., & Ortíz-Ramírez, G. (2021). You Can Bend Me but Can't Break Me: Vegetation Regeneration After Hurricane María Passed Over an Urban Coastal Wetland in Northeastern Puerto Rico. *Frontiers in Forests and Global Change*, *4*, 752328. <https://doi.org/10.3389/ffgc.2021.752328>
- Hernández, E. (2022). Ecophysiological responses of plant functional groups to environmental conditions in a coastal urban wetland, Ciénaga Las Cucharillas in Northeastern Puerto Rico. Dissertation. Ecolab. Department of Environmental Science. The University of Puerto Rico. <https://hdl.handle.net/11721/2860>
- Herrera, F., & Cuevas, E. (2003). Artrópodos del suelo como bioindicadores de recuperación de sistemas perturbados. *Venesuelos*, *11*(1-2), 67-78.
- IPCC. (2022). Summary for Policymakers. In H.-O. Pörtner, D. C. Roberts, E. S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Lösschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3-33). Cambridge University Press. <https://doi.org/10.1017/9781009325844.001>
- Kennaway, T., and Helmer, E. H. (2007). The forest types and ages cleared for land development in Puerto Rico. *GIScience Remote Sens.* *44*, 356–382. <https://doi.org/10.2747/1548-1603.44.4.356>
- Loranger-Merciris, G., Imbert, D., Bernhard-Reversat, F., Ponge, J. F., & Lavelle, P. (2007). Soil fauna abundance and diversity in a secondary semi-evergreen forest in Guadeloupe (Lesser Antilles): influence of soil type and dominant tree species. *Biology and Fertility of Soils*, *44*, 269-276. <https://doi.org/10.1007/s00374-007-0199-5>

- Lavelle P. (1997). Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Advances in Ecological Research*, 27(C), 94–132.
Retrieved from
<https://www.sciencedirect.com/science/article/pii/S0065250408600070>
- Lavelle, P. (1997). Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In *Advances in ecological research* (Vol. 27, pp. 93-132). Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60007-0](https://doi.org/10.1016/S0065-2504(08)60007-0)
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, 130-150. <http://dx.doi.org/10.2307/2389178>
- Lavelle, P., & Spain, A.V. (2001) *Soil Ecology*. Kluwer Academic Publishers, New York.
<https://doi.org/10.1007/978-94-017-5279-4>
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European journal of soil biology*, 42, S3-S15. <https://doi.org/10.1016/j.ejsobi.2006.10.002>
- Li, W., Dou, Z., Cui, L., Zhao, X., Zhang, M., Zhang, Y., Gao, C., Yang, Z., Lei, Y., & Pan, X. (2020). Soil fauna diversity at different stages of reed restoration in a lakeshore wetland at Lake Taihu, China. *Ecosystem Health and Sustainability*, 6(1), 1722034. <https://doi.org/10.1080/20964129.2020.1722034>
- Lukac, M. (2017). Soil biodiversity and environmental change in European forests. *Central European Forestry Journal*, 63(2-3), 59-65.
<https://doi.org/10.1515/forj-2017-0010>
- Mathieu, J., Antunes, A. C., Barot, S., Bonato Asato, A. E., Bartz, M. L., Brown, G. G., ... & Eisenhauer, N. (2022). Soil Fauna-a global synthesis effort on the drivers of soil macrofauna communities and functioning.
<https://agritrop.cirad.fr/601640/1/Mathieu2022SoilOrganisms.pdf>
- Mazhar, S., Pellegrini, E., Contin, M., Bravo, C., & De Nobili, M. (2022). Impacts of salinization caused by sea level rise on the biological processes of coastal soils-A review. *Frontiers in Environmental Science*, 1212.
<https://doi.org/10.3389/fenvs.2022.909415>
- Menta, C., & Remelli, S. (2020). Soil health and arthropods: From complex system to worthwhile investigation. *Insects*, 11(1), 54.
<https://doi.org/10.3390/insects11010054>
- Moore, J. C., & de Ruiter, P. C. (1991). Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. *Agriculture, ecosystems & environment*, 34(1-4), 371-397. [https://doi.org/10.1016/0167-8809\(91\)90122-E](https://doi.org/10.1016/0167-8809(91)90122-E)
- Mulder, C., Den Hollander, H. A., Vonk, J. A., Rossberg, A. G., op Akkerhuis, G. A. J., & Yeates, G. W. (2009). Soil resource supply influences faunal size-specific

- distributions in natural food webs. *Naturwissenschaften*, 96(7), 813.
<https://doi.org/10.1007/s00114-009-0539-4>
- National Weather Service. Climatological Data for La Puntilla Station (ID number 9755371), San Juan, Puerto Rico. Year 2020-2023. Available online:
https://www.ndbc.noaa.gov/station_page.php?station=sjnp4
- Nielsen, U. N., Ayres, E., Wall, D. H., & Bardgett, R. D. (2011). Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity–function relationships. *European Journal of Soil Science*, 62, 105-116.
<https://doi.org/10.1111/j.1365-2389.2010.01314.x>
- Nielsen, U. N. (2019). Soil fauna assemblages. Cambridge University Press.
<https://doi.org/10.1017/9781108123518.010>
- Office for Coastal Management Partners. (2018): 2018 USGS Lidar DEM: Post Hurricane Maria - Puerto Rico. NOAA National Centers for Environmental Information, <https://www.fisheries.noaa.gov/inport/item/60105>.
- Ortiz Ramírez, G. (2019). Topographic analyses for mapping spatial patterns of soil properties and runoff dynamics in an urban coastal wetland [Class Project]. CIAM 8925-GIS: GIS Advance Spatial Analysis, University of Puerto Rico.
- Ortiz-Ramírez G, Hernández E, Pinto-Pacheco S, Cuevas E. (2024). The Dynamics of Soil Mesofauna Communities in a Tropical Urban Coastal Wetland: Responses to Spatiotemporal Fluctuations in Phreatic Level and Salinity. *Arthropoda*. 2024; 2(1):1-27. <https://doi.org/10.3390/arthropoda2010001>
- Pereira, C.S., Lopes, I., Sousa, J.P. & Chelinho, S. (2015) Effects of NaCl and seawater induced salinity on survival and reproduction of three soil invertebrates species. *Chemosphere*, 135: 116–122. DOI: 10.1016/j.chemosphere.2015.03.094
- Pinto-Pacheco, S. (2023). Spatiotemporal water dynamics effects on plant functional types in a tropical urban coastal wetland: water sources and quality in the Ciénaga Las Cucharillas, northeastern Puerto Rico. Dissertation. Ecolab. Department of Environmental Science. The University of Puerto Rico. [Unpublished manuscript].
- Potapov AM, Beaulieu F, Birkhofer K, Bluhm SL, Degtyarev MI, Devetter M, Goncharov AA, Gongalsky KB, Klarner B, Korobushkin DI, Liebke DF, Maraun M, Mc Donnell RJ, Pollierer MM, Schaefer I, Shrubovych J, Semenyuk II, Sendra A, Tuma J, Tůmová M, Vassilieva AB, Chen TW, Geisen S, Schmidt O, Tiunov AV, Scheu S. (2022). Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biol Rev Camb Philos Soc*. 2022 Jun;97(3):1057-1117. doi: 10.1111/brv.12832. Epub 2022 Jan 20. PMID: 35060265.
- Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Pérès, G., & Rutgers, M. (2012). Soil biodiversity, biological indicators and soil ecosystem services—

- an overview of European approaches. *Current Opinion in Environmental Sustainability*, 4(5), 529-538. <https://doi.org/10.1016/j.cosust.2012.10.009>
- Pumarada-O'Neill, L. (1991). *Los Puentes Históricos de Puerto Rico*. Mayagüez: Centro de Investigación y Desarrollo, Recinto de Mayagüez, Universidad de Puerto Rico, 1991. <https://app.box.com/s/rm8asi7uz7k179at3vs3>
- Socarrás, A. (2013). Mesofauna edáfica: indicador biológico de la calidad del suelo. *Pastos y forrajes*, 36(1), 5-13. <https://www.redalyc.org/pdf/2691/269127587001.pdf>
- Sterzyńska, M., Pižl, V., Tajovský, K., Stelmaszczyk, M., Okruszko, T. (2015). Soil Fauna of Peat-Forming Wetlands in a Natural River Floodplain. *Wetlands* 35, 815–829. <https://doi.org/10.1007/s13157-015-0672-0>.
- Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems* (Vol. 5). Univ of California Press.
- Torres-Valcárcel, Á, Harbor, J., González-Avilés, C., and Torres-Valcárcel, A. (2014). Impacts of urban development on precipitation in the tropical maritime climate of Puerto Rico. *Climate* 2, 47–77. [doi: 10.3390/cli2020047](https://doi.org/10.3390/cli2020047)
- United States Department of Agriculture (USDA). (2023). NRCS Web Soils Survey. Ciénaga las Cucharillas. Available online: <https://websoilsurvey.usda.gov/> (accessed on June 16, 2023).
- van Dijk, J., Didden, W. A., Kuenen, F., van Bodegom, P. M., Verhoef, H. A., & Aerts, R. (2009). Can differences in soil community composition after peat meadow restoration lead to different decomposition and mineralization rates *Soil Biology and Biochemistry*, Volume 41, Issue 8, Pages 1717-1725, ISSN 0038-0717, <https://doi.org/10.1016/j.soilbio.2009.05.016>. (<https://www.sciencedirect.com/science/article/pii/S0038071709002090>)
- Wardle, D. A. (1995). Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. Editor(s): M. Begon, A.H. Fitter, *Advances in Ecological Research*, Academic Press, Volume 26, Pages 105-185, ISSN 0065-2504, ISBN 9780120139262, [https://doi.org/10.1016/S0065-2504\(08\)60065-3](https://doi.org/10.1016/S0065-2504(08)60065-3). (<https://www.sciencedirect.com/science/article/pii/S0065250408600653>)
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304(5677), 1629–1633. <https://doi.org/10.1126/science.1094875>
- Wharton, C. H. (1982). *The ecology of bottomland hardwood swamps of the Southeast: a community profile* (No. 81/37). US Fish and Wildlife Service. https://pubs.usgs.gov/publication/fwsobs81_37

Webb, R. M., and Gómez-Gómez, F. (1998). Synoptic Survey of Water Quality and Bottom Sediments, San Juan Bay Estuary System, Puerto Rico, December 1994-July 1995. Water Resources Investigations Report. Denver, CO: U.S. Geological Survey. [doi: 10.3133/wri974144](https://doi.org/10.3133/wri974144)

Wu, P., Zhang, H., & Wang, Y. (2015). The response of soil macroinvertebrates to alpine meadow degradation in the Qinghai–Tibetan Plateau, China. *Applied Soil Ecology*, Volume 90, Pages 60-67, ISSN 0929-1393, <https://doi.org/10.1016/j.apsoil.2015.02.006>.
(<https://www.sciencedirect.com/science/article/pii/S0929139315000499>)

CHAPTER 2: EFFECT OF PHYSICOCHEMICAL FACTORS (PH, SALINITY) AND PHREATIC LEVEL CONDITIONS IN SOIL ARTHROPODS ASSEMBLAGES

2.1 INTRODUCTION

Soil fauna is present in different soil types with most of their assemblages concentrated in hot spot zones or resource patches within the litter system which comprises both the loose litter layer and the top 1-5 cm of soil (Lavelle et al., 2001,2006, 2022; Mulder et al., 2009; Swift et al., 1979). Arthropods constitute approximately 85% of the soil fauna richness (Culliney, 2013). They are categorized into two main groups: macrofauna, which are organisms larger than 2 mm, and mesofauna, ranging in size from 100 μm to 2 mm (Briones, 2018; Chapter 1, Figure 3A, Figure 14). They play a significant role in

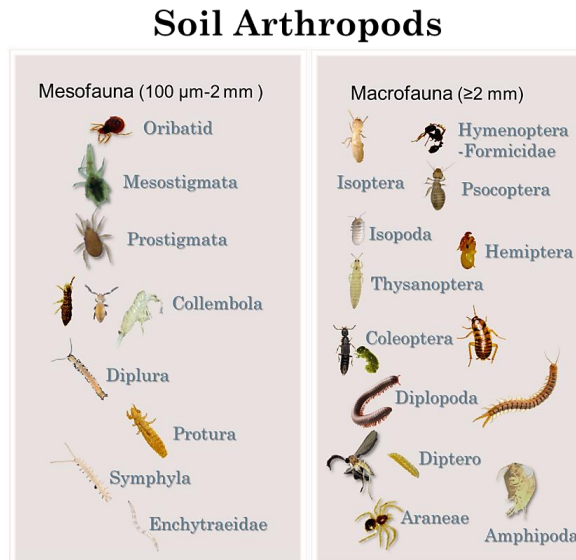


Figure 14: Classification of soil fauna based on body width and presence in various soil microhabitats. Adapted from Coleman et al., 2017; Culliney, 2013; Lavelle et al., 2003, 2013; Wardle et al., 2004.

maintaining soil quality and health, as well as providing ecosystem services: 1) involved in the translocation, breakdown, and decomposition of organic matter, contributing to

nutrient cycling, soil structure, aeration, and water regulation (Menta et al., 2020); and 2) promote the growth and dispersal of microbial populations and interact at various trophic levels through the litter decomposition process (Chapter 1, Figure 3B, page 8) (Lavelle et al., 1993; Wardle et al., 2004; Menta et al., 2020).

Soil arthropods can be considered sentinel species due to their inherent sensitivity to environmental modulations, facilitating the rapid detection and comprehension of the ecological alterations occurring within a given habitat (Menta et al., 2020; Socarrás, 2013). Their responsive dynamics to environmental fluctuations offer a rich repository of data, critical for interpreting the health and operational dynamics of wetland ecosystems (Lavelle et al., 2006; Menta et al., 2018).

Distribution patterns and interactions of soil fauna occur at different spatiotemporal dynamics (Coleman et al., 2017; Lavelle et al., 1993; Lavelle, 1997; Wardle et al., 2004), which are in turn regulated by scale-dependent variables such as climate (temperature and precipitation), edaphic properties (including porosity, structure, nutrients, humidity, pH, and salinity), vegetation (quality and quantity of resources), microtopography, and species-specific intra- and interspecific interactions (Wardle et al., 2004) (see Table 1, page 9). For example, a decrease in Isoptera (termites) diversity occurs concomitantly with reduced humidity and increased soil temperature (Menta et al., 2020). Higher soil temperatures and lower soil humidity may result in decreased population densities of Mesostigmata mites (Kagainis et al., 2017). Prostigmata mites tend to dominate in soils characterized by low nutrient content and low humidity, whereas Oribatid mites and Collembola (springtails) are typically found in nutrient-rich, humid environments (Coleman et al., 2017; Ghiglieno et al., 2020; Haarlov, 1955). The distribution of

springtails is associated with soil pore size, relative humidity, and the availability of food (Bezemer et al., 2010). Acari, Myriapoda, Isopoda, Coleoptera and Diptera larva generally have maximum abundances in acidic soils (pH <5) whereas earthworms prefer moderately acidic pH (5 to 6) (Petersen and Luxton, 1982; Lavelle et al., 1993). Diptera larvae are predominantly influenced by the influx of detritus and soil moisture levels, with which they exhibit a positive relationship (Menta et al.2020; Petersen et.al., 1882). A trophic cascade effect is observed where microtopography alters the soil environment and thus the diversity and composition of soil fungal communities (Batzer et al.,2006), which may subsequently influence the food resources and habitat quality for fungivores arthropods, such as Collembola and Oribatid (Barberena-Arias & Cuevas, 2018; Haarlov, 1955).

The hydrological regime (wetting cycles) primarily determines the physicochemical environment and biotic interactions in wetlands (Batzer et al., 2006). Spatiotemporal variations in the abundance and diversity of soil arthropods are influenced by the effects of drying and wetting cycles or hydro-patterns on soil bio-physicochemical conditions (Batzer et al.,2006; Chapter 1, Figure 5, page 14). General hydro-patterns, which are typically seasonal in water level variation (early dry, dry, early wet, and wet conditions; Chapter 1, Figure 6, page 15), exhibit significant variability across and within different wetlands types and climates conditions. Wetting cycles in wetlands include waterlogging or flooding time, frequency, duration, rate of water rise, and depth (Batzer et al.,2006; Kim et al., 2005). These cycles are modified by the relative magnitude of the water sources, including in-situ precipitation, freshwater inputs, and seawater flows (Hernández, 2021, 2022; Pinto-Pacheco, 2023). The interplay among these factors is

pivotal in shaping the spatiotemporal distribution and community dynamics of soil arthropods (Kagainis et al., 2017; Lawton, 1997). For example, in the in a lowland peat area in The Netherlands, ground-water levels affect the distribution of Collembola, with a shift in community composition observable along elevation gradients from regularly inundated areas to dry, seldom-flooded zones (van Dijk et al., 2009). In different wetlands sites in Canada, China, and southeast Florida, variations in hydro patterns induced spatial and temporal fluctuations in bio-physicochemical factors that influenced the diversity and abundance of Acari, Collembola and Insecta (Batzer et.al. 2016; Li et al., 2020; Wharton, 1982).

Natural and anthropogenic disturbances, which significantly affect overland water flow into the wetland influences the abundance, diversity, and composition of soil fauna by facilitating the redistribution of organic materials, sediments, contaminants, and the fauna themselves (Argerich et al., 2008; Coyle et al., 2017; Tronstad et al., 2005; Wheatcroft et al., 1997).

Anthropogenic modifications to Caribbean coastal wetlands since colonial times have engendered ecosystems distinguished by a mosaic of physicochemical conditions, habitats, and vegetation types (Batzer et.al., 2006; Briones, 2018; IPCC, 2022; Menta, 2020). These ecosystems are currently undergoing further stress from global and regional climate variability, sea-level rise, and changes in land use and cover (Chapter 1 Figure 1, page 6; Ortiz-Ramírez et al., 2024). The interplay between these anthropogenic stressors and the intrinsic mosaic characteristics of the wetlands significantly influences the hydrological regime, bio-physicochemical components, and soil arthropods diversity, abundance, and functional relationships among taxa (Barberena-Arias & Cuevas 2021;

Bardgett et al., 2005; Leal Filho et al., 2023). For instance, in a field experiment in the Zhanjiang Plain wetland, simulated variations in the phreatic level due to precipitation changes demonstrated that soil arthropods communities were significantly affected by changes in water level. Slight increases in total abundance were documented under natural water level dynamics, with significant reductions under constant high water level conditions (Wu et al., 2015). Mazhar et al. (2022) determined that sea level rise affects coastal soil processes and modifies ecosystems' net primary production due to variations in salinity, which have direct and indirect effects on soil arthropods diversity and function. Burton et al. (2022) found that land use changes significantly affect soil properties and vegetation cover, which in turn alters the composition of soil fauna communities.

The IPCC 2022 report for the Caribbean projects more frequent extreme precipitation events, rising temperatures, and increased sea levels, all resulting from shifts in global and regional climate patterns. These changes are anticipated to have significant impacts on the region's coastal wetland ecosystems (Yu et.al., 2019). Consequently, there is a pressing need for targeted research to understand wetland marine-terrestrial connectivity, bio-physicochemical components, and future climate change scenarios in these environments.

Given that soil arthropods play an essential role in coastal wetland biological processes and have specific environmental requirements, determining how weather variability, shifts in hydrological regime (wetting cycles) and variations in soil salinity and pH influence their composition, becomes an important tool to understand the ecosystem responses to global and regional climate change, sea level rise and increased anthropic

use of the region. An in-depth analysis of their biodiversity serves a dual purpose: a) elucidating the present ecological state of the wetland and b) underwriting adaptive management strategies anchored in a robust understanding of ecosystem dynamics (Wu et. al., 2015).

This chapter assess the effects of spatiotemporal variations in phreatic levels, pH, and salinity on soil arthropod assemblages within a tropical urban coastal wetland to address the fundamental question: How do fluctuations in phreatic level, pH, and salinity across various hydroperiods influence the composition and vertical distribution of soil arthropod assemblages within and across the study plots? The hypothesis posits that changes in hydroperiod phreatic level conditions, salinity and pH of the litter system will significantly influence the spatiotemporal composition of soil arthropods communities, with phreatic level being the strongest predictor. This, in turn, has consequential impacts on soil arthropods dynamics, altering their interactions within the soil system, thus changing how they impact their surrounding ecosystem.

2.2 METHODS

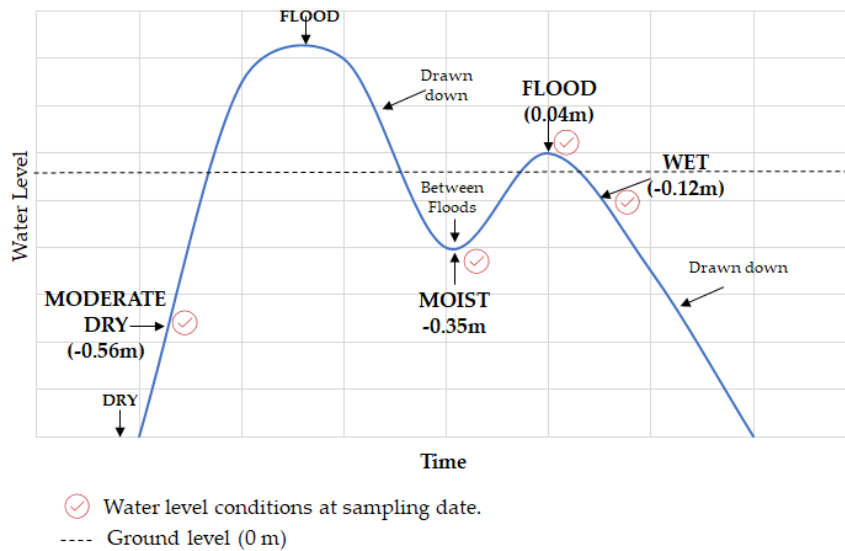
The methodology was designed to provide a comprehensive understanding of soil arthropods responses under diverse environmental stresses. Sampling was conducted based on the wetland hydroperiod dynamics to take account phreatic levels and weather conditions, as delineated in Chapter 1, and summarized in Figure 15 (Batzer et al., 2006; National Weather Service, 2023).

The study was conducted on five dates over the course of one year (from 2020 to 2021), with each date chosen to represent distinct hydroperiod conditions: Moderate Dry (June

18-25, 2020), Flood (October 23, 2020), Moist/Between Floods (March 19, 2021), and Wet (June 9, 2021). The hydroperiod classification in this study was primarily based on the phreatic level measurements recorded at sampling time. This approach was adopted due to the direct influence of phreatic level on soil microenvironment (reflecting soil antecedent patterns of drying/wetting cycles) (Batzer et al., 2006; Wu et al., 2015; Chen et al., 2014). Local precipitation data and the average tidal range for the 14 days prior to sampling date were also considered due to their impact on the wetland's dry and wet cycles, as well as site's phreatic level at the sampling time. For instance, during prolonged dry periods, bimodal high tide reaches the study site in 20 minutes, but this process can extend up to 2 hours during wet periods (Hernández, 2021).

Hydroperiod conditions on sampling day were categorized as "moderate dry" and "moist" at mean phreatic levels of -0.56 m and -0.38 m ground level, respectively. "Wet" and "flood" conditions were identified at mean phreatic levels of -0.12 m and at or above the ground level (0 m). It is noteworthy that the moist sampling period, which took place on March 19, 2021, occurred between flooding events. Specifically, the site experienced flooding both a week before and after the sampling date, although the week of the sampling itself was dry. The sampling for this period was conducted immediately following the first flood event. Additionally, the flood sampling date, which was October 23, 2020, coincided with the receding of floodwaters. Prior to this date, the wetland had been subjected to significant atmospheric events, including tropical storms Isaias and Laura, followed by a prolonged rainy period that lasted until the end of October 2020. This resulted in approximately three months of flooding at the site, spanning from August 2020 to October 2020 (National Weather Service, 2020).

A Hydrodynamics of Ciénaga Las Cucharillas Natural Reserve



B

Wetland Hydroperiod	Local Climate Conditions	Total Local Rainy Days	Total Local Precipitation (cm)	Mean Tidal Daily Range (m)	Mean Phreatic level (m)
	14 days before sampling date	7	4.93	0.44	-0.53
Moderate Dry (June 2020)	During sampling date	1	0	0.42	-0.56
	14 days before sampling date	9	12.34	0.52	0.0
Flood (Oct 2020)	During sampling date	0	0	0.5	0.04
	14 days before sampling date	4	1.73	0.44	-0.19
Moist (Mar 2021)	During sampling date	1	0.05	0.4	-0.38
	14 days before sampling date	10	8.81	0.49	-0.22
Wet (Jun 2021)	During sampling date	1	3.23	0.53	-0.12

Figure 15: A) Schematic diagram of the wetland hydrodynamics showing phreatic level (m) on the date of sampling, adapted from (Batzer et al., 2006). B) Overview of local total rainy days, precipitation (cm), mean tidal daily range, and mean phreatic level (m) for the 14-day period leading up to and including the sampling date (National Weather Service, 2023).

Sampling was conducted from 7:00 am to 10:00 am to ensure uniform environmental conditions across plots, specifically regarding soil temperature, water content, and tidal influence. This timing aligns with the transition from high to low tide (Table 3).

Table 3: Tide conditions at the time of sampling, detailing the tidal phase (low or high) corresponding to the sampling events. Data was obtained from the National Weather Service (2021).

Sampling Date	Sampling Time*	Tide (m)	Tide description
June 18, 2020	7:00	0.22	High
	10:00	0.05	Low
June 25, 2020	7:00	0.48	High
	10:00	0.23	Low
October 23, 2020	7:00	0.31	High
	10:00	0.14	Low
March 19, 2021	7:00	0.29	High
	10:00	0.15	Low
June 9, 2021	7:00	0.22	High
	10:00	0.10	Low

*Sampling occurred in the morning, between 7:00 am to 10:00 am.

Four study plots (3, 5, 6, and 10), each encompassing 100 square meters, were established in a research area within La Ciénaga las Cucharillas Natural Reserve, with each plot featuring distinct physicochemical factors and habitat type, representative of the inland part of the wetland (Chapter 1, Table 2, page 23). The distance of each study plot from the Malaria Channel (indicating freshwater influence) and the coast (indicating seawater influence) varies. Each plot is characterized by a dominant plant assemblage and displays variations in micro-elevations, vegetation cover, and soil type (Table 3). The plots, labeled as 3, 5, 6, and 10, correspond to their respective pre-established monitoring wells (Chapter 1, Figure 12, page 23), of which there are ten in total, in place since 2017. Within each sampling plot, five plant species were chosen based on their functional type and presence in all plots (Hernández, 2021): a) *Dalbergia ecastaphyllum* (L.) Taubert,

Fabaceae family (shrub); *b*) *Echinochloa polystachya* (Kunth) Hitchc. (grass), Poaceae family (grass); *c*) *Achrostichum.danaeifolium* Langsd. & Fisch, Pteridaceae family (fern) and *Laguncularia racemosa* L., Combretaceae family (tree). *D. ecastaphyllum* was present in two plots (6 and 10), *E. polystachya* was present in plot 10, while the three other species were present in plots 3, 5 and 6. In each plot, three plants per functional type were chosen.

Three substrate samples per plant/plot were collected every sampling date. Each sample measuring 7.62 cm diameter x 5 cm depth, was separated into loose litter (relatively undecomposed), and old litter (partly to fully decomposed) with organic soil. Phreatic level was measured *in-situ*. Collected samples were transported to the laboratory, where their fresh weight was recorded before being placed, in lighted Tullgren-Berlese extractors for one week. The extracted arthropods were preserved in 70% ethanol solution placed under each extractor (Barberena-Arias & Cuevas, 2018; Barberena-Arias, 2021; Herrera & Cuevas, 2003). Collected soil arthropods were taxonomically identified to the lowest category possible, either class, subclass, order or suborder, and family, and classified as adults or immatures. Collembola were not separated as adults or immatures due to the difficulty to differentiate among developments stages (Barberena-Arias & Cuevas, 2018; Barberena-Arias, 2021; Herrera & Cuevas, 2003). For each sample they were identified and counted using an Amscope SF2TRA stereoscopic binocular microscope or a Nikon Eclipse 80i microscope. After extraction, substrate samples were oven dried at 60°C for a period of seven days. A subsample was mixed with distilled water (1:1) and homogenized to determined salinity using EcoSense® conductivity meter and pH with Hanna Instruments® HI99121 pH/Temperature meter (USDA, 1999).

2.3 DATA ANALYSIS

Non-parametric statistical methods, including the Wilcoxon/Kruskal-Wallis test followed by post-hoc Steel Dwas's test, were employed to detect variations in phreatic levels, pH, and salinity among plots and hydroperiods. A multifactorial approach was employed to investigate the collective impact of these variables on the diversity, abundance, life stages and vertical distribution of soil arthropods. A density distribution table was employed to investigate the relationships between soil arthropod taxa and the combined effects of phreatic levels, pH, and salinity. By cataloging the frequency of occurrences for each unique combination of these factors in relation to taxa density, the analysis delineates the distribution patterns and occurrence frequencies of soil-dwelling arthropods. This methodology facilitated the extraction of insights into the adaptive mechanisms of these arthropods and their preferred environmental conditions. A heatmap was generated to visually represent this data. The G-test, also known as the log-likelihood ratio test, was applied to ascertain the presence of non-random associations among the categorical variables within the contingency tables. A p-value was employed to assess the statistical significance of these associations. In the distribution table, taxonomic groups were categorized as "dominant," "common," or "rare" according to their relative density. Dominant taxa were identified as those with a relative density of 10% or greater. Common taxa were those with a relative density between 1% and 10%, while rare taxa were defined by a relative density of less than 1% (Li et.al., 2012; Zheng et.al., 2022). Spearman's Rho correlation analysis was used to identify significant correlations among environmental factors. To further explore these relationships and quantify the effects of phreatic level, pH, and salinity on the dependent variables, a general linear model (GLM)

with a quasi-Poisson distribution was applied. Additionally, a quadratic model was utilized to delve deeper into these relationships.

Soil arthropod metrics, including the Menhinick's Index for diversity along with richness, abundance, and density (the latter representing the number of individuals per gram of sample), were quantified (Barberena-Arias & Cuevas, 2018; Yutan et al., 2019). The analysis was further structured by categorizing phreatic levels, pH, and salinity into specific ranges as outlined in Table 4, providing a systematic framework for examining the impact of these environmental factors on soil arthropod communities.

Table 4: Categorization of Environmental Factors. Each environmental factor was divided into specific ranges or categories to facilitate the examination of their effects on the dependent variables under study.

Environmental Factors Categories		
Phreatic Level (m)	pH (adapted from NRCS, 2023)	Salinity (ppt) (adapted from EPA, 2006)
High: >0.0	Strongly acidic: < 5.5	Freshwater: 0 to 0.5
Shallow: -0.01 to -0.12	Moderately Acidic: 5.6 to 6.0	Oligohaline: >0.5 to 5.0
Slightly Moderate: -0.13 to -0.36	Slightly Acidic: 6.1 to 6.5	Mesohaline: >5.0 to 18.0
Moderate: -0.37 to -0.43	Neutral: 6.6 to 7.3	Polyhaline: >18.0 to 33.0
Deep: <-0.44		

A Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to assess whether statistically significant differences exist in community composition, as quantified by Bray-Curtis distances, among plots across different hydroperiods.

The Soil Biological Quality-Arthropod Index (QBS-ar index, in Italian: Qualità Biologica del Suolo; Menta et al., 2018; Parisi et al., 2005) was calculated for different hydroperiods to serve as a benchmark for the study, and to assess soil quality and the impact of edaphic conditions on soil arthropods. The use of the QBS-ar index facilitates

worldwide comparisons of soil quality, providing a standardized tool for ecological assessments (Menta et al., 2018; Parisi et al., 2005). This index indicates that soils of superior biological quality possess a more diverse array of microarthropods that are well-adapted to their environment. Typically, the index values span from 1, representing epi-edaphic⁷ organisms with minimal soil adaptation, through hemi-edaphic⁸ organisms with an intermediate adaptation rating, to eu-edaphic⁹ forms that exhibit the highest degree of soil adaptation, with a maximum index value of 20. By integrating soil arthropod biodiversity with their vulnerability, the QBS-ar index serves as a tool to identify less favorable edaphic conditions, reflecting soil health. Notably, the use of the QBS-ar index facilitates worldwide comparisons of soil quality, providing a standardized tool for ecological assessments (Menta et al., 2018; Parisi et al., 2005).

Statistical analyses were performed using SAS JMP® Pro 16 and R statistical software (R Core Team, 2023). For the analysis of contingency tables and Generalized Linear Models (GLMs) in R, the packages gmodels, vcd, pheatmap, DescTools, MASS, stats, and car were utilized. The Permanova analysis was conducted using the adonis2 function from the vegan package, which is specifically designed for community ecology analysis.

⁷ Epi-edaphic organisms live on the soil surface rather than within the soil itself. These organisms are adapted to living in the leaf litter, dead wood, and other organic material that accumulates on the ground (Menta, 2012).

⁸ Hemi-edaphic organisms inhabit the soil's surface or the boundary layer between the soil and the air above it. These organisms live partially in the soil but may also venture to the surface or into the lower vegetation layers. They interact with both the soil environment and the above-ground environment (Menta 2012).

⁹ Eu-edaphic organisms are directly associated with the soil and its properties (Menta, 2012).

2.4 RESULTS

2.4.1 Study site variations in phreatic level, pH and salinity

There were significant ($p < 0.05$) fluctuations in phreatic levels, salinity, and pH within and among various plots during distinct hydroperiods (Table 5, Figure 16 and 17). In Plots 5 and 10, water levels varied from surface to shallow (-0.01 to -0.12 m) under flood conditions to moderately shallow depths (> -0.13 to -0.36 m) in wet periods. Salinity oscillated between oligohaline (>0.5 to 5.0 ppt) and fresh (0 to 0.5 ppt), with strongly acidic pH levels (< 5.0). In contrast, Plots 3 and 6 were characterized by elevated water levels (between 0.09 to 0.11 >0.0 m) during flood events and lower levels during wet phases (between -0.07 to -0.12), correlating with moderately to strongly acidic pH values ranging from (5.6 to 6.0) and transitioning salinity from oligohaline to fresh conditions. During the dry period, phreatic levels in Plots 3 and 5 were observed to be deep (-0.54 and -0.46 m, respectively), whereas in Plots 6 and 10, they transitioned to moderate depths (-0.43 m). Salinity assessments revealed conditions ranging from oligohaline to low mesohaline (mean values >5.0 to 8.0 ppt) in Plots 3 and 10. In contrast, Plots 6 and 5 exhibited salinities from high mesohaline to polyhaline (mean values >10.0 to 19.5 ppt). There were pH variations in all plots, which varied from neutral (6.6 to 7.3) to strongly acidic (<5.5). In the moist period, coinciding with a dry phase between flooding events, moderate phreatic levels (-0.37 to -0.43 m) and strongly acidic pH values were noted across all plots. Salinity levels ranged from polyhaline in plots 5 and 6, to mesohaline across all plots, and to oligohaline in plots 3 and 10. These variations reflect the dynamic interplay between hydrological conditions and chemical parameters throughout different periods and across various plot locations.

Table 5: Wilcoxon/Kruskal-Wallis analysis followed by post-hoc Steel-Dwass test showing significant variations in plots' phreatic levels (m), salinity (ppt), and pH values among hydroperiods. Values not connected by the same letter indicate significant differences ($p < 0.05$).

