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Understanding the mechanisms of hydrolytic enzyme mediated organic matter decomposition under different land covers within a subtropical preserve

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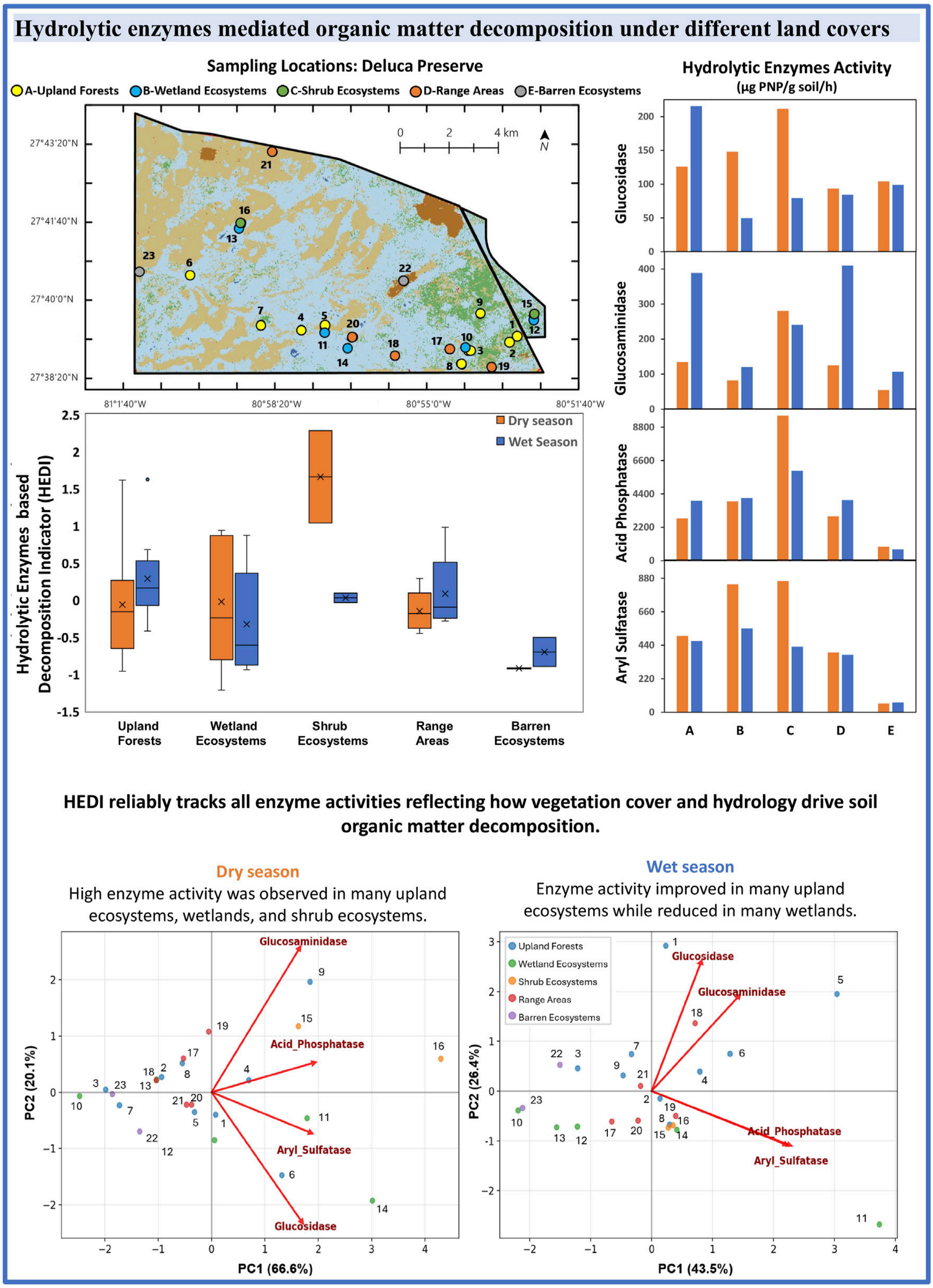
Soil Organic Matter (SOM) decomposition, vital to the carbon cycle, is influenced by land cover, hydrological conditions, and soil properties. However, understanding of how hydrolytic enzymes involved in SOM turnover vary under these factors remains limited. To address this, a study was conducted in a sub-tropical preserve in South Florida to assess hydrolytic enzyme activities across 23 diverse land covers (Categorized into five ecosystems: A-Upland Forests, B-Wetland ecosystems, C-Shrub ecosystems, D-Range Areas, and E-Barren ecosystems) during wet and dry seasons. The assessed enzymes were β-1,4 glucosidase (βG), β-1,4-N-acetyl glucosaminidase (β-NAG), Acid Phosphatase (AP), and Aryl Sulfatase (AS). A weighted index termed the Hydrolytic Enzyme Decomposition Indicator (HEDI) was derived using principal component analysis to summarize overall enzymatic activity as an indicator of decomposition. The results showed that among the land covers, βG, β-NAG, AP, and AS activities during the dry season ranged from 18.40 to 327.20, 14.71–351.90, 302.89–10,185.80, and 26.51–1,745.75 μg PNP/g soil/hr, respectively, while in the wet season, the activities for all enzymes except AS were higher, ranging from 4.08 to 398.66, 21.72–1,118.97, 372.38–11,960.36, and 28.26–1,475.09 μg PNP/g soil/hr. Among ecosystems, βG and β-NAG showed seasonal variability, with β-NAG consistently higher in A-Upland Forests, B-Range Areas, and C-Shrub. AP and AS showed minimal variation, with all enzymes showing lower activity in D-Barren ecosystems. HEDI values in the dry season A-Upland Forests exhibited the widest range (–0.962–1.613), indicating diverse decomposition rates, while Barren ecosystems showed consistently low activity (–0.928 to –0.916), suggesting lower decomposition. Correlation analysis revealed positive relationships between enzymatic activities and soil properties such as SOM (0.51–0.59), active carbon (0.46–0.58), soil protein (0.27–0.40), and cation exchange capacity (0.28–0.40), while bulk density showed negative correlations (–0.31 to –0.50). Overall, this study highlights the necessity of considering the complex interactions between soil properties, vegetation, moisture, and enzymatic activity in understanding SOM decomposition.

KEYWORDS

soil organic matter, decomposition, hydrolytic enzymes, land covers, wet season, dry season



GRAPHICAL ABSTRACT

1 Introduction

Soil Organic Matter (SOM) is an essential component of soil (Osman and Osman, 2013; Körschens, 2002) undergoing several transformative processes, including mineralization, immobilization, and decomposition (Filipović et al., 2024; Paul, 2016). Each of these processes plays a crucial role in the functioning of soil ecosystems, directly influencing soil fertility, structure, and overall soil health

(Murphy, 2015; Fageria, 2012). Mineralization is the process through which soil microbes convert SOM releasing inorganic forms of nutrients and making them available to plants. Immobilization on the other hand is the process, where inorganic forms of nutrients are converted back into organic forms, making them temporarily unavailable to plants (Mohammadi et al., 2011; Nieder and Benbi, 2008; Rice, 2002; Haynes, 1986). Decomposition which involves the breakdown of SOM by soil microorganisms is considered the most crucial process within the soil because it directly influences both mineralization and immobilization (Carter and Tibbett, 2008). During decomposition, the SOM can either undergo mineralization by soil microorganisms or be reincorporated into microbial biomass through immobilization (Findlay, 2021; Robertson and Paul, 2000; Haynes, 1986). Decomposition of SOM is a fundamental ecological process, vital for the recycling of nutrients, maintenance of soil structure and regulation of the carbon cycle (Raza et al., 2023; Nair et al., 2021; Angst et al., 2021; Paul and Collins, 2020). The rate at which SOM is decomposed also determines the balance between the carbon sequestered in soils and the carbon released into the atmosphere (Prescott, 2010; Swift, 2001), a balance with direct implications for climate change mitigation and the sustainability of diverse ecosystems (Goebel et al., 2011; Anderson, 1991).

The decomposition of SOM is a complex phenomenon influenced by several factors, including land cover, hydrological conditions, soil properties, climate, microbial community composition, nutrient availability, and human activities (Adl, 2003; Guo and Gifford, 2002; Robertson and Paul, 2000). Each factor contributes to the complex dynamics of SOM breakdown, affecting the rate and efficiency with which organic materials are decomposed (Cotrufo and Lavallee, 2022; Paul, 2016). For example, the nature of the land cover plays a significant role, with different vegetation and land uses providing varying SOM inputs and thus influencing the microbial consortia specialized for decomposition in these microhabitats (Ramesh et al., 2019; Moghimian et al., 2017; Deng et al., 2016; Muñoz-Rojas et al., 2015; Guo and Gifford, 2002). Soil type also directly influences the rate of SOM decomposition, affecting factors such as aeration, moisture retention, and nutrient cycling. These variations in soil properties create distinct microenvironments that impact microbial activity, enzyme production, and ultimately the efficiency of SOM decomposition and carbon turnover (Rittl, et al., 2020; Zheng et al., 2019; Frøseth and Bleken, 2015; Tumer et al., 2013; Dijkstra and Cheng, 2007; Scott et al., 1996). Biological properties, including microbial biomass and enzymatic activity, play a crucial role in driving decomposition processes (Wang and Allison, 2019; Glassman et al., 2018; Don et al., 2017 Condron, et al., 2010; Van Veen and Kuikman, 1990). Moreover, hydrological conditions, encompassing wet and dry seasons, particularly in humid sub-tropical climates like that of Central Florida (Lascody and Melbourne, 2002; Black, 1993) also play a crucial role in the decomposition of SOM (Harrison-Kirk et al., 2014; Zhu and Cheng, 2013; Lohse et al., 2009 Denef et al., 2001). For example, during wet periods, increased moisture levels can enhance microbial activity by improving the mobility of enzymes and substrates, thus potentially accelerating decomposition rates (Harrison-Kirk et al., 2014; Xiang et al., 2008; Williams and Rice, 2007). Conversely, dry periods may lead to a reduction in microbial activity due to moisture stress, which can slow down the decomposition process (Schimel, 2018; Ouyang and Li, 2013; Boddy, 1986).

Understanding the role of discussed factors in SOM decomposition is essential. However, to understand the mechanisms of SOM decomposition more comprehensively it is important to consider the effects of these factors on indicative soil parameters that can define SOM decomposition. Central to this understanding are a variety of enzymes that work synergistically to break down complex organic compounds. These include both hydrolytic enzymes such as β-1,4-glucosidase (βG), β-1,4-N-acetyl glucosaminidase (β-NAG), Acid Phosphatase (AP), and Aryl Sulfatase (AS) whichserve as critical mediators in the decomposition process (Bautista-Cruz and Ortiz-Hernández, 2015) and oxidative enzymes, like peroxidases and phenol oxidases, which are essential for degrading more recalcitrant components such as lignin (Hassan et al., 2013; Beckett et al., 2013). In this study, we specifically focus on hydrolytic enzymes due to their well-established role in catalyzing the breakdown of labile SOM fractions and their rapid responsiveness to environmental changes (Bautista-Cruz and Ortiz-Hernández, 2015). These enzymes are directly involved in the mineralization of key nutrients and are therefore considered sensitive indicators of microbial nutrient transformations under varying ecological conditions (Shi, 2010; Sinsabaugh et al., 2008). These enzymes, crucial for microbial nutrient transformations, significantly influence the rate-limiting steps of SOM decomposition (Koch et al., 2007; Speir et al., 2002) as theytarget specific substrates within the soil organic complex, facilitating the breakdown of SOM. βG plays a pivotal role in the carbon cycle by catalyzing the final step in cellulose compound breakdown and enabling the release of simple glucose to microorganisms (Tischer et al., 2015; Piotrowska and Koper, 2010). β-NAG, on the other hand, is vital for hydrolyzing N-acetylglucosamine from fungal chitin and bacterial murein, linking it to microbial turnover of carbon and nitrogen (Tischer et al., 2015). AP and AS contribute to the cycling of phosphorus and sulfur, respectively (Wang et al., 2019; Kang and Freeman, 1999). Despite the significant role of hydrolytic enzymes in SOM decomposition, more research is needed to understand how enzyme activities vary across different hydrological conditions and land cover types, as well as their implications for SOM decomposition. Current studies have primarily focused on controlled environments, leaving a gap in understanding enzyme activities under natural conditions with varying, soil types, and land covers (Burns et al., 2013). Moreover, there is a limited understanding of enzyme activity fluctuations across different hydrological periods, such as wet and dry seasons, which can significantly impact microbial activity and enzyme activity (Henry, 2013). These research gaps hinder our ability to understand SOM decomposition dynamics accurately and develop effective land management strategies for carbon sequestration and soil health improvement. Therefore, investigating these enzyme activities across different hydrological periods, soil types and land covers can provide insights into the temporal and spatial aspects of SOM decomposition. Furthermore, exploring how soil properties influence hydrolytic enzyme activity will enhance our understanding of the factors affecting SOM decomposition, supporting conservation efforts and carbon sequestration in less managed ecosystems.