Plots	Hydroperiod	Phreatic Level (m)			Salinity (ppt)			pH		
		Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***
3	Flood	729.50	22.39	A	169.17	-16.93	D	441.03	1.72	B
	Moderate									
	Dry	100.50	-22.24	D	629.66	14.47	B	700.22	19.23	A
	Moist	263.50	-8.07	C	680.08	13.43	A	135.60	-14.25	D
	Wet	477.00	5.76	B	330.78	-7.72	C	327.57	-8.01	C
5	Flood	757.50	21.95	A	390.49	-2.30	C	226.07	-12.77	C
	Moderate									
	Dry	256.00	-10.34	C	718.63	17.03	A	766.85	19.83	A
	Moist	87.00	-21.21	D	649.99	13.42	B	234.02	-11.55	C
	Wet	500.50	7.18	B	179.51	-23.02	D	473.48	4.38	B
6	Flood	740.00	18.98	A	188.64	-11.43	D	514.78	6.00	B
	Moderate									
	Dry	95.50	-21.97	D	660.53	17.55	A	709.50	20.87	A
	Moist	262.50	-8.41	C	607.12	11.68	B	195.03	-11.84	D
	Wet	505.00	11.32	B	253.23	-15.66	C	276.58	-13.21	C
10	Flood	1047.00	28.98	A	589.72	-1.59	C	696.75	5.27	B
	Moderate									
	Dry	83.50	-21.71	D	996.26	14.94	B	1144.25	20.71	A
	Moist	288.00	-16.77	C	1042.95	21.06	A	228.90	-18.94	D
	Wet	637.50	1.83	B	266.93	-26.44	D	561.66	-4.02	C

*Score Mean: Average rank within each group and illustrating the ranks' central tendency.

**Standardized Score: Deviation of group's mean rank. This serves as an indicator of the group's relative position or deviation from the norm.

*** Connectivity Letters: Steel-Dwass post-hoc comparison letters associated with each attribute.

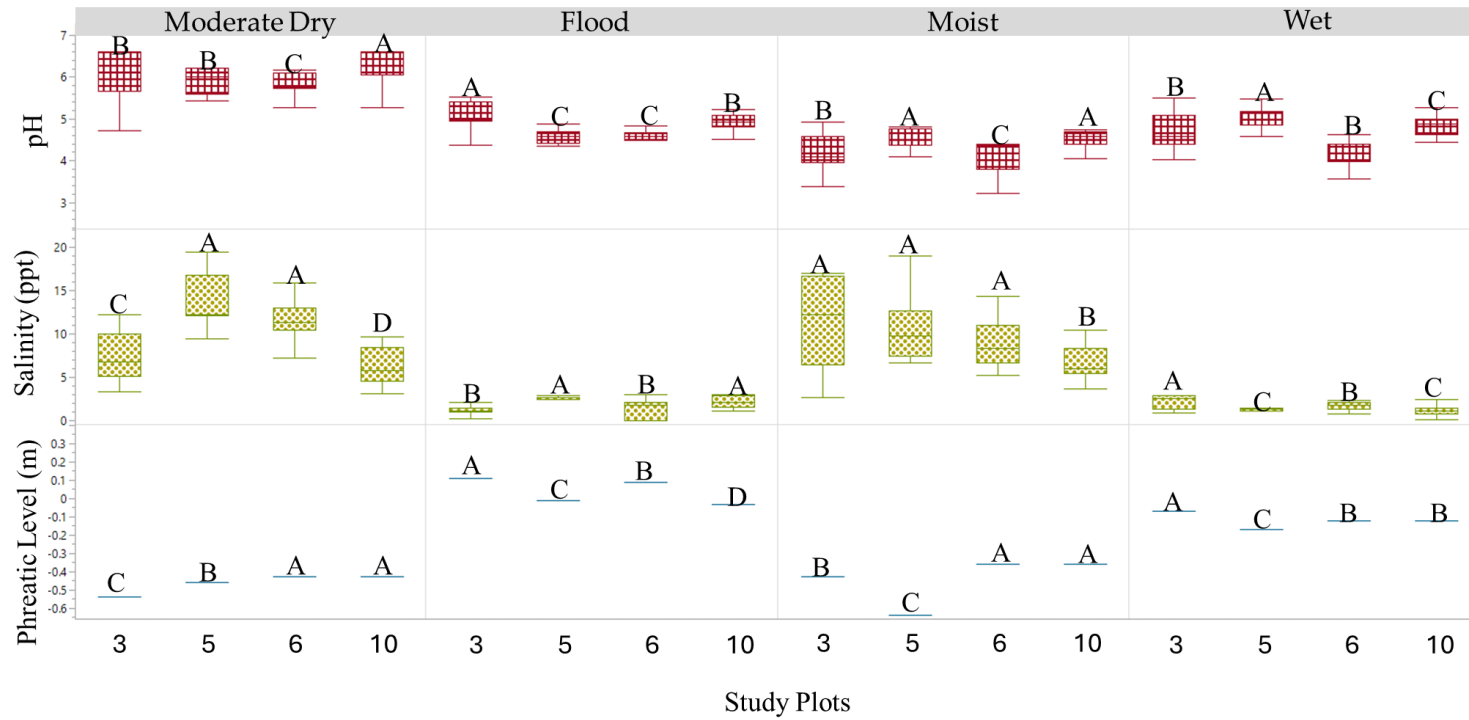


Figure 16: Significant differences in phreatic levels, salinity, and pH across plots during different hydroperiods. Values not connected by the same letter indicates significant differences ($p < .05$).

Furthermore, significant negative correlations between phreatic levels, salinity and pH across plots were identified, as illustrated in Table 6 and Figure 17. Freshwater and oligohaline salinity with strongly acidic conditions tended to prevail, when phreatic level was near the surface (with mean values of $-0.03 \pm 0.10\text{m}$ and $-0.11 \pm 0.10\text{m}$). Conversely, when the phreatic level was deeper, at approximately $-0.44 \pm 0.10\text{m}$ and $-0.57 \pm 0.08\text{m}$ (mean values), mesohaline and polyhaline conditions with slightly acidic and neutral pH became more dominant.

Table 6: Spearman's Rho correlation analysis showing significant correlations between phreatic level, salinity, and pH within plots.

Plots	Phreatic level by Salinity		Phreatic level by pH	
	Spearman ρ	Prob> ρ	Spearman ρ	Prob> ρ
3	-0.80	<0.0001	-0.30	<0.0001
5	-0.60	<0.0001	-0.20	<0.0001
6	-0.80	<0.0001	-0.30	<0.0001
10	-0.50	<0.0001	0.0	0.45

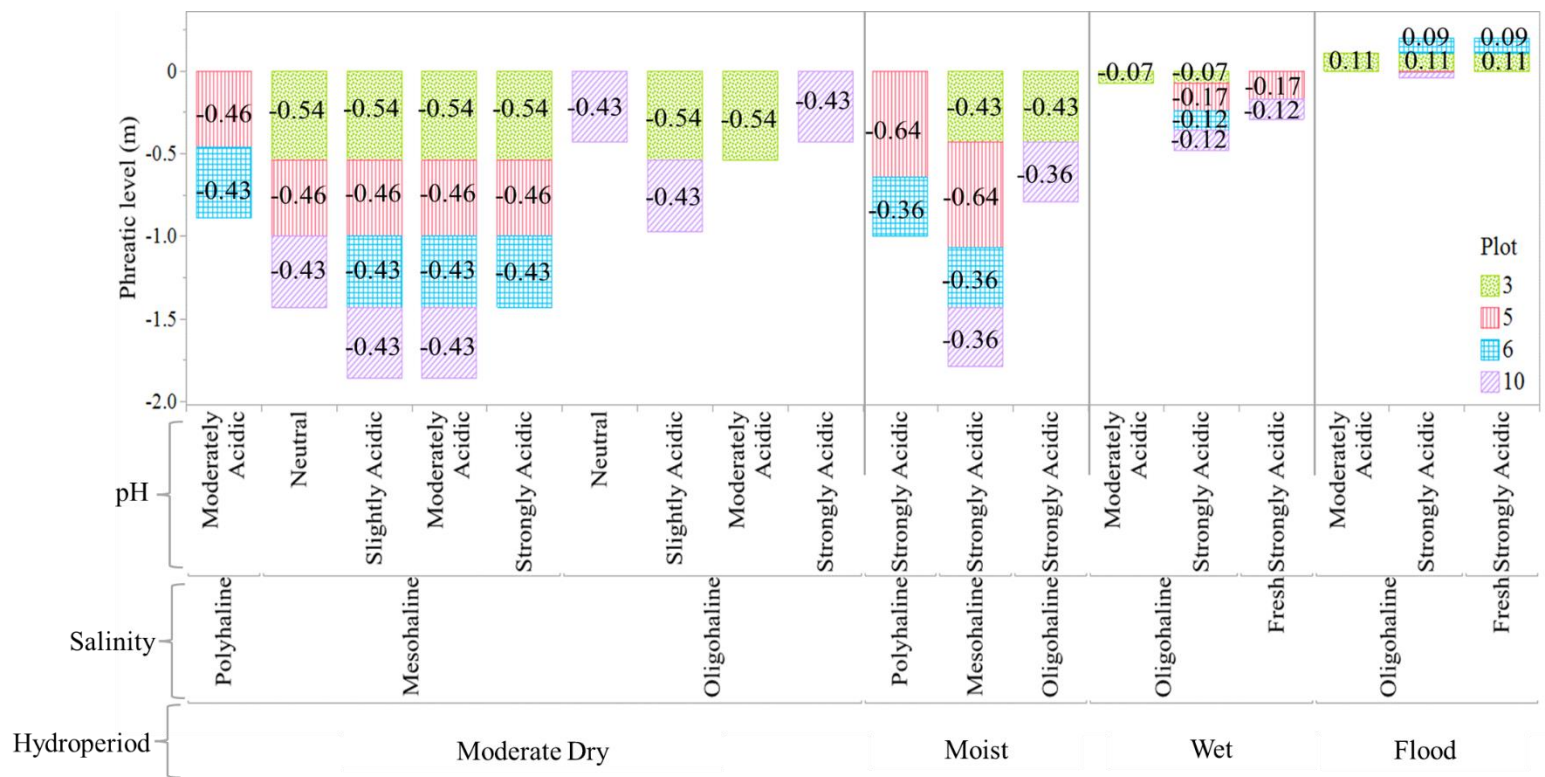


Figure 17: Variations in plot hydroperiod salinity and pH conditions correlated with phreatic level.

2.4.2 Influence of hydroperiods physicochemical factors on soil arthropods diversity and abundance

The application of a Generalized Linear Model (GLM) with a quasi-Poisson distribution to assess the impact of the environmental factors on the richness and abundance of soil arthropods yielded statistically significant effects for all included predictors, ($p < 0.01$, Table 7). For species richness, the model indicates negative correlations with phreatic level, salinity, and pH, each with substantial t-values suggesting strong effects.

Specifically, the negative coefficient for phreatic level (-0.32) with a t-value of -14.88 implies that higher water levels lead to reduced species richness. The influence of salinity and pH are less pronounced, reflected by a coefficient of -0.02 and -0.07 and a t-value of -30.33 and 18.37 respectively, yet they still significantly detract from species richness.

Table 7: Results from a Generalized Linear Model (GLM) analysis, utilizing a quasi-Poisson distribution to evaluate the influence of various environmental factors on the richness and abundance of soil arthropods.

Richness	Estimate coeficiente	Estimate Error	t value	p-value
Intercept	4.54	0.03	161.36	<0.01
Phreatic level	-0.32	0.02	-14.88	<0.01
Salinity	-0.02	0.00	-30.33	<0.01
pH	-0.07	0.00	18.37	<0.01
Abundance	Estimate coeficiente	Estimate Error	t value	p-value
Intercept	1.24	0.37	3.34	<0.01
Phreatic level	0.91	0.29	3.10	<0.01
Salinity	0.00	0.01	-0.10	<0.01
pH	0.03	0.05	0.71	<0.01

The application of a quadratic model to investigate the effects of phreatic levels on species richness and abundance provided insightful results, elucidating the nonlinear relationship between these variables (Table 8, Figure 18). In the case of species richness, the analysis demonstrated a significant unimodal response to phreatic levels. The

significant positive first-order term (t-value = 2.084, p = 0.0372) and the highly significant negative second-order term (t-value = -30.463, p < 2e-16) indicate a peak in species richness at an intermediate phreatic level. This peak suggests that species richness is highest during moderate wet conditions and decreases under both dryer conditions and extreme flooding, supporting the hypothesis of a unimodal (one peak) response to phreatic levels. The model for species abundance, while showing a less pronounced quadratic effect, still highlights important dynamics. The significant positive first-order term (t-value = 4.797, p = 1.67e-06) suggests that species abundance initially increases with rising phreatic levels. However, the second-order term, although not statistically significant (t-value = 1.128, p = 0.26), suggests a potential leveling off or slight decline as phreatic levels continue to rise, though this effect is not strong enough to be conclusive.

Table 8: Quadratic model results to investigate the effects of phreatic levels on species richness and abundance.

Richness	Estimate	Std Error	t value	p-value
Intercept	57.93	0.13	436.23	<0.01
Poly (Phreatic level, 2)1	16.87	8.09	2.08	<0.01
Poly (Phreatic level, 2)2	-246.54	8.09	-30.46	<0.01
Abundance	Estimate coeficiente	Estimate Error	t value	p-value
Intercept	2.69	0.08	34.46	<0.01
Poly (Phreatic level, 2)1	22.84	4.76	4.80	<0.01
Poly (Phreatic level, 2)2	5.37	4.76	1.13	0.26

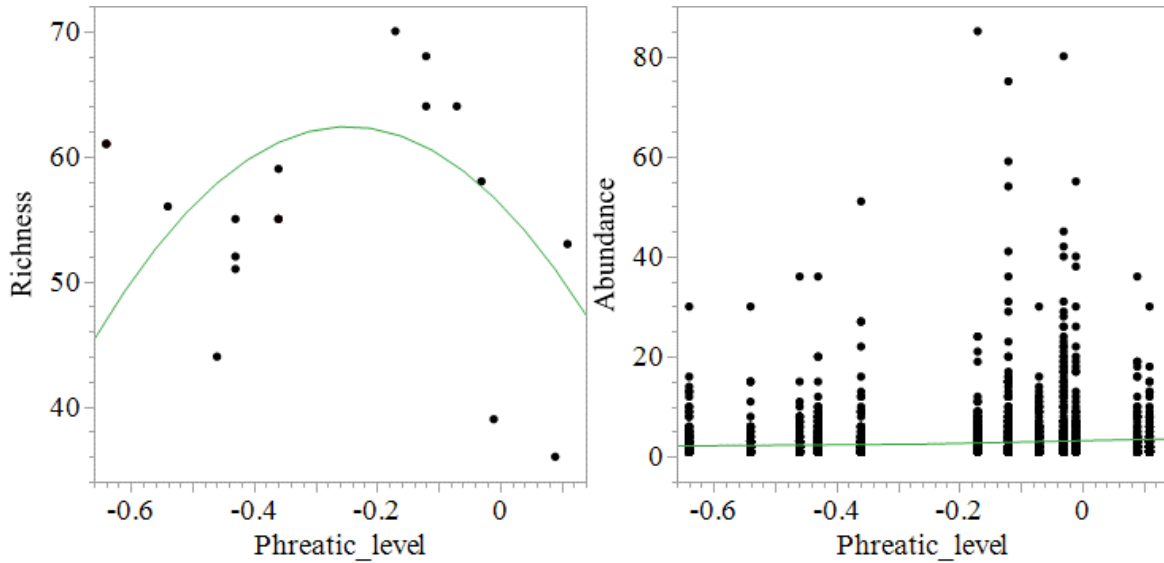


Figure 18: Quadratic model plots to investigate nonlinear effects of phreatic levels on species richness and abundance.

The multifactorial nonparametric analysis identified a combination of factors, including phreatic levels, salinity, and pH conditions across various hydroperiods, as delineated in Table 9 and Appendix 1.

Table 9: Combinations of factors, including phreatic levels, salinity, and pH conditions across various hydroperiods, as identified in the multifactorial analysis. Detailed specific range values for phreatic level, salinity, and pH categories can be found in Table 4.

Combination of environmental factors			
Hydroperiod	Phreatic level	Salinity	pH
Moderate Dry	Deep	Mesohaline	Neutral
			Moderately Acidic
			Slightly Acidic
			Strongly Acidic
	Moderate	Mesohaline	Moderately Acidic
			Slightly Acidic
Moist	Moderate	Mesohaline, Oligohaline	Strongly Acidic
Wet	Slightly Moderate	Mesohaline, Oligohaline	Strongly Acidic
	Shallow	Oligohaline	
Flood	High	Fresh Oligohaline	Strongly Acidic

This analysis revealed significant variations in the density (#individuals/grams), richness, and Menhinick index of soil arthropods across the study plots subjected to combine phreatic levels, salinity, and pH conditions (Figure 19 and Appendix 1). Notably, the combined effects of shallow phreatic levels (-0.01 to -0.12 meters), oligohaline salinity (>0.5 to 5.0), and strongly acidic pH (< 5.0) corresponded with markedly higher values of community parameters across all examined plots. Significant reductions in community parameters were documented in plots 5 and 3, both under deep phreatic conditions (deeper than -0.44 meters) and within a mesohaline salinity range (>5.0 to 18.0 ppt), with plot 5 exhibiting neutral pH values (6.6 to 7.3) and plot 3 showing slightly acidic pH (6.1 to 6.5). Comparable decreases were observed in plot 6 under moderate phreatic levels (-0.37 to -0.43 meters) with mesohaline salinity, spanning moderately to strongly acidic pH (5.6-6.0, < 5.0, respectively). In plot 10, declines were evident under slightly moderate (-0.13 to -0.36 meters), oligohaline, strongly acidic conditions.

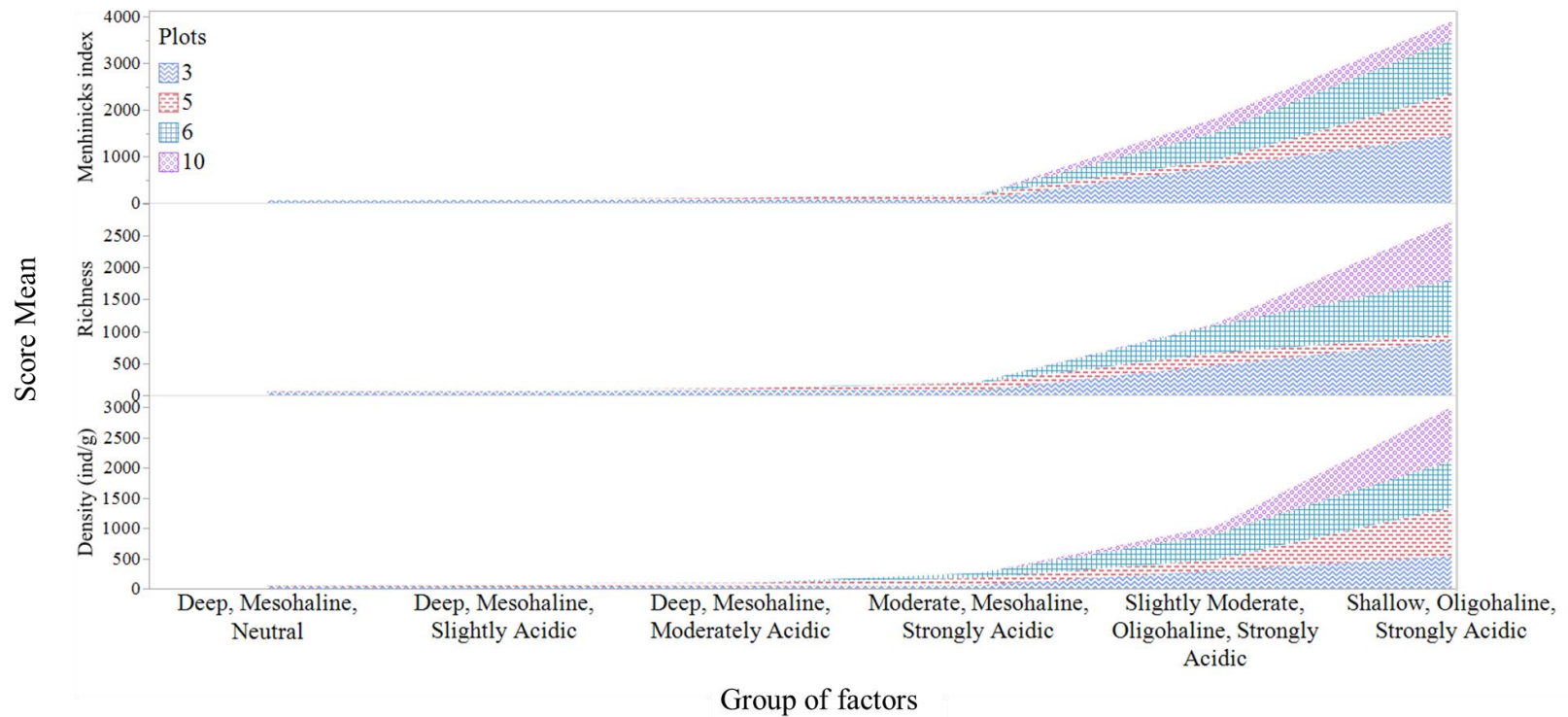


Figure 19: Multifactorial non-parametric analysis showing results with significant variation in soil arthropod density (individuals per gram), richness, and Menhinick index across plots under the combine effects of phreatic levels, salinity, and pH conditions. Group of factor categories are order as follow: phreatic level, salinity, and pH. The score mean of the analysis represents the average rank within each group, illustrating the ranks' central tendency.

The multifactorial nonparametric analysis further reveals that during the wet period, in shallow, oligohaline, and strongly acidic conditions, a significant distinction exists between adult and immature life stages, with the latter being more prevalent and both exhibiting notable higher densities compared to other combined factor conditions (Table 10). Under these conditions, the immature stages of Acari and Diptera dominate (Figure 20). Moreover, immature stages were also more abundant in flood period environments characterized by high (>0.0 meters), oligohaline, strongly acidic conditions. In these environments, the immature stages of Acari, Diptera, Diplopoda, Thysanoptera, Hemiptera, and Coleoptera were prevalent. The analysis also elucidated disparities in the distribution of soil arthropods among litter fractions, loose and old litter. It was determined that loose litter sustains a significantly greater density of arthropods, a pattern that was consistently maintained across all evaluated combinations of environmental factors (Figure 21). Notably, the highest densities were recorded during the wet period under oligohaline-acidic conditions.

Table 7: Multifactorial non-parametric analysis illustrating variations in the density of soil arthropod life stages (individuals per gram) under the combined effects of phreatic levels, salinity, and pH conditions. Distinct groups, identified by differing connectivity letters, indicate significant differences ($p < 0.05$) in density among the various environmental conditions analyzed.

Hydroperiod	Group of factors	Life Stage	Density (ind/g)		
			Score Mean**	Standardized Score***	Connectivity Letters****
Moderate Dry	Deep, Oligohaline, Moderately Acidic	Adult	10.56	-2.02	B
		Immature	17.20	2.02	A
	Moderate, Mesohaline, Slightly Acidic	Adult	65.05	-1.98	B
		Immature	79.68	1.98	A
	Moderate, Oligohaline, Slightly Acidic	Adult	14.04	-2.29	B
		Immature	28.00	2.29	A
Wet	Shallow, Oligohaline, Strongly Acidic	Adult	763.46	-4.59	B
		Immature	880.13	4.59	A
Flood	High, Oligohaline, Strongly Acidic	Adult	114.32	-2.40	B
		Immature	136.25	2.40	A

*Group of factor categories are order as follow: phreatic level, salinity, and pH
**Score Mean: Average rank within each group and illustrating the ranks' central tendency.
***Standardized Score: Deviation of group's mean rank. This serves as an indicator of the group's relative position or deviation from the norm.
****Connectivity Letters: Steel-Dwass post-hoc comparison letters associated with each attribute

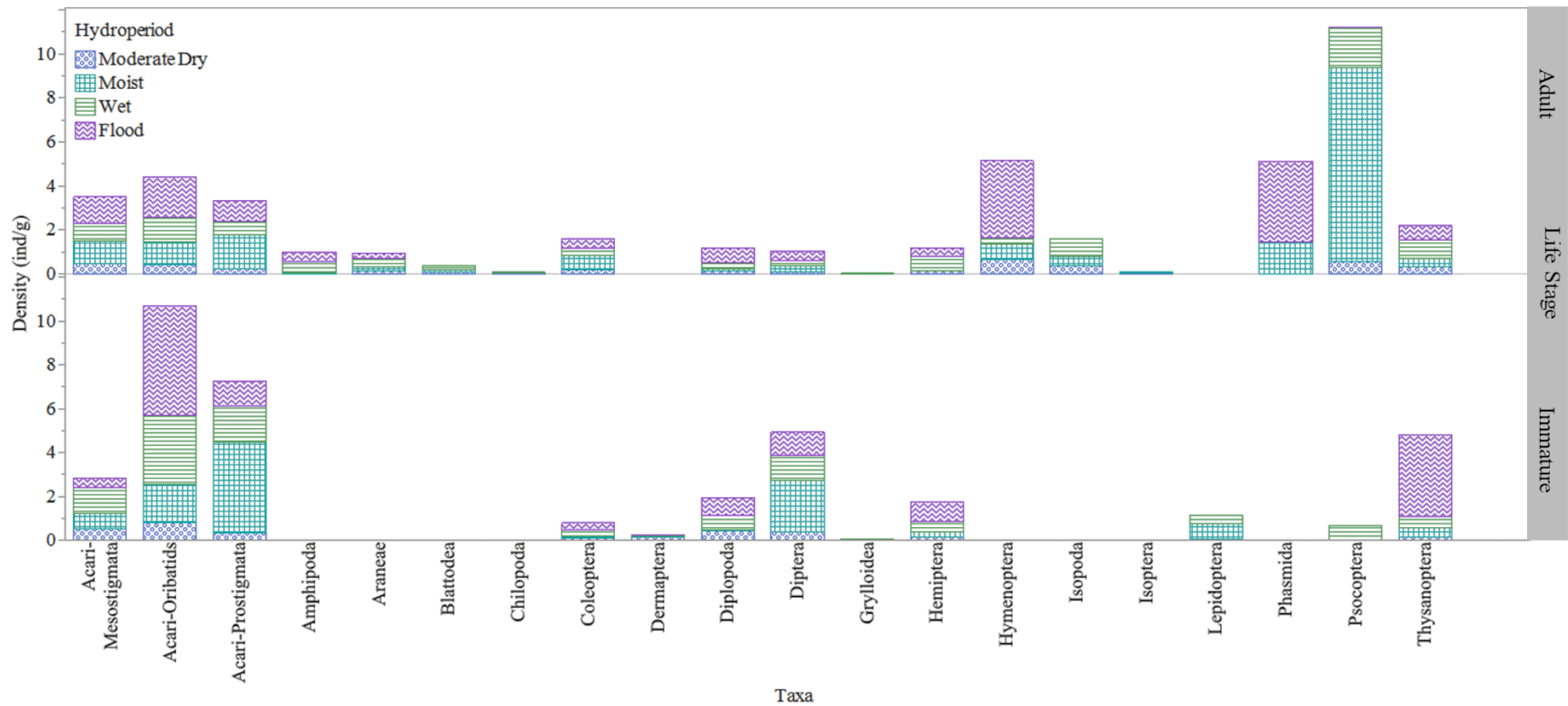


Figure 20: Fluctuations in the density of soil arthropod life stages (individuals per gram) across different hydroperiods. Significant differences were quantified for Oribatids during flood and wet periods, Coleoptera during moderate dry periods, and Diptera during flood, moderate dry, and wet periods, with a p-value < 0.05.

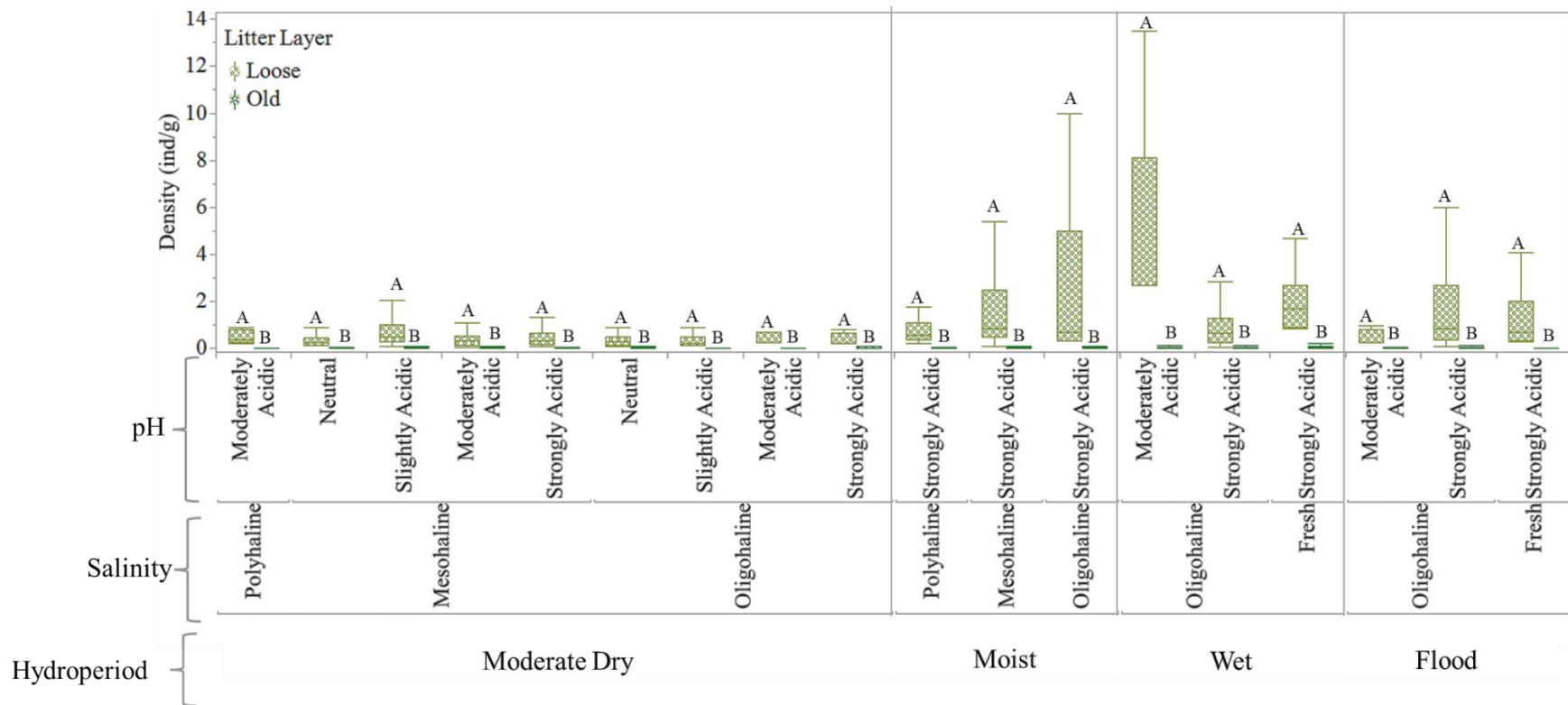


Figure 21: Multifactorial non-parametric analysis that demonstrates the variations in the distribution of soil arthropods within different litter fractions (loose and old litter mix with organic soil).

2.4.3 Effect of Hydroperiod Conditions on Soil Arthropod Assemblages

Twenty groups were identified and categorized via a density distribution table analysis into three levels of prevalence: dominant (69%), common (23%), and rare (8%).

Significant patterns in the densities of these groups were observed in environments characterized by shallow to slightly moderate phreatic levels, oligohaline salinity, and strongly acidic pH conditions (Table 11 and Figure 22). A significant presence of both dominant and common mesofauna groups was recorded in these environmental conditions, particularly Collembola (Arthropleona-19%), Oribatida (54%), Mesostigmata (7%), and Prostigmata (4%), as well as common macrofauna groups such as Diptera (7%), Hymenoptera (2%), Coleoptera (2%), and Hemiptera (1%). This indicates a specialized ecological niche for these organisms, with Oribatid mites and Collembola (Arthropleona) notably standing out among the arthropod groups.

Table 8: A density distribution table that illustrates the variation in soil arthropod density (individuals per gram) under combined environmental factors, highlighting conditions associated with elevated density metrics.

Order/Suborder	COMBINE FACTORS		Total Density (ind/g)*	Relative Density (%)**	Taxa Classification **
	Shallow-Oligohaline-Strongly Acidic	Slightly Moderate-Oligohaline-Strongly Acidic			
	Density (ind/g)	Density (ind/g)			
Amphipoda	3.43	0.00	3.43	0.13	Rare
Araneae	11.96	0.69	12.65	0.46	Rare
Arthropleona	460.89	51.59	512.48	18.81	Dominant
Blattodea	0.00	0.15	0.15	0.01	Rare
Coleoptera	46.86	3.28	50.14	1.84	Common
Dermaptera	0.15	0.00	0.15	0.01	Rare
Diptera	182.08	8.32	190.40	6.99	Common
Geophilomorpha	0.02	0.00	0.02	0.00	Rare
Hemiptera	31.04	2.70	33.74	1.24	Common

Order/Suborder	COMBINE FACTORS		Total Density (ind/g)*	Relative Density (%)**	Taxa Classification **
	Shallow-Oligohaline-Strongly Acidic	Slightly Moderate-Oligohaline-Strongly Acidic			
	Density (ind/g)	Density (ind/g)			
Hymenoptera	57.21	6.12	63.33	2.32	Common
Isopoda	17.93	8.42	26.35	0.97	Rare
Lepidoptera	4.45	1.92	6.37	0.23	Rare
Mesostigmata	162.40	26.24	188.64	6.92	Common
Oribatid	1320.15	140.25	1460.40	53.60	Dominant
Orthoptera	0.03	0.05	0.08	0.00	Rare
Phasmida	3.70	0.00	3.70	0.14	Rare
Polyzoniida	0.04	0.18	0.22	0.01	Rare
Prostigmata	104.07	9.67	113.74	4.17	Common
Psocoptera	6.42	0.82	7.24	0.27	Rare
Spirobolida	10.43	2.37	12.80	0.47	Rare
Symphyleona	23.15	0.45	23.60	0.87	Rare
Thysanoptera	11.31	3.94	15.25	0.56	Rare
Total (ind/g)	2457.72	267.16	2724.88		

*Total Density: Calculated as the sum of individual densities per taxa for each combined factor.

**Relative Density (%): Determined by dividing the total density per taxa by the sum of all taxa densities, expressed as a percentage.

***Taxa Classification: Taxonomic groups were classified as "dominant," "common," or "rare" based on their relative density.

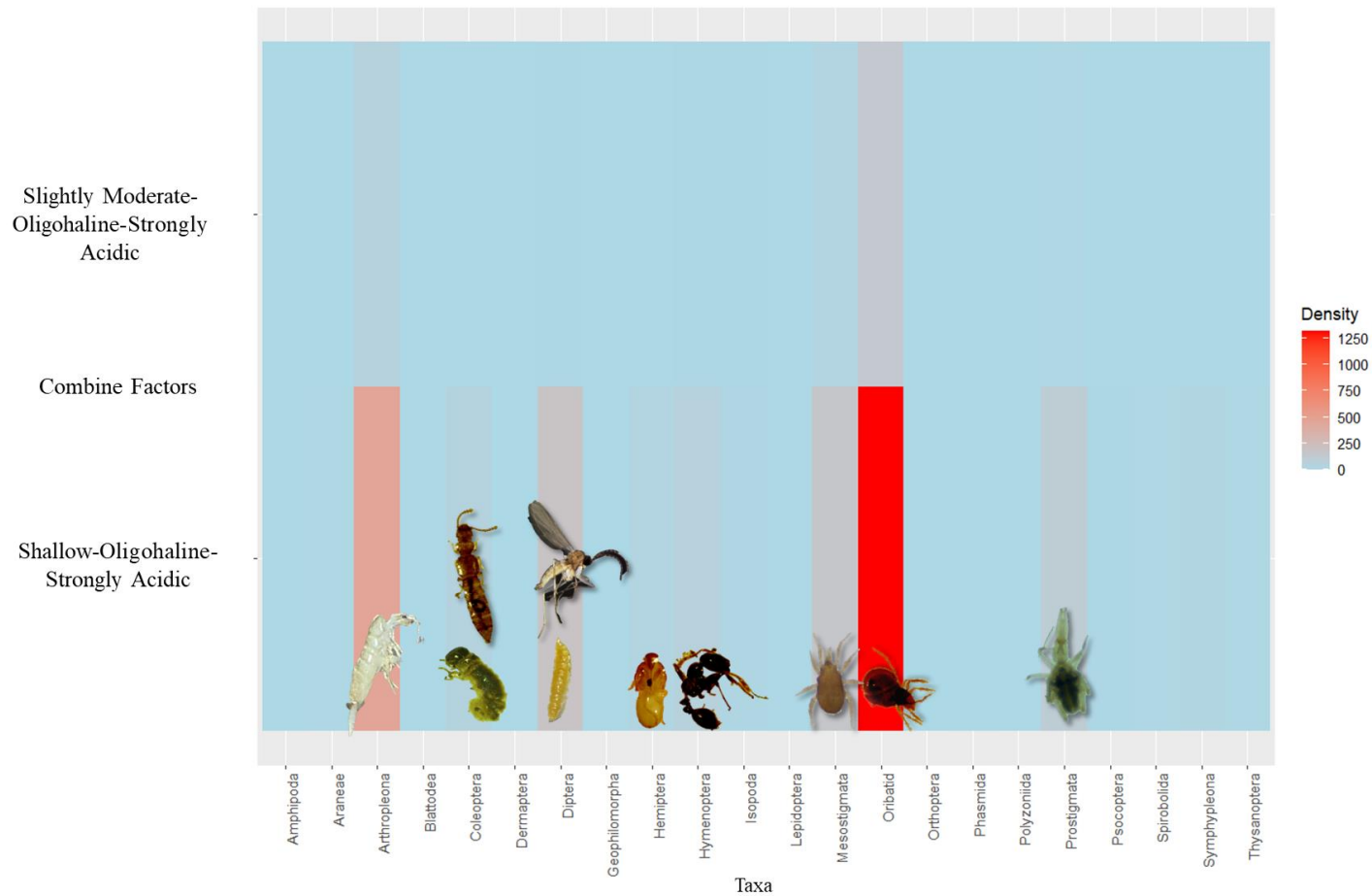


Figure 22: Heatmap showcasing the variability in soil arthropod densities under conditions of combine factors where significant higher values were quantified. Each cell represents density of a specific arthropod group, with color intensities ranging from blue (denoting rare groups) through light red (indicating common groups) to dark red (representing dominant groups), reflecting the gradient from low to high densities, respectively. The G-test results, with a G-value of 251.97, 87 degrees of freedom, and a p-value below 0.05, confirm a significant association among the study variables, suggesting that the distribution patterns observed are ecologically meaningful and not random.

In addition, significant variations were identified in soil arthropods assemblages attributable to differences among hydroperiods and the interaction between hydroperiods and plots (Table 12). The Permanova model indicated that hydroperiods alone account for a significant portion of the community composition variance, with a p-value of less than 0.01, explaining 43.0% of the total observed variation. Additionally, the interaction between hydroperiods and specific plots further contributes to the community composition variance (p-value < 0.01), which accounts for 24.0% of the variation.

Table 9: PERMANOVA analysis results, which reveals statistically significant differences in the community composition of soil arthropods. These differences are attributable to variations among hydroperiods as well as to the interaction between hydroperiods and plots.

Factors	Degrees of Freedom	Sum of squares	R ²	F-statistics	Level of significance
Hydroperiod	3	1.09	0.43	3.53	0.01
Hydroperiod:Plot	4	0.59	0.24	1.44	0.01
Residual	8	0.82	0.33		
Total	15	2.51	1.00		

The distribution patterns and the presence or absence of soil arthropods taxa across distinct hydroperiods (Figure 23 and Appendix 1 and 2), offer a rich source of data for understanding the adaptive responses and habitat preferences of these species. Of the ninety tree families from twenty arthropod groups identified, ninety percent (90%) were prevalent during the wet period, while a notable 36% of these families were absent during the flood period. This deficit included a diverse range of families from the mesofauna, such as Oribatida, Prostigmata and Mesostigmata, and macrofauna, including Araneae, Blattodea, Diptera, Coleoptera, Chilopoda, Orthoptera, Hemiptera, Hymenoptera, Isopoda, Isoptera, Lepidoptera, and Thysanoptera orders. During the moderate dry and moist period, an absence of 19.0% of the taxa was observed, which included families from the Oribatida and Prostigmata suborders, as well as those from the Araneae, Diptera,

Coleoptera, Orthoptera, Hemiptera, Hymenoptera, Lepidoptera, and Thysanoptera orders. Notably, the Phasmida order was present only during moist and flood periods, while the Phasmida and Amphipoda order was observed exclusively during wet and flood periods.

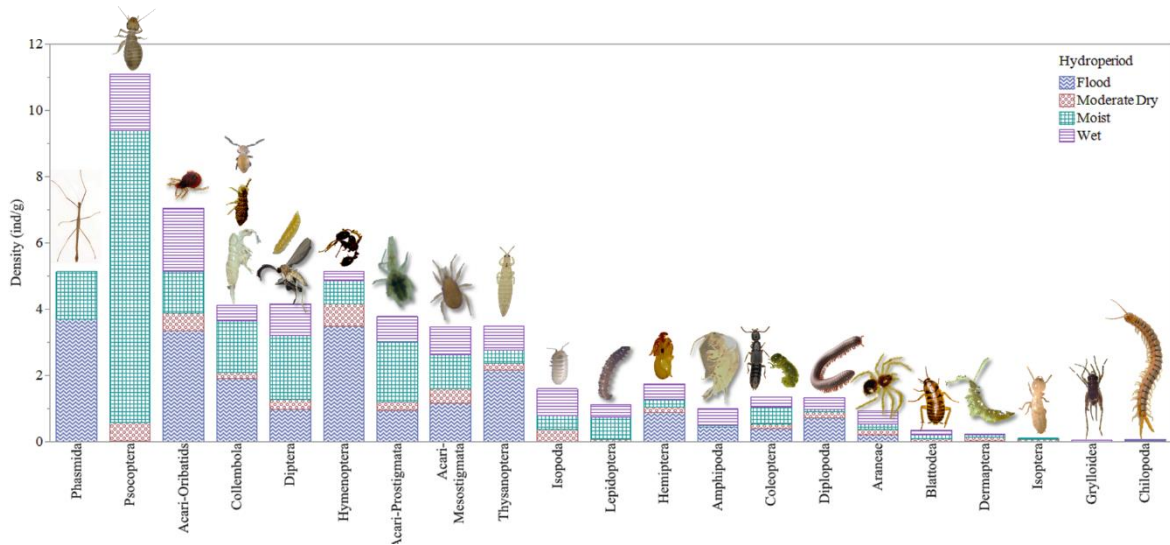


Figure 23: Soil arthropod assemblages across distinct hydroperiods.

2.4.4 Soil Biological Quality-Arthropod Index (QBS-ar index)

For the calculation of the Arthropod Biological Quality Index (QBS-ar), a total of 18 taxa were identified (Table 13). The taxa Acari and Collembola, along with Araneae, Coleoptera, Diptera, Hemiptera, and Hymenoptera, were consistently present across all plots and hydroperiods. During the flood period, taxa such as Blattodea, Chilopoda, Isopoda, and Lepidoptera were notably absent in all plots. Orthoptera were detected solely within plots 3 and 5 throughout the wet hydroperiod. Eu-edaphic 60-61 organisms, constituting 58% of the sampled fauna, and hemi-edaphic organisms, comprising 37%, demonstrated higher density during flood and wet conditions. In contrast, epi-edaphic organisms, representing a 4%, were more prevalent during moist and wet periods, as illustrated in Figure 24.

Table 10: Distribution and abundance of taxa across different hydroperiods: Moderate Dry, Moist, Wet, and Flood. It includes values for the QBS-ar Index, total number of individuals, and total number of taxa.

Taxon	Moderate Dry				Moist				Wet				Flood			
	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Acari	211	333	350	257	98	282	149	267	263	504	439	659	330	514	276	706
Araneae	5	2	6	5	2	10	1	12	3	10	8	24	3	2	3	4
Collembola	17	15	13	23	20	25	12	179	241	250	154	412	53	108	25	546
Blattodea	3	1			1	1	1	1		1						
Coleoptera	5	2	16	13	7	5	17	17	15	11	23	27	46	11	18	21
Coleoptera larvae	3	1	9	1	5	1	4	4	32	16	31	18	45	17	36	9
Dermaptera			1	3		1	1	3			1	3		1		
Diptera	1	5	4	5	3	1	0	3	9	6	6	10	11	1	3	8
Diptera larvae	31	1	25	7	14	12	9	7	70	31	70	60	48	76	38	50
Chilopoda	1	1		1	1	2	2		1							
Hemiptera	16	5	3	4	19	38	13	8	15	24	14	28	2	8	5	4
Hymenoptera	32	15	52	11	9	9	11	18	5	8	5	15	1	4	1	76
Isopoda	6	12	6	6	12	15	25	36	9	31	10	52				
Lepidoptera	2	2			2	5	1	3	13	6	7					
Orthoptera									1	1						
Diplopoda	8	1	1	5	1	4	3	6	2	6	4	2	2	4	0	10
Psocoptera	66	3	4		3	1	2		10	2	17	1	1			
Thysanoptera	5		1	1	1	13		3	12	8	6	7				2
N.Individual	415	404	497	352	201	430	257	577	704	920	801	1328	545	751	411	1446
N.Taxa	17	16	15	15	17	18	17	16	17	17	16	15	12	12	11	12
Plots QBS-ar	145	133	99	113	135	137	138	116	165	130	107	96	59	69	77	104
Hydroperiod QBS-ar	146				151				172				106			

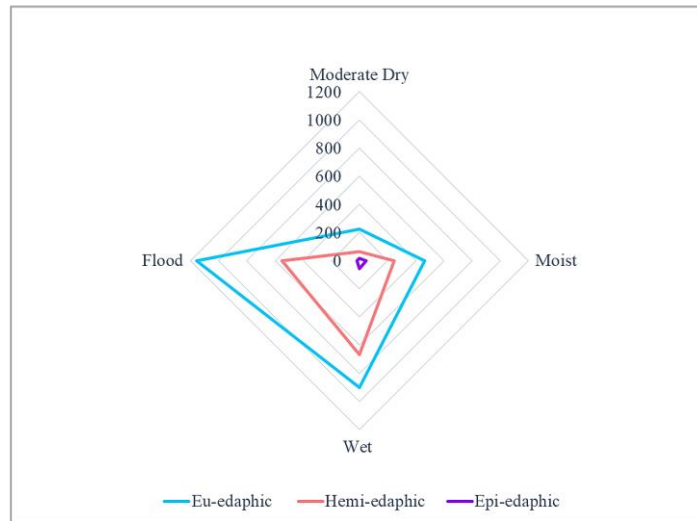


Figure 24: Abundance of eu-edaphic, hemi-edaphic, and epi-edaphic organisms across various hydroperiods.

The QBS-ar (Quality of Biological Soil) values obtained for each plot across various hydroperiods indicate enhanced soil conditions during the wet hydroperiod, as well as during moist and moderate dry conditions, with all measured plot values surpassing 93.7, as shown in Table 14. This threshold, as established by Menta et al. (2018), differentiates high-quality soils from those reflective of poorer conditions. In contrast, under flood conditions, Plots 3, 5, and 6 displayed QBS-ar values below 93.7, signaling poorer soil quality.

2.5 DISCUSSION

This study has examined the complex dynamics of soil arthropod assemblages within a tropical urban coastal wetland, with a specific focus on the influence of spatiotemporal fluctuations in phreatic levels, salinity, and pH on their diversity and abundance. The findings elucidate the intricate interplay between environmental factors and soil arthropod communities, highlighting the consequences of the initial hypothesis that posits a significant modulation of these communities by variations in hydroperiod phreatic levels, pH, and salinity.

2.5.1 Study site variations in phreatic level, salinity and pH

The observed variations in phreatic levels and physicochemical conditions across different hydroperiods and plots underscore the complex interplay between hydrological processes and habitat environments at the study site. The interplay is shaped by hydrological modifications that have been occurring since colonial times, further exacerbated by contemporary global and regional climate variability, sea-level rise, and recent historical changes in land use and cover. These factors serve as additional stressors

that lead to a wetland environment, characterized by a diverse mosaic of physicochemical conditions and habitats. The significant negative correlations between phreatic levels, salinity, and pH across plots highlight the crucial role these factors play in defining habitat conditions. The interactions between anthropogenic stressors and the intrinsic mosaic characteristics of wetlands are key determinants of the hydrological regime and the bio-physicochemical components (Leal Filho et al., 2023; Bardgett et al., 2005; Barberena-Arias & Cuevas, 2018, 2021). The study area's environment is shaped by the interactions among marine-terrestrial subsurface connectivity, local weather patterns, and regional climate fluctuations. These interactions dictate the influx of diverse water sources into the phreatic layers, including *in-situ* precipitation, freshwater inflows, and deep subsurface seawater ingress, thereby influencing the environmental dynamics at the site (Hernández, 2021; Pinto-Pacheco, 2022; refer to Figure 13 on page 25). Such diversity in water sources markedly affects the salinity and pH levels within the area (Environmental Protection Agency, 2006). Conditions during moderate dry and moist periods predominantly exhibit deeper and moderate phreatic levels, between -0.37 to -0.43 and <-0.44 respectively, with salinity in the mesohaline range and pH levels spanning from neutral to strongly acidic across plots. In dry periods, the site experiences a rapid bimodal high tide influx within 20 minutes, with deep subsurface seawater flow becoming the predominant contributor to phreatic levels (Pinto Pacheco 2022; Hernández, 2021). During flood period, water levels are high at plots 3 and 6, while they become shallow at plots 5 and 10. Conversely, at the wet period, water levels are shallow at plots 3 and 6 and slightly moderate at plot 5 and 10. Throughout both flood and wet periods, salinity levels transition from fresh to oligohaline, while pH levels consistently

remain strongly acidic. Under these conditions, freshwater inputs become the dominant factor influencing phreatic levels, and the bimodal high tide may take up to 2 hours to impact the study site (Pinto Pacheco 2022; Hernández, 2021). These dynamics underscore the intricate interactions among various water sources and their consequential impact on the hydrological and chemical attributes of the study site.

2.5.2 Influence of hydroperiods physicochemical factors on soil arthropods diversity and abundance

The role of the hydrological regime, notably through phreatic level fluctuations, emerges as a critical determinant in shaping the physicochemical environment and thereby influencing the distribution and dynamics of soil arthropod communities (Baxter et al., 2006; Kagainis et al., 2017; Lawton, 1997). Such variations have been shown to exert a considerable impact on both the richness and abundance of soil arthropods within the study area, as evidenced by the significant statistical findings. Specifically, a notable inverse relationship between phreatic levels and species richness, alongside a direct but weaker correlation with abundance, suggests that water table fluctuations play a complex role in mediating arthropod community structures. Moreover, these relationships suggest that as richness decreases and abundance increases with higher phreatic levels, interspecific competition may decrease, potentially leading to community dominance by a single or a few species that reproduce prolifically. The influence of pH on species richness, although less pronounced than that of phreatic levels, highlights the sensitivity of these communities to soil acidity changes. The significant statistical outcomes associated with pH underscore its role in modulating species richness, albeit with a relatively minor impact on overall abundance. Salinity's role, despite being the least influential on soil arthropods richness among the studied environmental factors, remains

statistically significant, pointing to its subtle yet important contribution to the ecological dynamics of soil arthropod communities, with its effects on abundance remaining inconsequential.

Interaction effects embody the collective influence of environmental factors on the dependent variable (Menta et al., 2018). This research demonstrated that the periodic interplay among phreatic level, salinity, and pH profoundly affects the dynamics and distribution of soil arthropods across diverse habitats, underscoring their vulnerability to the aggregate effects of these environmental factors.

In this study, the interactive effects on soil arthropod communities were analyzed across a spectrum of disturbance levels, with one sampling event conducted during each of the following hydroperiods: moderate dry, flood, moist, and wet. The moderate dry period, characterized by reduced precipitation, offered a distinct contrast to the moist period, which was defined by conditions between flood events, with samples collected immediately after the onset of flooding. The flood period was characterized by a three-month inundation phase leading up to the sampling, whereas the wet period corresponded to the receding of floodwaters after a cycle of alternating dry and flood conditions lasting five months. This spectrum of hydrological dynamics induced a variety of responses in the arthropod taxa, which can likely be attributed to the differences in their life cycle stages, physiological specializations, and behavioral adaptations.

During the moderate dry and moist periods, significant reductions in the density, richness, and Menhinick index of soil arthropods were documented, attributable to specific environmental conditions prevalent during these intervals. These conditions included fluctuations in phreatic levels from deep (below -0.44 meters) to moderate (-0.37 to -0.43

meters), mesohaline salinity (>5.0 to 18.0 ppt), and a pH spectrum extending from moderately acidic to neutral (5.6-6.0 to 6.6-7.3, respectively). Under such conditions, 19% of taxa was absent, indicating that the combination of environmental factors may exceed the resilience capacity of various arthropod taxa, resulting in reduced population density and diversity compared to other sampling periods (Bardgett et al., 2005; Bazter et al., 2016, 2020; Wardle et al., 2004). This reduction encompasses taxa from the Oribatida and Prostigmata suborders (microbivores and predators, respectively), as well as taxa from the orders Araneae, Diptera, Coleoptera, Orthoptera, Hemiptera, and families such as Formicidae, and orders Lepidoptera and Thysanoptera (encompassing predators, omnivores, detritivores, herbivores groups), suggesting significant shifts in community structure, attributed to prevailing environmental conditions.

The wet hydroperiod, marked by the co-occurrence of shallow phreatic levels (-0.01 to -0.12 meters), oligohaline salinity (>0.5 to 5.0), and strongly acidic pH (< 5.0), was associated with notable enhancements in soil arthropod density, richness, and Menhinick index across all surveyed plots and hydroperiods. This period created an ideal microenvironment that supported the growth of a diverse array of soil arthropods, as demonstrated by the Menhinick Index and the quadratic model, which indicate a peak in species richness at an intermediate phreatic level. This peak suggests that species richness is highest during wet conditions and decreases under both drier conditions and extreme flooding, supporting the hypothesis of a unimodal (one peak) response to phreatic levels. This was highlighted by the presence of 90% of all taxa during this period attributable to its unique environmental conditions. A plausible explanation for this trend is the series of flood and dry spells preceding this period. The flood and dry spells likely played a crucial

role in this trend, causing marked changes in soil moisture, salinity, pH, and resource availability, thus reshaping the habitat's ecological dynamics (Baxter et al., 2006; Cordes et al., 2022; Walter et al., 2013). In wetland ecosystems, the accumulation and subsequent decomposition of terrestrial and aquatic plant litter during flood and dry spells enrich the soil's humic content. This process, coupled with the receding floodwaters, creates fertile zones conducive to recolonization, enhancing microflora activity (Li et al., 2012) and facilitating the resurgence of meso- and macrofaunal populations (Kagainis et al., 2017; Ghiglieno et al., 2020). The notable presence of mesofauna such as Collembola, Oribatida, Mesostigmata, and Prostigmata, alongside macrofauna like Diptera, Hymenoptera, Coleoptera, and Hemiptera, delineates a specialized ecological niche fostering these groups. Among these, Oribatid mites and Collembola (Arthropleona) are particularly prominent, highlighting their significant role as regulators of microflora processes within the arthropod communities.

The flood sampling period, characterized by significant atmospheric phenomena leading to prolonged inundation, underscores the critical influence of disturbance frequency and duration on the adaptation and resilience of soil arthropod communities. Environmental conditions, marked by high phreatic levels, fresh to oligohaline salinity, and strongly acidic pH, led to a significant decrease in soil arthropod richness when compared to other sampling intervals, with around 64% of taxa managing to persist. The specific environmental tolerances of soil arthropods, particularly regarding water levels, significantly influence their populations during such events (Petersen and Luxton, 1982; Lavelle et al., 1995; Wu et al., 2015; Mazhar et al., 2022). Prolonged flooding exerts a more profound impact on soil arthropod communities, differentially affecting populations

due to the varying tolerance ranges of different taxonomic groups. The environmental selection process tends to favor hydrophilic or hydro-tolerant functional types, resulting in the predominance of species adept at surviving in aquatic habitats that emerge due to flooding (Baxter et al., 2016; Coyle et al., 2017). In such altered environments, these species often exhibit traits conducive to survival, including relative mobility, large body size, the ability to enter dormancy at the egg stage, and employing drifting strategies (Coyle et al., 2017).

Flooding effects were particularly evident in plots 3 and 6, characterized by lower micro-elevations, where water levels rose above the soil surface during flooding. Conversely, higher micro-elevations in plots 5 and 10 served as natural barriers against flooding, manifesting merely as a surface water film during such events. This phenomenon likely contributed to the higher soil arthropod densities observed in plots 5 and 10 compared to plots 3 and 6, emphasizing the influence of micro-elevation on the viability of arthropod habitats amidst flood conditions.

The variability in interactions between soil organisms and their environment, significantly influenced by life cycle stages within the soil matrix (Menta et. al., 2012), underpins the differences in the abundance of adult and immature life stages of soil arthropods across hydroperiod conditions (refer to Table 10). Immature stages density was significantly higher during the wet hydroperiod, characterized by shallow phreatic level, oligohaline salinity, and strongly acidic conditions. The distribution pattern of immature stages may be linked to the accumulation and subsequent exposure of organic materials in these environments, which create optimal conditions for the colonization by opportunistic groups (Li et al., 2012). This is supported by observations on the vertical

distribution across different litter fractions, where loose litter has been found to harbor a significantly higher density of arthropods, especially during this hydroperiod. The enhanced density in loose litter layers can be attributed to the availability of organic material, which, along with favorable microenvironmental conditions, promotes colonization. In such a scenario, the microhabitat supports the presence of immature stages of macrofauna taxa, including Diptera and Coleoptera, as well as the immature stages of mesofauna, particularly Acari, which were identified as the dominant group. These organisms play a crucial role in the recovery of the soil ecosystem, (Menta et. al., 2012). Their activities foster decomposition processes and nutrient mobilization, effectively utilizing the favorable conditions of the post-disturbance environment to support their development and the broader regeneration of soil arthropod communities (Coyle et.al., 2017; Baxter et. al., 2006; Cordes et. al., 2022; Walter et. al., 2013).

2.5.3 Effect of Hydroperiod Conditions on Soil Arthropod Assemblages

Variations in hydroperiods microenvironments act as a major determinant of community composition, accounting for 43.5% of the total variance observed, this finding highlighted the critical role of hydrological cycles in shaping the ecological dynamics of soil arthropod communities. Furthermore, the interaction between hydroperiods and individual plots significantly delineated their assemblages, accounting for 23.7% of the observed variation. This suggests that local conditions and spatial heterogeneity significantly influenced community assembly and dynamics, underscoring the complexity of ecological interactions governing soil arthropod communities. It demonstrates the considerable influence of hydrological patterns and spatial factors on these communities.

2.5.4 Soil Biological Quality-Arthropod Index (QBS-ar index)

The recorded QBS-ar values across hydroperiods surpassed the 93.7 threshold, which Menta et al. (2018) identify as demarcating high-quality soils from those of inferior quality. Notably, the wet period exhibited higher QBS-ar values, indicative of enhanced soil conditions. A sequential decline in the index was observed from moist to moderate dry and then to flood conditions, a pattern also evident within individual plots. This trend may be attributed to the effect of varying degrees of disturbance, resource availability, and the specific environmental conditions inherent to each hydroperiod. Notably plots 3, 5, and 6 recorded QBS-ar values beneath the 93.7 mark during flood conditions, suggesting less favorable microenvironmental conditions for soil quality during this period.

2.5.5 Findings in Relation to Objectives, Questions, and Hypotheses

This research aimed to assess the effects of spatiotemporal variations in phreatic levels, pH, and salinity on soil arthropod assemblages within a tropical urban coastal wetland.

This research seeks to address the fundamental question: How do fluctuations in phreatic level, pH, and salinity across various hydroperiods influence the composition of soil arthropod assemblages within and across the study plots? The hypothesis posited that fluctuations in phreatic levels, litter system salinity, and pH would substantially dictate the spatiotemporal composition of soil arthropod communities, with phreatic levels anticipated as the pivotal determinants.

This research provides compelling evidence that spatiotemporal variations in phreatic levels, pH, and salinity significantly shape the soil arthropod assemblages in a tropical

urban coastal wetland (Figure 25). The study supports the hypothesis that these environmental fluctuations, with a particular emphasis on phreatic levels, are critical determinants of the spatial and temporal patterns of soil arthropod communities (Lugo et al., 2019).

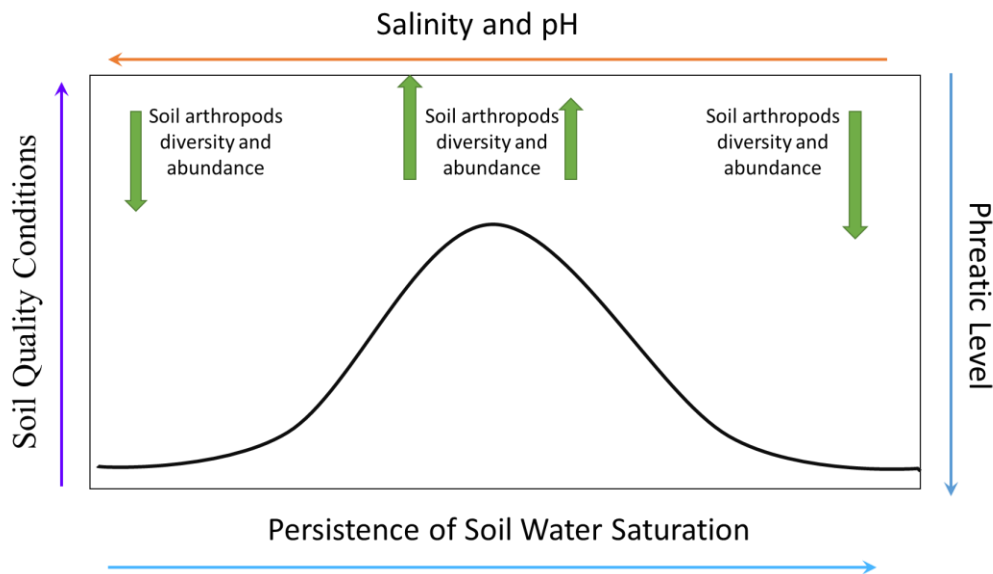


Figure 25: Schematic diagram of the factors and gradients on wetlands that contribute to soil arthropods diversity and abundance (Adapted from Lugo et al., 2019).

During the wet period, following sequences of flooding and drying, the conditions were found to be most favorable for the proliferation of a broad spectrum of soil arthropods. This is evidenced by elevated community metrics, alongside a significant increase in the QBS-ar index, which indicates enhanced soil quality (Leone et.al., 2023) conducive to arthropod diversity and abundance. In contrast, moderate dry and moist periods exhibited marked reductions in soil arthropod density, richness, and diversity, as reflected by lower Menhinick index values. These periods, characterized by deep and moderate phreatic levels and mesohaline salinity conditions within a wide pH range, seemed to exceed the resilience capacities of numerous arthropod taxa, resulting in diminished populations.

The QBS-ar index during these times revealed intermediate soil quality, suggesting that the environmental conditions were less than optimal for sustaining diverse arthropod communities. Flood periods, however, were associated with a significant downturn in arthropod richness, with a shift in community composition towards taxa more tolerant of waterlogged conditions. The QBS-ar index further declined during these flood periods, highlighting the adverse effects of prolonged flooding on soil quality and, consequently, on the viability of soil arthropod habitats.

These findings emphasize the significant impact of hydroperiod variations on soil arthropod assemblages, offering insights into the community composition and functional dynamics of soil meso- and macrofauna. They reveal how various groups adapt to the changing conditions associated with different hydroperiods, thus broadening our understanding of ecological responses within these communities.

2.6 CONCLUSIONS

The study underscores the significance of understanding soil arthropods' intricate inter- and intra-specific responses to fluctuations in wetland hydroperiod phreatic levels, pH and salinity conditions. The diverse range of responses exhibited by these communities in a coastal urban wetland emphasizes their varying degrees of adaptability and resilience to changes in their microenvironment. The study highlighted the necessity to consider both temporal fluctuations and spatial variability in understanding the ecological dynamics that shape community composition in soil ecosystems, serving as a crucial tool for effective wetland management. This approach is especially pertinent in the context of multiple stressors such as global and regional climate change, sea level rise, and human activities. The bio-sensor capacity of these organisms emerges as a crucial tool for

monitoring and adaptive ecosystems management to ensure their long-term health and sustainability.

2.7 REFERENCES

- Argerich, A., Martí, E., Sabater, F., Ribot, M., von Schiller, D., & Riera, J. L. (2008). Combined effects of leaf litter inputs and a flood on nutrient retention in a Mediterranean mountain stream during fall. *Limnology and Oceanography*, 53(2), 631-641. <https://doi.org/10.4319/lo.2008.53.2.0631>
- Barberena-Arias, F. M., Cuevas, E. (2018). Physicochemical Foliar Traits Predict Assemblages of Litter / Humus Detritivore Arthropods, 1–20. [DOI:10.5772/intechopen.75076](https://doi.org/10.5772/intechopen.75076)
- Barberena-Arias, F. M., & Cuevas, E. (2021). Vertical Arthropod Dynamics across Organic Matter Fractions in Relation to Microclimate and Plant Phenology. [IntechOpen. doi: 10.5772/intechopen.94747](https://doi.org/10.5772/intechopen.94747)
- Bardgett, R. D.; Yeates, G. W.; Anderson, J. M. (2005). Patterns and determinants of soil biological diversity. *Biological diversity and function in soils*; pp. 100-118. *Ecology of Freshwater and Estuarine Wetlands*. The University of California
- Batzer, P. D, Sharitz, R.R. (2006). *Ecology of Freshwater and Estuarine Wetlands*. The University of California.
- Batzer, D., Wu, H., Wheeler, T., & Eggert, S. (2016). Peatland invertebrates. In: Batzer, D.P., Boix, D. (Eds.), *Invertebrates in Freshwater Wetlands*. pp. 219–250. Springer International Publishing, Cham, Switzerland. https://doi.org/10.1007/978-3-319-24978-0_7
- Batzer, D. P., & Wu, H. (2020). Ecology of terrestrial arthropods in freshwater wetlands. *Annual Review of Entomology*, 65, 101-119. <https://doi.org/10.1146/annurev-ento-011019-024902>
- Bezemer, T. M., Fountain, M. T., Barea, J. M., Christensen, S., Dekker, S. C., Duyts, H., Van Hal, R., Harvey, J. A., Hedlund, K., Maraun, M., Mikola, J., Mladehov, A. G., Robin, C., De Ruiter, P. C., Scheu, S., Setälä, H., Šmilauer, P., & van der Putten, W. H. (2010). Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. *Ecology*, 91(10), 3027-3036. <https://doi.org/10.1890/09-2198.1>
- Briones, M. J. (2018). The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. *Frontiers in Environmental Science*, 6, 149. <https://doi.org/10.3389/fenvs.2018.00149>
- Burton, V. J., Contu, S., De Palma, A., Hill, S. L., Albrecht, H., Bone, J. S., ... & Purvis, A. (2022). Land use and soil characteristics affect soil organisms differently from above-ground assemblages. *BMC Ecology and Evolution*, 22(1), 135. <https://doi.org/10.1186/s12862-022-02089-4>

- Chen, Y.; Wang, B.; Pollino, C. A.; Cuddy, S. M.; Merrin, L. E.; Huang, C. (2014). Estimate of flood inundation and retention on wetlands using remote sensing and GIS. *Ecohydrology*, 7(5), 1412-1420.
- Coleman, D. C., Callaham, M., & Crossley Jr, D. A. (2017). *Fundamentals of soil ecology*. Academic press. Cambridge, MA, USA.
- Cordes, P.; Maraun, M.; Schaefer, I. (2022). Dispersal patterns of oribatid mites across habitats and seasons. *Experimental and Applied Acarology*, 86. Available online: <https://doi.org/10.1007/s10493-022-00686-y>.
- Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., & Callaham Jr, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, 110, 116-133. <https://doi.org/10.1016/j.soilbio.2017.03.008>
- Culliney, T.W. (2013). Role of Arthropods In Maintaining Soil Fertility. Plant Epidemiology and Risk Analysis Laboratory, Plant Protection, and Quarantine, Center for Plant Health Science and Technology, USDA-APHIS. *Agriculture* 2013, 3, 629-659; [doi:10.3390/agriculture3040629](https://doi.org/10.3390/agriculture3040629)
- Leone, D., Mirabile, M., Altieri, G. M., Zimone, A., Torrisci, B., Tarasco, E., & Clausi, M. (2023). Assessment of soil quality in wetlands in Eastern Sicily. *Ecological Indicators*, 153, 110428. <https://doi.org/10.1016/j.ecolind.2023.110428>
- Environmental Protection Agency. (2006). Chapter 14 of the Volunteer Estuary Monitoring Manual, A Methods Manual, Second Edition, EPA-842-B-06-003.
- Ghiglieno, I., Simonetto, A., Orlando, F., Donna, P., Tonni, M., Valenti, L., & Gilioli, G. (2020). Response of the arthropod community to soil characteristics and management in the Franciacorta viticultural area (Lombardy, Italy). *Agronomy*, 10(5), 740. <https://doi.org/10.3390/agronomy10050740>
- Haarlov, N. (1995). Vertical Distribution of Mites and Collembola in Relation to Soil Structure. In: *Soil Zoology*; Mc Kevan, D.K.E., Ed.; Butter Worths: London; pp. 167-179.
- Hernández, E., Cuevas, E., Pinto-Pacheco, S., & Ortíz-Ramírez, G. (2021). You Can Bend Me but Can't Break Me: Vegetation Regeneration After Hurricane María Passed Over an Urban Coastal Wetland in Northeastern Puerto Rico. *Frontiers in Forests and Global Change*, 4, 752328. <https://doi.org/10.3389/ffgc.2021.752328>
- Hernández, E. (2022). Ecophysiological responses of plant functional groups to environmental conditions in a coastal urban wetland, Ciénaga Las Cucharillas in Northeastern Puerto Rico. Dissertation. Ecolab. Department of Environmental Science. The University of Puerto Rico. <https://hdl.handle.net/11721/2860>
- Herrera, F., & Cuevas, E. (2003). Artrópodos del suelo como bioindicadores de recuperación de sistemas perturbados. *Venesuelos*, 11(1-2), 67-78.