The Deluca preserve, with its diverse ecosystems and well-defined wet and dry seasons, offers a prime setting for the investigation of all these research gaps. The preserve's location within a humid subtropical climate zone in central Florida, characterized by distinct hydrological patterns, and its diverse array of ecosystems, from woodlands to wetlands offer a microcosm through which the complex relationship between hydrolytic enzyme activity and SOM decomposition can be observed. This study explores how hydrolytic enzyme activities differ across various land covers and between wet and dry seasons within the DeLuca Preserve, aiming to uncover patterns in enzyme activity that may influence SOM decomposition. Additionally, it investigates the associations between hydrolytic enzyme activities and soil physicochemical properties, seeking to understand how these relationships contribute to SOM dynamics in different environmental contexts within the preserve. The study was conducted with the following objectives. (i) To investigate the variations in hydrolytic enzyme activities in different land covers in dry and wet seasons and their implications on SOM decomposition and (ii) to examine the relationship between soil physiochemical properties and hydrolytic enzyme activities in dry and wet season, and how these interactions affect SOM decomposition.

2 Materials and methods

2.1 Study location

This study was conducted on the Deluca preserve located in Central Florida (South of SR 60, West of FL Turnpike) about 11 km east of the Kissimmee River, geographically located between 27°38′ 20′′ to 27°44′ 10′′ N, and 80°51′ 40′′ to 81°1′ 40′′ W (Figure 1). The site is located in a tropical climate zone with an average annual high and low temperature of 28.89°C, and 17.22°C, and a mean yearly rainfall of approximately 1,204 mm. The preserve is characterized by cyclical patterns of a wet rainy season from June to September and a dry, cool winter season beginning from December to February, which are referred to as the "wet" and "dry" seasons, respectively (Figure 1). This natural hydroperiod of seasonally flooded and desiccated conditions on an annual basis is the major driver creating a favorable condition for the diverse land covers on the preserve (Exum, 2020).

2.2 Soil sampling and processing

Based on the major vegetation categories in the Deluca preserve, 23 unique land covers were selected for the study (Figure 2; Table 1). Topsoil samples (0–15 cm) were collected from these land covers during two seasons: the dry season (January 2021) and the wet season (August 2022). To capture spatial variability and minimize the impact of sampling point selection on soil properties, composite samples were taken from three locations within each land cover type. At each location, soil was collected within a 1-m diameter and mixed to form a single composite sample, ensuring representativeness for each sample (Supplementary Table S1 in the Supplementary Material for geographic coordinates of sampling locations).

Considering the overall ecological setting, including dominant vegetation type, hydrological characteristics, land management and land-use history, these 23 land covers were further classified into five distinct ecosystems (Table 1; Supplementary Figure S1 in the Supplementary Material for more detailed views of land cover and ecosystems). This classification aimed to facilitate a more structured analysis of regional ecological patterns and to minimize the impact of sampling point selection on observed soil properties. The collected soil samples were oven-dried at 50°C for chemical analysis and air-dried for enzymatic analysis. All samples were then sieved to 2 mm prior to laboratory analysis.

2.3 Ecological setting

The Deluca preserve, across 109.05 square kilometers (km^2), is a mix of diverse ecosystems and land uses (Figure 3). The area distribution includes several diverse ecosystems as described below:

i. *Wetland, Watercourse, and Waterbody Areas (27.02 km^2):* Encompassing herbaceous prairies, marshes, and forested wetlands, these areas are essential for water purification, groundwater recharge, and providing habitats for species such as the eastern indigo snake and Florida sandhill crane.
ii. *Upland Forests (21.61 km^2):* Consisting of mesic hammocks, Florida scrub, mesic flatwoods, and scrubby flatwoods, these forests support a wide range of flora and fauna, including rare habitats for the red-cockaded woodpecker and gopher tortoise.
iii. *Native Range Areas (30.02 km^2):* Dominated by dry prairie habitats with indigenous vegetation, these areas are vital for the conservation of species like the Florida grasshopper sparrow, maintained through light grazing and regular fires.
iv. *Cultivated Agricultural Areas (3.28 km^2):* Including active citrus groves and lands previously utilized for row crops, these areas are now mainly used for cattle grazing on bahiagrass, reflecting the agricultural heritage of the preserve.
v. *Improved Pasture Areas (26.68 km^2):* Primarily used for cattle grazing, these pastures have been enhanced for forage with bahiagrass, aiding in the conservation and agricultural management of the landscape.
vi. *Intensive Use Areas (0.44 km^2):* These areas are allocated for more concentrated activities, likely including the infrastructure and facilities essential for the management and operations of the preserve.

2.4 Soils geology and hydrology

Based on the NRCS soil survey for Osceola County, a comprehensive analysis has identified a total of 38 distinct soil types and 6 soil orders within the DeLuca Preserve (Exum, 2020), as detailed in Figure 4 and summarized in Table 2. Table 3, derived from the Soil Survey Geographic Database (National Resources Conservation Service, 2024), provides key soil hydrological properties across various land cover types, including parameters such as available water storage, water table depth, saturated hydraulic conductivity, and moisture content. These parameters

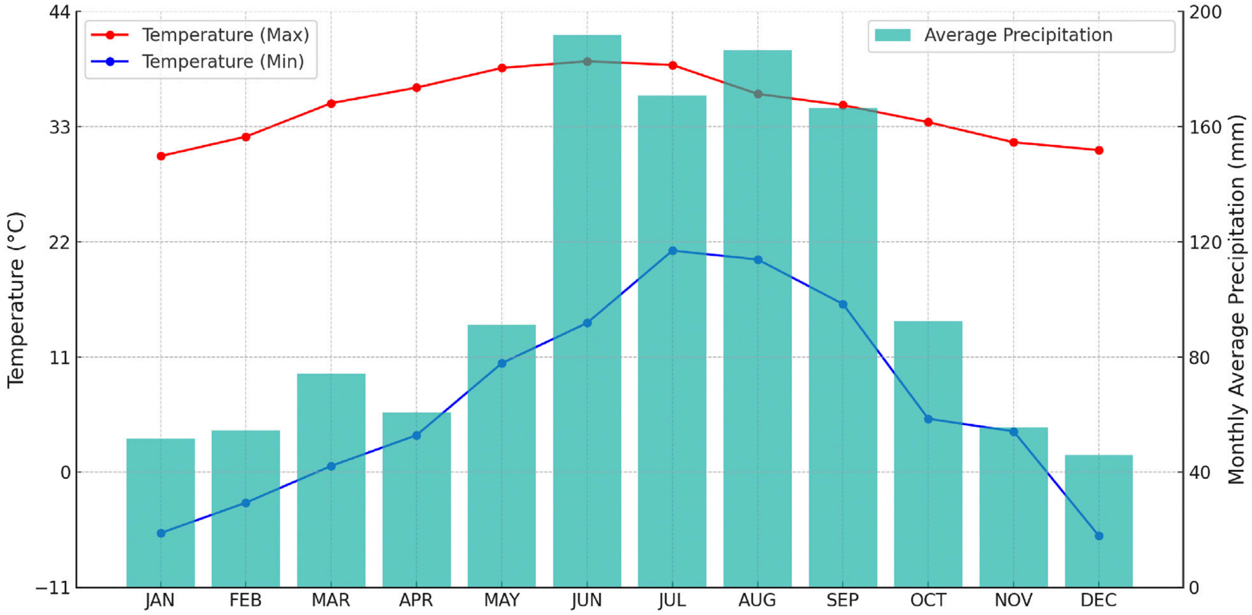


FIGURE 1
Monthly Temperature and Precipitation Averages for DeLuca preserve (1981–2023) Source: NASA/POWER CERES/MERRA2 Climatology Data 2024.

remain relatively stable and serve as a comprehensive source of information, offering a detailed description of hydrological attributes for different land cover and ecosystems. Wetland and poorly drained soils have higher water retention capacities and hydric soil presence, while xeric and sandy soils, such as those in hammocks and abandoned citrus groves, exhibit lower available water capacities and higher drainage. Additional details on specific soil types and their distributions can be found in Supplementary Materials S2, S3.

2.5 Laboratory analysis

All soil samples were subjected to physicochemical analyses following standard procedures. For Enzymatic analysis, air-dried soil samples were sieved through a 2 mm sieve for analysis of βG and β-NAG, AP, and AS by the method described by Tabatabai (1994). Enzyme activities were expressed in µg PNP/g dry soil/h, representing the micrograms of p-nitrophenol released per gram of dry soil per hour. To examine the relationship between soil physiochemical properties and hydrolytic enzyme activities, ten soil properties were analysed: pH, bulk density (BD), maximum water holding capacity (MWHC), cation exchange capacity (CEC), SOM, active carbon (AC), soil protein (SP), total phosphorus (TP), total potassium (TK), and total Kjeldahl nitrogen (TKN). Soil pH (soil/water suspension of 1.5:15) was determined using a pH meter (Amgain, Martens-Habbena, and Bhadha, 2022). BD was measured by filling a 25 mL graduated cylinder with oven-dry soil and dividing the soil mass by the cylinder volume (25 cm^3) (Xu et al., 2022). MWHC was measured following a modified protocol by Jenkinson and Polson (1976). SOM was determined using the loss on ignition method at 550°C. CEC was determined using the ammonium acetate method (Sumner, Miller, and Sparks, 1996). AC was measured using the Potassium Permanganate ($KMnO_4$) method (Schindelbeck et al., 2016). SP was measured using the sodium citrate extraction method under autoclaving at high temperature and pressure (Schindelbeck et al., 2016). TP and TK were measured by ashing samples at 550°C in a muffle furnace for at least 5 h (not exceeding 16 h), followed by extraction with 6 M HCl and analysis using ICP-OES. TKN was analyzed using the Kjeldahl method (Bremner and Mulvaney, 1982).

2.6 Statistical analysis

All statistical analyses were performed using statistical software R-4.4.0 (R Development Core Team, 2024). Data were tested for normality, and transformations were applied as necessary to meet assumptions. For the first objective, a two-way ANOVA was conducted with land cover and season as factors to examine their interaction and main effects on the response variables. Mean comparisons were conducted using Bonferroni adjustments at a 5% significance level, separately between land covers and between seasons. Similarly a two-way ANOVA was also performed with the five ecosystems and years as factors to provide an overall understanding of SOM decomposition across a broader scale, reflecting the aggregated ecosystem groups from the 23 distinct land covers. Mean comparisons were conducted using Bonferroni adjustments at a 5% significance level, separately between ecosystems and between seasons.