- IPCC. (2022). Summary for Policymakers. In H.-O. Pörtner, D. C. Roberts, E. S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3-33). Cambridge University Press.
<https://doi.org/10.1017/9781009325844.001>
- Kagainis, U.; Jucevica, E.; Salmane, I.; Ventins, J.; Melecis, V. (2017). Does Climate Warming Affect Soil Mesofauna? Conference: 2nd Global Soil Biodiversity Conference. At: Nanjing, China.
<https://www.researchgate.net/publication/320559698>
- Kim, J.; Lee, J.; Cheong, T.; Kim, R.; Koh, D.; Ryu, J.; Chang, H. (2005). Use of time series analysis for the identification of tidal effect on groundwater in the coastal area of Kimje, Korea. *Journal of Hydrology*, 300, 188-198.
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, 130-150. <http://dx.doi.org/10.2307/2389178>
- Lavelle, P. (1997). Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In *Advances in ecological research* (Vol. 27, pp. 93-132). Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60007-0](https://doi.org/10.1016/S0065-2504(08)60007-0)
- Lavelle, P., & Spain, A.V. (2001) *Soil Ecology*. Kluwer Academic Publishers, New York.
<https://doi.org/10.1007/978-94-017-5279-4>
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European journal of soil biology*, 42, S3-S15.
<https://doi.org/10.1016/j.ejsobi.2006.10.002>
- Lavelle, P., Mathieu, J., Spain, A., Brown, G., Fragoso, C., Lapied, E., & Zhang, C. (2022). Soil macroinvertebrate communities: A world-wide assessment. *Global Ecology and Biogeography*, 31(7), 1261-1276. [doi: 10.1111/geb.13492](https://doi.org/10.1111/geb.13492)
- Leal Filho, W., Nagy, G. J., Setti, A. F. F., Sharifi, A., Donkor, F. K., Batista, K., & Djekic, I. Handling the impacts of climate change on soil biodiversity. *Science of The Total Environment*, 869, 161671. (2023).
<https://doi.org/10.1016/j.scitotenv.2023.161671>
- Li, K.; Bihan, M.; Yooseph, S.; Methé, B.A. (2012). Analyses of the microbial diversity across the human microbiome. *PLoS One* 7(6), e32118.
<https://doi.org/10.1371/journal.pone.0032118>.
- Li, W., Dou, Z., Cui, L., Zhao, X., Zhang, M., Zhang, Y., Gao, C., Yang, Z., Lei, Y., & Pan, X. (2020). Soil fauna diversity at different stages of reed restoration in a lakeshore wetland at Lake Taihu, China. *Ecosystem Health and Sustainability*, 6(1), 1722034. <https://doi.org/10.1080/20964129.2020.1722034>

- Lawton, J. (1997). Biology of springtails. *Insecta: Collembola*. By Stephen P. Hopkin. (Oxford: Oxford University Press. 344 pp. ISBN 0 19 8540484 1. *Bulletin of Entomological Research*, 88(1), 106-106. [doi:10.1017/S0007485300041651](https://doi.org/10.1017/S0007485300041651)
- Mazhar, S., Pellegrini, E., Contin, M., Bravo, C., & De Nobili, M. (2022). Impacts of salinization caused by sea level rise on the biological processes of coastal soils-A review. *Frontiers in Environmental Science*, 1212. <https://doi.org/10.3389/fenvs.2022.909415>
- Menta, C., Conti, F. D., Pinto, S., & Bodini, A. (2018). Soil Biological Quality index (QBS-ar): 15 years of application at global scale. *Ecological Indicators*, 85, 773-780. <https://doi.org/10.1016/j.ecolind.2017.11.030>
- Menta, C., & Remelli, S. (2020). Soil health and arthropods: From complex system to worthwhile investigation. *Insects*, 11(1), 54. <https://doi.org/10.3390/insects11010054>
- Mulder, C., Den Hollander, H. A., Vonk, J. A., Rossberg, A. G., op Akkerhuis, G. A. J., & Yeates, G. W. (2009). Soil resource supply influences faunal size-specific distributions in natural food webs. *Naturwissenschaften*, 96(7), 813. <https://doi.org/10.1007/s00114-009-0539-4>
- National Weather Service. Climatological Data for La Puntilla Station (ID number 9755371), San Juan, Puerto Rico. Year 2020-2021. Available online: https://www.ndbc.noaa.gov/station_page.php?station=sjnp4
- National Weather Service, 2020. Tropical Storm Laura August 21-23, 2020. Weather.gov. [Tropical Storm Laura - August 21-23, 2020 \(weather.gov\)](https://www.weather.gov/storm-laura)
- Ortiz-Ramírez G, Hernández E, Pinto-Pacheco S, Cuevas E. (2024). The Dynamics of Soil Mesofauna Communities in a Tropical Urban Coastal Wetland: Responses to Spatiotemporal Fluctuations in Phreatic Level and Salinity. *Arthropoda*. 2024; 2(1):1-27. <https://doi.org/10.3390/arthropoda2010001>
- Parisi, V., Menta, C., Gardi, C., Jacomini, C., & Mozzanica, E. (2005). Microarthropod communities as a tool to assess soil quality and biodiversity: a new approach in Italy. *Agriculture, ecosystems & environment*, 105(1-2), 323-333. <https://doi.org/10.1016/j.agee.2004.02.002>
- Pinto-Pacheco, S. (2023). Spatiotemporal water dynamics effects on plant functional types in a tropical urban coastal wetland: water sources and quality in the Ciénaga Las Cucharillas, northeastern Puerto Rico. Dissertation. Ecolab. Department of Environmental Science. The University of Puerto Rico. [Unpublished manuscript].
- Petersen, H., & Luxton, M. (1982). A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. *Oikos*, 39(3), 288-388. <https://doi.org/10.2307/3544689>
- Socarrás, A. (2013). Mesofauna edáfica: indicador biológico de la calidad del suelo. *Pastos y forrajes*, 36(1), 5-13. <https://www.redalyc.org/pdf/2691/269127587001.pdf>

- Tronstad, L. M., Tronstad, B. P., & Benke, A. C. (2005). Invertebrate seedbanks: rehydration of soil from an unregulated river floodplain in the south-eastern US. *Freshwater Biology*, 50(4), 646-655. [https://doi.org/10.1672/0277-5212\(2005\)025\[0583:IRTDWL\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2005)025[0583:IRTDWL]2.0.CO;2)
- Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems* (Vol. 5). Univ of California Press.
- USDA Soil Quality Institute. (1999). *Soil Quality Test Kit*. Agricultural Research Service. Natural Resources Conservation Service.
- van Dijk, J., Didden, W. A., Kuenen, F., van Bodegom, P. M., Verhoef, H. A., & Aerts, R. (2009). Can differences in soil community composition after peat meadow restoration lead to different decomposition and mineralization rates *Soil Biology and Biochemistry*, Volume 41, Issue 8, Pages 1717-1725, ISSN 0038-0717, <https://doi.org/10.1016/j.soilbio.2009.05.016>. (<https://www.sciencedirect.com/science/article/pii/S0038071709002090>)
- Walter, D.E.; Proctor, H.C. (2013). *Life Cycles, Development and Size*. In: *Mites: Ecology, Evolution & Behaviour*; Springer: Dordrecht. Available online: https://doi.org/10.1007/978-94-007-7164-2_4.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304(5677), 1629–1633. <https://doi.org/10.1126/science.1094875>
- Wharton, C. H. (1982). *The ecology of bottomland hardwood swamps of the Southeast: a community profile* (No. 81/37). US Fish and Wildlife Service. https://pubs.usgs.gov/publication/fwsobs81_37
- Wheatcroft, R. A., Sommerfield, C. K., Drake, D. E., Borgeld, J. C., & Nittrouer, C. A. (1997). Rapid and widespread dispersal of flood sediment on the northern California margin. *Geology*, 25(2), 163-166. [https://doi.org/10.1130/0091-7613\(1997\)025%3C0163:RAWDOF%3E2.3.CO;2](https://doi.org/10.1130/0091-7613(1997)025%3C0163:RAWDOF%3E2.3.CO;2)
- Wu, P., Zhang, H., & Wang, Y. (2015). The response of soil macroinvertebrates to alpine meadow degradation in the Qinghai–Tibetan Plateau, China. *Applied Soil Ecology*, Volume 90, Pages 60-67, ISSN 0929-1393, <https://doi.org/10.1016/j.apsoil.2015.02.006>. (<https://www.sciencedirect.com/science/article/pii/S0929139315000499>)
- YuTan, WanqinYang, XiangyinNi, BoTan, KaiYue, RuiCao, ShuLiao, and FuzhongWu. (2019). Soil fauna affects the optical properties in alkaline solutions extracted (humic acid-like) from forest litters during different phenological periods. *Canadian Journal of Soil Science*. 99(2): 195-207. <https://doi.org/10.1139/cjss-2018-0081>
- Zheng, X.; Wang, H.; Tao, Y.; Kou, X.; He, C.; Wang, Z. (2022). Community diversity of soil meso-fauna indicates the impacts of oil exploitation on wetlands.

Ecological Indicators, 144, 109451.

<https://www.sciencedirect.com/science/article/pii/S1470160X22009244>.

Appendix 1: Multifactorial non-parametric analysis showing variation in soil arthropod density (individuals per gram), richness, and Menhinick index across plots under the combine effects of phreatic levels, salinity, and pH conditions. Groups not sharing the same connectivity letter denote significant differences ($p < 0.05$).

Plots	Group of factors Phreatic level, Salinity, pH	Density (ind/g)			Richness			Menhinicks index		
		Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***
3	Deep, Mesohaline, Moderately Acidic	38.40	-2.80	B	80.00	9.79	A	80.00	9.79	A
5		54.98	2.80	A	31.50	-9.79	B	31.50	-9.79	B
3	Deep, Mesohaline, Neutral	44.41	1.02	A	56.50	9.11	A	56.50	9.11	A
5		38.68	-1.02	B	14.50	-9.11	B	14.50	-9.11	B
3	Deep, Mesohaline, Slightly Acidic	35.20	-2.31	B	60.50	8.94	A	60.50	8.94	A
5		47.24	2.31	A	20.00	-8.94	B	20.00	-8.94	B
3	Deep, Mesohaline, Strongly Acidic	71.50	-1.16	B	22.00	-8.38	B	22.00	-8.38	B
5		85.96	1.16	A	91.54	8.38	A	91.54	8.38	A
6	Moderate, Mesohaline, Moderately Acidic	36.67	0.14		29.50	-8.42	B	29.50	-8.42	B
10		35.79	-0.14		65.50	8.42	A	65.50	8.42	A
6	Moderate, Mesohaline,	70.27	0.33		47.50	-11.70	B	47.50	-11.70	B

Plots	Group of factors Phreatic level, Salinity, pH	Density (ind/g)			Richness			Menhinicks index		
		Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***
10	Slightly Acidic	67.85	-0.33		116.50	11.70	A	116.50	11.70	A
3	Moderate, Mesohaline,	58.98	-2.99	B	80.00	11.27	A	80.00	11.27	A
6	Strongly Acidic	81.77	2.99	A	16.00	-11.27	B	16.00	-11.27	B
3	Moderate, Oligohaline,	17.90	-1.62		24.00	6.06	A	24.00	6.06	A
10	Strongly Acidic	24.67	1.62		5.00	-6.06	B	5.00	-6.06	B
6	Slightly Moderate, Mesohaline,	160.02	-1.35		69.50	-18.30	B	267.50	18.30	A
10	Strongly Acidic	174.41	1.35		237.50	18.30	A	99.50	-18.30	B
5	Slightly Moderate, Oligohaline,	176.10	3.18	A	192.00	18.36	A	147.00	-18.36	B
10	Strongly Acidic	126.52	-3.18	B	23.00	-18.36	B	316.00	18.36	A
3	Shallow, Oligohaline,	535.82	-10.21	C	858.00	2.49	A	1459.50	26.49	A
5	Strongly Acidic	803.44	0.21	AB	95.50	-23.47	B	889.50	3.03	C
6		772.42	-1.12	B	858.00	2.89	A	1155.00	16.61	B
10		894.17	8.42	A	918.08	10.97	A	397.50	-35.41	D
3		23.25	-1.16		45.50	7.20	A	27.00		

Plots	Group of factors Phreatic level, Salinity, pH	Density (ind/g)			Richness			Menhinicks index		
		Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***	Score Mean*	Standardized Score**	Connectivity Letters***
6	High, Fresh, Strongly Acidic	28.62	1.16		19.00	-7.20	B	27.00		
3	High, Oligohaline,	125.94	0.55		170.00	15.68	A	124.00		
6	Strongly Acidic	120.73	-0.55		46.50	-15.68	B	124.00		

*Score Mean: Average rank within each group and illustrating the ranks' central tendency.

**Standardized Score: Deviation of group's mean rank. This serves as an indicator of the group's relative position or deviation from the norm.

*** Connectivity Letters: Steel-Dwass post-hoc comparison letters associated with each attribute.

Appendix 2: Soil arthropod density (ind/g) across distinct hydroperiods. The table displays the diversity at the family and higher taxonomic levels, specifically the orders, suborders, and superfamily.

Hydroperiod		Flood				Moderate Dry				Moist				Wet			
Order	Family	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Amphipoda	Talitridae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3
Araneae	Dipluridae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Araneae	Oonopidae	0	0	1	0	0	1	1	1	0	1	0	1	0	1	1	10
Araneae	Salticidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Araneae	Sicariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arthropleona	Brachystomellidae	3	10	5	24	0	0	2	0	0	4	0	34	2	8	11	44
Arthropleona	Entomobryidae	0	0	0	0	1	0	0	0	0	2	0	3	8	5	2	6
Arthropleona	Isotomidae	4	9	1	296	1	1	2	2	2	0	69	8	9	17	15	30
Blattodea	Blattidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Coleoptera	Curculionidae	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	7
Coleoptera	Dystiscidae	2	3	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Coleoptera	Hydraenidae	5	0	1	6	0	0	0	0	1	0	1	3	0	0	0	4
Coleoptera	Hydrophilidae	0	0	0	0	0	0	0	1	0	0	15	0	0	2	1	1
Coleoptera	Passalidae	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Coleoptera	Ptiliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coleoptera	Scarabaeidae	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Coleoptera	Staphylinidae	3	0	5	4	0	0	3	0	1	1	1	1	5	2	6	7
Dermaptera	Labiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Ceratopogonidae	5	1	3	19	0	0	1	0	0	0	33	0	3	0	2	3
Diptera	Chironomidae	4	3	1	22	1	0	0	0	2	0	0	0	1	2	0	16
Diptera	Culcinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Culicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Diptera	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Dolichopodidae	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Drosophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Hydroperiod		Flood				Moderate Dry				Moist				Wet			
Order	Family	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Diptera	Psychodidae	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
Diptera	Scatopsidae	7	31	7	6	3	0	4	2	0	1	2	6	3	5	15	27
Diptera	Sciaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diptera	Simuliidae	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Diptera	Sphaeroceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Stratiomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Stratiomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	Syrphidae	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0
Diptera	Tabanidae	0	0	0	2	0	0	0	1	1	1	1	0	2	0	0	1
Diptera	Tipulidae	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Geophilomorpha	Oryidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hemiptera	Aphididae	0	8	1	0	1	1	0	0	0	5	0	0	1	3	1	1
Hemiptera	Cicadellidae	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	8
Hemiptera	Delphacidae	0	0	0	4	1	0	0	0	0	1	0	0	0	1	0	1
Hemiptera	Lygaeidae	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	3
Hemiptera	Miridae	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	5
Hemiptera	Pentatomidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hemiptera	Pseudococcidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hymenoptera	Aphelinidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	Ceraphronidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hymenoptera	Chalcidoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	Formicidae	0	2	0	5	4	3	2	1	1	1	5	2	0	1	2	3
Hymenoptera	Ichneumonidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Isopoda	Porcellionidae	0	0	0	0	0	2	2	1	0	1	6	7	2	8	2	14
Isoptera	Kalotermitidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	Crambidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Lepidoptera	Lycaenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	Pyralidae	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0

Hydroperiod		Flood				Moderate Dry				Moist				Wet			
Order	Family	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Lepidoptera	Tineidae	0	0	0	0	0	0	0	0	0	4	0	1	1	1	0	0
Mesostigmata	Ascidae	3	1	2	54	3	2	14	3	1	5	9	19	6	14	11	36
Mesostigmata	Blattisociidae	0	1	0	6	0	0	2	1	0	0	0	0	0	0	2	2
Mesostigmata	Digamasellidae	0	0	0	1	0	0	1	0	0	0	0	0	0	1	4	9
Mesostigmata	Laelapidae	1	0	0	1	1	2	1	0	0	9	1	0	1	5	5	13
Mesostigmata	Pachylaelapidae	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Mesostigmata	Sejidae	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0
Mesostigmata	Uropodidae	1	0	0	1	1	0	5	0	0	0	0	1	1	0	1	1
Mesostigmata	Veigaiidae	0	0	0	0	0	1	0	0	0	0	0	2	1	0	3	
Oribatid	Acaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oribatid	Astigmata	0	0	0	34	0	0	1	0	1	1	0	0	0	0	1	0
Oribatid	Ceratozetidae	7	43	8	46	3	14	9	4	7	28	3	20	4	7	7	36
Oribatid	Cryptognathidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Oribatid	Damaeidae	3	9	1	39	4	12	10	9	9	16	6	22	10	5	3	49
Oribatid	Eniochthoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Oribatid	Galumnidae	1	0	0	1	1	2	3	0	0	0	0	0	0	1	3	1
Oribatid	Glycyphagidae	2	0	0	0	0	0	0	0	0	19	3	0	0	1	2	1
Oribatid	Haplozetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Oribatid	Hermanniidae	0	0	0	0	0	0	0	1	0	1	2	5	0	72	0	0
Oribatid	Histiostomatidae	0	0	0	33	0	0	1	0	0	0	1	4	0	0	0	0
Oribatid	Hypochthoniidae	6	16	26	24	3	1	10	8	1	32	13	18	11	12	18	43
Oribatid	Lohmanniiae	0	0	0	0	0	0	0	1	1	7	1	3	0	1	0	1
Oribatid	Lohmanniidae	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0
Oribatid	Malaconothridae	9	29	29	154	2	6	17	16	1	26	9	5	8	24	38	196
Oribatid	Nothridae	0	0	0	0	0	0	0	0	1	0	0	5	0	7	0	8
Oribatid	Unknown	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	8
Oribatid	Unknown	9	0	1	13	0	1	3	1	0	3	1	7	1	1	3	6
Oribatid	Phthiracaridae	4	0	0	1	1	0	0	2	1	9	1	3	1	1	0	3

Hydroperiod		Flood				Moderate Dry				Moist				Wet			
Order	Family	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Oribatid	Schlerobatidae	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Oribatid	Stigmaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oribatid	Suctobelbidae	0	0	0	0	0	1	1	2	0	0	0	0	0	3	0	3
Oribatid	Tectocepheidae	6	5	7	2	0	0	1	1	0	0	0	0	0	1	3	14
Oribatid	Tegoribatidae	27	8	37	19	5	2	16	3	1	5	1	6	0	7	11	16
Oribatid	Trhypochthoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthoptera	Grylotalpidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Orthoptera	Phalangopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phasmida	Phasmatidae	0	0	0	4	0	0	0	0	0	1	0	0	0	0	0	0
Polyzoniida	Polydesmidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polyzoniida	Sinphonotidae	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Prostigmata	Bdellidae	0	0	0	0	0	0	0	0	0	4	33	0	0	0	1	0
Prostigmata	Cheyletidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prostigmata	Cunaxidae	1	1	11	19	1	0	2	1	1	8	0	0	5	3	17	7
Prostigmata	Digamasellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Prostigmata	Erythraeidae	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Prostigmata	Eupodidae	0	1	0	9	0	0	0	0	0	0	2	6	0	0	11	4
Prostigmata	Prostigmata	6	0	0	1	0	2	1	0	0	0	1	6	1	3	1	3
Prostigmata	Rhagidiidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Prostigmata	Scutacaridae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Prostigmata	Stigmaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prostigmata	Tydeidae	2	0	0	1	0	0	0	0	0	0	0	4	4	2	1	1
Psocoptera	Liposcelididae	0	0	0	0	8	2	0	0	1	1	34	0	2	1	4	0
Spirobolida	Rhinocricidae	0	0	0	4	0	0	0	0	0	0	1	0	0	2	1	0
Spirobolida	Trigoniulidae	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1
Spirobolida	Unknown	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Symphyleona	Sminthuridae	1	2	0	10	0	0	0	0	0	0	0	0	1	0	5	5
Thysanoptera	Aeolothripidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Hydroperiod		Flood				Moderate Dry				Moist				Wet			
Order	Family	3	5	6	10	3	5	6	10	3	5	6	10	3	5	6	10
Thysanoptera	Phlaeothripidae	0	0	0	1	0	0	0	0	0	0	0	0	5	4	0	1
Thysanoptera	Thripidae	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Thysanoptera	Thysanoptera	0	0	0	4	0	0	0	0	0	0	0	0	1	0	1	1
Total Density (ind/g)		127	261	152	1196	48	55	137	63	31	210	286	242	140	242	254	683

CHAPTER 3: EFFECTS OF PLANT FUNCTIONAL TYPES SUBSTRATES ON SOIL ARTHROPOD COMMUNITY IN COASTAL URBAN WETLANDS

3.1 INTRODUCTION

Aboveground-belowground interactions are fundamental to ecosystem structure and function (Wardle et al., 2004). Plants supply detritus resources such as litter, while soil arthropods, via their trophic activities, mediate the breakdown of plant litter and contribute significantly to organic matter turnover and nutrient availability, which are essential for plant growth (Facelli and Pickett, 1991; Wardle et.al., 2012; Whigham et al.,1978). These complex bidirectional relationships between plant communities and soil arthropods enhance soil health, ecosystem services, and ecosystem resilience and stability (Bardgett & Van Der Putten, 2014; Mitsch et.al., 2009).

The soil-litter system is characterized by the interdependent dynamics of litter inputs and arthropod responses, moderated by the spatial and temporal distribution of detrital resources and the diversity and abundance of arthropod functional groups, including micro-predators, litter transformers, and ecosystem engineers (Culliney, 2013; Lavelle et al., 1993, 1997, 2001, 2006, 2022; Swift et al., 1979). The nutritional content, physical structure, and decomposition stage of plant litter generate a diverse array of habitats and resources, catering to the specific needs and feeding strategies of various arthropod groups. This diversity influences the composition and structure of soil arthropod communities (Barberena-Arias et. al., 2018; Culliney, 2013; Haynert et al., 2017; Lavelle et al., 2006; Mulder et al., 2009; Swift et al., 1979). For example, in agroforestry plantations, soil arthropod diversity is greater in plots with thicker litter layers and

enhanced nutrient content (Tongkaemkaew et al., 2018). Diplopoda (millipedes) and Isopoda (woodlice) species show increased richness and abundance in response to food quality, as well as soil temperature and humidity (Menta et al., 2020). Collembola (springtails) exhibit significant aggregation at small spatial scales, influenced by litter quality and quantity, and microclimatic conditions, potentially driven by pheromonal signaling that directs them to optimal micro-environments (Lavelle et al., 2006).

Moreover, as detritus decomposition proceeds, arthropod assemblages experience successional changes in the food web as a result of changes in resource quality and habitat microclimate conditions (Bastow, 2012; Barberena-Arias et al., 2018; Haynert et al., 2017; Lavelle et al., 2006; Mulder et al., 2009; Swift et al., 1979). The “sleeping beauty paradox” (Lavelle et al. 1995) states that dormant microbial communities need a “Prince Charming”, be it a microorganism, a physical process or an environmental factor, which “awakens them” by facilitating their contact with the nutrient pools. Schoenly et al., (1987), showed that colonization, succession, and subsequent decline of arthropod assemblages on detritus followed a predictable sequence: initial of surface-dwelling species such as ants, beetles, and flies, transitioning to an intermediate stage dominated by soil-dwelling organisms like mites and springtails (collembolas), and ultimately evolving into a decline phase where the assemblage is predominantly comprised by more specialized species.

In wetland ecosystems the availability and spatial distribution of detrital resources are influenced by the hydroperiods and drying and wetting dynamics. During dry periods, terrestrial plant litter accumulates and undergoes partial in-situ decomposition. Upon flooding, both loose and decomposed litter is redistributed, creating a mixture of fresh,

comminuted and partly decomposed organic substrate. This process yields microhabitats and food resources unevenly distributed across time and space, thus modulating soil arthropods responses (Anderson et al., 1989; Batzer et al., 2006, 2016, 2020; Culliney, 2013; Lavelle et al., 2001, 2006, 2022). In the soils of floodplain forests, wetting and drying cycles trigger a rapid mineralization burst, leading to a high C:N ratio and significant mass and carbon losses from decomposing litter (Batzer et al., 2006, 2016; Lockaby, 1996; Yang, 2022). These alterations subsequently modulate soil arthropods trophic assemblages (Culliney, 2013; Zhang et al., 2023) by fostering the development of two interactive decomposition channels: bacterial or fungal-based food webs, sensu Coleman et al. (2007). Bacteria utilize the labile components of plant litter for their growth, while the more recalcitrant resources (such as cellulose and lignin) are consumed by fungi. This succession in bacterial and fungal communities cascades up to higher trophic levels. In the bacterial-based food web, bacteria, protozoa, and nematodes predominate. Conversely, in the fungal-based food web, fungi and mesofauna (such as mites and springtails) are involved (Barberena-Arias et al., 2018; Moore et al., 1991; Swift et al., 1979).

The complexity, heterogeneity, distribution, and accumulation of plant litter is recognized to significantly influence the overarching structure of their associated soil food webs and their effect on soil organic accumulation and nutrient dynamics (Lavelle et al., 2006, 2022; Swift et al., 1979). However, there remains a research gap in Caribbean Coastal Wetlands (Table 14). The lack of prior research is particularly noteworthy given the critical importance of plant-soil interactions in developing management strategies for ecosystem conservation (Wardle, 2002). In critically endangered areas such as the

Caribbean: the fourth primary biodiversity hotspot worldwide which represents one of the world's most complex mosaics of marine freshwater and terrestrial habitats (Figure 26), this gap emphasizes the need for focused fundamental investigations in this unique ecological setting (González & Barberena-Arias, 2017). Their significance is further underscored within the framework of global and regional challenges, including climate change, sea-level rise, and anthropogenic impacts.

Table 11: Global Studies on the Effects of Vegetation on Soil Arthropod Communities in Various Wetland Ecosystems

Study Reference	Wetland Location	Key Findings
Guo et. al., 2022	Qinghai-Tibetan Plateau Peatland.	Water table decline significantly arthropod community structure by shifting plant communities and leaf nutrient profiles
Ward et. al., 2015	Peatlands National Nature Reserve, Northern England	Litter quality and changes in vegetation composition play a significant role in regulating short-term litter decomposition and belowground communities. These influences are found to have a more pronounced effect than that of moderate warming.
Krab et, al., 2013	Abisko Subarctic Peat Bogs, North Sweden	The influence of litter quality on Collembola populations is more significant than its indirect effects on microclimate.
García-Gómez et. al.,2014	National Park Reefs of Cozumel Island in the South of Mexico	This study provides valuable insights into the seasonal dynamics of arthropod diversity in relation to the dominant mangrove species and climatic conditions.
Weilhoefer et. al., 2017	Smith and Bybee Wetlands Natural Area in Portland, OR, USA	Influence of reed canary grass on the arthropod community is predominantly indirect, mediated through alterations in habitat structure and conditions, rather than by directly changing the food resources available to the arthropods.

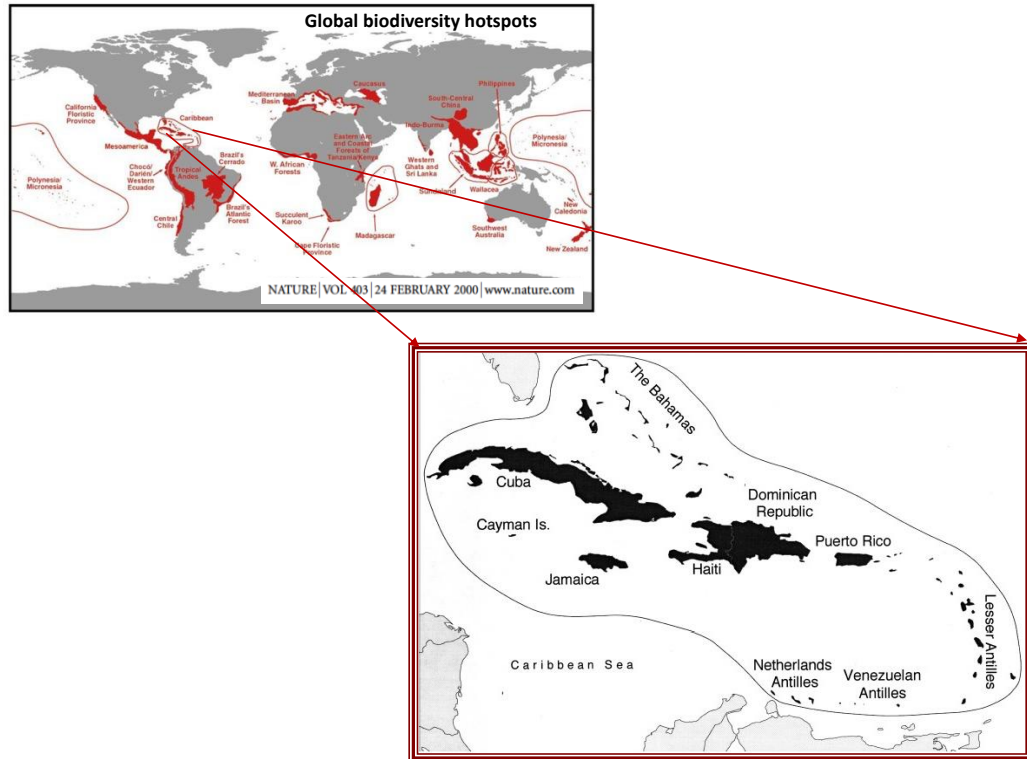


Figure 26: Caribbean Area: the fourth primary biodiversity hotspot worldwide (adapted from Myers et.al., 2000).

A thorough understanding of arthropod responses to variations in litter quality, distribution, and accumulation is essential for elucidating the functioning of the wetland litter system and its impact on ecosystem dynamics, which encompass both aboveground and belowground processes (Barberena-Arias, 2008; Bardgett et al., 2005; Coleman et al., 2017; Culliney, 2013; Cuevas, 2019; Lavelle et al., 1997, 2013; Moore et al., 1991; Swift et al., 1979; Wardle, 2002; Wardle et al., 2004, 2012).

The aim of this research is to determine the influence of plant functional types on soil arthropods community structure and composition. It addresses the central question; how does plant litter cover, through their associated litter quantity and quality, modulate the assemblages of soil arthropod groups across wetland hydroperiods? The hypothesis posits that the synchrony and synlocation of soil arthropod community structure and

composition are influenced by specific plant functional types. This influence is mediated through the composition of plant residues, the quality and accumulation of litter, and the dynamics dictated by hydroperiod variations. This research endeavor seeks to fill the existing knowledge gap by providing insights into the nuanced interactions between plant litter characteristics and soil arthropod communities in a coastal urban wetland, thereby contributing to the effective management and conservation of wetland ecosystems under the current global environmental challenges.

3.2 METHODS

Four study plots each encompassing 100 square meters, were established in a research area within La Ciénaga las Cucharillas Natural Reserve (Figure 12 and Table 2, page 23). Five plant species were chosen based on their functional type and occurrence within the study plots (Table 16, Box, 1981; Hernández, 2022; Medina, 2024; Mehltreter et. al., 2010; Native Plant Trust, 2024; Pérez-Harguindeguy, 2013): *Dalbergia ecastaphyllum* (L.) Taub (shrub), *Echinochloa polystachya* (Kunth) Hitchc. (grass), Poaceae family (grass), *Acrostichum danaeifolium* Langsd. & Fisch. (fern) and *Laguncularia racemosa* C.F.Gaertn (tree). *D. ecastaphyllum* was present in two plots, *E. polystachya* in one plot, while the remaining species were found in three plots each (Table 2, page 23). The chemical composition and structure of plant residues vary among different types, influencing their decomposition dynamics and nutrient cycling processes (Table 15).

Table 12: General description of dominant plant functional types within the study plots (adapted from Alegre et al., 2004; Box, 1981; Hernández, 2022; Medina, 2024; Mehltreter et al., 2010; Native Plant Trust, 2024; Pérez-Harguindeguy, 2013; Pradisty et al., 2021).

Functional Type	Definition	Taxa	General Description	Chemical composition of litter
Fern	Small plants with prostrate, underground stems and large, erect, compound leaves called fronds.	<i>A. danaeifolium</i>	Non-flowering, vascular plants with large and robust fronds, from the ferns family (Pteridaceae) common in brackish swamps.	High concentrations of fiber, lignin, and tannins, further contributing to their slow decomposition.
Shrub	Woody plant ~5 m tall. with multiple stems arising at or near the base.	<i>D. ecastaphyllum</i>	Leguminous shrub. Grows in non-forested areas generally forming monospecific stands.	Low lignin, high in organic carbon (C) and nitrogen (N) largely because of the plant's ability to fix atmospheric nitrogen.
Grass	Narrow, flat, linear-leaved herb, growing from well-developed underground rootstocks.	<i>E. polystachya</i>	Annual, biennial, or perennial plants can be terrestrial or aquatic, with leaves that are evergreen or deciduous, usually much longer than they are wide. They typically grow, forming tufts or mats. Perennial grass with decumbent erects stems that could reach 2 m height. It is commonly found in flooding areas.	Grasses are characterized by high silica content and a relative scarcity of phosphorus (P), which enhances their structural rigidity and resistance to decomposition.
Tree	Woody plant usually >5 m tall, with a trunk supporting branches and leaves forming a	<i>L. racemosa</i>	A representative species of mangrove trees; characterized by a solitary or clustered trunk, gray bark. Elliptic to	High carbon-to-nitrogen (C/N) and lignin-to-nitrogen (lignin/N) ratios, which are indicative

Functional Type	Definition	Taxa	General Description	Chemical composition of litter
	characteristic crown.		oblong-shaped leaves.	of slower decomposition rates.

Within each plot, three specimens of each functional type were selected, and three litter samples per plant were collected on each sampling date. Sampling was prioritized in areas with a higher quantity of litter. Each sample was collected using a sampling ring, measuring 7.62 cm in diameter and 5 cm in depth, which was pressed into the ground. Collected samples were then divided into two fractions: 1) loose litter, consisting of relatively undecomposed material found within the top 1 cm of the ring (above the soil surface), and 2) a mixture of older litter, ranging from partly to fully decomposed, combined with organic soil. Substrate samples were collected on five dates, each chosen to represent distinct hydroperiod conditions (Figure 15, page 42; Table 3, page 43): Moderate Dry (June 18-25, 2020), Flood (October 23, 2020), Moist/Between Floods (March 19, 2021), and Wet (June 9, 2021). The collected samples were transported to the laboratory, where their fresh weight was recorded before being placed, in lighted Tullgren-Berlese extractors for one week. The extracted arthropods were preserved in 70% ethanol solution placed under each extractor (Barberena-Arias & Cuevas, 2018, 2021). Collected soil arthropods were taxonomically identified to the lowest category possible, either class, subclass, order or suborder, and family, and classified as adults or immatures. Collembola were not separated as adults or immatures because it is difficult to differentiate among developments stages (Barberena-Arias & Cuevas, 2018, 2021; Herrera & Cuevas, 2003). Soil arthropods were also categorized within the soil food web

framework based on the predominant feeding habit of the group (Table 16; Barberena-Arias, 2008; Lavelle et al., 2003; Nielsen, 2019; Potapov et. al., 2022).

Table 13: Basal resources and corresponding trophic guilds within the soil food web framework (Adapted from Barberena-Arias & Cuevas, 2018; Lavelle et al., 2001; Nielsen, 2019; Potapov et. al., 2022).

Trophic guild	Basal resource	Description	Ecological contribution
Detritivores (animal primary decomposers)	Detritus	They feed directly on organic matter	Litter transformation (comminution), decomposition, nutrient mobilization, soil formation, structural stabilization
Herbivores (phytophages)	Plant material	Living vascular plants shoots, sap, and roots	Nutrient cycling, soil aggregation, respiration
Microbivore (secondary decomposers)	Microflora	Fungi and organic matter, eating also the bacteria growing on it.	Biological control, nutrient cycling
Fungivores (mycophages)	Fungi	Fungi and lichen associated fungi	Biological control, nutrient cycling
Omnivores	Organic matter, plants, small arthropods	Plant material, fungi, detritus, and smaller soil organisms.	Organic matter redistribution, microbe dispersal, nutrient cycling, soil aggregation
Predators	Soil organisms	Smaller arthropods, nematodes, and various soil invertebrates	Nutrient cycling, soil aggregation, biological control

For each sample, organisms were identified and counted using an Amscope SF2TRA stereoscopic binocular microscope or a Nikon Eclipse 80i microscope. After extraction, the samples were oven-dried at 60°C for a period of seven days, and the dry weight of the sample fractions was determined. Loose litter samples were homogenized to a 5 µm size using a Retsch® grinding mill, while old litter and organic soil were ground using a mortar and pestle until they passed through a 20-mesh sieve. A 5.00 mg subsample from

each sample was taken for carbon-to-nitrogen (C:N) ratio, carbon (C) percentage, and nitrogen (N) percentage analysis using a Vario EL Cube organic elemental analyzer.

3.3 DATA ANALYSIS

Non-parametric statistical approaches, including the Wilcoxon/Kruskal-Wallis test followed by the post-hoc Steel-Dwass test, were employed to detect variations in litter mass (g), as well as C %, N%, and the carbon-to-nitrogen (C:N) ratio in substrate fractions among plant functional types and hydroperiods. To further explore these relationships and quantify the effects of these variables on soil arthropods diversity and abundance, a general linear model (GLM) with a quasi-Poisson distribution was applied. The analysis was further refined by categorizing the C:N ratio into specific ranges (Table 17), defined by mineralization and immobilization rates of organic material (Brust, 2019; Liu et al., 2013). This categorization provided a systematic framework to assess the impact of the C:N ratio on soil arthropod communities.

Table 14: C:N ratio categories, defined by mineralization and immobilization rates of organic material (Brust, 2019; Liu et al., 2013)

C:N Ratio	Process	Description
Below 20:1	Mineralization	Mineralization is occurring, indicating a relatively high availability of nitrogen for microbes.
20:1 to 30:1	Balance between Mineralization and Immobilization	Optimal range for microbial activity, indicating a balance between mineralization and immobilization.
Above 30:1	Immobilization	Immobilization is likely to occur as microbes require nitrogen for their growth, leading to the sequestration of nitrogen in microbial biomass.

Soil arthropod metrics, including Menhinick's Index for diversity, along with richness, abundance, and density (density being quantified as the number of individuals per gram of soil), were determined (Barberena-Arias & Cuevas, 2018; Tan et al., 2019). A two-way

non-parametric analysis was implemented to examine the influence of plant functional types and hydroperiods on these metrics. A density distribution table was employed to investigate the relationships between soil arthropod taxa and the combined effects of plant functional types and hydroperiods. Taxonomic classifications were designated as "dominant," "common," or "rare" based on their relative densities, facilitating comparisons of community compositions via the Bray-Curtis similarity index and Non-metric Multidimensional Scaling (NMDS). Dominant taxa were identified as those with a relative density of 10% or greater. Common taxa were those with a relative density between 1% and 10%, while rare taxa were defined by a relative density of less than 1% (Li et.al., 2012; Zheng et.al., 2022). A PERMANOVA (Permutational Multivariate Analysis of Variance) and Multi-Response Permutation Procedure (MRPP) were conducted to elucidate the combined effects of vegetation types and hydroperiods on the community composition and structure of soil arthropods.

These statistical analyses were performed using SAS JMP® Pro 16 and RStudio (R Core Team, 2023) statistical software. Statistical analyses in RStudio were completed using the following packages: 'stats', 'vegan', 'gplots', and 'pheatmap'.

3.4 RESULTS

3.4.1 Substrate Quality and Quantity Across Plant Functional Type and Hydroperiod

Significant variations were identified in the C% and N%, as well as in the C:N ratios, through two comprehensive analyses. The first analysis investigated the influence of varying hydroperiods on these parameters within each distinct plant functional type (Figure 27). In contrast, the second analysis compared these metrics across plant

functional types under differing hydroperiods (Figure 28, Table 18). These significant differences were observed in both loose litter and old litter-organic soil fractions. Results from the first analysis (Figure 27), centered on loose litter fractions, indicated that variations in N% content between flood and moderate dry periods were not statistically significant. However, when considered collectively, these conditions displayed significant contrast from those observed during moist and wet periods, which presented lower values. Under flood conditions, the loose litter fractions from grasses, shrubs, and ferns exhibit significantly elevated nitrogen levels, whereas shrubs and trees demonstrate a markedly higher carbon percent content across both substrate fractions, with all values statistically distinct from those observed in other hydroperiods. C:N ratios within the old litter-organic soil fractions are significantly lower than those observed in the loose litter fractions, a trend consistent across all vegetation types and hydroperiods. When comparing these metrics across plant functional types under differing hydroperiods (Figure 28, Table 18), it was found that within both substrate fractions, shrubs consistently exhibited the highest C% and N% in all conditions. In contrast, trees were characterized by having the highest carbon-to-nitrogen (C:N) ratios. These distinctions, which were statistically significant, differentiate shrubs and trees from other plant functional types and are related to the chemical composition of the residues from these specific types (Table 15).

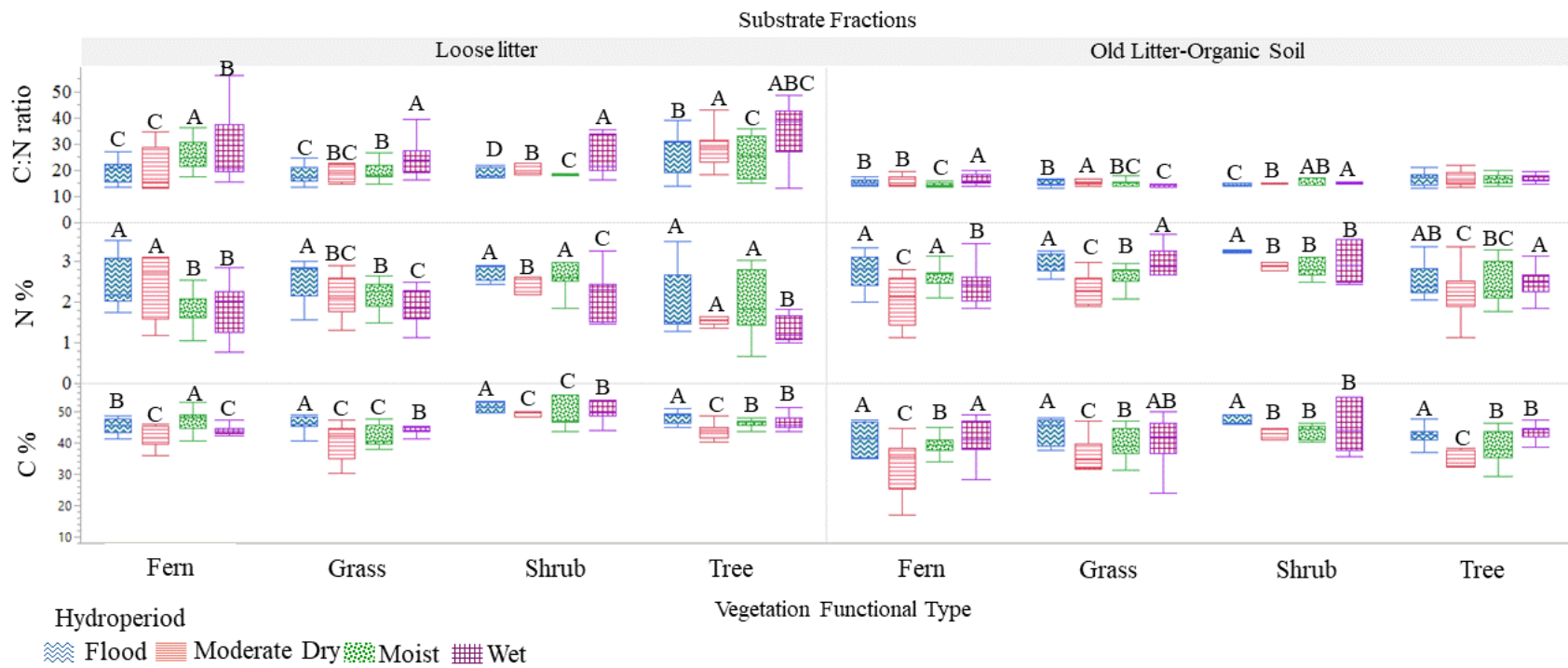


Figure 27: Significant variations in C% and N%, as well as in C:N ratios, across different hydroperiods within each plant functional type, segmented by substrate fractions. Values not connected by the same letter indicate significant differences ($p < 0.05$).

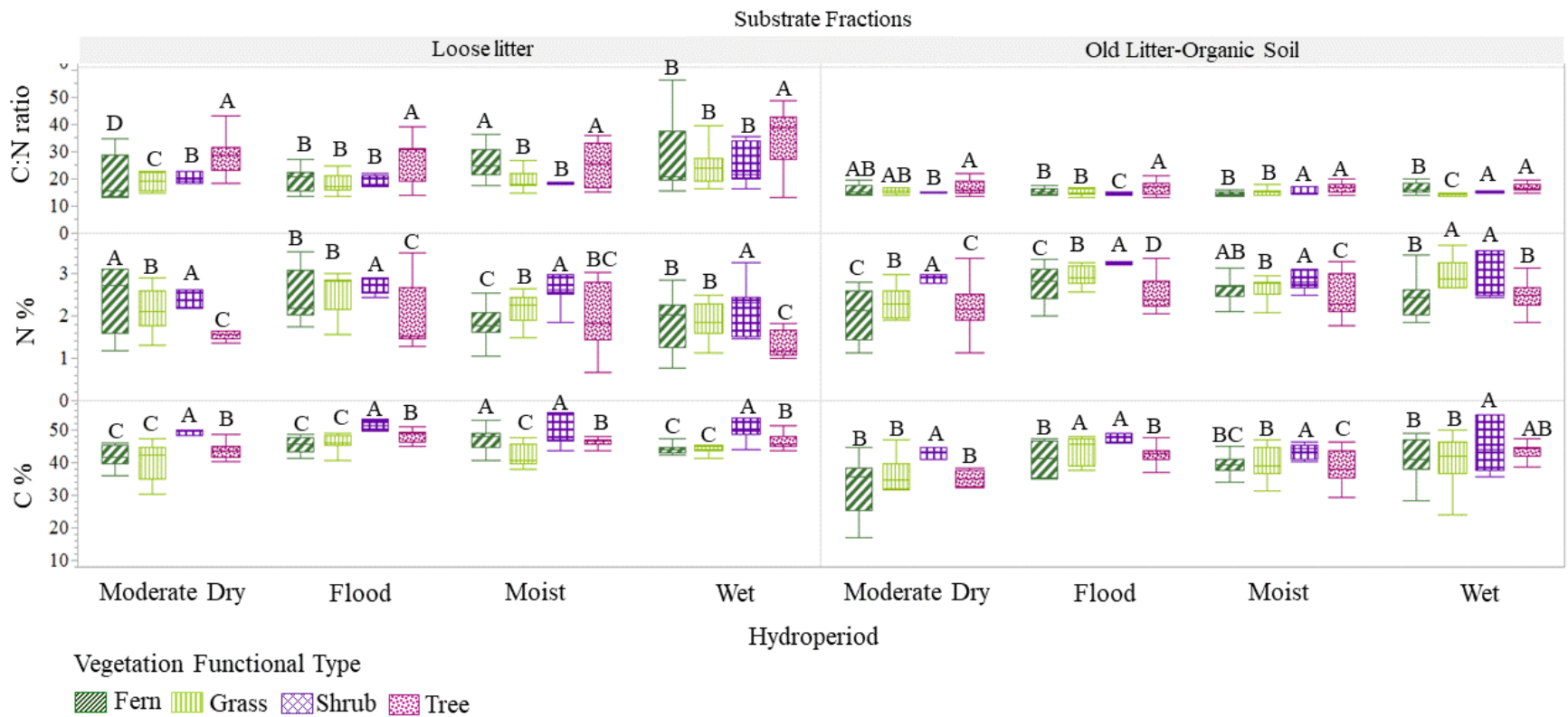


Figure 28: Significant variations in C% and N% contents, as well as in C:N ratios, across plant functional types within different hydroperiods within each substrate fraction. Values not connected by the same letter signify significant differences ($p < 0.05$).

Table 15: Mean and standard deviation of carbon (C) and nitrogen (N) percentage contents, as well as the C:N ratio, for different plant functional types across hydroperiods within loose litter and old litter-organic soil fractions.

Flood																
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C:N ratio	18.60	3.75	18.12	3.75	18.48	2.01	24.04	8.09	15.38	1.32	15.08	1.08	14.43	0.41	16.41	2.38
N% (mg/g)	2.44	0.57	2.49	0.48	2.78	0.20	2.00	0.80	2.71	0.44	2.87	0.36	3.26	0.03	2.54	0.39
C%(mg/g)	45.45	2.20	45.12	4.11	51.31	1.49	48.18	1.87	41.68	4.73	43.30	5.39	47.00	1.23	41.76	3.41

Moderate Dry																
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C:N ratio	17.98	7.45	19.57	5.70	20.44	2.04	27.82	6.92	15.92	1.95	15.71	0.95	14.91	0.14	17.24	7.48
N% (mg/g)	2.34	0.73	2.05	0.51	2.42	0.21	1.58	0.30	2.06	0.58	2.34	0.36	2.87	0.10	2.15	0.50
C%(mg/g)	42.03	3.16	40.20	5.96	49.41	0.61	43.87	3.17	32.77	8.04	36.80	5.16	42.85	1.76	36.99	5.20

Moist																
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C:N ratio	25.67	8.10	19.73	4.99	18.82	2.39	23.10	9.31	14.76	1.00	14.97	1.14	15.72	2.68	16.23	1.93
N% (mg/g)	1.86	0.49	2.13	0.34	2.61	0.29	2.02	0.71	2.65	0.32	2.66	0.34	2.77	0.36	2.39	0.51
C%(mg/g)	47.79	3.49	42.02	3.39	49.17	4.14	46.59	3.11	39.11	3.43	39.78	4.61	43.62	2.24	38.71	5.33

Wet																
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C:N ratio	23.15	12.47	23.18	6.01	22.77	7.08	31.31	10.61	16.48	1.86	14.42	1.16	15.21	0.37	16.80	1.75
N% (mg/g)	1.91	0.61	1.88	0.41	2.21	0.62	1.48	0.69	2.50	0.45	2.75	0.75	2.98	0.42	2.53	0.37
C%(mg/g)	44.16	1.72	43.57	1.88	50.28	2.86	46.48	2.10	41.26	6.28	39.64	9.39	45.41	7.12	42.48	3.82

Litter mass was significantly elevated during the moderate dry period across all vegetation types, with trees and shrubs displaying augmented litter mass relative to the others (Table 19; Figure 29).

Table 19: Mean and standard deviation of litter mass (g), for different plant functional types across hydroperiods within loose litter and old litter-organic soil fractions.

Litter mass (g)	Flood								Moderate Dry							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
	0.07	0.07	0.06	0.04	0.07	0.02	0.10	0.06	0.09	0.06	0.10	0.04	0.20	0.05	0.19	0.11
Litter mass (g)	Moist								Wet							
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
	0.04	0.04	0.05	0.03	0.08	0.04	0.05	0.05	0.05	0.03	0.03	0.01	0.09	0.03	0.11	0.09

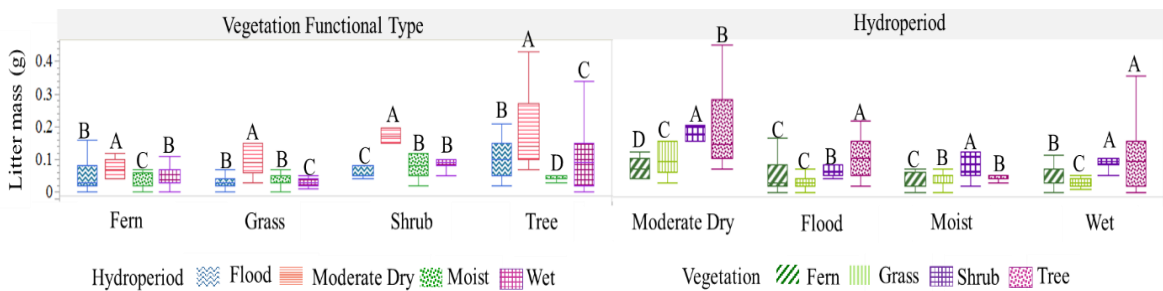


Figure 29: Significant differences in vegetation functional type litter mass (g) across hydroperiods. Values not connected by the same letter indicate significant differences ($p < 0.05$).

Notably, during the moist and flood periods, there is a redistribution of both loose and decomposed litter. As a result, the loose litter collected under ferns and grasses was an amalgamation of fresh and aged organic materials originating from disparate plant sources (Figure 30). Conversely, the loose litter collected under shrub and tree types was homogeneous, consisting of materials from the same vegetation type, without a mixture of different plant sources. During the moist period, the composition under fern vegetation was 88% from trees, grasses, and shrubs, and 12% from ferns; under grass, the composition was 79% from trees and shrubs, and 21% from grasses. In the flood period, the litter composition under fern vegetation constituted 62% from trees, grasses, and

shrubs, and 38% from ferns; while under grass, was 91% from trees, grasses, and shrubs, and 9% from grasses. Given the diverse quality of these residues, attributable to their distinct plant types (Table 15), their presence contributes to a habitat with heterogeneous resources beneath both fern and grass vegetation.

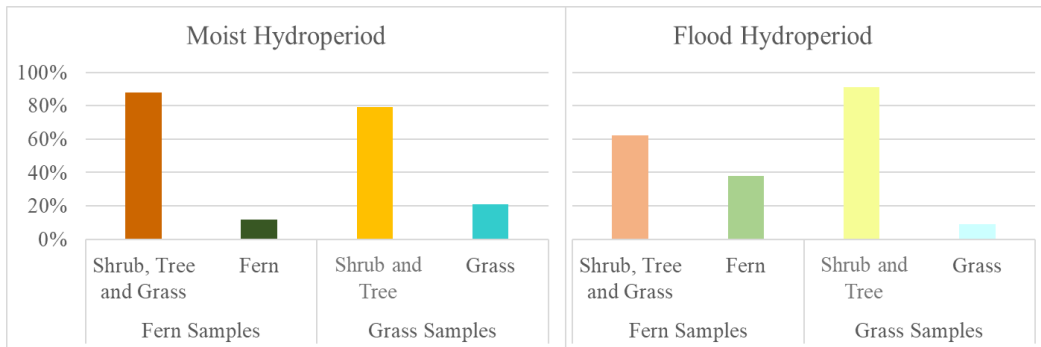


Figure 30: Percentage (%) composition of mixed loose litter types collected under fern and grass vegetation, during moist and flood periods.

3.4.2 Soil Arthropod Community Responses

3.4.2.1 Influence of Loose Litter Mass, Carbon and Nitrogen Content, and C:N Ratio on soil arthropods communities

The application of Generalized Linear Models (GLM) has demonstrated statistically significant correlations (p -values < 0.01) between the percentage of carbon (%C), nitrogen (%N), and loose litter mass with species richness and abundance (Table 20). The analysis revealed that while %C has relatively smaller coefficients of 0.01 for richness and 0.02 for abundance, its influence is statistically significant, underscored by high t -values of 13.70 for richness and 4.29 for abundance. Litter mass showed more substantial coefficients of 0.20 for richness and 0.93 for abundance, with corresponding t -values of 2.61 and 2.26, respectively. These results suggest that litter mass has a more pronounced quantitative impact on both richness and abundance. In contrast, nitrogen (%N) exhibited a complex influence on the ecological metrics. It negatively affected species richness, as

indicated by a coefficient of -0.06 and a t-value of -7.80, suggesting a suppressive effect on diversity. However, nitrogen (%N) also showed a positive influence on species abundance, with a coefficient of 0.09 and a t-value of 1.97. While this t-value indicates statistical significance, it is comparatively lower than those observed for other variables, suggesting a more subtle effect.

Table 16: Results from a Generalized Linear Model (GLM) analysis, utilizing a quasi-Poisson distribution to assess the effects of loose litter mass, carbon content, and nitrogen content on the richness and abundance of soil arthropods.

Quality Factors	Richness				Abundance			
	Estimate coefficient	Estimate Error	t value	p-value	Estimate coefficient	Estimate Error	t value	p-value
%C	0.01	0.001	13.70	<0.01	0.02	0.005	4.29	<0.01
%N	-0.06	0.007	-7.80	<0.01	0.09	0.045	1.97	<0.01
Litter mass	0.20	0.067	2.61	<0.01	0.93	0.412	2.26	<0.01

The impact of the C:N ratio on soil arthropod communities indicated that all trophic guild densities (ind/g) were significantly elevated in conditions where the C:N ratio ranged between 20:1 and 30:1, denoted as the equilibrium phase of the mineralization-immobilization continuum, and during the immobilization phase, characterized by a C:N ratio greater than 30:1 (Figure 31). No statistical differences were observed between these two phases. However, both phases were statistically distinct from the mineralization phase, identified by a C:N ratio less than 20:1. During the mineralization phase, lower densities were quantified. Herbivores exhibited statistically significant differences compared to detritivores and microbivores, whereas microbivores differed significantly from predators (Figure 32).

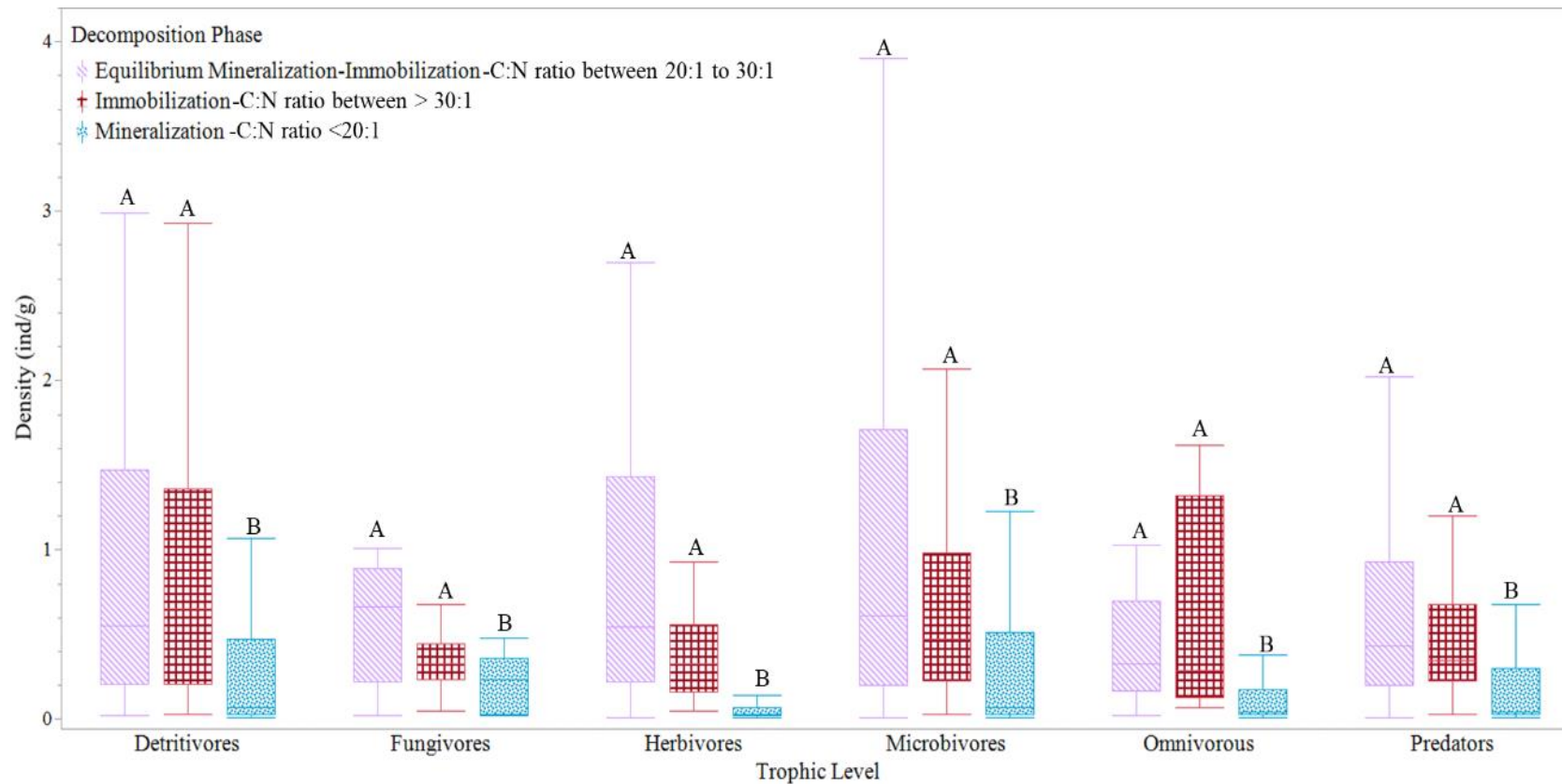


Figure 31: Abundance of various trophic guilds across different decomposition phases (individuals per gram), categorized by C:N ratio ranges. The graphic illustrates how abundance varies within each trophic guild during distinct decomposition stages. Statistical differences are indicated by non-overlapping letters, with values not connected by the same letter considered significantly different ($p < 0.05$).

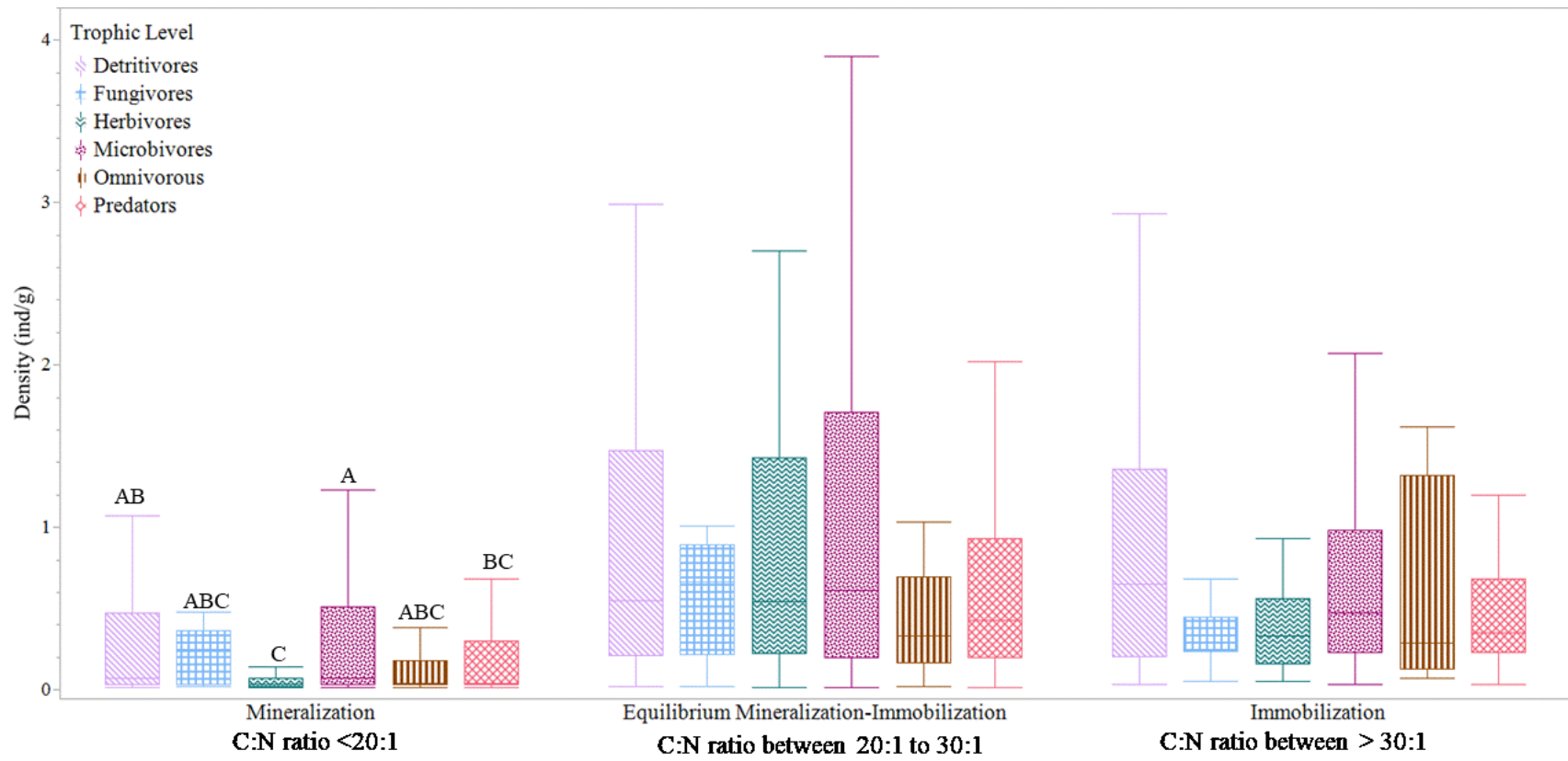


Figure 32: Statistical differences in trophic guild densities (individuals per gram) across various decomposition phases, as delineated by C:N ratio ranges. Values not connected by the same letter indicate significant differences ($p < 0.05$).

3.4.2.2 Hydroperiod Influences on Soil Arthropod Diversity Across Vegetation Types

The two-way non-parametric analysis demonstrated significant variations in the diversity matrices among plant functional types across different hydroperiods for both mesofauna and macrofauna, as delineated in Figure 33. Macrofauna densities were significantly elevated within the fern, grass, and tree vegetation types during flood and wet hydroperiods. Regarding mesofauna, significantly higher densities were quantified in association with grass and shrub types during the flood, wet, and moist hydroperiods, while the peak density within tree type was recorded during the flood period. Richness was significantly higher for fern, shrub, and tree functional types during the wet period, in contrast to grass, where higher richness was observed during the moderate dry period. Furthermore, the Menhinick's Index revealed an enhanced diversity during moist hydroperiods for fern, shrub, and tree types, and during the moderate dry period for grass types. These patterns of richness and diversity were consistent across both mesofauna and macrofauna groups.

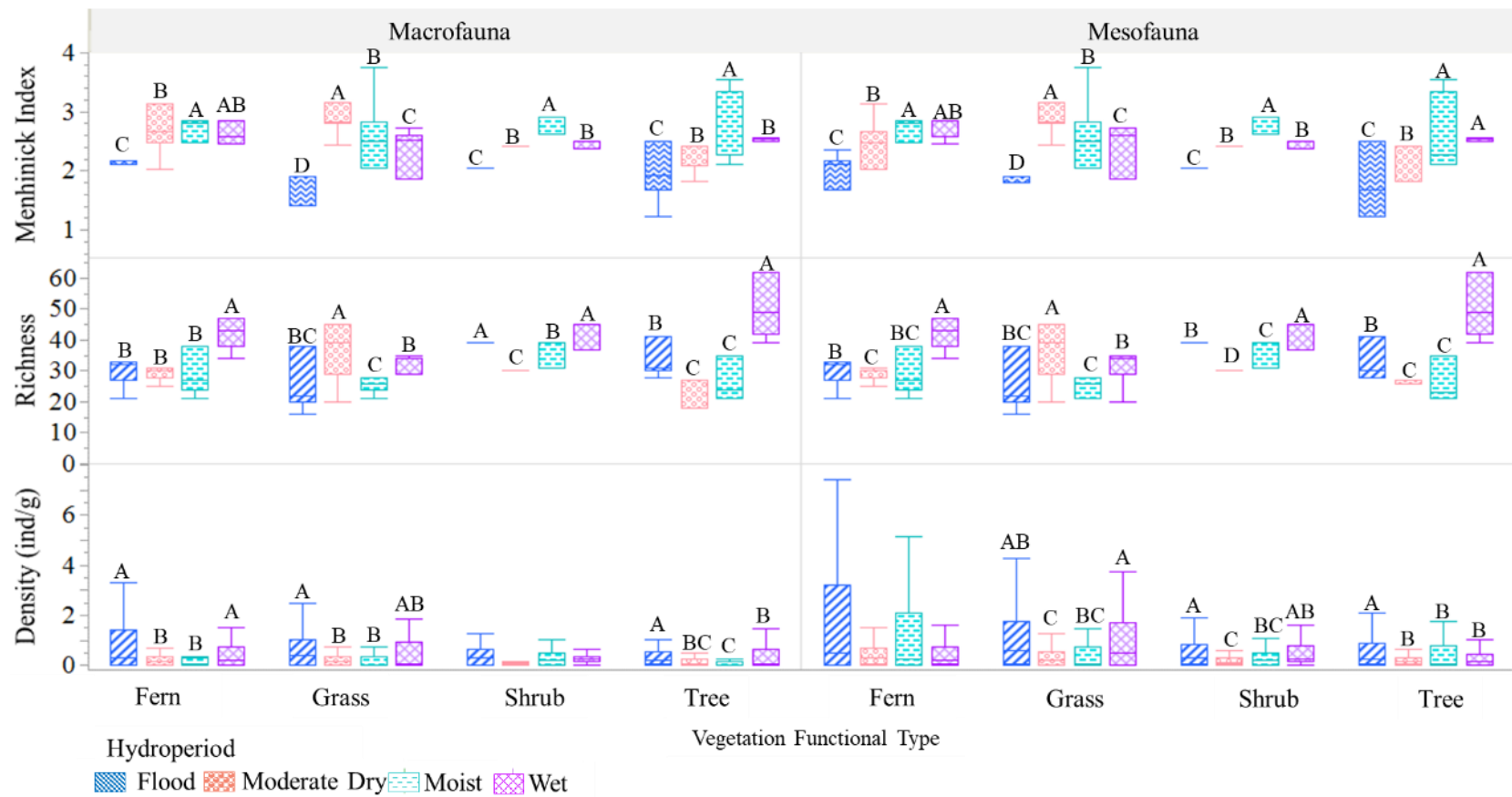


Figure 33: Statistical differences of macro and mesofauna density (ind/g), richness and Menhinick's Index within vegetation functional types among hydroperiods. Values not connected by the same letter indicates significant differences ($p < .05$).

Significant variations in macro and mesofauna density (individuals per gram), richness, and diversity were observed across different vegetation functional types under varying hydroperiods, as detailed in Figure 34. During the moist and wet hydroperiods, macrofauna density associated with shrub vegetation was found to differ significantly from that observed within tree vegetation. Significant disparities in mesofauna density were observed between shrub and grass vegetation types compared to tree vegetation during the moderate dry period, whereas in wet periods, the density within tree vegetation was markedly different from that in other types. In wet periods, richness levels of macrofauna and mesofauna associated with tree vegetation were found to significantly exceed those observed in other vegetation types. In contrast, during the moderate dry period, the highest richness was observed in grass vegetation. Furthermore, shrub vegetation not only exhibited higher richness compared to other types during the moist and flood period but also recorded the highest values of the Menhinick's Index.