Principal Component Analysis (PCA) was performed on all four hydrolytic enzymes to determine their combined effect on SOM decomposition. Using the results from the PCA, an index termed the PCA-based hydrolytic enzymes decomposition indicator (HEDI)

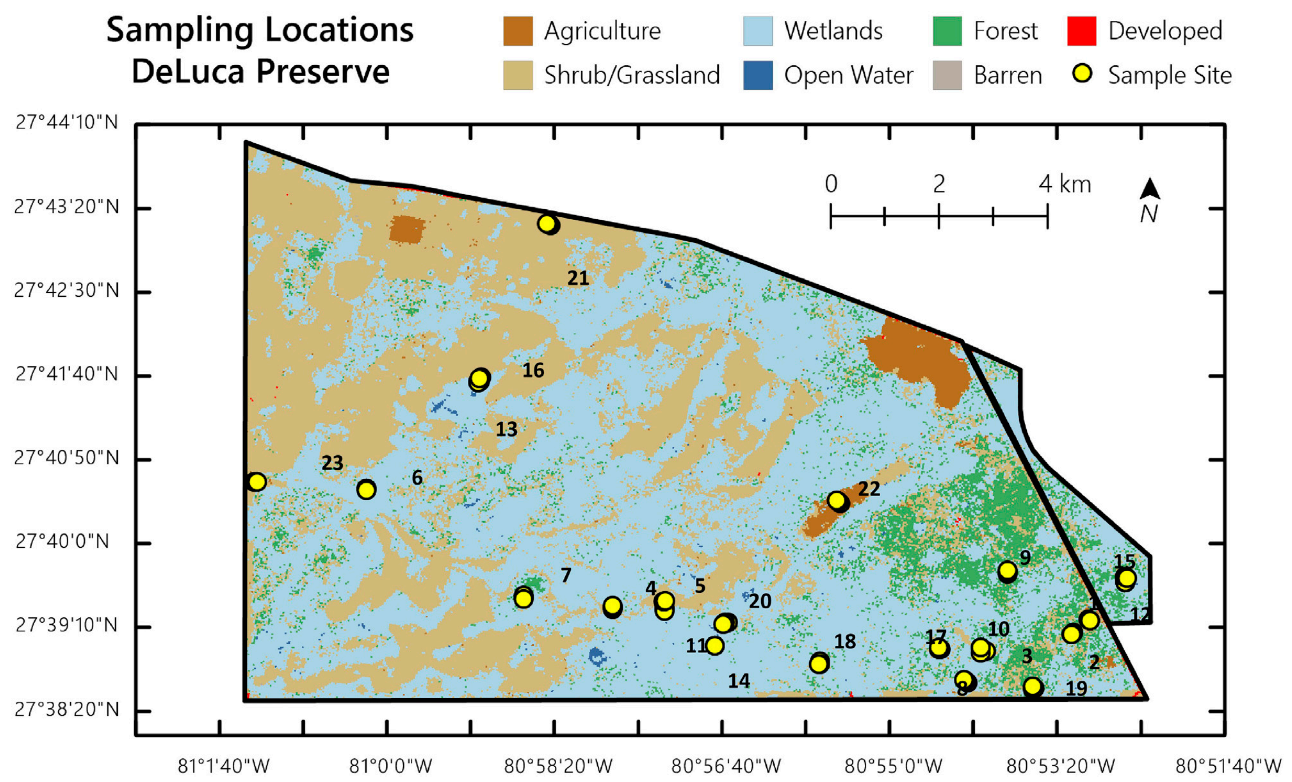


FIGURE 2
Deluca preserve, Florida with sampling locations.

was calculated to represent the overall enzymatic activity which can act as an indicator of decomposition. This index incorporates the weighted methodology that considers the principal components (PC) scores. The weight of each PCs score is given by the proportion of variance it explains. HEDI was calculated with the following equation:

$$\mathbf{HEDI} = (\mathbf{PC1} \times \mathbf{V1}) + (\mathbf{PC2} \times \mathbf{V2}) + \ldots + (\mathbf{PCn} \times \mathbf{Vn})$$

Where PCn is the score for principal component n, and Vn is the variance explained by that component. Similar approaches of using weighted PCA scores has been employed to assess soil quality and variability, where PCA scores, weighted by explained variance, serve as critical indicators (Martin-Sanz et al., 2022; Karaca et al., 2021; Kumar et al., 2012). This study adapts and modifies these established methodologies to develop HEDI. Seasonal comparisons using the HEDI are not feasible because the index is calculated based on distinct principal components derived from the dry and wet seasons, which prevents a direct comparison of enzymatic activity between these periods. However, to facilitate relative comparisons of enzymatic activity across seasons, the activities in each season were classified into quartiles. PCA scores for the dry and wet seasons are provided in Supplementary Tables S2A, B, and the PCA Biplot is illustrated in Supplementary Figure S4.

For second objective, Spearman correlation analysis was conducted to explore the interactions between hydrolytic enzyme activities and the soil parameters across different land covers. This method was directly applied due to its suitability for non-normal, non-transformed data and its ability to capture both monotonic and non-linear relationships. Multiple regression analyses were performed for each of the four enzymes, using all soil physicochemical properties and other enzyme activities as predictors. Standardized coefficients were calculated for each equation to identify significant predictors and compare their relative effects on soil hydrolytic enzymes.

3 Results

3.1 Variations in hydrolytic enzyme activities in different land covers in dry and wet seasons and their implications on SOM decomposition

3.1.1 Hydrolytic enzyme activities across land covers

Distinct patterns in hydrolytic enzyme activities emerged from seasonal comparisons across various land covers, with a significant interaction ($p < 0.05$) observed between land cover and season for all enzymes (Figures 5–8).

Among different land covers during the dry season, βG activity ranged from 18.40 to 327.20 μg PNP/g soil/hr (Figure 5) with highest values observed in 14-Wetland-4, which was not significantly different ($p > 0.05$) from nine other land cover types, reflecting consistent enzymatic activity across multiple ecosystems. On the other hand, in the wet season, βG activity showed a wider range, from 4.02 to 398.66 μg PNP/g soil/hr, with the highest value in 1-

TABLE 1 Characterization of the 23 land covers present at the Deluca preserve.

S.No	Land cover	Vegetation cover	Soil order	T[a] (°C)	P[a] (mm)	Texture	Ecosystems
1	Flatwood	Oak (*Quercus virginiana*)	Spodosols	23	1,245	Sandy	Group A Upland Forests (Forested ecosystems/ Natural Tree Cover)
2	Mesic flatwood	Saw palmetto (*Serenoa repens*)/Gall berry (*Ilex glabra*)/Slash pine *(Pinus elliottii)*	Spodosols	23	1,245	Sandy	
3	Dry hammock	Sabal palm (*Sabal palmetto*)/Live oak *(Quercus virginiana)*	Alfisols	23	1,372	Loamy	
4	Xeric hammock	Live oak *(Quercus virginiana)*/Sabal palm (*Sabal palmetto*)	Alfisols	23	1,295	Loamy	
5	Palm hammock (Xeric)	Oak (Quercus *sp.*)	Spodosols	23	1,245	Sandy	
6	Cypress	Natural tree cover	Spodosols	23	1,320	Sandy	
7	Pinewood-1	Slash pine *(Pinus elliottii)*/Sabal palm (*Sabal palmetto*)	Entisols	23	1,270	Sandy	
8	Hammock	Oak (*Quercus virginiana*), pines (*Pinus*), palmettos	Spodosols	23	1,245	Sandy	
9	Pinewood-2	Pine (*Pinus*)/saw palmetto (*Serenoa repens*)/Gall berry (*Ilex glabra*)	Spodosols	23	1,320	Sandy	
10	Canal (wet)	Cattails (*Typha*)/Pickerelweed (*Pontederia cordata*)	Alfisols	23	1,372	Loamy	Group B Wetland ecosystems (Wetland, Watercourse, and Waterbody Areas)
11	Wetland-1	Aquatic plants	Entisols	22	1,282	Sandy	
12	Wetland-2	Aquatic plants, 15-inch depth	Entisols	22	1,320	Loamy	
13	Wetland-3	Juncus/hypericum/Panicum	Alfisols	23	1,265	Loamy	
14	Wetland-4	Sawgrass (*Cladium*), 8-inch depth	Entisols	22	1,320	Loamy	
15	Sawtooth palmetto	Sawtooth palmetto (*Serenoa repens*)/Gallberry (*Ilex glabra*)	Entisols	22	1,320	Loamy	Group C Shrub ecosystems
16	Sabal palmetto	Saw palmetto (*Serenoa repens*)/Sabal palm (*Sabal palmetto*)/black berry (*Rubus* sp.)	Alfisols	23	1,265	Loamy	
17	Dry Prairie-1	Gall berry (*Ilex glabra*)/Saw palmetto (*Serenoa repens*)/Running oak (*Quercus* sp.)	Entisols	23	1,321	Sandy	Group D Range Areas (Grassland and Prairie ecosystems)
18	Dry Prairie-2	Andropogon (*Andropogon*)/wiregrass (*Aristida stricta*)	Entisols	23	1,321	Sandy	
19	Dry Prairie-3	Slash pine *(Pinus elliottii)*/Saw palmetto (*Serenoa repens*)	Spodosols	23	1,245	Sandy	
20	Native pasture	Panic grass (*Panicum*)	Spodosols	23	1,245	Sandy	
21	Improved pasture	Bahia grass (*Paspalum notatum*)/Andropogon (*Andropogon*)	Spodosols	23	1,320	Sandy	
22	Abandoned citrus grove	Abandoned Citrus Plantation	Spodosols	23	1,320	Sandy	Group E Barren ecosystems
23	Sandy spoil	No vegetation	Entisols	23	1,282	Loamy	

[a]*T* stands for Mean Annual Air Temperature in degrees Celsius, and *P* stands for Mean Annual Precipitation in millimetres.

Flatwood which was not significantly different ($p > 0.05$) from ten other land cover types. For β-NAG activity, values during the dry season ranged from 14.71 to 351.90 µg PNP/g soil/hr (Figure 6), with the highest levels observed in 9-Pinewood-2, which were not significantly different ($p > 0.05$) from 16 other land covers. In the wet season, however, β-NAG activity showed a broader range of 21.72 to 1,118.97 µg PNP/g soil/hr, with the highest value observed in 17-Dry Prairie-1. These values were not significantly different ($p > 0.05$) from 1-Flatwood and 5-Palm Hammock (Xeric) but were statistically higher than other land covers, indicating more variability among land covers compared to the dry season. AP activity showed the largest range of activity among all enzymes. During the dry season, AP ranged from 302.89 to 10,185.80 µg PNP/g soil/hr (Figure 7), with the highest levels observed in 16-Sabal Palmetto. These values were not significantly different ($p > 0.05$) from those in 11-Wetland-1, 14-Wetland-4, and 15-Sawtooth Palmetto. In the wet season, AP activity displayed a broader range, from 372.38 to 11,960.36 µg PNP/g soil/hr, with 11-

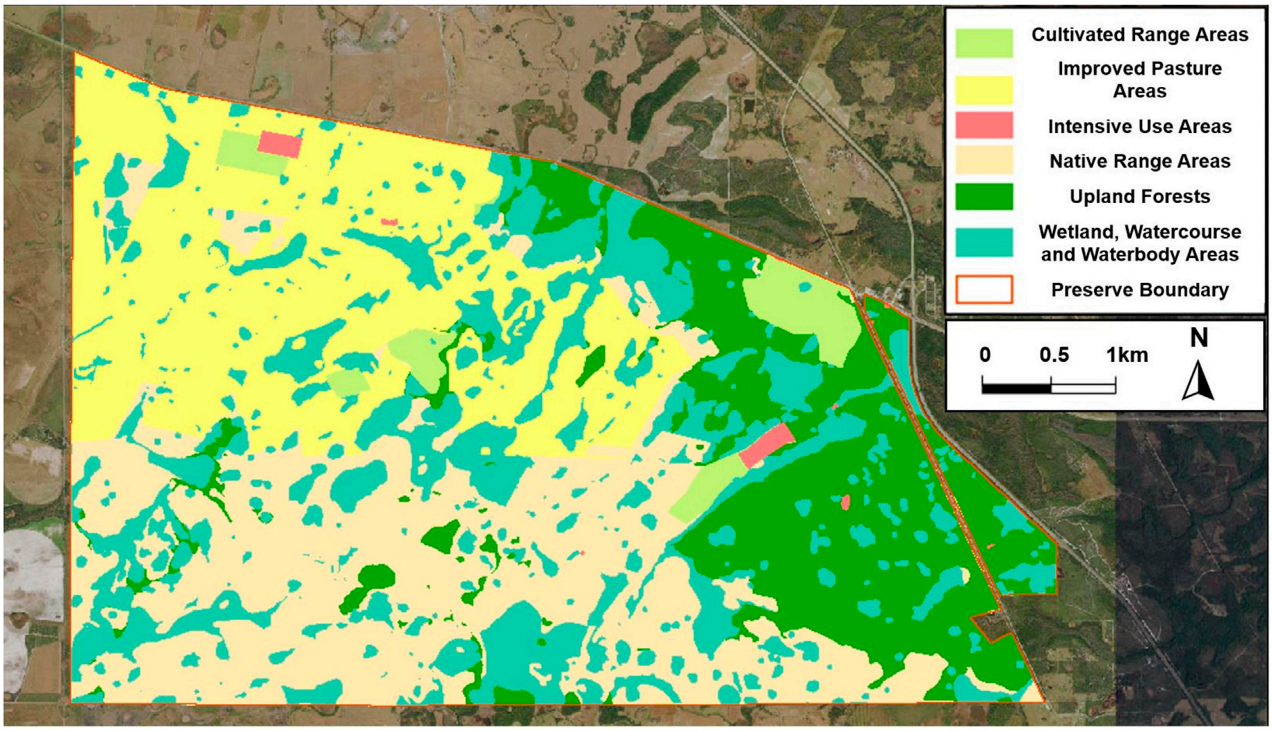


FIGURE 3
Land use categories and distribution within the DeLuca preserve.