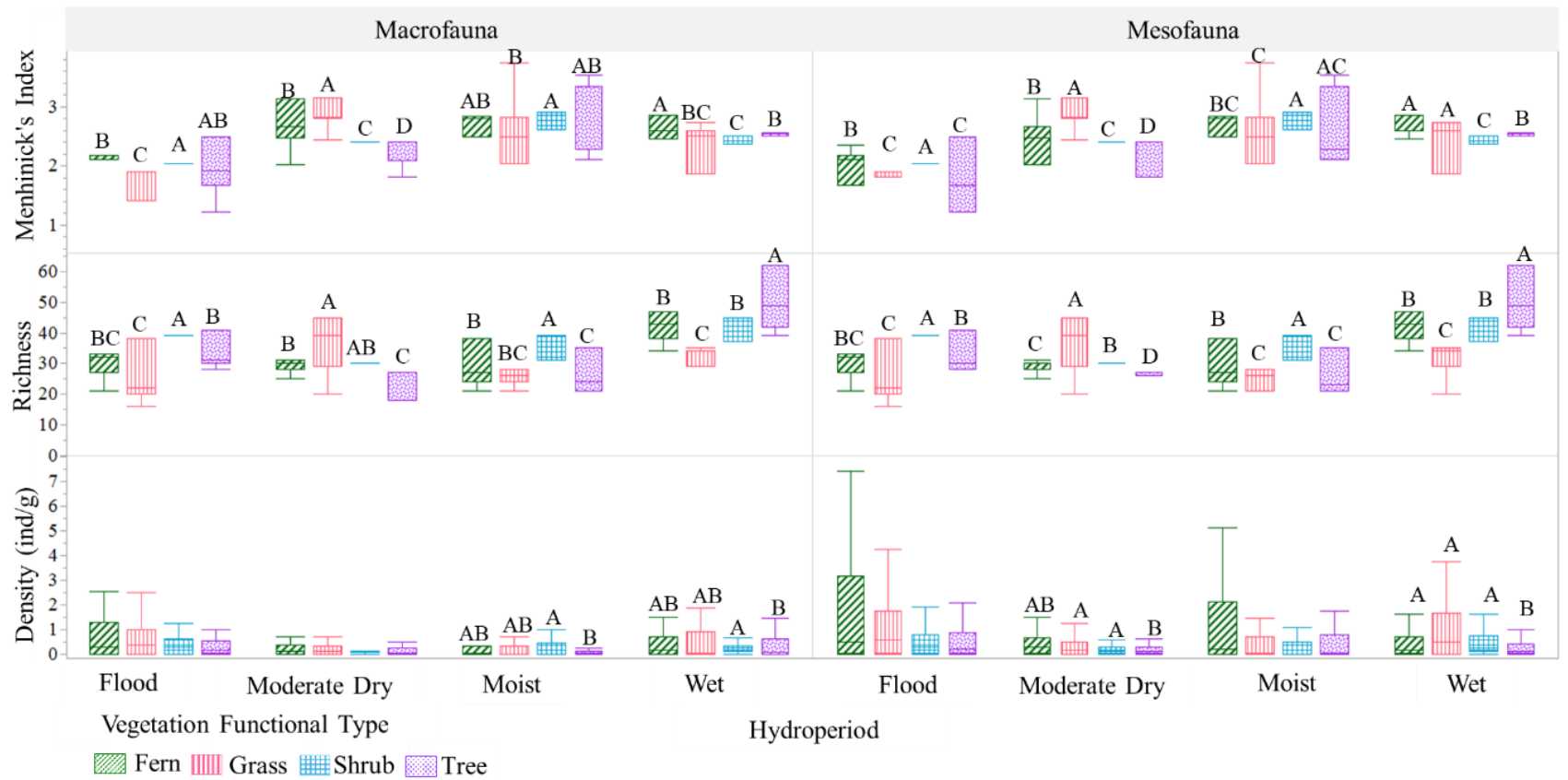


Figure 34: Statistical differences of macro and mesofauna density (ind/g), richness and Menhinick's Index within hydroperiods among vegetation functional types. Values not connected by the same letter indicates significant differences ($p < .05$).

3.4.2.3 Relationships between soil arthropod taxa and the combined effects of plant functional types and hydroperiods.

A total of 9,881 soil arthropods, encompassing 93 families across 20 taxonomic groups (Orders and Suborders), were identified (Figure 35). Of these, 43 were classified within the mesofauna¹⁰ group, while 50 were attributed to macrofauna.

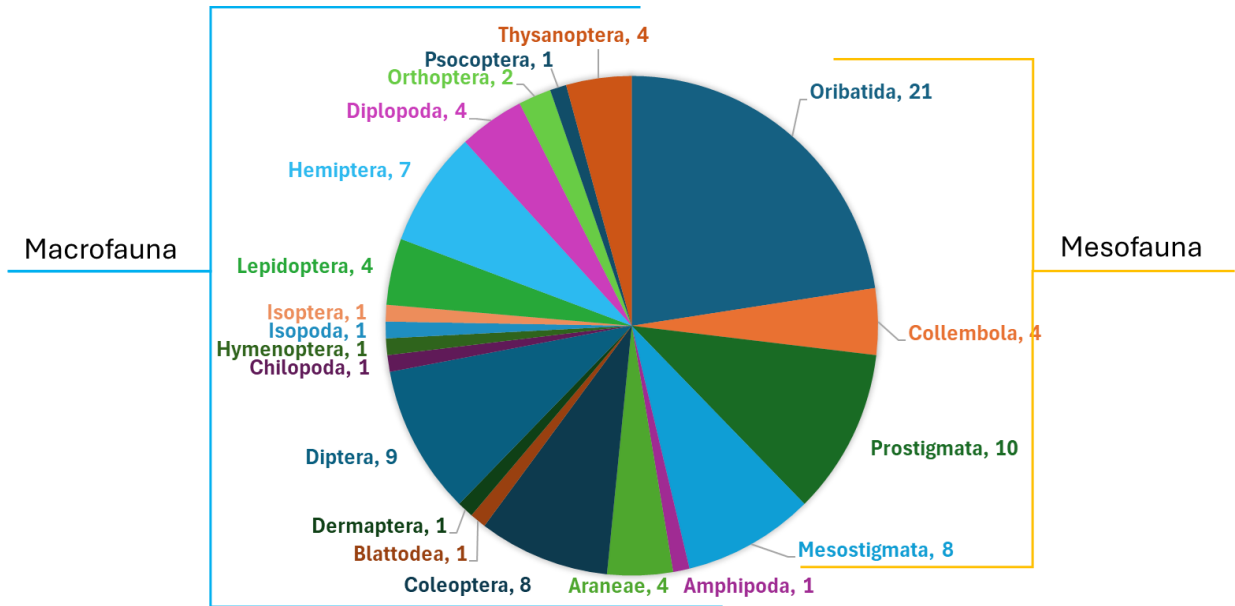


Figure 35: Total number of families identified by taxa. Within these categories, 93 families comprising 9,881 organisms were documented. The classes Collembola and Diplopoda were further subdivided into two subgroups each: the suborders Arthropleona and Symphypleona for Collembola; and the orders Polyzoiniida and Spirobolida for Diplopoda. This resulted in a total of 22 taxonomic classifications.

Biodiversity variations, classified into dominant, common, and rare taxa, were quantified across various vegetation functional types subject to differing hydroperiods (Table 21). Among all hydroperiods, common and rare taxa relative density exceeded the dominant groups across all functional types. The moist period exhibited the greatest relative density of common taxa among all vegetation types, with observed percentages of 66.7% for

¹⁰ Soil fauna classification by body width and the degree of presence in soil microhabitats 1) mesofauna (size ranges between 100 µm to 2 mm), 2) macrofauna (organisms larger than 2 mm).

ferns, 60.0% for grasses and shrubs, and 68.4% for trees. The highest relative densities for rare taxa groups were quantified under wet conditions, while the flood period was for dominant taxa, with rare taxa presenting values of 36.84% for ferns, 42.86% for grasses, 33.33% for shrubs, and 42.11% for trees, and dominant groups exhibited densities of 23.08% for ferns, 15.38% for grasses, 27.27% for shrubs, and 18.18% for trees.

In the moist period, notable common taxa included Arthropleona and Hemiptera for both fern and tree vegetation types, Coleoptera and Prostigmata for grasses, and Arthropleona and Mesostigmata for shrubs. During wet conditions distinct rare taxa include Lepidoptera and Thysanoptera for ferns; Araneae, Hymenoptera and Isopoda for grasses; Hymenoptera and Hemiptera for shrubs, alongside Araneae, Hymenoptera and Psocoptera for trees. It is noteworthy that Oribatida maintained dominance across all hydroperiods within all vegetation functional types, while Arthropleona was predominant during both flood and wet periods (Figure 36).

Table 17: Biodiversity variations, classified into dominant, common, and rare taxa, across various vegetation functional types subject to differing hydroperiods.

Taxa	Flood				Moderate Dry				Moist				Wet			
	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree
Amphipoda	0.3%								1.2%			1.8%	1.3%	0.1%		0.3%
Araneae	0.5%	0.4%	0.3%	0.3%	1.1%	1.5%	0.7%	0.8%	1.7%	2.1%	1.0%	2.1%	1.8%	0.6%	2.5%	0.6%
Arthropleona	14.5%	20.0%	14.3%	30.4%	3.2%	2.6%	14.0%	3.3%	9.7%	39.1%	6.4%	7.9%	25.8%	40.2%	15.6%	22.1%
Blattodea					0.2%	0.4%		0.3%	0.2%	0.3%		0.6%				0.1%
Coleoptera	6.3%	4.2%	3.6%	8.7%	1.5%	4.6%		4.3%	3.1%	5.6%	1.9%	5.9%	5.0%	4.9%	3.9%	4.7%
Dermoptera		0.1%			0.2%	0.4%	0.7%			0.5%	0.6%	0.3%	0.4%			
Diptera	10.6%	4.3%	4.8%	6.4%	4.2%	4.0%	1.3%	4.3%	3.5%	2.1%	2.2%	3.2%	8.9%	3.1%	3.2%	7.1%
Geophilomorpha						0.2%	0.7%	0.3%	0.7%		0.3%	0.3%				0.1%
Hemiptera	0.7%	1.3%		0.4%	1.7%	1.6%	1.3%	2.0%	9.9%	3.5%	1.9%	5.0%	2.5%	4.0%	0.5%	1.8%
Hymenoptera	0.7%	2.2%	13.4%	1.1%	12.9%	5.5%	1.3%	1.0%	2.6%	3.2%	2.2%	4.4%	1.2%	0.6%	0.7%	0.6%
Isopoda					3.4%	0.2%	3.3%	1.5%	4.5%	0.3%	13.8%	7.4%	4.2%	0.6%	5.4%	1.8%
Isoptera					0.2%					1.9%	0.3%					
Lepidoptera								1.0%	1.2%		0.6%	1.2%	0.6%	0.3%	0.2%	1.1%
Mesostigmata	2.0%	3.6%	8.7%	6.3%	13.1%	7.9%	12.0%	5.8%	5.7%	2.7%	6.1%	1.5%	7.3%	5.9%	10.9%	7.7%
Oribatida	59.0%	56.6%	46.9%	43.4%	51.7%	64.7%	61.3%	55.4%	48.3%	32.7%	59.3%	50.3%	30.7%	31.6%	41.3%	39.3%
Orthoptera													0.2%			
Polyzoniida						1.1%	0.7%					0.3%	0.1%			0.2%
Prostigmata	4.3%	5.3%	4.2%	1.8%	2.1%	3.1%	2.7%	6.8%	4.2%	4.3%	2.2%	4.1%	6.2%	2.8%	7.5%	7.8%
Psocoptera		0.1%			3.4%	0.9%		12.5%	0.5%	0.3%		0.9%	0.4%		3.0%	0.6%
Spirobolida	0.3%	0.4%	0.9%	0.2%	0.2%	0.7%		0.5%	0.2%	1.3%		1.8%	0.4%	0.3%	0.2%	0.2%
Symphyleona	0.8%	1.3%	2.7%	1.0%		0.4%		0.3%	0.5%				2.2%	4.9%	3.5%	2.9%
Thysanoptera	0.1%		0.3%		0.8%	0.4%		0.3%	2.4%		1.0%	1.2%	0.8%		1.8%	1.0%
Dominant	23.08%	15.38%	27.27%	18.18%	18.75%	5.56%	25.00%	11.76%	5.56%	13.33%	13.33%	5.26%	10.53%	14.29%	20.00%	10.53%
Rare	53.85%	30.77%	27.27%	36.36%	31.25%	44.44%	33.33%	35.29%	27.78%	26.67%	26.67%	26.32%	36.84%	42.86%	33.33%	42.11%
Common	23.08%	53.85%	45.45%	45.45%	50.00%	50.00%	41.67%	52.94%	66.67%	60.00%	60.00%	68.42%	52.63%	28.57%	46.67%	47.37%
Richness	13	13	11	11	16	18	12	17	18	15	15	19	19	14	15	19
Abundance	761	694	335	1309	526	547	150	399	424	373	312	340	926	674	571	1540

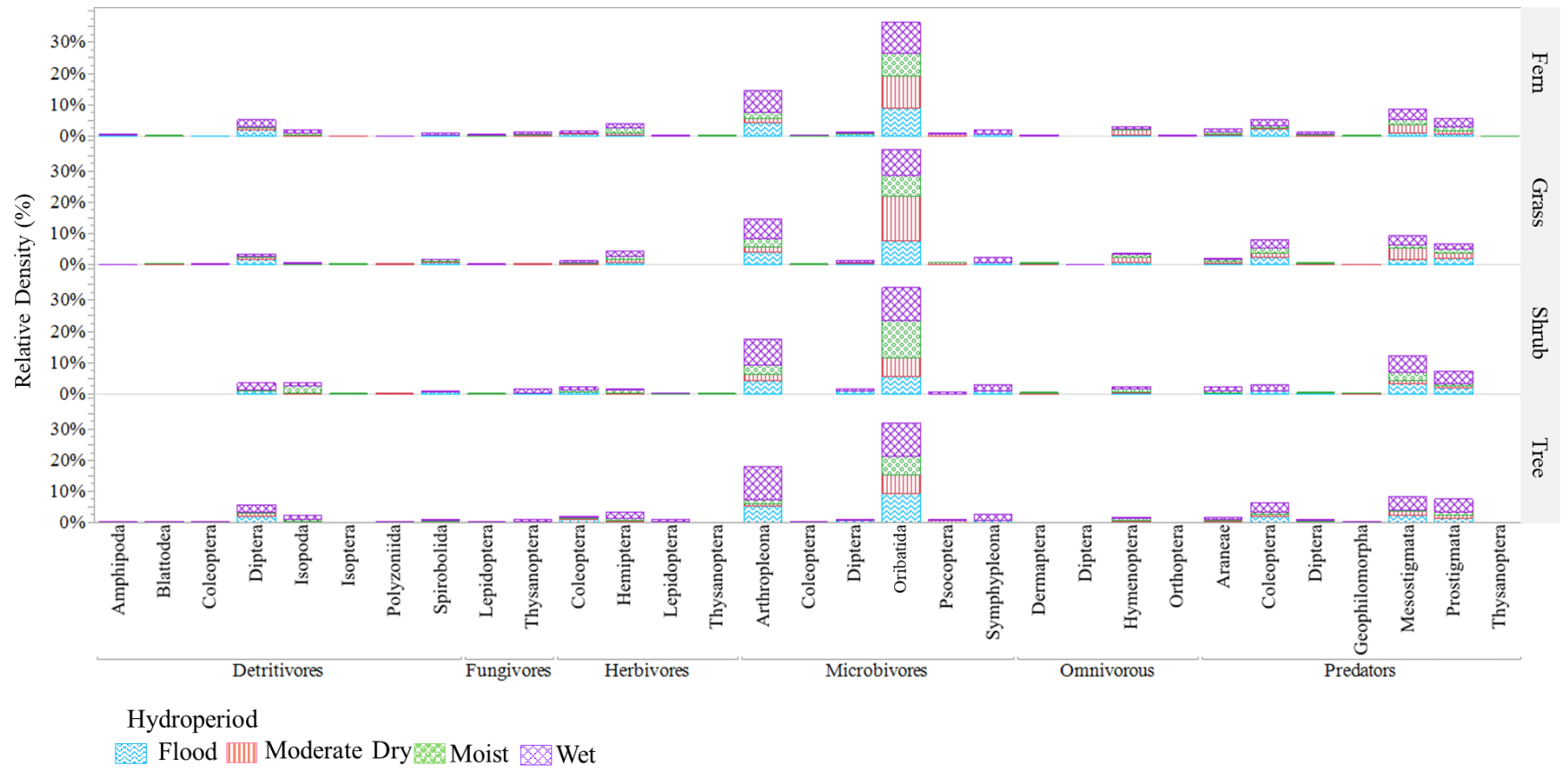


Figure 36: Soil arthropods assemblages and trophic structure across various vegetation functional types subject to differing hydroperiods.

Across all vegetation types and hydroperiods, seven taxonomic groups of soil arthropods were consistently present, establishing a similarity of approximately 32% among plants/hydroperiods (Figure 37). The remaining 68% of the taxa, which were not shared, contributed to assemblages' variations between types across hydroperiods. These non-shared groups included Amphipoda (scuds or side-swimmers), Blattodea (cockroaches), Coleoptera (beetles), Dermaptera (earwigs), Geophilomorpha (soil centipedes), Hemiptera (true bugs), Isopoda (woodlice), Isoptera (termites), Lepidoptera (moths and butterflies), Orthoptera (grasshoppers and crickets), Polyzoia (a group of millipedes), Psocoptera (barklice or booklice), Spirobolida (a group of millipedes), Symphypleona (a subgroup of springtails), and Thysanoptera (thrips).

The Bray-Curtis Index and Non-metric Multidimensional Scaling (NMDS) analyses revealed that the variations in assemblages between different types across hydroperiods yield the following combinations with the highest similarity, as illustrated in Figures 38 and 37: Fern-Flood and Grass-Flood (64%), Moderate Dry-Fern and Moderate Dry-Grass (74%), Wet-Fern and Wet-Grass (65%), Wet-Tree and Wet-Fern (65%), and Moist-Tree and Moist-Shrub (64%). Conversely, the combinations showing the least similarity include Wet-Tree and Moderate Dry-Shrub (16%), and Moderate Dry-Shrub and Flood-Tree (17%).

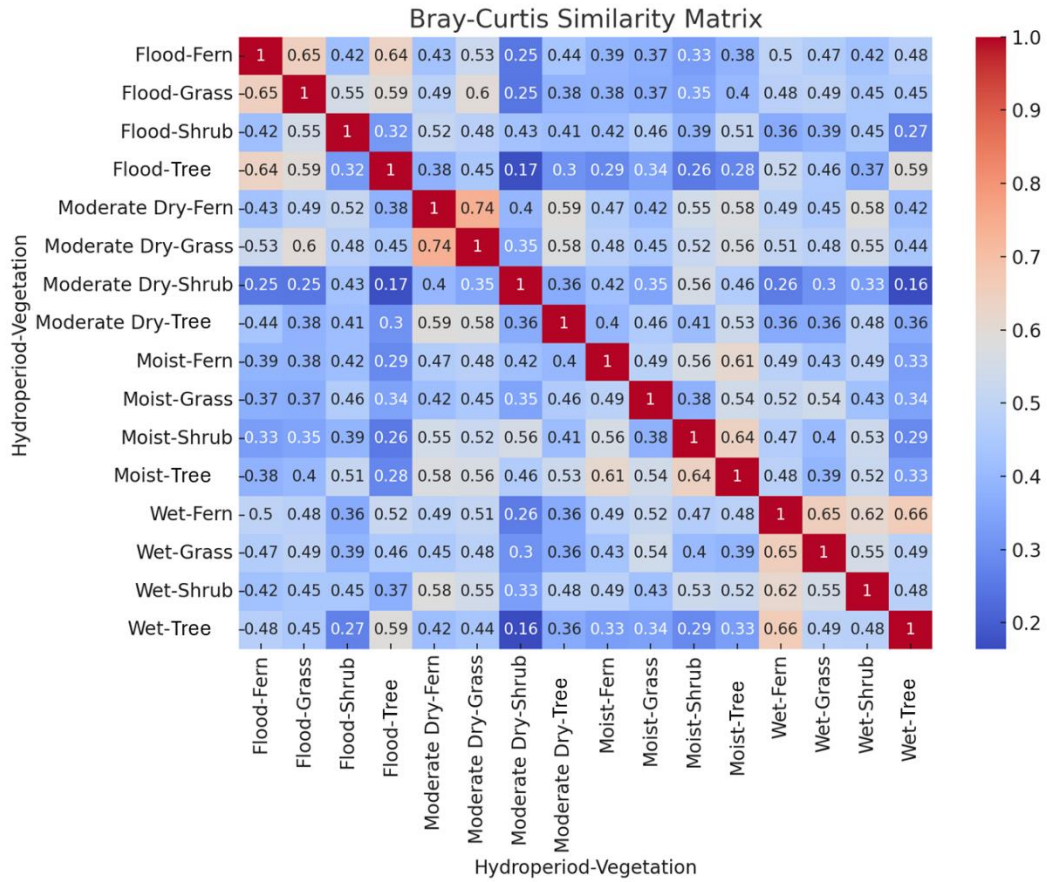


Figure 37: Bray-Curtis Similarity Matrix, which displays combinations of vegetation types and hydroperiods along with a gradient of color indicative of similarity among soil arthropod communities. Values approaching 1 are depicted in red, denoting higher similarity, while values closer to 0 are represented in blue, indicating greater dissimilarity.

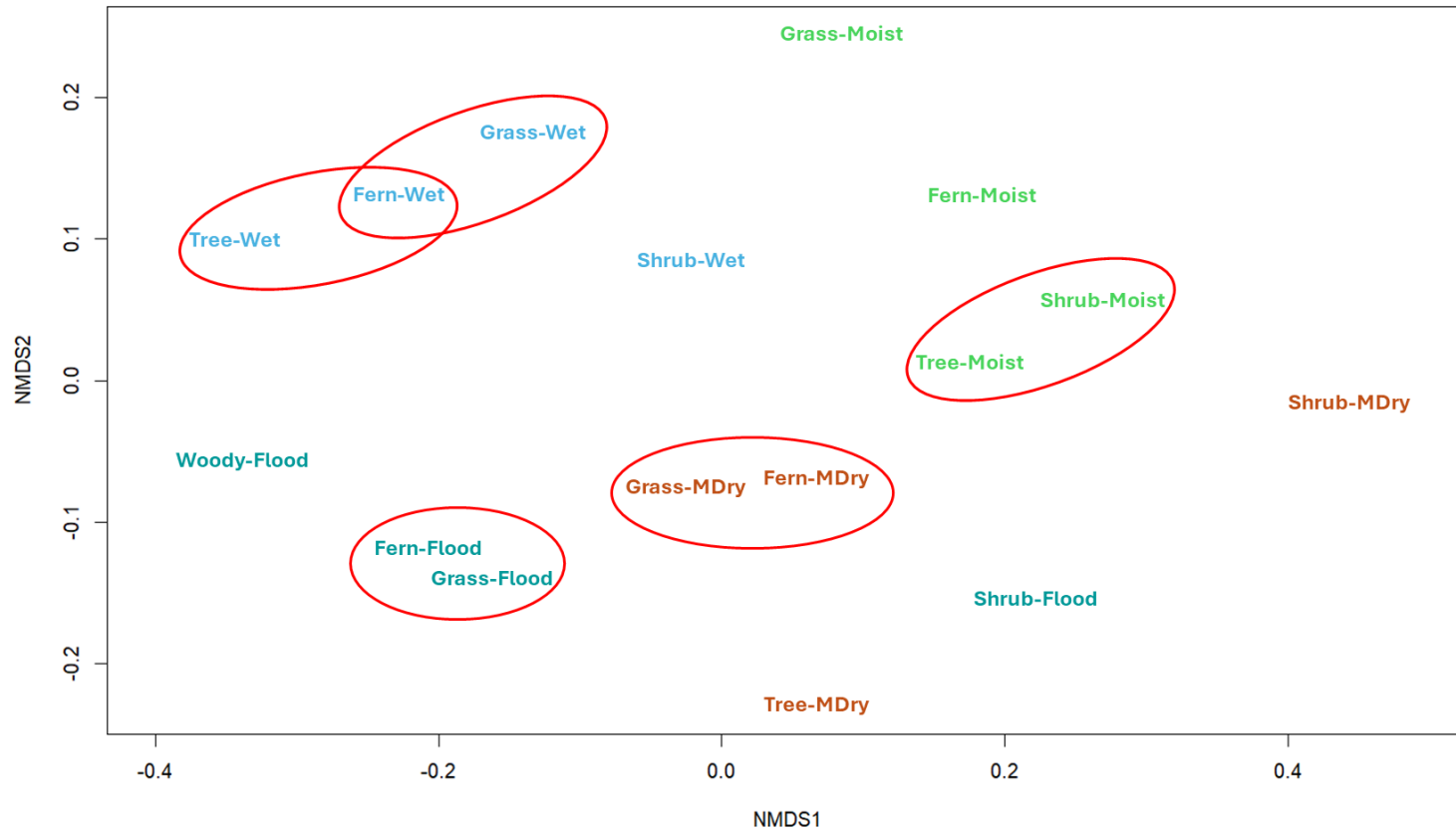


Figure 38: NMDS (Non-metric Multidimensional Scaling) analysis plot depicting the relationships between combinations of vegetation types and hydroperiods in terms of similarity among soil arthropod communities. Points that are closer together (red circles) indicate higher similarity, whereas points that are more distant from one another signify greater dissimilarity.

3.4.2.4 Combined effects of vegetation types and hydroperiods on the community composition and structure of soil arthropods

The PERMANOVA and Multi-Response Permutation Procedure (MRPP) analyses reveal significant variations in soil arthropods assemblages and trophic structure attributable to differences among hydroperiods and vegetation (Table 22 and 23, Appendix 3). The significant p-values obtained from the PERMANOVA analysis (Hydroperiod: $p = 0.0$; Vegetation: $p = 0.01$) indicate that both factors distinctly influence the community composition. Hydroperiods account for 43.0% of the total observed variation, while vegetation functional type explains 22% of the variation. These results are echoed by the MRPP analysis, where the overall significance of delta ($p = 0.001$) underscores notable variations in trophic level composition. The MRPP analysis identified combinations with a high degree of dissimilarity (high delta values) in community structure within plant types, such as Shrub in Moderate Dry conditions at the Microbivores trophic level (delta = 6.17), and in Wet conditions at the Omnivorous trophic level (delta = 5.29). Fern in Moist conditions at the Microbivores trophic level (delta = 4.36), and in Flood conditions at the Detritivores trophic level (delta=3.44). Conversely, more similar combinations include Grass in Flood conditions at the Fungivores trophic level and Shrub in Wet conditions at the Herbivores trophic level, both with a delta of 0.00, and Fern in Moist conditions at the Fungivores trophic level (delta = 0.22).

Table 18: PERMANOVA analysis, which reveals statistically significant differences in the community composition of soil arthropods. These differences are attributable to variations among hydroperiods and vegetation functional types.

Factors	Degrees of Freedom	Sum of squares	R ²	F-statistics	Level of significance
Hydroperiod	3	1.01	0.42	3.55	0.01
Vegetation	3	0.52	0.22	1.81	0.01
Residual	9	0.85	0.36		
Total	15	2.38	1		

Table 19: Multi-Response Permutation Procedure (MRPP) analysis, which categorizes combinations by their degree of dissimilarity (indicated by high delta values) or similarity (indicated by low delta values) in trophic level composition between groups. Sample sizes (n) associated with each group denote the number of observations or data points utilized to evaluate the trophic level composition within each category.

Vegetation Type	Hydroperiod	Trophic Level	Delta (Δ)	n
Fern	Moist	Microbivores	4.36	152
	Flood	Detritivores	3.44	24
	Wet	Detritivores	2.68	41
	Moderate Dry	Herbivores	2.52	19
	Moist	Detritivores	2.33	14
	Moderate Dry	Omnivorous	2.00	89
	Moderate Dry	Detritivores	1.83	18
	Moist	Fungivores	0.22	9
	Wet	Fungivores	0.17	12
Grass	Moist	Omnivorous	2.67	6
	Wet	Microbivores	2.12	125
	Moderate Dry	Detritivores	1.64	13
	Flood	Detritivores	1.07	8
	Flood	Detritivores	0.93	20
	Moist	Detritivores	0.77	13
	Moist	Herbivores	0.75	25
	Wet	Detritivores	0.70	14
	Flood	Fungivores	0.00	13
Wet	Fungivores	0.00	2	
Shrub	Moderate Dry	Microbivores	6.17	110
	Wet	Omnivorous	5.29	17
	Wet	Detritivores	2.77	18
	Flood	Detritivores	2.72	26
	Moist	Detritivores	2.69	16
	Moderate Dry	Detritivores	1.40	5
	Flood	Fungivores	1.00	7
Wet	Herbivores	0.00	17	
Tree	Moist	Microbivores	3.77	86
	Wet	Detritivores	2.63	52
	Wet	Omnivorous	1.60	5
	Moist	Detritivores	1.43	25
	Flood	Detritivores	1.18	14
	Moderate Dry	Detritivores	1.18	14
	Flood	Fungivores	1.16	11
	Moderate Dry	Herbivores	1.11	16
	Moist	Fungivores	0.86	11

3.5 DISCUSSION

This research elucidates the significant impact of plant functional types on soil arthropods community structure and composition. By investigating the effects of litter cover variations—particularly its quantity and quality—on soil arthropod assemblages across different wetland hydroperiods, our research addresses the pivotal question of how traits of plant-derived litter influence these assemblages. The findings offer a detailed insight into the ecological interconnections among plant litter attributes, environmental hydroperiod variations, and their collective effects on the biodiversity of soil arthropods. The study makes a valuable contribution to the broader ecological questions, emphasizing the critical role of vegetation in determining the dynamics of soil ecosystems.

3.5.1 Substrate Quality and Quantity Across Plant Functional Type and Hydroperiod

Significant variations in the contents of substrate fractions of carbon (C) and nitrogen (N), as well as in the carbon to nitrogen (C:N) ratios found under different plant functional types across hydroperiods, highlight the intricate relationships between vegetation and hydrological regimes. These relationships influence the quality and decomposition rate of plant litter, which varies among functional types, affecting the accumulation or depletion of soil nutrients. This underlines the complexity of soil ecosystems and the critical role of decomposition processes in shaping the habitat and nutrient availability for soil arthropods. C:N ratios within old litter-organic soil fractions were significantly lower compared to those in loose litter fractions, a pattern consistent across all plant types and hydroperiods. Such distinctions suggest varying decomposition stages or nutrient release patterns between the two soil fractions, contributing to a diverse mosaic of substrate qualities that influence soil arthropod dynamics (Moore et al., 2004;

Bastow, 2013). Upon comparing these metrics across plant functional types under various hydroperiods, the shrub type, a nitrogen-fixing plant, consistently exhibited the highest carbon (C) and nitrogen (N) percentages under all conditions, indicating a richer nutrient profile in their litter compared to other types. This enhanced nutrient availability can accelerate microbial decomposition processes and subsequently influence soil nutrient dynamics. In contrast, trees exhibited the highest carbon-to-nitrogen (C:N) ratios, marking them significantly different from other plant functional types. These high C:N ratios are indicative of a slower decomposition rate due to the more recalcitrant nature of their litter. High C:N ratios in tree litter result from a higher proportion of lignin and cellulose, which are more resistant to rapid breakdown and thus persist longer in the soil. The differentiation in litter quality among plant types highlights unique traits that significantly influence soil arthropod communities by modulating their interactions within the decomposition process. Litter quality is determined by their chemical and structural characteristics, such as nitrogen, lignin, and cellulose content, which affect the rate and manner of decomposition. These characteristics give rise to two primary energetic channels for decomposition: the bacterial channel and the fungal channel, which in turn shape the trophic assemblages of soil arthropods communities. In low C:N ratio litter, where lignin and cellulose are less abundant, decomposition is typically dominated by bacteria. This leads to a rapid transformation cycle of carbon, creating an environment where bacteria, along with protozoa, nematodes, and earthworms, thrive. The abundance of these primary decomposers also supports a diverse array of predators that depend on them for food, further modulating the community structure. Conversely, high C:N ratio litter, characterized by a higher content of complex compounds such as

lignin, humic or phenolic acids, and cellulose, tends to decompose more slowly. This slower process is primarily facilitated by fungi, which can break down these resistant compounds. As a result, the fungal decomposition channel becomes more prominent, supporting a different structure of soil organisms, predominantly consisting of mesofauna such as mites and springtails. Thus, the quality of litter, dictated by the type of plant and its litter's chemical and structural properties, plays a crucial role in determining the decomposition pathways and the associated trophic interactions among soil arthropods.

The results underscored the significant influence of hydroperiods on both the mass and composition of plant litter. A marked increase in plant litter mass was observed during moderate dry periods across all examined vegetation types, with the most substantial accumulations being recorded in microenvironments dominated by trees and shrubs. This pronounced accumulation can be attributed to the specific characteristics of leaf fall and senescence associated with these plant types. Trees and shrubs typically undergo a distinct leaf-fall season, which is notably observed in mangrove forests where seasonal patterns of leaf litter production are prominent during warmer months, often associated with air temperature increases (Shang et al., 2015, as cited in Medina, 2024). This phenomenon contributes significantly to the litter mass, as observed in various ecosystems (Box, 1981). Unlike trees and shrubs, grasses and ferns do not have a distinct leaf-fall season (Box, 1981; Wardle et. al., 2006). They continuously grow new leaves from the base while older leaves die off gradually. This growth pattern results in a more constant but less noticeable contribution to the litter layer. Furthermore, the study revealed that during moist and flood periods, there was a notable redistribution of litter, particularly around ferns and grasses (Figure 30). Given the diverse decomposition rates

of these residues, attributable to their distinct chemical compositions (Table 15), this redistribution leads to heterogeneous decomposition rates beneath both fern and grass vegetation. The distinct leaf fall, litter redistribution, and decomposition patterns associated to these plant types at the study site, contribute to the spatial variability in litter quantity and quality.

3.5.2 Influence of Loose Litter Mass, Carbon and Nitrogen Content, and C:N Ratio on Soil Arthropods Communities

Loose litter mass, substrate carbon (%C) and nitrogen (%N) content demonstrate statistically significant correlations with the richness and abundance of soil arthropods, each influencing ecological metrics in distinct ways. Although %C exhibits relatively smaller coefficients (0.01 for richness and 0.02 for abundance), its significant impact, highlighted by high t-values (13.70 for richness and 4.29 for abundance), suggests that even minor increases in carbon content can significantly affect species metrics.

Conversely, litter mass exerts a more substantial quantitative effect with coefficients of 0.20 for richness and 0.93 for abundance, underlining its vital role in enhancing ecological diversity and abundance through nutrient provision and habitat creation. %N exhibits a dual effect on these ecological parameters. While it positively influences species abundance—likely due to its role in enhancing growth and reproductive rates among microflora, which soil arthropods help to regulate—it adversely affects arthropod richness. This negative impact could lead to reduced ecological diversity due to the competitive exclusion of less dominant species. The substantial difference in the t-values for %N's impact on abundance (1.97) versus richness (-7.8) underscores its complex role in ecological dynamics, suggesting that its effects are context-dependent and may vary across different ecological or environmental conditions.

The effect of the C:N ratio on soil arthropod communities, across trophic guilds such as detritivores, fungivores, herbivores, microbivores, omnivores, and predators, offers insightful observations into ecosystem dynamics. Densities of soil arthropod trophic guilds were notably higher within the equilibrium phase (C:N ratio between 20:1 and 30:1) and the immobilization phase (C:N ratio >30:1) of decomposition, with no significant differences observed either between these phases or among the trophic guilds within them. This pattern underscores the indirect influence of C:N ratios on soil arthropods by affecting the availability of microbial communities, thereby shaping the conditions that support a diverse spectrum of soil arthropods and sustain high densities across various trophic guilds (Bastow, 2013; Lavelle et. al., 2006; Swift et. al. 1979).

The distinct separation from the mineralization phase (C:N ratio < 20:1) highlights the sensitivity of soil arthropod communities to nitrogen availability, suggesting that nitrogen's role in this context is mediated significantly by its effects on microbial decomposition processes and the subsequent availability of nutrients. In environments where nitrogen is more readily available for mineralization, significant shifts occur in the composition and interaction patterns among detritivores, fungivores, herbivores, microbivores, omnivores, and predators (Figure 39; Bastow, 2013; Lavelle et. al., 2006; Swift et. al. 1979). The observed statistical differences within the mineralization phase, especially among herbivores, detritivores, and microbivores, as well as between microbivores and predators, highlight the nuanced changes in food web dynamics under nitrogen-rich conditions. These variances may point to competition for resources, as well as potential shifts in predator-prey relationships (Wardle et.al., 2006). Furthermore, it emphasizes the critical role of primary and secondary decomposers, such as detritivores

(Diplopoda, Blattodea) and microbivores (Oribatida and Collembola), in the initial stages of loose litter decomposition through mechanical and physical management, setting the

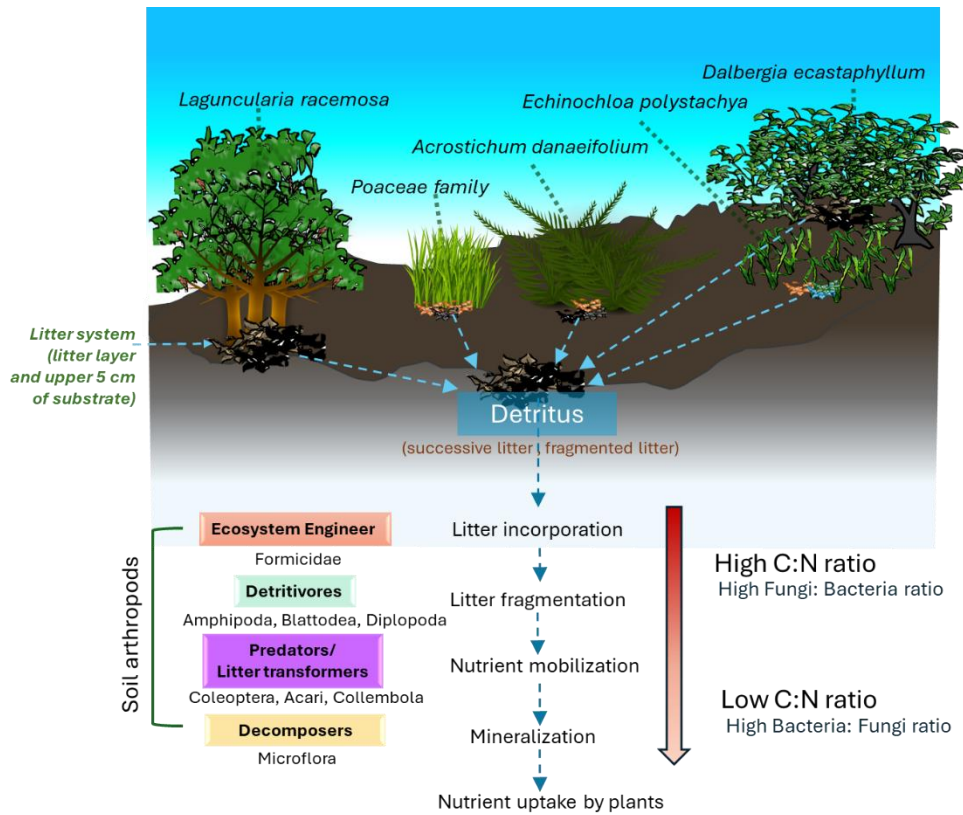


Figure 39: Soil arthropods belonging to different functional groups (groups of species with similar traits and effects on processes) involve in carbon and nutrient mobilization from litter (dead plant residues). Adapted from Bastow, 2013.

stage for microbial action and further decomposition (Bastow, 2013; Lavelle et. al., 2006; Swift et. al. 1979).

3.5.3 Hydroperiod Influences on Soil Arthropod Diversity Across Vegetation Types

The two-way non-parametric analysis revealed significant dependencies of soil arthropods on their microhabitats (plant functional types), which vary with hydrological conditions (Figure 33 and 34). This variability underscores the complex interplay between hydrological conditions, plant functional types, and faunal diversity for both mesofauna and macrofauna.

Macrofauna densities significantly increased within fern, grass, and tree vegetation types during the flood and wet hydroperiods, including Detritivores (Diptera, Isopoda), Predators (Coleoptera, Araneae), Omnivores (Formicidae), and Herbivores (Hemiptera). Conversely, mesofauna densities were higher during flood, wet, and moist hydroperiods, particularly within grass and shrub vegetation types, with the highest densities observed in tree vegetation types during the flood period. This included Microbivores (Oribatida, Collembola-Arthropleona) and Predators (Mesostigmata, Prostigmata). These distribution pattern can likely be attributed to the enhanced availability of habitats and resources¹¹ inherent to each vegetation type, driven by fluctuations in substrate quality and quantity (Wardle et al., 2006; Barberena-Arias & Cuevas, 2018; Moore et al., 1991; Swift et al., 1979). These fluctuations are intricately connected to the effects of the hydrological regime before the sampling intervals on litter redistribution (Bardgett et. al., 2014; Batzer et. al., 2006).

The timing of the flood sampling aligned with the receding floodwaters following significant atmospheric events, leading to prolonged flooding. The moist period sampling occurred during a dry interval between flood events, while the wet hydroperiod was marked by a series of flooding and drying cycles preceding the sampling. Variations in these wetting cycles led to the redistribution of both loose and decomposed plant litter, creating patches of fresh and aged organic material from various plant sources, notably under fern and grass vegetation types (Figure 30) (Bardgett et. al., 2014; Batzer et. al., 2006). This redistribution induced notable variations in substrate Carbon to Nitrogen

¹¹ The fluctuations in substrate quality and quantity influence the types and availability of food resources, as well as shelter for soil fauna.

(C:N) ratios across different vegetation types, linked to different decomposition stages, from immobilization and an equilibrium phase to mineralization (Figure 28 and Table 18).

The mixing of litter and the presence of diverse decomposition stages prompted shifts in microflora communities, ranging from fungi, which break down more recalcitrant resources (such as cellulose and lignin), to bacteria that decompose more readily available components (Figure 39). This bacterial and fungal succession influences the composition of soil arthropod communities, which undergo significant changes as decomposition progresses. Initially, surface-dwelling macrofauna predominated, facilitating the physical breakdown of litter. As decomposition continues, the community composition shifts towards a dominance of soil-dwelling mesofauna, well-adapted to exploit the microhabitats created by litter breakdown (Figure 39; Bastow, 2013; Barberena-Arias & Cuevas, 2018; Moore et al., 1991; Swift et al., 1979).

Regarding soil arthropods' richness and Menhinick's Index, further analysis illustrates significant variations among macrofauna and mesofauna groups within the contexts of fern, shrub, and tree functional types exhibiting higher values during the wet, flood and moist periods, respectively. In contrast, grass types exhibited significantly higher values under moderate dry conditions. This variation underscores the adaptive strategies employed by different faunal groups in response to resource and habitat availability (Bastow, 2013; Lavelle et. al., 2006; Swift et. al. 1979). Certain groups seem to prefer drier conditions with abundance of resources (litter mass) (Peng et.al., 2023), which typify the moderate dry phase, succeeding months of reduced precipitation. It should be emphasized that shrub vegetation exhibited higher diversity during moist and flood

periods for both mesofauna and macrofauna. This suggests that shrubs play a crucial functional role in aiding the recovery of microhabitats for other vegetation types following disturbances.

The patterns of density, richness, and diversity among soil arthropods reveal a distinct interaction between faunal assemblages and their microhabitat conditions, emphasizing the importance of temporal changes in resource availability on biodiversity patterns. In the case of fern and grass vegetation types, these variations are influenced by litter mixing beneath them, where loose litter from shrubs and trees predominates following flooding events.

3.5.4 Relationships between soil arthropod taxa and the combined effects of plant functional types and hydroperiods.

Biodiversity variations, classified into dominant, common, and rare taxa provided a distinctive understanding of species distribution across varying hydroperiods. The analysis revealed that common and rare taxa consistently outnumbered the dominant groups in all functional vegetation types across the different hydroperiods (Table 21 and Figure 36), suggesting a high level of ecological diversity and niche specialization within these ecosystems. This diversity suggests efficient niche utilization and conditions of high-quality soil that are resilient to disturbances (Briones, 2018; Menta et al., 2020; Wardle et al., 2006). Sampling during the moist period, conducted immediately after the recession of floodwaters, revealed the greatest relative density of common taxa across all vegetation types (64% mean value), including diverse taxonomic groups such as Predators (Araneae, Coleoptera, Mesostigmata, Prostigmata), Detritivores (Diptera), Herbivores (Hemiptera), and Omnivores (Hymenoptera). The moist period can be seen as

an early stage of ecological succession following the disturbance created by flooding. Early successional stages are often characterized by a higher presence of opportunistic species that can quickly take advantage of changing conditions (Cuevas, 2024). The presence of exposed, nutrient-rich litter post-flooding provides an ideal environment for rapid colonization and growth (Batzer et. al., 2006; Mulder et. al., 2009; Yang et.al., 2022). Common taxa, with their generalist ecological requirements, are particularly well-equipped to prosper under such conditions (Dee et.al., 2019). Their capacity for rapid response and recovery, attributed to characteristics like large body size, dormancy in egg stage and high mobility, that enables species to quickly immigrate or recolonize sites post-flooding, and versatile dietary preferences, allows them to effectively utilize the newly available resources (Coyle et. al., 2017; Bardgett et. al., 2014; Gerisch et. al., 2012). These traits play a pivotal role in ecosystem stability and recovery following disturbances. Furthermore, disturbances lead to the convergence of species traits due to uneven resource exploitation, thereby enhancing the ability of these adaptable taxa to fill available ecological niches amid low functional evenness (Coyle et. al., 2017; Wardle, 2022). Such dynamics during the critical window for ecosystem recovery and diversification highlight the significant impact of post-disturbance phases on community composition and biodiversity.

In the wet sampling period, characterized by alternating flooding and drying cycles leading up to the sample collection, we observed the highest relative densities of rare taxa groups, averaging 39%. This period included a wide array of taxonomic groups, such as Predators (Araneae), Detritivores (Amphipoda, Spirobolida, Polyzoniida), Herbivores (Lepidoptera), Microbivores (Psocoptera), and Omnivores (Hymenoptera). The

predominance of these rare taxa may be attributed to the specific environmental conditions prevalent during the wet period, which likely included a mix of detritus at various stages of decomposition due to the preceding cycles of prolonged drying and shorter flooding (Appendix 6). This variability in detritus quality and quantity, further compounded by the unique litter traits of different plant functional types, may have created specialized niches. Rare taxa, though fewer in number, possess a unique combination of traits that enable them to exploit these niches, thriving in habitats or fulfilling dietary requirements not readily available to more generalized species (Dee et.al., 2019). Their success during this period underscores the complex interplay between hydrological dynamics, litter traits, and biodiversity, highlighting how specific environmental conditions can facilitate the flourishing of specialized organisms within soil ecosystems. During these intermediate stages, a gradual increase in diversity occurs as rare species begin to establish, supported by the stabilizing environment. This phase marks a critical period in ecological succession, where the conditions become increasingly conducive for a broader array of species to thrive, further enriching the ecosystem's complexity and resilience.

It's important to note that some taxa appear both as common and rare across different sampling periods, reflecting their adaptive strategies and ecological plasticity. These species possess a broad range of ecological tolerances that allow them to quickly capitalize on the post-flood abundance of resources, yet their presence as 'rare' in other periods indicates a sensitivity to changing environmental dynamics, such as alternating wet and dry conditions. This duality underscores the complexity of ecological niches and

the flexibility of species in responding to the mosaic of habitat conditions presented by varying hydroperiods.

The dominant taxa, characterized by Oribatida mites (Microbivores), account for an average of 48% across various vegetation types and hydroperiods (Table 22 and Figure 36). This significant dominance underscores their resilience and adaptability to a wide range of environmental conditions, terrestrial, aquatic, and semi-aquatic, and establishes their critical role as keystone species in regulating decomposition processes, nutrient cycling, and overall soil health (Behan-Pelletier et. al., 2023). They are instrumental within the soil food web, playing a pivotal role in shaping soil microbial communities, regulating their proliferation and diversity, and serving as a connecting node between microflora and a diverse array of invertebrate predators (Menta et. al., 2020; Potapov et. al., 2022). As the dominant group, Oribatida mites not only support ecosystem recovery and stability through their interactions within the soil food web but also play a vital role in preserving biodiversity and ecosystem services under varying environmental conditions.

Overall, vegetation types exhibit approximately 32% similarity in soil arthropod taxa across hydroperiods, underscoring the presence of distinct ecological communities among vegetation types, with a significant 68% of taxa unique to specific assemblages. This diversity includes non-shared groups such as Amphipoda, Blattodea, Coleoptera, Dermaptera, Geophilomorpha, Hemiptera, Isopoda, Isoptera, Lepidoptera, Orthoptera, Polyzoniida, Psocoptera, Spirobolida, Symphypleona, and Thysanoptera, highlighting the rich biodiversity within these ecosystems. The Bray-Curtis Index and Non-metric Multidimensional Scaling (NMDS) analyses further uncover significant patterns in these

community assemblages, revealing that combinations like Fern-Flood and Grass-Flood (64%), and Moderate Dry-Fern and Moderate Dry-Grass (74%), exhibit high similarity, in contrast to the low similarity observed between Wet-Tree and Moderate Dry-Shrub (16%). These findings emphasize the critical role that hydroperiods and vegetation types play in shaping the diversity and composition of soil arthropod communities, reflecting both the shared and unique environmental niches that these communities inhabit across different conditions.

3.5.5 Combined effects of vegetation types and hydroperiods on the community composition and structure of soil arthropods

The influence of hydroperiods and vegetation functional types on the assemblages and trophic structure of soil arthropods (Figure 40), explaining 43% and 22% of the observed variations, respectively, emphasizes the intricate bidirectional interactions between plant communities and soil arthropods, shaped by the wetland's hydrological conditions across time and space (Culliney, 2013; Batzer et al., 2006; Lavelle et al., 2001, 2006, 2022; Swift et al., 1979). Complex ecological structures predominate during wet hydroperiods, whereas simpler structures are characteristic of flood periods (Figure 40). This pattern emerges from the cumulative effects of interspecific differences on vegetation type substrates, including their chemical and structural compositions, as well as hydrological regimes.

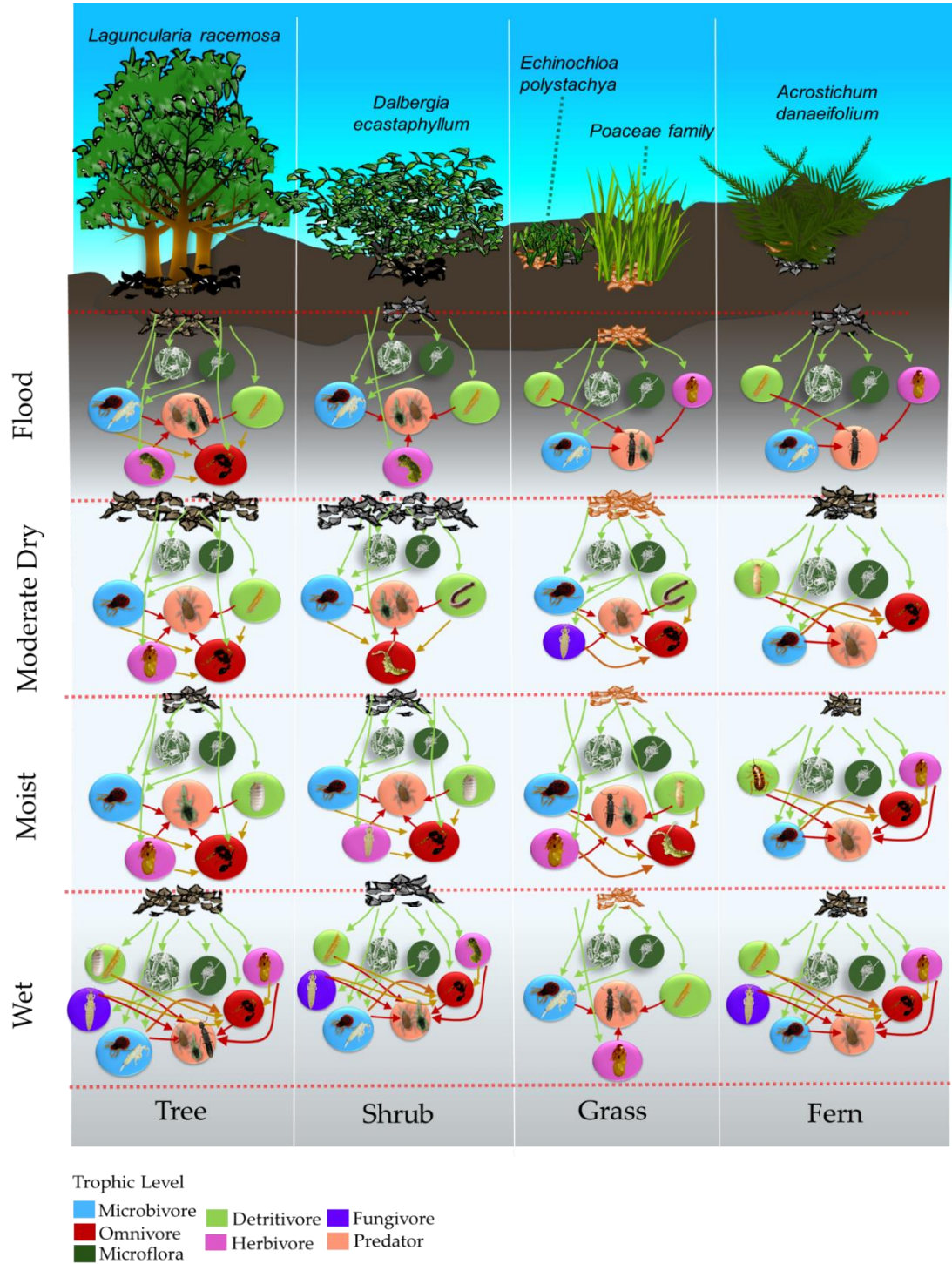


Figure 40: Soil arthropods community structure across vegetation types among hydroperiods.

Significant dissimilarities in community structure among different conditions were detected in combinations such as Shrub in Moderate Dry conditions at the Microbivores trophic level ($\Delta = 6.17$), Fern in Moist conditions at the Microbivores level ($\Delta = 4.36$), and Shrub in Wet conditions at the Omnivorous level ($\Delta = 5.29$). These variations are attributable to the adaptation and specialization of arthropod communities within their unique habitats. In contrast, more homogeneous community structures were observed in specific conditions, such as Fern in Moist conditions at the Fungivore level ($\Delta = 0.22$), suggesting that certain environmental conditions, particularly those following disturbance events, may promote more uniform community structures. Within the framework of soil ecosystems and the decomposition food web dynamics, the impact of disturbances on substrate availability and quality significantly influencing the activity of fungi on less labile (more difficult to decompose) materials. Such post-disturbance conditions create specific ecological niches that favor fungivores, as these organisms feed on and regulate fungal resources. Furthermore, the creation of new niches and resources, following disturbances, establishes fertile grounds for colonization, thereby encouraging the formation of more homogeneous community structures among soil-dwelling organisms, including fungivores (Coyle et. al., 2017; Gerisch et. al., 2012).

3.5.6 Findings in Relation to Objectives, Questions, and Hypotheses

Soil biota's reactions to variations in vegetation types and hydroperiods can be attributed to several mechanisms: 1) Variations in resource quantity and quality due to interspecific differences, 2) the interplay of bottom-up and top-down dynamics, and 3) the creation and alteration of microhabitats (Wardle, 2002). The observed concomitant changes in the soil arthropods community structure and decomposition substrates C:N ratios indicate the

critical role resource quality in shaping microbial community availability and, consequently, supporting a diverse array of soil arthropods. Soil arthropod trophic guild densities peak in both the equilibrium (C:N ratio between 20:1 and 30:1) and immobilization (C:N ratio >30:1) phases of decomposition. The distinct separation from the mineralization phase (C:N ratio < 20:1) underscores a) soil arthropod communities' sensitivity to nitrogen availability, b) interactions and potential shifts in bottom-up and top-down regulatory mechanisms, c) the role of primary and secondary decomposers in ecosystem processes. There is a succession of taxa-dependent interactions related to decomposition stages, where, common, rare, and dominant groups interact, illustrating the complex interplay among different arthropod groups that contribute to the nitrogen cycling and organic matter breakdown in soil ecosystems. Common groups such as predators (Araneae, Coleoptera, Mesostigmata, Prostigmata), detritivores (Diptera), herbivores (Hemiptera), and omnivores (Hymenoptera), which colonize early in successional stages, are characterized by a higher presence of opportunistic taxa (Cuevas, 2024; Dee et.al., 2019). These taxa swiftly adapt to changing conditions, playing a vital role in contributing to ecosystem stability and recovery post-disturbance. Rare groups, including predators (Araneae), detritivores (Amphipoda, Spirobolida, Polyzoniida), herbivores (Lepidoptera), microbivores (Psocoptera), and omnivores (Hymenoptera), typically establish at intermediate stages. As these rare taxa begin to settle, a gradual increase in diversity is supported by the stabilizing environment, marking a critical period in ecological succession (Bastow, 2013). The presence of taxa in both common and rare categories across different hydroperiods highlights their ecological versatility and the nuanced balance between competition, adaptation, and specialization. Shifts in taxa

dominance and rarity accentuate the fluid nature of ecological communities, where taxa adjust their roles and abundances in response to the ever-changing environmental conditions and resource availability. The ongoing dialogue between taxa traits and ecosystem processes shapes the intricate web of life within these dynamic habitats. Dominant groups, particularly Oribatida mites (microbivores), emerge as key regulators of decomposition processes, nutrient cycling, and overall soil health, being instrumental within the soil food web by shaping soil microbial communities, regulating their proliferation and diversity, and acting as a bridge between microflora and various invertebrate predators (Behan-Pelletier et. al., 2023). The group interactions across vegetation and hydroperiods underline the integral role that each arthropod group—common, rare, and dominant—plays at different stages of decomposition, highlighting their collective contribution to the soil ecosystem's dynamics (Bastow, 2013; Dee et.al., 2019).

An observed increase in litter mass during moderate dry periods, coupled with its redistribution in flood and moist periods, identified trees and shrubs as major contributors to litter across all hydroperiods. Additionally, shrubs play a crucial functional role in aiding the recovery of microhabitats constituted by other vegetation types following disturbances within wetland ecosystems. Litter mass, carbon and nitrogen concentration are pivotal determinants of soil arthropod richness and abundance, with variations attributed to hydroperiods and plant functional types. The significant observed variations in soil arthropod diversity across different vegetation types and hydroperiods, collectively highlight the combined influence of plant-hydroperiod interactions on habitat and resource availability and its influence on soil arthropods assemblages and trophic

structure. Complex ecological structures predominate during wet hydroperiods, whereas simpler structures are characteristic of flood periods (Figure 38). This pattern emerges from the cumulative effects of interspecific differences on vegetation type substrates, including their chemical and structural compositions, as well as hydrological regimes. These interactions highlight the dynamic adaptability of soil arthropods to fluctuating microhabitat conditions and the functional role of plant-soil dynamics in the resilience of the wetland ecosystem.

3.6 CONCLUSIONS

This research contributes to a deeper understanding of the intricate ecological interconnections between plant litter attributes, environmental hydroperiods, and soil arthropod biodiversity. It underscores the integral role of vegetation and water in shaping soil ecosystem dynamics. The findings bolster the hypothesis that synchrony and synlocation of soil arthropod communities are influenced by the specific plant functional type and the characteristics of its associated litter, with hydroperiod dynamics playing a crucial role. Directly addressing the research question regarding the modulation of arthropod assemblages by plant-derived litter characteristics, providing new insights into the ecological interconnections that shape soil ecosystem dynamics.

By elucidating the complex interdependencies between plant functional types, litter quality and quantity, and soil arthropod assemblages, the study offers valuable insights for ecosystem management and conservation strategies aimed at preserving biodiversity and ecosystem functionality in wetland environments.

3.7 REFERENCES

- Alegre, J., Alonso-Blázquez, N., de Andrés, E. et al. Revegetation and reclamation of soils using wild leguminous shrubs in cold semiarid Mediterranean conditions: Litterfall and carbon and nitrogen returns under two aridity regimes. *Plant and Soil* 263, 203–212 (2004).
<https://doi.org/10.1023/B:PLSO.0000047735.73030.41>
- Barberena-Arias, F. M., Cuevas, E. (2018). Physicochemical Foliar Traits Predict Assemblages of Litter / Humus Detritivore Arthropods, 1–20.
[DOI:10.5772/intechopen.75076](https://doi.org/10.5772/intechopen.75076)
- Barberena-Arias, F. M., & Cuevas, E. (2021). Vertical Arthropod Dynamics across Organic Matter Fractions in Relation to Microclimate and Plant Phenology.
[IntechOpen. doi: 10.5772/intechopen.94747](https://doi.org/10.5772/intechopen.94747)
- Bardgett, R. D., & Van Der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, 515(7528), 505-511. [doi:10.1038/nature13855](https://doi.org/10.1038/nature13855)
- Bastow, J. (2013). Succession, resource processing, and diversity in detrital food webs. In D.H. Wall (Ed.), *Soil Ecology and Ecosystem Services*. Oxford Academic.
<https://doi.org/10.1093/acprof:oso/9780199575923.003.0013>
- Batzer, P. D, Sharitz, R.R. (2006). *Ecology of Freshwater and Estuarine Wetlands*. The University of California.
- Batzer, D., Wu, H., Wheeler, T., & Eggert, S. (2016). Peatland invertebrates. In: Batzer, D.P., Boix, D. (Eds.), *Invertebrates in Freshwater Wetlands*. pp. 219–250. Springer International Publishing, Cham, Switzerland.
https://doi.org/10.1007/978-3-319-24978-0_7
- Batzer, D. P., & Wu, H. (2020). Ecology of terrestrial arthropods in freshwater wetlands. *Annual Review of Entomology*, 65, 101-119. <https://doi.org/10.1146/annurev-ento-011019-024902>
- Behan-Pelletier, V., & Lindo, Z. (2023). *Oribatid Mites: Biodiversity, Taxonomy and Ecology*. CRC Press. <https://doi.org/10.1201/9781003214649>
- Box, E.O. (1981). *Macroclimate and plant forms* (Vol. 1). Springer, Dordrecht.
https://doi.org/10.1007/978-94-009-8680-0_1
- Briones, M. J. (2018). The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. *Frontiers in Environmental Science*, 6, 149.
<https://doi.org/10.3389/fenvs.2018.00149>
- Brust, G.E. (2019). Management strategies for organic vegetable fertility. In *Safety and Practice for Organic Food* (pp. 193-212). Academic Press.
<https://doi.org/10.1016/B978-0-12-812060-6.00009-X>
- Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., ... & Callahan Jr, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, 110, 116-133.

- Coleman, D. C., & Wall, D. H. (2007). Fauna: the engine for microbial activity and transport. In *Soil microbiology, ecology, and biochemistry* (pp. 163-191). Academic Press. <https://doi.org/10.1016/B978-0-08-047514-1.50011-1>
- Cuevas, E. (2024). Personal communication. April 2, 2024.
- Culliney, T.W. (2013). Role of Arthropods In Maintaining Soil Fertility. *Plant Epidemiology and Risk Analysis Laboratory, Plant Protection, and Quarantine, Center for Plant Health Science and Technology, USDA-APHIS. Agriculture* 2013, 3, 629-659; [doi:10.3390/agriculture3040629](https://doi.org/10.3390/agriculture3040629)
- Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, 34(8), 746-758.
- Facelli, J. M., & Pickett, S. T. (1991). Plant litter: its dynamics and effects on plant community structure. *The botanical review*, 57, 1-32.
- García-Gómez, A., Castaño-Meneses, G., Vázquez-González, M. M., & Palacios-Vargas, J. G. (2014). Mesofaunal arthropod diversity in shrub mangrove litter of Cozumel Island, Quintana Roo, México. *Applied Soil Ecology*, 83, 44-50. <https://doi.org/10.1016/j.apsoil.2014.04.007>
- Gerisch, M., Agostinelli, V., Henle, K. and Dziock, F. (2012), More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, 121: 508-515. <https://doi.org/10.1111/j.1600-0706.2011.19749.x>
- Gergócs, V., & Hufnagel, L. (2016). The effect of microarthropods on litter decomposition depends on litter quality. *European Journal of Soil Biology*, 75, 24-30.
- González, G., & Barberena, M. F. (2017). Ecology of soil arthropod fauna in tropical forests: A review of studies from Puerto Rico. *The Journal of Agriculture of the University of Puerto Rico*, 101(2), 185-201.
- Guo, J., Zhao, C., Zhang, L., Han, Y., Cao, R., Liu, Y., & Sun, S. (2022). Water table decline alters arthropod community structure by shifting plant communities and leaf nutrients in a Tibetan peatland. *Science of The Total Environment*, 814, 151944. <https://doi.org/10.1016/j.scitotenv.2021.151944>
- Haynert, K., Kiggen, M., Klarner, B., Maraun, M., & Scheu, S. (2017). The structure of salt marsh soil mesofauna food webs—The prevalence of disturbance. *PLoS One*, 12(12), e0189645. <https://doi.org/10.1371/journal.pone.0189645>
- Hernández, E. (2022). Ecophysiological responses of plant functional groups to environmental conditions in a coastal urban wetland, Ciénaga Las Cucharillas in Northeastern Puerto Rico. Dissertation. Ecolab. Department of Environmental Science. The University of Puerto Rico. <https://hdl.handle.net/11721/2860>
- Herrera, F., & Cuevas, E. (2003). Artrópodos del suelo como bioindicadores de recuperación de sistemas perturbados. *Venesuelos*, 11(1-2), 67-78.

- Krab, E. J., Berg, M. P., Aerts, R., van Logtestijn, R. S., & Cornelissen, J. H. (2013). Vascular plant litter input in subarctic peat bogs changes Collembola diets and decomposition patterns. *Soil Biology and Biochemistry*, 63, 106-115. <https://doi.org/10.1016/j.soilbio.2013.03.024>
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, 130-150. <http://dx.doi.org/10.2307/2389178>
- Lavelle, P. (1997). Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In *Advances in ecological research* (Vol. 27, pp. 93-132). Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60007-0](https://doi.org/10.1016/S0065-2504(08)60007-0)
- Lavelle, P., & Spain, A.V. (2001) *Soil Ecology*. Kluwer Academic Publishers, New York. <https://doi.org/10.1007/978-94-017-5279-4>
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European journal of soil biology*, 42, S3-S15. <https://doi.org/10.1016/j.ejsobi.2006.10.002>
- Lavelle, P., Mathieu, J., Spain, A., Brown, G., Fragoso, C., Lapied, E., & Zhang, C. (2022). Soil macroinvertebrate communities: A world-wide assessment. *Global Ecology and Biogeography*, 31(7), 1261-1276. [doi: 10.1111/geb.13492](https://doi.org/10.1111/geb.13492)
- Li, K., Bihan, M., Yooseph, S., & Methé, B.A. (2012). Analyses of the microbial diversity across the human microbiome. *PLoS One*, 7(6), e32118. <https://doi.org/10.1371/journal.pone.0032118>
- Liu, C., & Sun, X. (2013). A review of ecological stoichiometry: Basic knowledge and advances. *Reference Module in Earth Systems and Environmental Sciences*. Elsevier. <https://doi.org/10.1016/B978-0-12-409548-9.05519-6>
- Lockaby, B.G., Murphy, A.L., & Somers, G.L. (1996). Hydroperiod influences on nutrient dynamics in decomposing litter of a floodplain forest. *Soil Science Society of America Journal*, 60(4), 1267. <https://doi.org/10.2136/sssaj1996.03615995006000400039x>
- Lonard, R.I., Judd, F.W., DeYoe, H.R., & Stalter, R. (2020). Biology and ecology of the halophyte *Laguncularia racemosa* (L.) Gaertn. f.: A review. In M.N. Grigore (Ed.), *Handbook of Halophytes*. Springer, Cham. https://doi.org/10.1007/978-3-030-17854-3_71-1
- Medina E (2024). *Principios de ecofisiología vegetal*. Ediciones IVIC, Instituto Venezolano de Investigaciones Científicas. Caracas, Venezuela. 414 pp.
- Medina, E. (2024). Personal communication, April 22.
- Mehltreter, K., Walker, L. R., & Sharpe, J. M. (Eds.). (2010). *Fern ecology*. Cambridge University Press.
- Menta, C., & Remelli, S. (2020). Soil health and arthropods: From complex system to worthwhile investigation. *Insects*, 11(54). <https://doi.org/10.3390/insects11010054>

- Mitsch, W. J., Gosselink, J. G., Zhang, L., & Anderson, C. J. (2009). *Wetland ecosystems*. John Wiley & Sons.
- Moco, M.K.S., Gama-Rodrigues, E.F., Gama-Rodrigues, A.C., Machado, R.C., & Baligar, V.C. (2010). Relationships between invertebrate communities, litter quality, and soil attributes under different cacao agroforestry systems in the south of Bahia, Brazil. *Applied Soil Ecology*, 46(3), 347-354.
- Moore, J. C., & de Ruiter, P. C. (1991). Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. *Agriculture, ecosystems & environment*, 34(1-4), 371-397. [https://doi.org/10.1016/0167-8809\(91\)90122-E](https://doi.org/10.1016/0167-8809(91)90122-E)
- Mulder, C., Den Hollander, H. A., Vonk, J. A., Rossberg, A. G., op Akkerhuis, G. A. J., & Yeates, G. W. (2009). Soil resource supply influences faunal size-specific distributions in natural food webs. *Naturwissenschaften*, 96(7), 813. <https://doi.org/10.1007/s00114-009-0539-4>
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Native Plant Trust. (2024). Go Botany: Discover thousands of New England plants. <https://gobotany.nativeplanttrust.org/>
- Nielsen, U. N. (2019). *Soil fauna assemblages*. Cambridge University Press.
- Peng, Y., Vesterdal, L., Peñuelas, J., Peguero, G., Wu, Q., Heděnc, P., Yue, K. and Wu, F. (2023). Soil fauna effects on litter decomposition are better predicted by fauna communities within litterbags than by ambient soil fauna communities. *Plant Soil* 487, 49–59. <https://doi.org/10.1007/s11104-023-05902-1>
- Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., & Cornelissen, J.H.C. (2013). New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167-234. <https://doi.org/10.1071/BT12225>
- Potapov, A. M., Beaulieu, F., Birkhofer, K., Bluhm, S. L., Degtyarev, M. I., Devetter, M., ... & Scheu, S. (2022). Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biological Reviews*, 97(3), 1057-1117. <https://doi.org/10.1111/brv.12832>
- Potapov, A.M. (2022). Multifunctionality of belowground food webs: resource, size and spatial energy channels. *Biol Rev*, 97: 1691-1711. <https://doi.org/10.1111/brv.12857>

- Pradisty, N.A., Amir, A.A. & Zimmer, M. (2021). Plant species- and stage-specific differences in microbial decay of mangrove leaf litter: the older the better? *Oecologia* 195, 843–858. <https://doi.org/10.1007/s00442-021-04865-3>
- Schoenly, K., & Reid, W. (1987). Dynamics of Heterotrophic Succession in Carrion Arthropod Assemblages: Discrete Seres or a Continuum of Change? *Oecologia*, 73(2), 192–202. <http://www.jstor.org/stable/4218351>
- Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. M. (1979). Decomposition in terrestrial ecosystems (Vol. 5). Univ of California Press.
- Tongkaemkaew, U., Sukkul, J., Sumkhan, N., Panklang, P., Brauman, A., & Roslan Ismail, R. I. (2018). Litterfall, litter decomposition, soil macrofauna, and nutrient content in rubber monoculture and rubber-based agroforestry plantations. <http://dx.doi.org/10.24259/fs.v2i2.4431>
- Ward, S. E., Orwin, K. H., Ostle, N. J., Briones, M. J., Thomson, B. C., Griffiths, R. I., ... & Bardgett, R. D. (2015). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, 96(1), 113-123. <https://doi.org/10.1890/14-0292.1.sm>
- Wardle, D. A. (2002). *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. United Kingdom: Princeton University Press.
- Wardle, D. A.; Bardgett, R. D.; Klironomos, J. N.; Setälä, H.; Van Der Putten, W. H.; Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science* 2004, 304(5677), 1629–1633. <https://doi.org/10.1126/science.1094875>
- Wardle, D. A. (2006). The influence of biotic interactions on soil biodiversity. *Ecology letters*, 9(7), 870-886. <https://doi.org/10.1111/j.1461-0248.2006.00931.x>
- Wardle, D. A., Jonsson, M., Bansal, S., Bardgett, R. D., Gundale, M. J., & Metcalfe, D. B. (2012). Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of ecology*, 100(1), 16-30.
- Weilhoefer, C. L., Williams, D., Nguyen, I., Jakstis, K., & Fischer, C. (2017). The effects of reed canary grass (*Phalaris arundinacea* L.) on wetland habitat and arthropod community composition in an urban freshwater wetland. *Wetlands Ecology and Management*, 25, 159-175. <https://doi.org/10.1007/s11273-016-9508-5>
- Whigham, D. F., & Bayley, S. E. (1978). Nutrient dynamics in freshwater wetlands. *Wetland functions and values: The state of our understanding*.
- Yang, Y., Zhou, H., Wang, W., Zhu, C., Cui, D., & Ye, Z. (2022). Transient flooding and soil covering interfere with decomposition dynamics of *Populus euphratica* leaf litter: Changes of mass loss and stoichiometry of C, N, P, and K. *Forests*, 13(3), 476. <https://doi.org/10.3390/f13030476>
- Tan, Y., Yang, W., Ni, X., Tan, B., Yue, K., Cao, R., ... & Wu, F. (2019). Soil fauna affects the optical properties in alkaline solutions extracted (humic acid-like) from

forest litters during different phenological periods. Canadian journal of soil science, 99(2), 195-207.<https://doi.org/10.1139/cjss-2018-0081>

Zhang, L., Liu, J., Yin, R., et al. (2023). Soil fauna accelerated litter C and N release by improving litter quality across an elevational gradient. Ecological Processes, 12, 47. <https://doi.org/10.1186/s13717-023-00459-4>

Zheng, X., Wang, H., Tao, Y., Kou, X., He, C., & Wang, Z. (2022). Community diversity of soil meso-fauna indicates the impacts of oil exploitation on wetlands. Ecological Indicators, 144, 109451. <https://www.sciencedirect.com/science/article/pii/S1470160X22009244>

Appendix 3: Results of the Wilcoxon/Kruskal-Wallis analysis indicating significant differences in plant functional type carbon (C) and nitrogen (N) percentage contents, as well as the C:N ratio, across hydroperiods within loose litter and old litter-organic soil fractions. The "Score Mean" represents the average rank within each group, illustrating the ranks' central tendency. The "Standardized Score" indicates the deviation of the group's mean rank, serving as a measure of the group's relative position or deviation from the norm.