Wetland-1 recording statistically higher value ($p < 0.05$) than all other land covers. In contrast to βG, β-NAG and AP, AS activity showed opposite trends from the dry to wet season. In the dry season, AS activity ranged from 26.51 to 1,745.75 μg PNP/g soil/hr (Figure 8), with the highest levels observed in 14-Wetland-4 not significantly different ($p > 0.05$) from 16-Sabal Palmetto, 9-Pinewood-2 and 10-Canal (wet). In the wet season, AS activity exhibited a narrower range, from 28.26 to 1,475.09 μg PNP/g soil/hr, with the highest levels observed in 11-Wetland-1 not significantly different ($p > 0.05$) from 6-Cypress. Overall, the highest enzymatic activity exhibited variable trends between the dry and wet seasons, while the lowest enzymatic activity remained consistently lowest in 10-Canal (wet) across all enzymes during the dry season. This trend was similar in the wet season with minimum values of β-NAG and AS in 10-Canal (wet).

3.1.2 Hydrolytic enzyme activities across seasons

For pairwise seasonal comparisons for each land cover, hydrolytic enzyme activities displayed variable patterns for different enzymes. βG activity increased significantly in 5-Palm hammock (Xeric) and 10-Canal (wet), while decreased significantly in 11-Wetland-1, 12-Wetland-2, 14-Wetland-4, 16-Sabal palmetto, and 17-Dry Prairie-1. For β-NAG, only a significant increase was recorded in 1-Flatwood, 2-Mesic flatwood, 3-Dry hammock, and 18-Dry Prairie-2. AP activity exhibited significant increases in 5-Palm hammock (Xeric), 7-Pinewood-1, 10-Canal (wet), and 19-Dry Prairie-3, while decreased significantly in 9-Pinewood-2, 12-Wetland-2, 16-Sabal palmetto, and 23-Sandy spoil. Additionally, AS activity showed a significant increase in 3-Dry hammock and decreased significantly in 9-Pinewood-2, 12-Wetland-2, and 16-Sabal palmetto. Other land covers such as 6-Cypress, 8-Hammock, 15-Sawtooth Palmetto, 20-Native Pasture, 21-Improved Pasture, and 22-Abandoned Citrus Grove, exhibited no significant seasonal differences in enzymatic activity.

3.1.3 Ecosystems comparison

Across different ecosystems, a visible pattern emerged with the transition from dry to wet conditions (Figure 9). Overall, the C-Shrub ecosystems demonstrated the highest range of enzymatic activity, spanning from 79.42 to 9,561.07 μg PNP/g soil/hr, while the D-Barren ecosystems exhibited the lowest range, from 54.94 to 106.58 μg PNP/g soil/hr.

Among different ecosystems in the dry season, βG activity showed no significant differences; however, it varied more in the wet season, with βG being highest in A-Flatwoods, not statistically different ($p > 0.05$) to the C-Shrub and D-Barren ecosystems. For β-NAG, the highest activity in the dry season was observed in the C-Shrub ecosystems, not statistically different ($p > 0.05$) to the B-Range Areas and A-Upland Forests. Similarly, in the wet season, β-NAG was highest in the B-Range Areas not statistically different ($p > 0.05$) to A-Flatwoods C-Shrub ecosystems. The results indicated that β-NAG activity was consistently higher in these three ecosystems (A-Upland Forests, B-Range Areas, and C-Shrub ecosystems) across both seasons. AP activity was significantly higher in the C-Shrub ecosystems during the dry season.

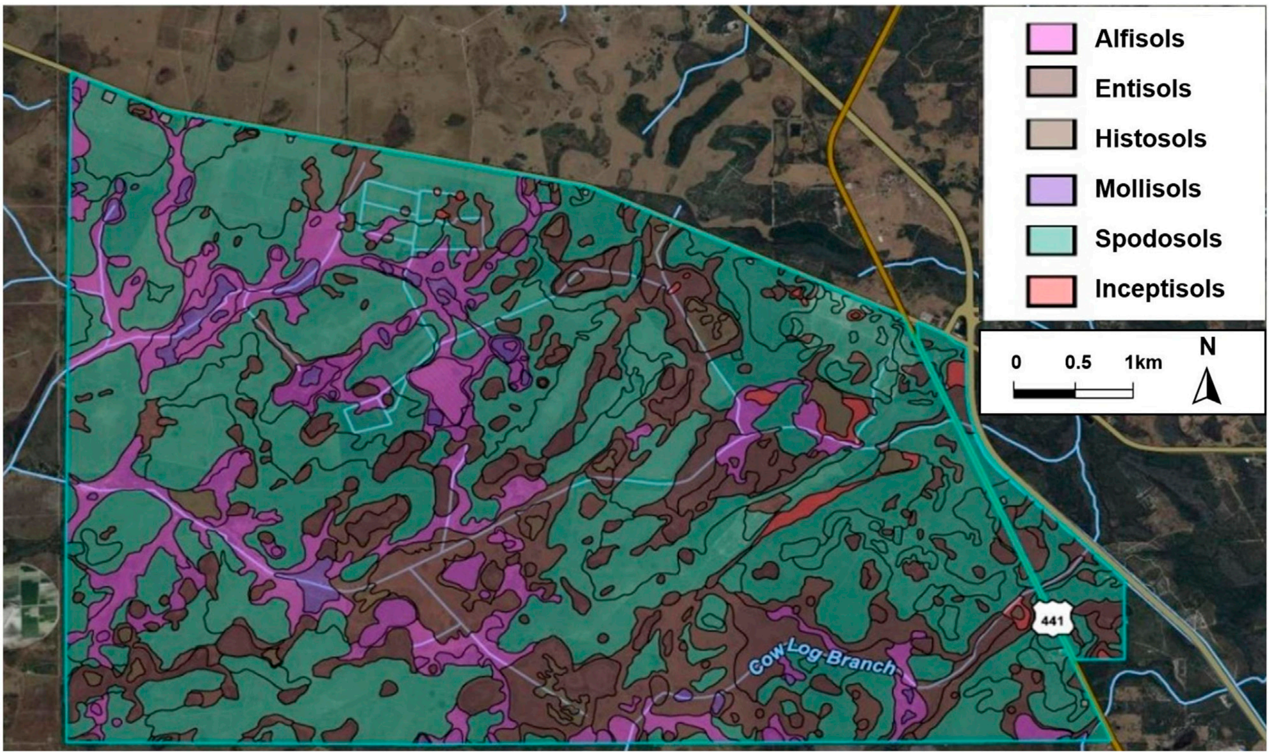


FIGURE 4
Soil taxonomy map of soil orders across the preserve. Source: (U.S. Department of Agriculture, [USDA]-NRCS, 2024).

TABLE 2 Soil Characteristics in the DeLuca preserve.

Soil texture	Area (km^2)	Percent	Soil order	Area (km^2)	Percent	Soil type	Area (km^2)	Percent
Fine Sand	105.57	96.43	Spodosols	61.72	61.7	Smyrna fine sand	33.17	30.4
Muck	2.00	1.82	Entisols	27.86	27.9	Myakka fine sand	11.46	10.5
Loamy Fine Sand	1.07	0.98	Alfisols	15.38	15.4	Eaugallie fine sand	11.37	10.4
Sand	0.84	0.77	Histosols	1.99	2.0	Basinger fine sand, depressional	11.02	10.1
			Mollisols	1.62	1.6	Basinger fine sand	9.22	8.5
			Inceptisols	0.86	0.9	Others	33.19	30.1

However, in the wet season, AP activity showed no significant differences, except for the D-Barren ecosystems, which showed significantly lower values. AS showed minimal variation among ecosystems in both seasons, with no statistical difference ($p > 0.05$) among all ecosystems except for the D-Barren ecosystems which showed significantly lower activity in both seasons. Overall, the results indicate that both AP and AS activities remained relatively stable across most ecosystems, highlighting the distinct differences in enzymatic responses based on seasonal changes.

From dry to wet seasons, βG increased significantly in A-Flatwoods, while it decreased significantly in both B-Wetlands and C-Shrub ecosystems. β-NAG showed significant increases in A-Flatwoods and B-Range Areas, with no significant decreases observed in any ecosystem. Both AP and AS demonstrated no significant changes from dry to wet season across all ecosystems.

3.1.4 HEDI across different land covers and ecosystems

The HEDI values demonstrated significant variability across different land covers and seasons (Table 4). Among different land covers during the dry season, HEDI values ranged from a minimum of −1.217 in 10-Canal (wet) to a maximum of 2.281 in 16-Sabal palmetto, indicating a spectrum of enzymatic activity. In the wet season however, the HEDI values exhibited a narrower range, with the lowest value at −0.943 again in 10-Canal (wet) and the highest at 1.623 in 5-Palm Hammock (Xeric). Land covers such as 1-Flatwood, 6-Cypress, 11-Wetland-1, 15-Sabal palmetto, and 16-Sawtooth palmetto consistently showed higher HEDI values, classifying in the highest quartile classes (I or II) in both seasons, which reflects overall higher enzymatic activity. In contrast, several land covers, including 3-Dry hammock, 10-Canal (wet), 12-Wetland-2, 13-

TABLE 3 Soil hydrological characteristics of the 23 land covers present at the Deluca preserve.

S.No	Land cover	Available water storage (cm)				Water table depth annual minimum (cm)	Drainage class - dominant condition	Hydric soils presence (%)	Saturated hydraulic conductivity (μm/s)	Water content, 15 bar (%)	Water content, 0.33 bar (%)	Available water capacity (cm/cm)	Moisture Subclass
		0–25	0–50	0–100	0–150								
1	Flatwood	2.03	4.09	10.38	14.51	31	Poorly drained	5	23.0	4.4	11.2	0.08	Aeric
2	Mesic flatwood	2.01	4.20	10.35	14.44	15	Poorly drained	90	92.0	3.0	9.5	0.08	Typic
3	Dry hammock	2.01	4.03	8.12	12.16	0	Very poorly drained	99	92.0	5.3	12.2	0.08	Typic
4	Xeric hammock	1.45	2.90	6.51	10.95	31	Poorly drained	9	20.0	2.2	6.6	0.06	Typic
5	Palm hammock (Xeric)	2.03	4.09	10.38	14.51	31	Poorly drained	5	23.0	4.4	11.2	0.08	Aeric
6	Cypress	2.06	4.05	10.08	14.79	15	Poorly drained	86	28.2	2.3	8.4	0.08	Typic
7	Pinewood-1	1.45	2.90	6.51	10.95	31	Poorly drained	9	20.0	2.2	6.6	0.06	Typic
8	Hammock	1.85	4.08	7.84	11.47	0	Very poorly drained	97	91.7	8.6	15.0	0.07	Typic
9	Pinewood-2	2.00	4.69	8.85	13.05	31	Poorly drained	6	28.2	4.9	11.7	0.08	Aeric
10	Canal (wet)	2.01	4.03	8.12	12.16	0	Very poorly drained	99	92.0	5.3	12.2	0.08	Typic
11	Wetland-1	1.85	4.08	7.84	11.47	0	Very poorly drained	97	91.7	8.6	15.0	0.07	Typic
12	Wetland-2	1.85	4.08	7.84	11.47	0	Very poorly drained	97	91.7	8.6	15.0	0.07	Typic
13	Wetland-3	2.01	4.02	8.10	14.09	0	Very poorly drained	100	28.2	5.3	12.2	0.08	Typic
14	Wetland-4	1.85	4.08	7.84	11.47	0	Very poorly drained	97	91.7	8.6	15.0	0.07	Typic
15	Sawtooth palmetto	2.03	4.09	10.38	14.51	31	Poorly drained	5	23.0	4.4	11.2	0.08	Aeric
16	Sabal palmetto	2.01	4.20	10.35	14.44	15	Poorly drained	90	92.0	3	9.5	0.08	Typic
17	Dry Prairie-1	2.00	4.69	8.85	13.05	31	Poorly drained	6	28.2	4.9	11.7	0.08	Aeric

(Continued on following page)

TABLE 3 (*Continued*) Soil hydrological characteristics of the 23 land covers present at the Deluca preserve.

S.No	Land cover	Available water storage (cm)				Water table depth annual minimum (cm)	Drainage class - dominant condition	Hydric soils presence (%)	Saturated hydraulic conductivity (µm/s)	Water content, 15 bar (%)	Water content, 0.33 bar (%)	Available water capacity (cm/cm)	Moisture Subclass
		0–25	0–50	0–100	0–150								
18	Dry Prairie-2	2.01	4.20	10.35	14.44	15	Poorly drained	90	92.0	3.0	9.5	0.08	Typic
19	Dry Prairie-3	2.00	4.69	8.85	13.05	31	Poorly drained	6	28.2	4.9	11.7	0.08	Aeric
20	Native pasture	2.01	4.20	10.35	14.44	15	Poorly drained	90	92.0	3.0	9.5	0.08	Typic
21	Improved pasture	2.00	4.69	8.85	13.05	31	Poorly drained	6	28.2	4.9	11.7	0.08	Aeric
22	Abandoned citrus grove	1.07	2.14	4.48	6.70	76	Somewhat poorly drained	4	210.0	2.2	8.2	0.04	Aquic
23	Sandy spoil	2.00	4.01	8.09	14.15	15	Poorly drained	96	28.2	5.3	12.2	0.08	Typic

Source: (USDA-NRCS, 2024).

Wetland-3, 21-Improved pasture, 22-Abandoned citrus grove, and 23-Sandy spoil, remained in the lower quartile classes (III and IV) for HEDI values, indicating minimal enzymatic activity.

Among different ecosystems in the dry season, A-Upland Forests showed the widest range of HEDI values, ranging from −0.962 to 1.613, indicating a wide variation of enzymatic activity. C-Shrub ecosystems demonstrated the highest values of HEDI ranging from 1.035 to 2.280, suggesting high hydrolytic enzyme activity. In contrast, E-Barren ecosystems showed lowest HEDI values between −0.928 and −0.916, emphasizing limited enzymatic activity. In the wet season, A-Upland Forests again showed a wide range of HEDI values, from −0.421 to 1.623, along with B-Wetland ecosystems ranging from −0.942 to 0.870, indicating a diverse enzymatic activity across these ecosystems. Similarly, E-Barren ecosystems remained consistent with low HEDI of −0.897 to −0.505 in the wet season as well, indicating persistently limited enzymatic activity across both seasons.

3.2 Relationship between soil physiochemical properties and hydrolytic enzyme activities in wet and dry seasons

The analysis of the relationship between soil biogeochemical properties and hydrolytic enzyme activities revealed significant insights, particularly in understanding the differences between wet and dry seasons (Figure 10). SOM, SP, AC, CEC, and MWHC showed positive correlations with all enzymes in both seasons, while BD showed consistently negative correlations, and pH showed no significant correlations. Other parameters, such as TP, TKN, and TK, showed more variable correlation values. During the dry season, SOM and AC showed significant positive correlations at $p < 0.001$ with all enzymes. The correlations for SOM were 0.59, 0.54, 0.51, and 0.55, and for AC, were 0.58, 0.58, 0.46, and 0.50, with βG, β-NAG, AP, and AS, respectively. In the wet season, although SOM and AC retained positive correlations with enzymatic activities, they showed greater variability, with significant correlations at $p < 0.001$ observed only with AS (0.51 with SOM and 0.50 with AC). A general trend of decreasing correlation strength was observed from the dry to wet season for most relationships, with exceptions such as SP with AP (Dry: 0.27, $p < 0.05$; Wet: 0.32, $p < 0.01$) and AS (Dry: 0.30, $p < 0.05$; Wet: 0.40, $p < 0.001$), MWHC with AS (Dry: 0.28, $p < 0.05$; Wet: 0.61, $p < 0.001$), and CEC with AS (Dry: 0.28, $p < 0.05$; Wet: 0.28, $p < 0.01$). Other important correlations included SP, TKN and TP, which exhibited positive relationships during dry seasons which was more variable during wet season. The correlations between enzymes were all positive and generally exhibited significant reduction from the dry to wet season, with exceptions for AP and AS (Dry: 0.60, $p < 0.001$; Wet: 0.63, $p < 0.001$) and β-NAG and AP (Dry: 0.50, $p < 0.001$; Wet: 0.39, $p < 0.001$), with no significant reduction.

Based on the Multiple Linear regression analysis (Table 5), the predictors influencing enzyme activities varied between the dry and wet seasons, reflecting dynamic soil-enzyme interactions. For βG and β-NAG, the R^2 values decreased between seasons, with βG dropping from 0.71 in the dry season to 0.41 in the wet season and β-NAG declining from 0.48 to 0.31 ($p < 0.001$). Conversely, for AP and AS, the R^2 values increased between seasons. AP rose from 0.51 in

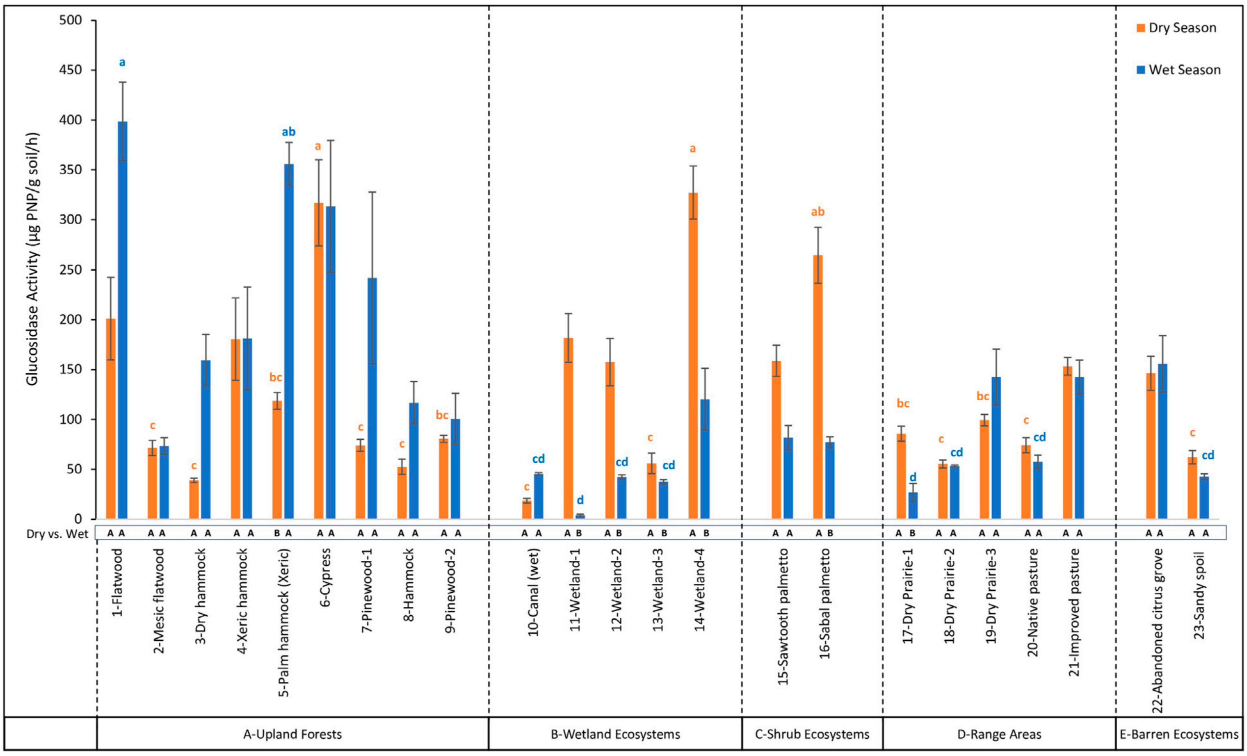


FIGURE 5
Comparison of β-1,4 glucosidase (βG) activity across 23 land cover types at the DeLuca Preserve in wet and dry seasons (Error bars represent ±standard error of the mean. Lowercase letters above bars indicate significant differences among land covers within each season (Bonferroni-adjusted, $p < 0.05$), with blue letters denoting differences in the wet season and orange letters in the dry season. Capital letters below bars denote significant seasonal differences (dry vs wet) within each land cover type (Bonferroni-adjusted, $p < 0.05$). To enhance clarity, only the extreme significance labels are displayed; detailed comparisons are provided in the Supplementary Table S3. Land cover types are grouped by ecosystem categories (A–E), separated by dashed lines).

the dry season to 0.74 in the wet season, while AS increased from 0.56 to 0.71 ($p < 0.001$). HEDI, representing overall enzymatic activity, had a high R^2 of 0.80 in the dry season and was predicted by a broader range of soil properties, including AP, β-NAG, AS, MWHC, CEC, and AC. In the wet season, HEDI had a slightly lower R^2 of 0.72, with fewer significant predictors, including β-NAG, AP, and pH.

4 Discussion

4.1 Variations in hydrolytic enzyme activities in different land covers in wet and dry seasons and their implications on SOM decomposition

4.1.1 Hydrolytic enzyme activities across land covers

Among different enzymes the observed activities for βG in both seasons and β-NAG in the dry season demonstrate consistently high activity across several land covers, likely driven by the combined effects of vegetation type, hydrological, and soil properties regulating microbial activity and enzyme production (Wang et al., 2020; Simpson et al., 2019; Salazar et al., 2011). This suggests that βG and β-NAG enzymes play a key role in stabilizing decomposition processes across these land covers (Sherene, 2017), facilitating consistent SOM turnover under varying environmental conditions. Additionally, environmental factors such as rainfall and temperature (Mariscal-Sancho et al., 2018; Rastin et al., 1988), along with soil characteristics like substrate availability (Mir et al., 2023), likely influenced the βG and β-NAG activities, contributing to the observed results. β-NAG activity exhibits greater variability among land covers during the wet season compared to the dry season, suggesting that increased moisture availability may contribute to the broader range of β-NAG activity and decomposition processes (Borowik and Wyszkowska, 2016; Zhang et al., 2011). AP and AS exhibited different trends compared to βG and β-NAG during the dry season, with their activities showing greater variability across land covers, possibly because these enzymes are more influenced by factors such as land cover characteristics (Mayor et al., 2016; Salam et al., 2001) and soil type (Nedyalkova et al., 2020) indicating varying levels of SOC decomposition. Overall, all enzymes exhibited increased activity ranges from the dry to wet season, indicating enhanced SOC decomposition, except for AS, which showed an opposite trend. This divergence may result from AS's regulation by sulfate availability and its sensitivity to wetting and drying cycles, which can suppress activity (Kunito et al., 2022; Cooper, 1972). In contrast,