Flood																	
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil								
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree		
	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	
N% (mg/g)	285.67	2.36	284.15	2.06	373.39	7.36	171.17	-9.68	159.43	-0.96	193.84	2.57	286.73	7.97	125.92	-6.37	
C% (mg/g)	160.71	-9.13	178.27	-6.96	466.71	13.42	302.05	4.58	147.54	-2.38	195.99	2.78	253.97	5.78	142.52	-3.82	
C:N ratio	226.66	-3.07	204.70	-4.71	206.29	-3.49	349.71	9.77	163.38	-0.49	144.43	-2.25	87.51	-5.35	205.12	5.76	

Moderate Dry																	
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil								
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree		
	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	
N% (mg/g)	258.74	5.23	212.96	-0.25	287.77	4.11	115.60	-8.74	113.02	-3.10	146.07	1.75	238.64	6.41	110.17	-2.90	
C% (mg/g)	186.56	-3.40	171.70	-5.23	404.00	10.68	238.37	2.05	118.41	-2.37	129.97	-1.05	232.25	6.01	134.92	-0.12	
C:N ratio	163.34	-6.17	195.76	-2.32	222.34	0.41	322.48	9.45	136.75	0.10	137.61	0.28	82.23	-3.36	151.78	1.77	

Moist																	
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil								
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree		
	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	
N% (mg/g)	92.65	-5.92	125.62	-1.24	200.11	8.63	119.48	-1.95	207.53	0.73	219.89	1.93	256.69	4.20	146.23	-6.01	
C% (mg/g)	168.58	4.10	57.26	-8.41	168.71	4.30	127.14	-1.12	178.26	-2.54	199.22	-0.18	301.72	7.59	169.89	-3.41	
C:N ratio	184.15	6.15	106.11	-3.29	101.47	-4.97	156.09	2.01	161.81	-4.37	163.94	-3.79	220.58	1.47	263.83	6.89	

Wet																	
Substrate Quality Parameters	Loose litter								Old litter-Organic Soil								
	Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree		
	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	Score Means	Std Score	
N% (mg/g)	383.66	1.29	401.78	1.99	503.37	10.19	230.06	-12.20	283.93	-3.66	401.22	4.96	470.65	5.54	297.32	-3.49	
C% (mg/g)	201.66	-12.41	190.69	-9.92	596.90	17.16	405.20	3.46	314.64	-0.99	306.15	-1.31	380.79	2.10	332.82	0.83	
C:N ratio	303.98	-4.71	293.88	-4.10	295.94	-5.25	505.87	12.46	364.09	3.31	141.57	-12.15	209.40	-4.47	399.34	8.93	

Appendix 4: Results of the Wilcoxin/Kruskal-Wallis analysis indicating significant differences in plant functional type litter mass (g) across hydroperiods. The "Score Mean" represents the average rank within each group, illustrating the ranks' central tendency. The "Standardized Score" indicates the deviation of the group's mean rank, serving as a measure of the group's relative position or deviation from the norm.

Flood								Moderate Dry							
Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std
Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score
359.105	-4.983	320.32	-6.909	415.03	-0.569	550.325	11.066	244.777	-9.55	312.119	-3.849	579.833	9.743	470.827	8.379
Moist								Wet							
Fern		Grass		Shrub		Tree		Fern		Grass		Shrub		Tree	
Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std	Score	Std
Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score	Means	Score
252.59	-7.34	349.83	0.88	464.82	8.99	316.13	-1.72	581.21	-6.35	345.83	-14.96	925.79	9.85	826.74	9.94

Appendix 5: Density (ind/g), assemblages and trophic structure of soil arthropod within various vegetation types across distinct hydroperiods. The table showcases the diversity at both the family level and higher taxonomic ranks, including orders, suborders, and superfamilies.

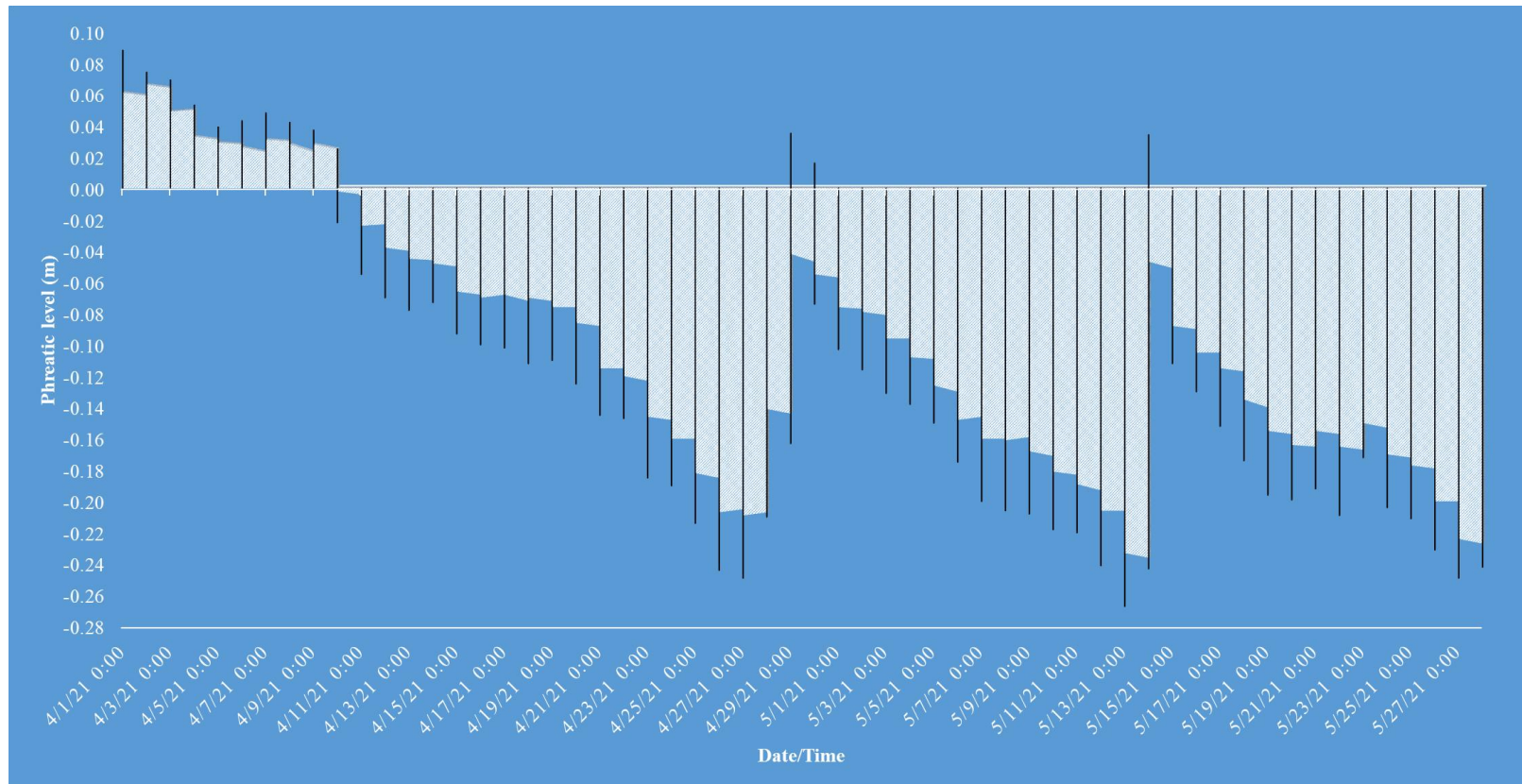
Trophic Guild	Taxa	Family	Flood				Moderate Dry				Moist				Wet			
			Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree
Detritivores	Amphipoda	Talitridae	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	2.3	1.2	0.0	0.1
Detritivores	Blattodea	Blattidae	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.2
Detritivores	Coleoptera	Passalidae	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.5	0.0	0.0
Detritivores	Coleoptera	Scarabaeidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Detritivores	Diptera	Chironomidae	13.6	3.9	2.5	4.6	0.0	0.0	0.0	0.4	1.0	0.0	0.0	0.8	2.0	0.9	0.3	14.2
Detritivores	Diptera	Psychodidae	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Detritivores	Diptera	Scatopsidae	21.4	10.9	0.3	19.0	5.0	2.3	0.3	1.0	0.3	1.5	1.0	15.4	32.0	10.2	2.0	30.0
Detritivores	Diptera	Stratiomyidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Detritivores	Isopoda	Porcellionidae	0.0	0.0	0.0	0.0	2.6	0.2	0.5	0.4	0.5	0.0	8.3	4.2	17.0	1.7	4.3	3.2
Detritivores	Isoptera	Kalotermitidae	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Detritivores	Polyzoniida	Polydesmidae	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Detritivores	Polyzoniida	Sinphonotidae	0.0	0.0	0.0	0.0	0.0	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Detritivores	Spirobolida	Rhinocricidae	0.0	2.4	1.6	0.0	0.0	0.2	0.0	0.0	0.0	0.5	0.0	0.1	2.5	0.5	0.3	0.2
Detritivores	Spirobolida	Trigoniulidae	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	1.3
Fungivores	Lepidoptera	Tineidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.5	0.7	0.5	0.9	0.0	1.0
Fungivores	Thysanoptera	Phlaeothripidae	0.0	0.0	0.6	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.5	7.0	0.0	1.0	2.4
Fungivores	Thysanoptera	Thysanoptera	3.7	0.0	0.0	0.0	0.0	0.4	0.0	0.1	0.0	0.0	0.4	0.0	0.7	0.0	1.5	1.0
Herbivores	Coleoptera	Curculionidae	1.6	0.0	0.0	0.3	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.7	3.4	0.5	2.6
Herbivores	Coleoptera	Hydraenidae	1.9	0.0	0.7	8.8	0.3	0.0	0.0	0.0	0.0	0.0	1.5	2.9	1.0	0.0	0.8	2.6
Herbivores	Coleoptera	Scarabaeidae	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.1
Herbivores	Hemiptera	Aphididae	0.2	5.1	0.0	2.8	0.5	0.6	0.0	0.5	1.9	2.8	0.2	0.6	1.4	2.2	0.0	1.1
Herbivores	Hemiptera	Cicadellidae	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.6	7.6	0.0	0.0

Trophic Guild	Taxa	Family	Flood				Moderate Dry				Moist				Wet			
			Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree
Herbivores	Hemiptera	Delphacidae	3.7	0.0	0.0	0.0	0.0	0.4	0.2	0.0	1.7	0.1	0.4	0.2	1.9	0.0	0.4	0.9
Herbivores	Hemiptera	Lygaeidae	0.7	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	3.3	0.2	0.0
Herbivores	Hemiptera	Miridae	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.3	0.1	0.1	0.0	0.0	0.7	3.4	0.6	0.1
Herbivores	Hemiptera	Pentatomidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Herbivores	Hemiptera	Pseudococcidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Herbivores	Lepidoptera	Crambidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.4	0.3	0.0	0.0	1.1
Herbivores	Lepidoptera	Lycaenidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Herbivores	Lepidoptera	Pyralidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.2	2.2
Herbivores	Thysanoptera	Thripidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Microbivores	Arthropleona	Brachystomellidae	14.6	5.9	2.4	17.8	1.0	0.7	0.0	0.1	4.3	33.7	0.5	0.0	19.5	18.3	11.3	15.3
Microbivores	Arthropleona	Entomobryidae	0.2	0.0	0.3	0.4	0.6	0.3	0.1	0.1	1.5	0.4	0.7	2.7	5.5	3.1	2.6	9.5
Microbivores	Arthropleona	Isotomidae	141.7	74.8	8.7	84.6	2.4	1.1	2.1	0.5	71.4	0.6	2.8	4.1	8.5	36.0	11.0	15.4
Microbivores	Coleoptera	Ptiliidae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Microbivores	Diptera	Ceratopogonidae	13.0	1.8	1.7	5.6	0.6	0.7	0.0	0.2	33.4	0.0	0.0	0.0	1.3	1.3	1.0	3.1
Microbivores	Oribatida	Acaridae	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microbivores	Oribatida	Astigmata	3.8	12.7	17.6	0.4	0.8	0.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.8	0.2	0.4
Microbivores	Oribatida	Ceratozetidae	45.2	14.6	14.8	29.3	12.6	8.8	0.1	8.3	13.0	26.9	1.6	16.0	13.6	4.2	7.0	28.6
Microbivores	Oribatida	Cryptognathidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Microbivores	Oribatida	Damaeidae	29.4	8.4	6.6	8.2	14.9	10.6	2.5	6.8	10.8	18.0	8.3	15.6	15.3	27.4	21.7	29.4
Microbivores	Oribatida	Eniochthoniidae	0.0	0.0	0.0	0.5	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Microbivores	Oribatida	Galumnidae	0.0	0.1	0.0	0.9	2.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.1	0.8	0.7
Microbivores	Oribatida	Glycyphagidae	1.7	0.0	0.0	0.0	0.0	0.2	0.0	0.0	18.7	0.0	2.5	0.0	0.3	0.5	1.6	0.0
Microbivores	Oribatida	Haplozetidae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.5	0.2
Microbivores	Oribatida	Hermanniidae	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3	1.5	5.0	1.7	0.0	1.9	7.9	0.2	62.1
Microbivores	Oribatida	Histiostomatidae	18.7	14.8	0.0	0.4	0.0	0.1	0.1	0.0	3.3	0.0	0.7	0.0	0.1	0.0	0.0	0.0
Microbivores	Oribatida	Hypochthoniidae	166.2	31.6	2.5	51.9	8.1	11.9	0.4	1.1	34.1	12.5	5.1	11.5	22.6	30.2	5.6	24.7

Trophic Guild	Taxa	Family	Flood				Moderate Dry				Moist				Wet			
			Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree
Microbivores	Oribatida	Lohmanniiae	0.0	0.0	0.0	0.0	0.0	0.3	0.1	0.4	6.6	0.5	0.6	2.9	1.3	0.0	0.0	0.0
Microbivores	Oribatida	Lohmanniidae	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.2	0.0	0.7	1.7	1.2	1.0	0.0	0.2
Microbivores	Oribatida	Malaconothridae	72.0	48.8	9.2	91.2	17.0	19.8	3.4	0.6	27.7	2.3	15.9	30.1	54.7	57.0	19.1	135.5
Microbivores	Oribatida	Nothridae	0.0	0.0	0.0	0.4	0.0	0.0	0.2	0.0	0.9	5.0	0.0	0.0	5.6	3.4	0.7	4.9
Microbivores	Oribatida	Oribatid	0.3	0.0	0.0	0.5	0.0	0.7	0.0	0.0	0.0	0.7	0.0	0.0	0.6	0.0	6.9	0.2
Microbivores	Oribatida	Oribatida	12.5	1.5	0.6	9.3	2.6	1.3	0.0	0.1	8.7	0.8	1.0	0.0	2.2	4.7	1.1	1.6
Microbivores	Oribatida	Phthiracaridae	1.6	0.6	0.3	2.3	0.9	1.0	1.2	0.2	5.9	3.5	2.7	1.0	1.6	0.5	0.0	2.1
Microbivores	Oribatida	Schlerobatidae	0.0	0.0	0.0	0.4	0.6	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Microbivores	Oribatida	Stigmaeidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microbivores	Oribatida	Suctobelbidae	0.0	0.0	0.0	0.0	2.1	0.3	0.8	0.3	0.0	0.0	0.0	0.0	3.5	0.1	1.2	1.4
Microbivores	Oribatida	Tectocephidae	14.3	4.7	1.5	7.6	0.0	1.1	0.0	0.3	0.0	0.0	0.0	0.0	0.6	4.2	0.5	13.2
Microbivores	Oribatida	Tegoribatidae	58.9	77.1	2.3	105.9	9.0	12.7	1.0	2.7	5.4	0.8	1.3	5.4	8.2	12.9	1.4	11.6
Microbivores	Oribatida	Trhypochthoniidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Microbivores	Psocoptera	Liposcelididae	0.0	0.0	0.0	0.0	2.8	1.1	0.0	5.6	33.7	1.5	0.0	0.1	8.1	0.0	4.3	2.9
Microbivores	Symphyleona	Sminthuridae	0.5	7.0	0.5	4.7	0.0	0.4	0.0	0.2	0.4	0.0	0.0	0.0	0.8	0.8	3.5	6.8
Omnivorous	Dermaptera	Labiidae	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.0	0.0	0.1	0.2	0.0	0.1	0.0	0.0	0.0
Omnivorous	Diptera	Culcinidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Omnivorous	Hymenoptera	Formicidae	1.8	9.7	14.2	26.2	21.3	4.8	0.3	0.9	6.3	9.0	1.4	1.3	3.0	0.9	0.9	1.0
Omnivorous	Orthoptera	Gryllotalpidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Omnivorous	Orthoptera	Phalangopsidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Predators	Araneae	Dipluridae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.0
Predators	Araneae	Oonopidae	0.5	0.4	0.3	0.4	1.3	0.6	0.2	0.1	0.5	0.2	0.8	1.2	3.0	1.0	2.8	4.2
Predators	Araneae	Salticidae	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Predators	Araneae	Sicariidae	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Predators	Coleoptera	Dystiscidae	3.3	2.2	0.2	1.9	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	1.3
Predators	Coleoptera	Hydrophilidae	0.3	0.0	0.3	0.2	0.0	0.6	0.0	0.0	0.0	14.8	0.0	0.0	0.0	1.0	0.5	0.8

Trophic Guild	Taxa	Family	Flood				Moderate Dry				Moist				Wet			
			Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree	Fern	Grass	Shrub	Tree
Predators	Coleoptera	Staphylinidae	3.0	5.2	0.6	4.1	0.7	1.6	0.0	1.7	0.5	1.0	0.0	0.2	4.6	3.9	1.0	9.4
Predators	Diptera	Ceratopogonidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0
Predators	Diptera	Dolichopodidae	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Predators	Diptera	Tabanidae	0.0	1.0	0.3	0.1	0.2	0.9	0.0	0.3	0.1	1.4	0.8	0.0	2.4	0.0	0.0	1.3
Predators	Geophilomorpha	Oryidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Predators	Mesostigmata	Ascidae	14.0	14.2	6.4	33.9	14.9	3.7	1.9	2.0	18.7	9.7	4.2	0.8	18.3	13.3	7.4	27.0
Predators	Mesostigmata	Blattisociidae	0.1	1.1	0.3	3.7	1.5	0.8	0.1	0.0	0.0	0.0	0.0	0.0	0.7	1.1	0.0	1.4
Predators	Mesostigmata	Digamasellidae	0.0	0.0	0.6	0.4	1.0	0.0	0.0	0.2	0.0	0.0	0.3	0.0	5.2	1.4	1.8	5.9
Predators	Mesostigmata	Laelapidae	0.0	0.6	1.3	1.0	2.3	0.9	0.0	0.2	7.6	0.8	0.2	0.3	8.5	8.1	5.3	1.2
Predators	Mesostigmata	Pachylaelapidae	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	1.5	0.5	0.0	0.0	0.9	0.0	0.8	0.2
Predators	Mesostigmata	Sejidae	0.0	1.1	0.3	0.2	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Predators	Mesostigmata	Uropodidae	0.0	0.0	0.6	0.3	5.2	1.2	0.0	0.0	1.4	0.0	0.3	0.0	1.2	0.0	0.3	0.5
Predators	Mesostigmata	Veigaiidae	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	3.3
Predators	Prostigmata	Bdellidae	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	37.0	0.0	0.2	0.0	0.0	0.8	0.0	0.3
Predators	Prostigmata	Cheyletidae	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4
Predators	Prostigmata	Cunaxidae	16.5	13.7	1.9	0.8	1.1	1.9	0.1	0.9	7.9	1.0	0.0	0.7	16.0	2.3	8.0	6.4
Predators	Prostigmata	Digamasellidae	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.6	0.0
Predators	Prostigmata	Erythraeidae	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Predators	Prostigmata	Eupodidae	4.3	1.6	1.6	1.1	0.2	0.2	0.0	0.0	1.9	0.0	2.0	4.5	13.2	0.0	2.2	0.4
Predators	Prostigmata	Prostigmata	2.7	0.6	0.1	2.3	0.7	0.0	0.0	2.0	1.4	5.0	0.0	10.0	0.0	0.0	0.3	24.4
Predators	Prostigmata	Rhagidiidae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Predators	Prostigmata	Scutacaridae	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Predators	Prostigmata	Stigmaeidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Predators	Prostigmata	Tydeidae	0.0	1.6	0.6	1.6	0.3	0.2	0.0	0.3	0.0	0.0	0.0	0.0	1.2	1.5	0.0	6.3
Predators	Thysanoptera	Aeolothripidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 6: Variations in phreatic level (m) at the study site prior to June 9, 2021, sampling date during the Wet period. Data were collected hourly from sampling well 6 utilizing Hobo data loggers.



CHAPTER 4: CONCLUDING REMARKS

4.1 SUMMARY OF FINDINGS

This research explored the intricate dynamics of soil arthropod assemblages in a tropical urban coastal wetland, illustrating how abiotic factors, plant-substrate interactions, and varying hydrologic regimes significantly influence these communities. The findings reveal that fluctuations in phreatic levels, pH, and salinity are critical in shaping the composition and diversity of soil arthropods, particularly under different hydroperiods. During wet periods, favorable conditions such as shallow phreatic levels and acidic, oligohaline environments support a rich diversity of arthropods, whereas more extreme conditions in dry, moist and flood periods challenge their resilience, often leading to shifts in community composition towards more tolerant species.

Plant-substrate dynamics further demonstrate how variations in litter quality and quantity impact community structure across hydroperiods, with trophic guild densities peaking during key phases of decomposition. This reflects the soil arthropods' sensitivity to nitrogen availability and their role in nutrient cycling and organic matter breakdown, facilitated by the interactions among common, rare, and dominant groups at different stages of ecological succession.

Overall, the study underscores the complex interplay between species traits, ecosystem processes, and environmental changes, emphasizing the adaptability of soil arthropods. This is particularly significant for the Caribbean region, recognized as the fourth primary biodiversity hotspot worldwide. Such insights are crucial in the context of conservation,

highlighting the importance of developing strategies that consider temporal and spatial variability, as well as plant functional diversity, in managing wetlands.

4.2 DETAILED FINDINGS

This research has provided several key insights into soil arthropods spatiotemporal dynamics and ecological roles:

- **Soil Biota Dynamics:** The dynamics are driven by a synergy of mechanisms, including interspecific variations in resource quantity and quality, the interplay of bottom-up and top-down dynamics, ecological strategies, environmental changes, and the creation and alteration of microhabitats.
- **Environmental Influences:** Fluctuations in phreatic levels, pH, and salinity shape the composition and diversity of soil arthropod communities, with the phreatic level being the factor with the strongest influence, emphasizing their sensitivity to hydrological changes.
- **Hydroperiod Effects:**
 - Wet Periods: Favorable conditions such as shallow to moderate phreatic levels, strongly acidic pH, and oligohaline conditions support a rich diversity of arthropods, enhancing community metrics and complexity.
 - Moderate Dry and Moist Periods: These periods feature deeper phreatic levels and wider pH ranges, often surpassing the resilience of many arthropod taxa and leading to population declines.
 - Flood Periods: Characterized by high phreatic levels and waterlogged conditions, these periods shift the community composition towards more tolerant taxa.

- **Trophic Dynamics:**
 - Soil arthropod densities increase during the equilibrium (C:N ratio between 20:1 and 30:1) and immobilization (C:N ratio >30:1) phases of decomposition, without significant differences among trophic guilds, but decrease when the C:N ratio is below 20:1. In the mineralization phase, herbivores show statistical differences compared to detritivores and microbivores, while microbivores significantly differ from predators.
 - This pattern across the distinct phases of decomposition underscores their sensitivity to nitrogen, the impact of ecological interactions, and the crucial role of decomposers in ecosystem processes.
 - Litter mass and nitrogen concentration are pivotal determinants of soil arthropod richness and abundance, with variations attributed to hydroperiods and plant functional types.
- **Groups Interactions and Succession:**
 - Interactions among common, rare, and dominant groups during different decomposition stages reflect complex trophic dynamics.
 - Common groups characterized by opportunistic species adapt swiftly and play crucial roles in ecosystem stability and recovery post-disturbance.
 - Rare groups establish during intermediate stages, supporting a gradual increase in diversity as environmental conditions stabilize.
- **Group Traits and Ecosystem Processes:**
 - Shifts in species dominance and rarity accentuate the fluid nature of ecological communities, where species adjust their roles and abundances

in response to the ever-changing environmental conditions and resource availability.

- The ongoing dialogue between groups traits and ecosystem processes shapes the intricate web of life within these dynamic habitats.
- Dominant groups, such as Oribatida mites, regulate decomposition processes and act as key intermediaries in the soil food web.
- **Vegetation and Hydroperiod Interactions:** The significant variations in soil arthropod diversity across different vegetation types and hydroperiods underline the combined influence of plant-hydroperiod interactions on habitat and resource availability.

4.3 RECOMMENDATIONS FOR FUTURE ACTION

To enhance the understanding of the crucial role soil arthropods, play in ecosystem processes and their broader implications for ecosystem functioning and management in tropical urban coastal wetlands, further research and soil conservation efforts are essential. Based on this research findings, the following recommendations are presented:

- **Advancing Research**

Species Identification and Genetic Techniques:

- Identify soil arthropod groups down to the species level using DNA metabarcoding techniques.
- Incorporate stable isotopes, fatty acid profiles, and DNA gut content analysis to assess the trophic relationships of soil consumers.

Ecological Dynamics and Interaction Studies:

- Study the dynamics of soil arthropods associated with grasses and ferns, focusing not only on the analysis of litter such as fronds and leaves found on the substrate but also on senescent leaves that are still attached to the plant.
- Incorporate the examination of aquatic macroinvertebrates dynamics during flooding periods.

Environmental Impact and Decomposition Process:

- Investigate the impact of changing environmental conditions, such as flooding, drought, and variations in vegetation, on the relationship between soil arthropods and the decomposition process.
- **General Management Recommendations**
 - Research is essential for understanding spatiotemporal dynamics and crafting strategies that bolster ecosystem resilience and promote assisted management. It is crucial that research endeavors operate in tandem with ecosystem management efforts to effectively address environmental challenges.
- **Soil Conservation**
 - Encourage the existing diverse array of plant species to ensure a range of litter quality and quantity. The current variety of vegetation functional types found in the study area reflects a response to the diverse mosaic of substrate physicochemical properties.

- Protect and enhance microhabitats through the conservation of fallen logs, leaf litter, and other natural debris. These habitats are crucial for many soil arthropod species, offering shelter and feeding grounds.
- Minimize the use of shortcut paths and establish designated trails to prevent soil compaction in sensitive areas.
- Minimize pollution inputs, such as pesticides and herbicides, that can adversely affect soil arthropod communities. Encourage the adoption of organic planting practices and the implementation of assisted succession strategies.

Final Supplementary Data and Material

Appendix A: Scientific Publication



Article

The Dynamics of Soil Mesofauna Communities in a Tropical Urban Coastal Wetland: Responses to Spatiotemporal Fluctuations in Phreatic Level and Salinity

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Abstract: Coastal wetlands, vital for ecological diversity, have been significantly altered by anthropogenic activities, particularly in the Caribbean. These changes have created a complex mosaic of habitats and physicochemical conditions, further stressed by climate variability and sea-level rise. This study, conducted in Las Cucharillas Natural Reserve, a tropical urban coastal wetland in Puerto Rico, aimed to determine the effects of spatiotemporal variations in phreatic levels and salinity on soil mesofauna assemblages, crucial bio-indicators of environmental change. In 2020 and 2021, soil samples were collected from five diverse habitat types during different hydroperiods. Each sample was taken under four randomly selected plant types and processed using lighted Tullgren-Berlese extractors. Phreatic level and salinity were also measured. A total of 43 families were quantified, underscoring distinct habitat differences, similarities, and overall ecosystem diversity. Moderate correlations between phreatic levels, salinity, and mesofauna richness and abundance were determined. Peak richness and abundance were quantified at shallow (−0.03 to −0.07 m) and slightly moderate (−0.12 to −0.17 m) phreatic levels where oligohaline salinity (>0.5 to 5.0 ppt) prevails. The study highlights the adaptability of mesofauna to environmental shifts and their potential as biosensors for effective coastal wetland management amid climatic and anthropogenic pressures.

Keywords: urban wetland; coastal wetlands; Puerto Rico; hydroperiods; phreatic level; salinity conditions; soil mesofauna; biodiversity



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1. Introduction

Wetlands provide heterogeneous ecological niches for unique soil arthropod assemblages, with mesofauna communities being the most abundant and diverse [1–3]. Among these, Acari (mites) and Collembola (springtails) are the most prevalent groups, consisting of microarthropods that range in size from 0.1 to 2 mm. They are present in different soil types, with most of their assemblages concentrated in hot spot zones or resource patches within the litter system, which consists of the loose litter layer and the upper 1–5 cm of the soil [4–6]. In the ecosystem, mites and springtails significantly influence decomposition processes and nutrient mobilization, serving as plant litter transformers through (a) fragmentation and comminution, (b) the ingestion of plant debris, and (c) the deposition of feces, which enhances mineralization by soil microflora (fungi and bacteria) [7–9]. They also foster the growth and dispersal of microbial populations and interact at different trophic levels through the litter decomposition process [10–13]. These microarthropods are sentinel species due to their inherent sensitivity to environmental modulations, thus facilitating the rapid detection and comprehension of the

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Appendix B: Taxa, Trophic Guilds, Density (individuals/gram), and Abundance of Soil Arthropods.

Taxa	Trophic Level	Density (ing/g)	Abundance
Acari-Mesostigmata	Predators	280	651
Acari-Oribatids	Microbivores	2200	4527
Acari-Prostigmata	Predators	219	460
Amphipoda	Detritivores	5	31
Araneae	Predators	20	100
Blattodea	Detritivores	1	9
Chilopoda	Predators	0	9
Coleoptera	Detritivores	3	4
	Herbivores	30	84
	Microbivores	0	10
	Predators	35	158
Coleoptera Larvae	Detritivores	0	1
	Herbivores	2	16
	Predators	30	215
Collembola	Microbivores	665	2093
Dermaptera	Omnivorous	1	14
Diplopoda	Detritivores	12	51
Diptera larvae	Detritivores	197	449
	Microbivores	64	57
	Omnivorous	0	2
	Predators	20	38
Grylloidea	Omnivorous	0	2
Hemiptera	Herbivores	50	206
Hymenoptera	Omnivorous	103	257
Isopoda	Detritivores	43	220
Isoptera	Detritivores	0	9
Lepidoptera larvae	Fungivores	8	15
	Herbivores	5	26
Psocoptera	Microbivores	60	110
Thysanoptera	Fungivores	20	46
	Herbivores	2	11
	Predators	1	1
Total		4074	9882

Appendix C: Richness of Soil Arthropods by Taxa.

Taxa	Richness
Acari-Oribatids	25
Diptera	15
Acari-Prostigmata	11
Acari-Mesostigmata	8
Coleoptera	8
Hemiptera	7
Hymenoptera	5
Araneae	4
Collembola	4
Diplopoda	4
Lepidoptera larvae	4
Thysanoptera	4
Grylloidea	2
Amphipoda	1
Blattodea	1
Chilopoda	1
Dermaptera	1
Isopoda	1
Isoptera	1
Phasmida	1
Psocoptera	1
Total	109