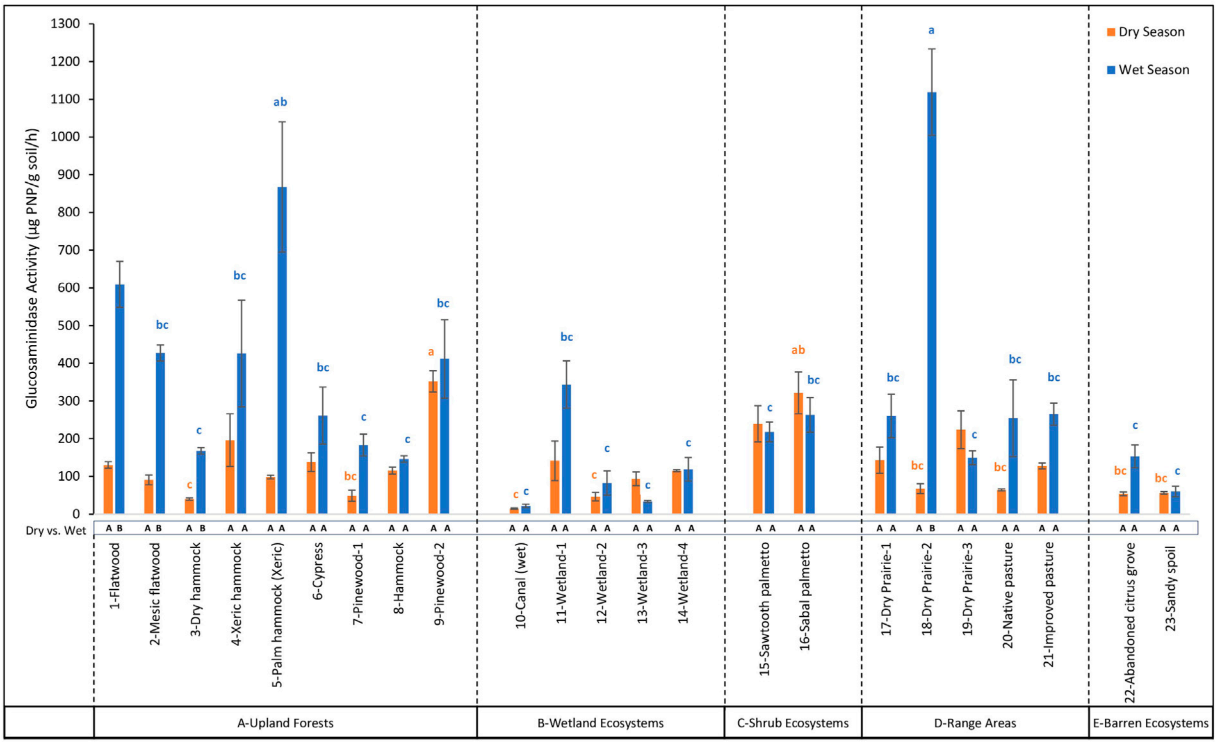


FIGURE 6
Comparison of β-1,4-N-acetyl glucosaminidase (β-NAG) activity across 23 land cover types at the DeLuca Preserve in wet and dry seasons (Error bars represent ±standard error of the mean. Lowercase letters above bars indicate significant differences among land covers within each season (Bonferroni-adjusted, $p < 0.05$), with blue letters denoting differences in the wet season and orange letters in the dry season. Capital letters below bars denote significant seasonal differences (dry vs wet) within each land cover type (Bonferroni-adjusted, $p < 0.05$). To enhance clarity, only the extreme significance labels are displayed; detailed comparisons are provided in Supplementary Table S3. Land cover types are grouped by ecosystem categories (A–E), separated by dashed lines).

βG, β-NAG, and AP activities were positively influenced by increased moisture, consistent with studies showing enhanced enzyme activities during wet seasons or after rewetting (Hammerl et al., 2019; Kapila et al., 2017; Liao et al., 2016). These results emphasize the critical role of hydrology in regulating enzyme-mediated SOC decomposition.

Among land covers in the dry season, 11-Wetland-1, 14-Wetland-4, 15-Sawtooth palmetto, and 16-Sabal palmetto generally showed higher enzymatic activity. This could be attributed to specific characteristics of these land covers, such as very poorly drained loamy soils, which are known to enhance water retention and support microbial activity (Kim, 2015). Additionally, these soils are typically associated with a high moisture class and high available water storage capacity, creating favourable conditions for microbial processes and enzyme production (Kim, 2015; Wu et al., 2021). These conditions may have maintained sufficient soil moisture even during dry periods, supporting microbial activity and enzyme production (Sinsabaugh et al., 2008). Whereas the lowest enzymatic activities during the dry season in the 10-Canal (wet) ecosystem for all enzymes could have resulted from over-saturated conditions, which may hinder oxygen diffusion and microbial activity necessary for enzyme production (Furtak et al., 2020; Borowik and Wyszkowska, 2016). The persistence of minimum values for β-NAG and AS in 10-Canal (wet) across both seasons, again suggests that prolonged wetland conditions might consistently inhibit these enzymes. This inhibition could be due to factors such as reduced oxygen availability or changes in substrate accessibility under saturated conditions (Veres et al., 2015; Daunoras et al., 2024). Moreover, the 23-Sandy spoil land cover also showed consistently lower enzymatic activity, which could be attributed to lower substrate availability in this type of soil (Allison et al., 2011; Babcock and Esen, 1994).

4.1.2 Hydrolytic enzyme activities across seasons

Insignificant seasonal differences in the enzymatic activity across several land covers like 6-Cypress, 8-Hammock, 15-Sawtooth Palmetto, 20-Native Pasture, 21-Improved Pasture, and 22-Abandoned Citrus Grove could be a result of the interactions of several soil and environmental factors with a diverse range of vegetation (Shao et al., 2015; Ullah et al., 2013; Wallenstein et al., 2009; Boerner et al., 2005; Kang and Freeman, 1999). This interaction might have resulted in insignificant changes in enzyme activity from dry to wet season enzymatic activity, minimally influencing SOM decomposition rates and the turnover of SOM components. The presence of aeric moisture subclass in most of these ecosystems is characterized by a well-aerated soil environment (Soil Survey Staff, 2003; Soil Survey Staff, 1999) potentially could also cause these results. The sufficient

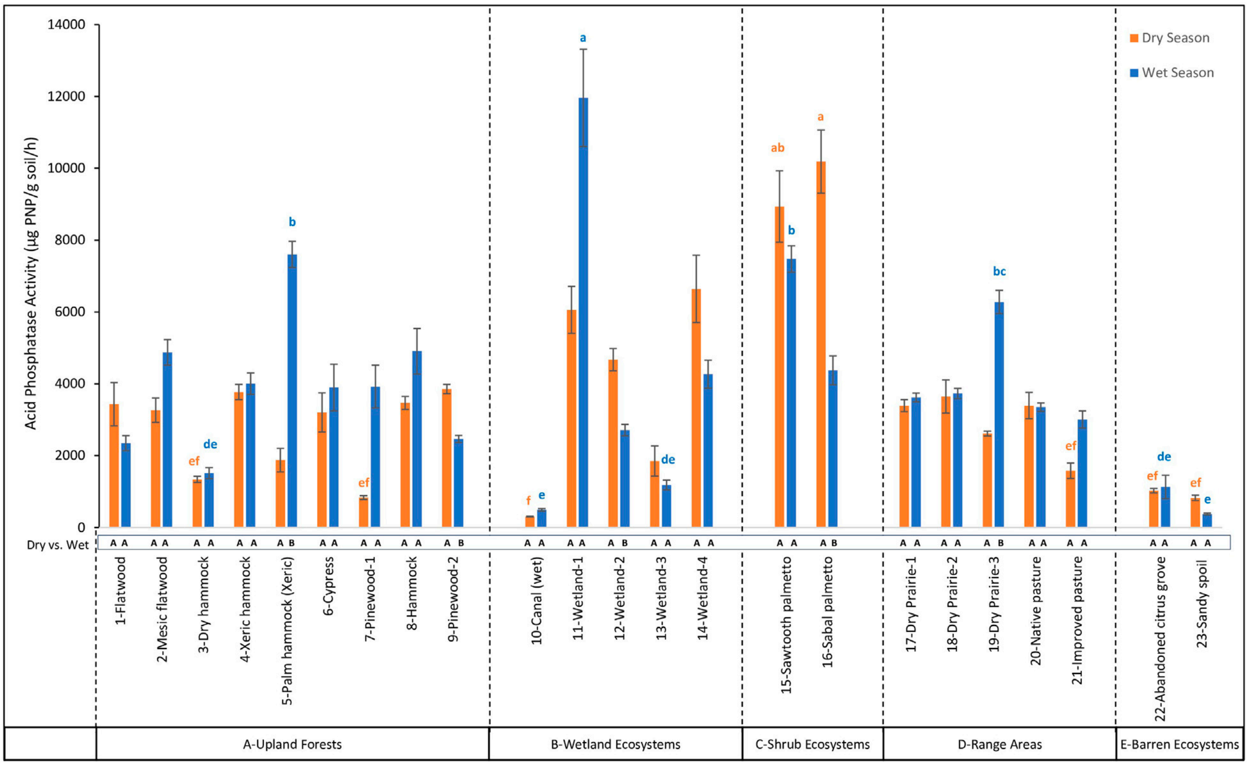


FIGURE 7
Comparison of Acid Phosphatase (AP) activity across 23 land cover types at the DeLuca Preserve in wet and dry seasons (Error bars represent ±standard error of the mean. Lowercase letters above bars indicate significant differences among land covers within each season (Bonferroni-adjusted, $p < 0.05$), with blue letters denoting differences in the wet season and orange letters in the dry season. Capital letters below bars denote significant seasonal differences (dry vs wet) within each land cover type (Bonferroni-adjusted, $p < 0.05$). To enhance clarity, only the extreme significance labels are displayed; detailed comparisons are provided in Supplementary Table S3. Land cover types are grouped by ecosystem categories (A–E), separated by dashed lines).

aeration could have led to consistent enzymatic activity, making the transition to wetter conditions less impactful on enzymatic processes and SOM decomposition (Wang et al., 2022; Ge et al., 2020). Moreover, the presence of Spodosols soil order with sandy texture (McKeague et al., 1983) and poor drainage capacity in most of these ecosystems may have promoted consistent hydrological conditions resulting in insignificant changes in enzyme activity.

The increase in some specific enzymatic activity in land covers like 1-Flatwood, 2-Mesic flatwood, 3-Dry hammock, 5-Palm hammock (Xeric) and 7-Pinewood-1 A- Upland ecosystems, during the transition from dry to wet season can be attributed to the inherent attributes of trees and their environmental interactions, enhancing SOM decomposition (Błońska et al., 2021). Trees such as oaks and pines contribute rich SOM through leaf litter, enhancing substrate availability for microbes and facilitating the decomposition of both labile and stable SOM components thereby promoting enzymatic activity (Prescott and Vesterdal, 2021; Prescott and Grayston, 2013; Hättenschwiler, 2005). Similarly diverse root exudates from species like sabal palm can stimulate microbial communities to produce enzymes further enhancing SOM decomposition (Zhang, et al., 2019; Grayston et al., 1997). The presence of adequate moisture in this resource-rich environment in wet season could also have increased enzymatic activity (Brockett, et al., 2012). On the other hand, the nonsignificant differences among the majority of land covers within this ecosystem demonstrate that the forest canopy creates a stable microclimate, maintaining consistent conditions that protect microbial enzymatic activity from seasonal extremes ensuring stable SOM decomposition rates (De Frenne, et al., 2021; Breshears et al., 1998). Contrarily to this, 9-Pinewood-2 land cover despite having similar vegetative and soil conditions as other upland forests, showed a significant reduction in AP and AS. This reduction may stem from unique interactions between pine root exudates, microbial communities, and other soil and environmental factors under wet conditions (Prescott and Grayston, 2013; Shi et al., 2011). The composition of root exudates, particularly organic acids, significantly influences soil bacterial community structure and diversity (Shi et al., 2011), and some pine root exudates may reduce soil enzyme activity (Zhang et al., 2015). For instance, certain exudates may favor microbes that produce fewer extracellular enzymes, thereby decreasing the breakdown of organic matter (Kawasaki et al., 2021; Ferreira et al., 2024). These factors, along with some other soil and environmental factors, could have affected AP and AS activity uniquely in wet conditions (Huang et al., 2011; Baligar et al., 2005). The decline in enzymatic activities among land covers like 11-Wetland-1, 12-Wetland-2, and 14-Wetland-4 within Group B Aquatic and Wetland ecosystems could be attributed to the saturated conditions of these ecosystems, which may hinder oxygen diffusion and microbial activity necessary for

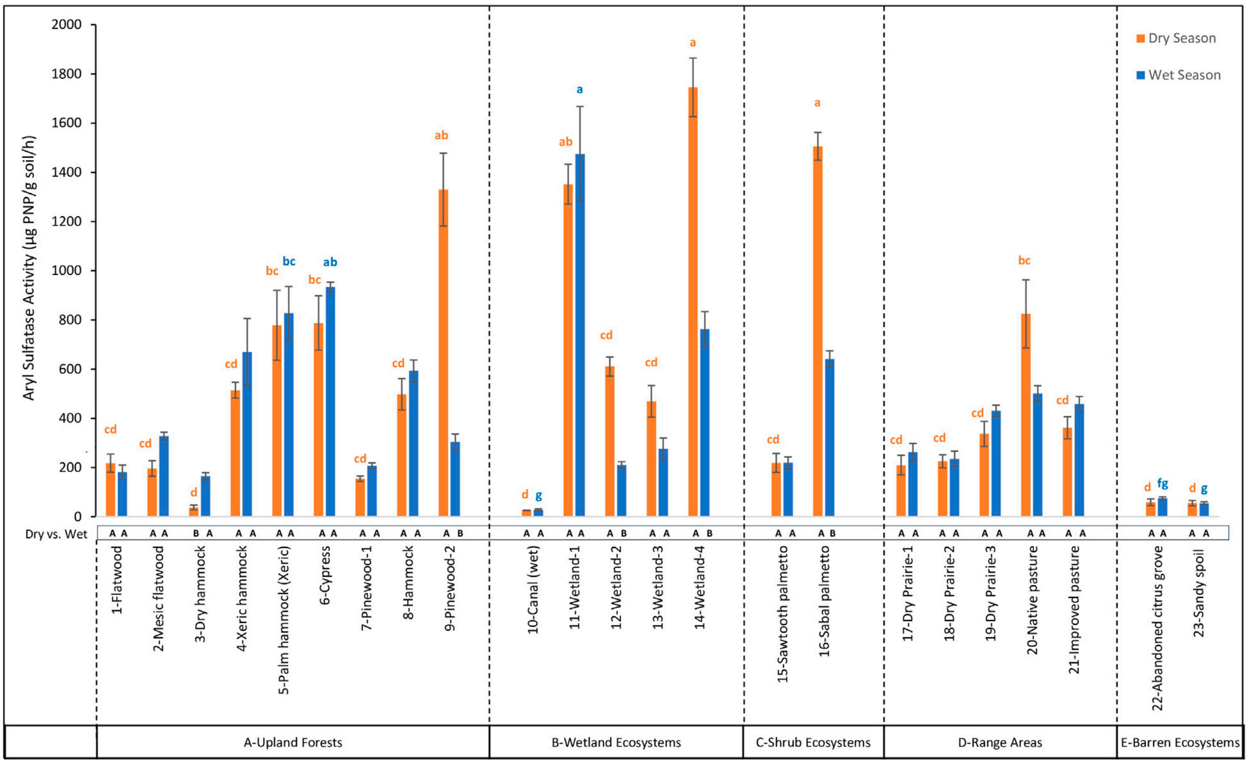


FIGURE 8
Comparison of Aryl Sulfatase (AS) activity across 23 land cover types at the DeLuca Preserve in wet and dry seasons. (Error bars represent ± standard error of the mean. Lowercase letters above bars indicate significant differences among land covers within each season (Bonferroni-adjusted, $p < 0.05$), with blue letters denoting differences in the wet season and orange letters in the dry season. Capital letters below bars denote significant seasonal differences (dry vs. wet) within each land cover type (Bonferroni-adjusted, $p < 0.05$). To enhance clarity, only the extreme significance labels are displayed; detailed comparisons are provided in Supplementary Table S3. Land cover types are grouped by ecosystem categories (A–E), separated by dashed lines).

enzyme production thus detrimentally affecting decomposition of SOM (Borowik and Wyszkowska, 2016; de Macedo et al., 2002; Eswaran, 1982). Aquatic plants typically thrive in water-saturated soils, which may experience enzymatic dilution or washout due to excessive wetness leading to a significant reduction in βG activity in the wet season also indicating a decline in the decomposition rates (Długosz et al., 2023; Xue et al., 2018). However, the significant increase in βG and AP activities in the 10-canal (wet) land cover, with similar conditions highlights the fact that wetland plants like Cattails and Pickerelweed growing in land cover might have enhanced the microbial substrate (Mallison et al., 2001; Sistani et al., 1999) and conditions conducive to enzymatic reactions during wet seasons (Rejmánková and Sirová, 2007). These land covers, along with some others exhibiting decreased enzymatic activity, was observed to fall under Alfisols or Entisols, suggesting soil orders may play a role in enzymatic responses to moisture changes. Alfisols, with their finer textures and higher nutrient contents, tend to retain moisture but may become waterlogged in wet conditions, inhibiting oxygen flow and reducing the activity of aerobic microbes responsible for enzymatic production (de Maced eta al., 2002; Russell, 1978; Rust, 1983). Entisols, conversely, are often sandy and well-drained, leading to rapid moisture percolation. In wet seasons, this could have resulted in the leaching of nutrients necessary for microbial activity, thus reducing enzymatic activity (Grossman, 1983). These all observations emphasize the critical roles of vegetation, soil type, and hydrological conditions in regulating enzymatic activities, reflecting the complex ecological processes that govern SOM decomposition. Vegetation influences enzyme activity through the type and quality of organic inputs, including litter and root exudates, which act as substrates for microbial metabolism. For instance, flatwood ecosystems dominated by pine, oak and palms, wetlands with aquatic plants, prairie grasses, and shrublands each contribute distinct litter chemistry and root exudates, thereby shaping microbial communities and enzyme production (Zhang et al., 2022; Schroeter et al., 2022; Meena and Rao, 2020). These plant-soil-microbe interactions directly influence the expression of enzymes involved in nutrient cycling. Soil type further modulates enzymatic activity through its inherent physical and chemical properties. Soils classified as Entisols and Alfisols, which dominate large portions of the study area, differ in their development, organic matter content, and nutrient-holding capacity. In particular, loamy textured soils typically provide higher water retention and improved aeration (Zega, 2024). Compared to sandy soils, supporting more stable microbial habitats and enhancing enzyme activity (Kim, 2015; Schnecker et al., 2014; Sinsabaugh et al., 2008). Hydrological conditions, especially the contrast between wet and dry seasons, strongly influence soil enzyme dynamics. In dry conditions, moderate moisture and aerobic environments enhance microbial respiration and promote the activity of hydrolytic enzymes. In

TABLE 4 HEDI with corresponding Quartile class among different land covers and ecosystems in dry and wet season.

Land cover	Dry season		Wet season		Ecosystems	HEDI value	
	HEDI value	Quartile class	HEDI value	Quartile class		Dry season	Wet season
1-Flatwood	−0.160	II	0.678	I	Group A Upland Forests	−0.962 to 1.613	−0.421 to 1.623
2-Mesic flatwood	−0.394	III	0.160	II			
3-Dry hammock	−0.962	IV	−0.421	III or IV			
4-Xeric hammock	0.374	I or II	0.337	I or II			
5-Palm hammock (Xeric)	−0.209	III	1.623	I			
6-Cypress	0.152	II	0.375	I			
7-Pinewood-1	−0.913	IV	−0.029	II			
8-Hammock	−0.085	II	−0.099	III			
9-Pinewood-2	1.613	I	−0.048	II or III			
10-Canal (wet)	−1.217	IV	−0.943	IV	Group B Wetland ecosystems	−1.217 to 0.937	−0.942 to 0.870
11-Wetland-1	0.797	I	0.870	I			
12-Wetland-2	−0.242	III	−0.610	IV			
13-Wetland-3	−0.397	III	−0.813	IV			
14-Wetland-4	0.937	I	−0.151	III			
15-Sawtooth palmetto	1.036	I	0.092	II	Group C Shrub ecosystems	1.035 to 2.280	0.092 to −0.035
16-Sabal palmetto	2.281	I	−0.036	II			
17-Dry Prairie-1	−0.102	II	−0.286	III	Group D Range Areas	−0.454 to 0.288	−0.286 to 0.978
18-Dry Prairie-2	−0.454	III or IV	0.979	I			
19-Dry Prairie-3	0.289	II	0.035	II			
20-Native pasture	−0.184	II or III	−0.210	III			
21-Improved pasture	−0.314	III	−0.099	III			
22-Abandoned citrus grove	−0.916	IV	−0.505	IV	Group E Barren ecosystems	−0.928 to −0.916	−0.897 to −0.505
23-Sandy spoil	−0.928	IV	−0.898	IV			

contrast, wet conditions, especially in poorly drained wetland systems can lead to waterlogging, reduce oxygen availability, and lower redox potential, thereby suppressing enzyme production and microbial function (Hammerl et al., 2019; Kapila et al., 2017; Liao et al., 2016). Together, these interrelated factors along with other environmental variables shape the biochemical and microbial environment, ultimately driving the decomposition of SOM across diverse ecosystems.

4.1.3 Comparison across ecosystems

Among different ecosystems, the broad range of enzymatic activity in C-Shrub ecosystems in dry season can be attributed to dense and diverse shrub vegetation, such as Saw palmetto and Gal berry, which contribute significant plant debris to the soil. This debris serves as a rich source of SOM, enhancing a variety of enzymes necessary for decomposing plant material (Charlebois, et al., 2010; Archibold and Archibold, 1995). On the other hand, the absence of vegetation in barren ecosystems might also contribute to the lowest enzymatic activities observed (Minick et al., 2022).

Across different ecosystems, higher βG activities in the wet season under A-Flatwoods and C-Shrub ecosystems can be attributed to the combined influence of higher available water storage capacity and sufficient substrate availability (Diédhiou et al., 2020; Bracho et al., 2008), which are favorable conditions indicative of high SOM decomposition (Blonska et al., 2020; Weintraub et al., 2013). For β-NAG, higher activities in A-Upland Forests, B-Range Areas, and C-Shrub ecosystems during both seasons can be attributed to optimal moisture levels (Borowik and Wyszkowska, 2016) combined with sufficient substrate availability (Song et al., 2021; Yao et al., 2019), conditions that promote SOM decomposition (Blonska et al., 2020; Blonska et al., 2020; Weintraub et al., 2013). Moreover, higher AP activity in C-Shrub ecosystems during the dry season could be attributed to the role of shrubs in maintaining soil moisture and stimulating microbial activity under dry conditions (Diédhiou et al., 2020; Bach and Hofmockel, 2016), which likely enhances enzymatic activity in these ecosystems. AS showing minimal variation in both seasons indicates its relatively insensitive nature (Moreira et al., 2017;

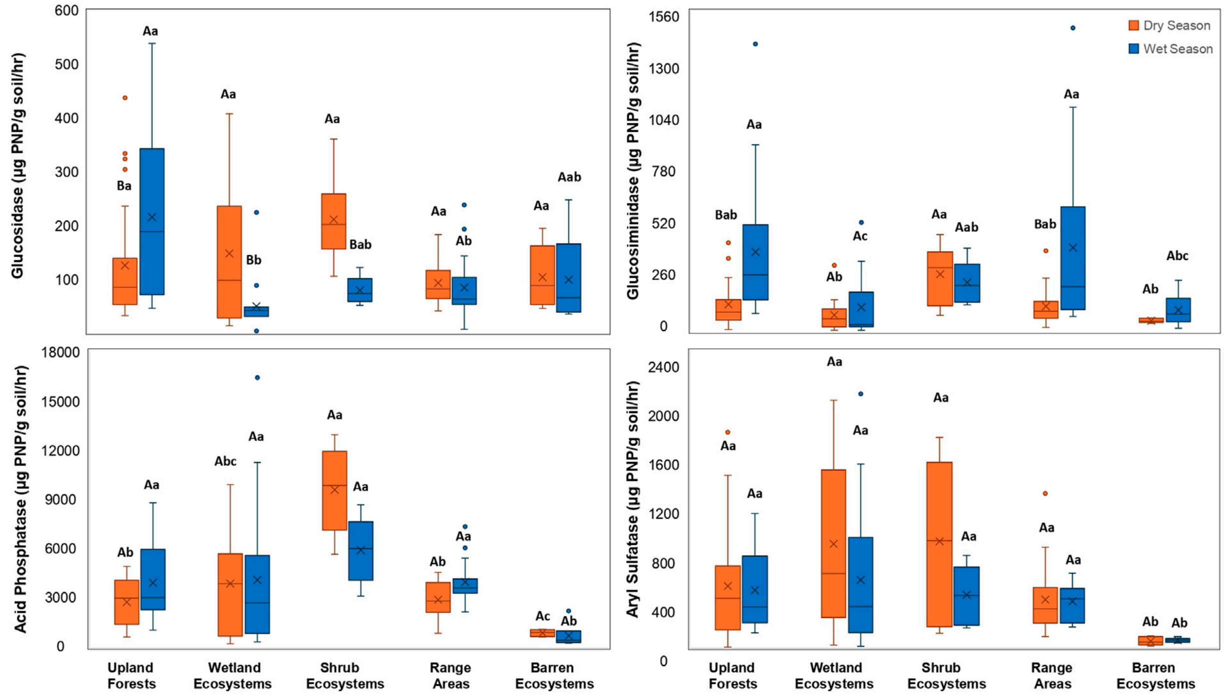


FIGURE 9
Comparison of hydrolytic enzyme activities- β-glucosidase, β-1,4-N-acetylglucosaminidase (β-NAG), acid phosphatase (AP), and arylsulfatase (AS) across five ecosystem categories at the DeLuca Preserve in wet and dry seasons. (Error bars represent ±standard error of the mean. Each ecosystem comprises multiple land cover types (Table 1). Capital letters above each box indicate significant seasonal differences within an ecosystem (dry vs. wet), while lowercase letters denote significant differences among ecosystems within each season (Bonferroni-adjusted, $p < 0.05$).

Wyszkowska et al., 2010). Several studies suggest that while some enzymes are sensitive to environmental changes, AS often exhibits stability under varying conditions (Moreira et al., 2017; Wyszkowska et al., 2010; Ekenler and Tabatabai, 2003; Bergstrom et al., 1998).

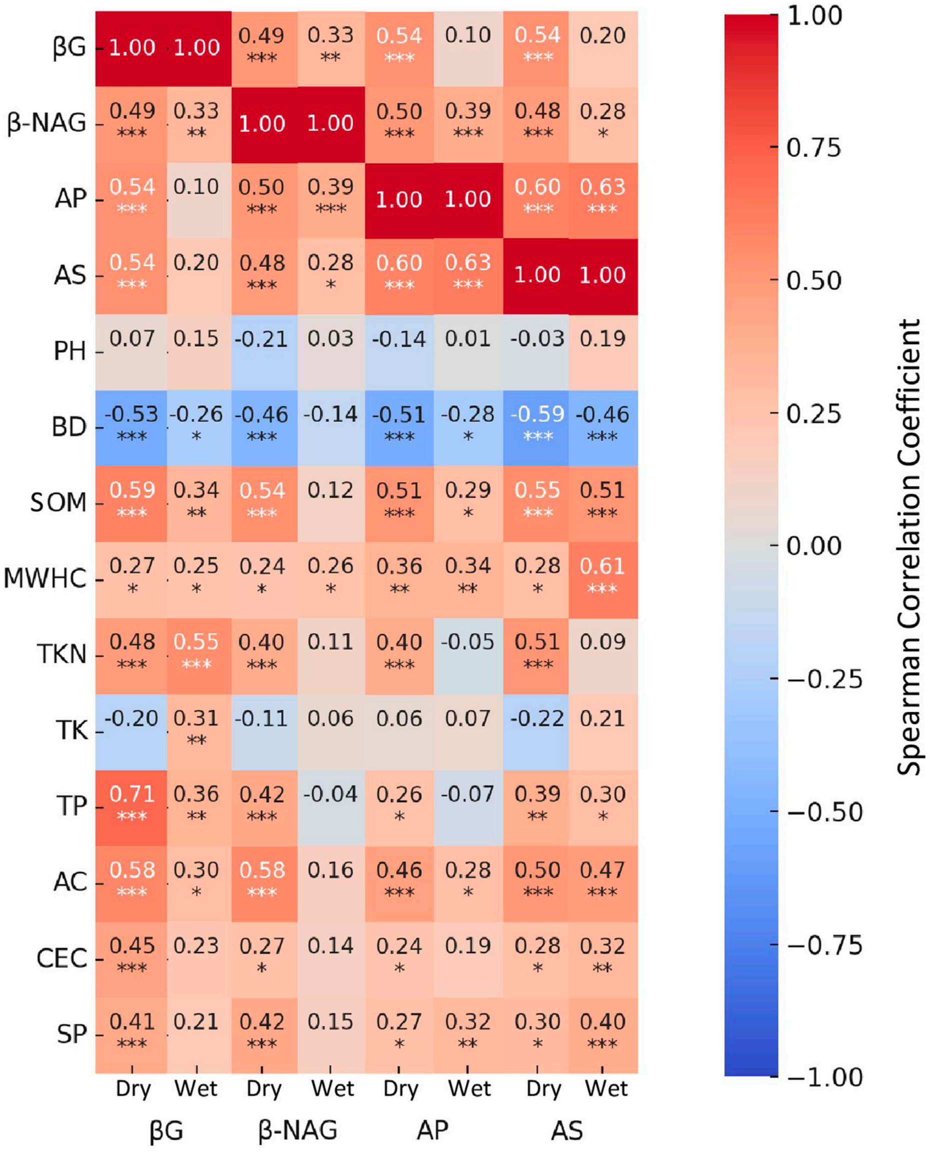
From dry to wet seasons the increase in βG and β-NAG activity in A-Upland Forests possibly due to the presence of Spodosols. These soils, with their sandy texture, can retain moisture without becoming waterlogged (New York State College of Agriculture and United States Soil Management Support Services, 1985). This moist yet aerated environment, enriched with organic material from varied vegetation (Prescott and Vesterdal, 2021; Prescott and Grayston, 2013; Hättenschwiler, 2005), likely encouraged microbial proliferation and enzymatic activity during the wet season. The decline in βG activity from the dry to the wet season within the B-Wetlands and C-Shrub ecosystems may be attributed to reduced microbial activity during the wet season, as during the dry season the presence of aeric and typic moisture subclasses likely promote greater microbial activity due to higher oxygen availability (Soil Survey Staff, 2003; Dekker et al., 1984). Conversely, in the wet season, the loamy soils with very poorly drained textures might lead to anaerobic, water-logged conditions, diminishing microbial activity and, consequently, enzymatic activities (Bogati et al., 2023; Steinweg et al., 2012).

4.1.4 HEDI across different land covers and ecosystems

The observed variability in the HEDI across different land covers and seasons shows the complex interplay of ecological factors influencing soil enzymatic activity and subsequent SOM decomposition (Wang, et al., 2020; Simpson et al., 2019). Low HEDI values, particularly in Canal (wet), indicate environments where conditions might be limiting for enzymatic processes, potentially due to factors like water saturation which could impede oxygen diffusion and thus microbial activity (Borowik and Wyszkowska, 2016).

The variation within ecosystems, particularly the contrast between the broad variability in Upland Forests and the consistently low activity in Barren ecosystems, highlights the role of vegetation (Li et al., 2015; Yin et al., 2014; Caldwell, et al., 1999) and soil characteristics (Błońska et al., 2017) in shaping enzymatic activity. Upland Forests, with a mix of vegetation supplying sufficient SOM, create conditions that can either foster or inhibit microbial activity depending on seasonal changes (Prescott and Vesterdal, 2021; Prescott and Grayston, 2013). For example, in favorable conditions, such as during moderate moisture and temperature, this vegetation-derived SOM provides abundant substrates that stimulate microbial growth and enzyme production (Osman, 2013; Baldrian and Štursová, 2010). However, in wet conditions, excess organic matter can lead to reduced oxygen availability or the accumulation of inhibitory compounds (e.g., polyphenols), which may suppress microbial processes (Zak et al., 2019; Zak et al., 2015; Myers et al., 2001). In Barren ecosystems, the minimal fluctuation in HEDI values suggests that the lack of vegetation and potentially poor soil conditions provide limited organic substrates for microbial decomposition, leading to consistently low enzymatic activity regardless of season (De Varennes and Torres, 2011; Badiane et al., 2001).

The observed shift towards higher HEDI values in A-Upland Forests, D-Range Areas and E-Barren ecosystems and lowering



	βG		β-NAG		AP		AS	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
βG	1.00	1.00	0.49 ***	0.33 **	0.54 ***	0.10	0.54 ***	0.20
β-NAG	0.49 ***	0.33 **	1.00	1.00	0.50 ***	0.39 ***	0.48 ***	0.28 *
AP	0.54 ***	0.10	0.50 ***	0.39 ***	1.00	1.00	0.60 ***	0.63 ***
AS	0.54 ***	0.20	0.48 ***	0.28 *	0.60 ***	0.63 ***	1.00	1.00
PH	0.07	0.15	-0.21	0.03	-0.14	0.01	-0.03	0.19
BD	-0.53 ***	-0.26 *	-0.46 ***	-0.14	-0.51 ***	-0.28 *	-0.59 ***	-0.46 ***
SOM	0.59 ***	0.34 **	0.54 ***	0.12	0.51 ***	0.29 *	0.55 ***	0.51 ***
MWHC	0.27 *	0.25 *	0.24 *	0.26 *	0.36 **	0.34 **	0.28 *	0.61 ***
TKN	0.48 ***	0.55 ***	0.40 ***	0.11	0.40 ***	-0.05	0.51 ***	0.09
TK	-0.20	0.31 **	-0.11	0.06	0.06	0.07	-0.22	0.21
TP	0.71 ***	0.36 **	0.42 ***	-0.04	0.26 *	-0.07	0.39 **	0.30 *
AC	0.58 ***	0.30 *	0.58 ***	0.16	0.46 ***	0.28 *	0.50 ***	0.47 ***
CEC	0.45 ***	0.23	0.27 *	0.14	0.24 *	0.19	0.28 *	0.32 **
SP	0.41 ***	0.21	0.42 ***	0.15	0.27 *	0.32 **	0.30 *	0.40 ***

FIGURE 10
Spearman correlation heatmaps showing the relationships between hydrolytic enzyme activities- β-glucosidase, β-1,4-N-acetylglucosaminidase (β-NAG), acid phosphatase (AP), and arylsulfatase (AS) and soil physicochemical parameters under dry and wet season conditions at the DeLuca Preserve. Each cell displays the Spearman correlation coefficient (ρ) between a given enzyme and soil property. Statistical significance is denoted by asterisks: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. Non-significant correlations are unmarked. Abbreviated soil variables: bulk density (BD), soil organic matter (SOM), maximum water holding capacity (MWHC), total nitrogen (TKN), total potassium (TK), total phosphorus (TP), active carbon (AC), cation exchange capacity (CEC), and soil protein (SP).

down in B-Wetland ecosystems and C-Shrub ecosystems during the wet season, underlines the complexity of SOM decomposition dynamics (Lehmann and Kleber, 2015; Schnitzer and Khan, 1975). While moisture is generally favorable for decomposition but only in optimum amount, it can also lead to conditions that may not always benefit enzymatic activity, as seen in the Range Areas where excessive moisture may not yield increased enzymatic action (Brockett et al., 2012; Hinojosa et al., 2004).

4.2 Relationship between soil physiochemical properties and hydrolytic enzyme activities in wet and dry seasons

The study revealed significant seasonal variations in soil enzyme-property relationships, emphasizing the dynamic nature of soil enzymes. Enzyme activities, strongly associated with microbial activity, showed positive correlations with OM (Kouchou et al., 2017; Madejón et al., 2001), SP (Theng, 2012; Ladd, 1985), and AC (Bhaduri et al., 2016; Zhongmei and Changchun, 2008), highlighting their roles in substrate availability and SOC decomposition (Smith et al., 2018; Kumar and Sharma, 2019). Additionally, enzyme activities are influenced by nutrient concentration and cycling (Ndlovu et al., 2023), as nutrients regulate microbial metabolism and enzyme synthesis (Liu et al., 2022; Chettri et al., 2020), aligning with the positive correlation observed with CEC. MWHC, meanwhile, improves water retention and provides essential nutrients for soil microorganisms (Mohammadi et al., 2011). The negative correlation between bulk density and enzyme activities across seasons supports Wang et al.'s

TABLE 5 Regression equations for hydrolytic enzyme activities across seasons.

Enzyme	Season	Equation	R^2
βG	Dry	$\beta G = 0.43 + 0.51TP + 0.34AP - 0.12TK$	0.71
	Wet	$\beta G = 0.08 + 0.49TKN + 0.18CEC$	0.41
β-NAG	Dry	$\beta\text{-}NAG = -0.09 + 0.32AC + 0.36AP$	0.48
	Wet	$\beta\text{-}NAG = -0.53 + 0.67AP + 0.24\beta G$	0.31
AP	Dry	$AP = 1.91 + 0.33AS + 0.35\beta\text{-}NAG$	0.51
	Wet	$AP = 2.41 + 0.50AS - 0.35TP + 0.19AC$	0.74
AS	Dry	$AS = 1.23 + 0.77AP - 1.43BD - 0.63TK$	0.56
	Wet	$AS = -2.69 + 0.76AP + 1.24MWHC + 0.30TP - 0.08CEC$	0.71
HEDI	Dry	$HEDI = -3.23 + 0.86AP + 0.59\ \beta\text{-}NAG + 0.51AS - 1.18MWHC + 0.24CEC - 0.21AC$	0.80
	Wet	$HEDI = -6.34 + 0.62\beta\text{-}NAG + 0.69AP + 3.46pH$	0.72

All predictors were significant at $p < 0.05$. The R^2 values represent the proportion of variance explained by the regression equation.

(2019) conclusions on the impact of soil compaction on microbial processes. Moreover, BD is negatively related to SOM (Tanveera et al., 2016; Ahad et al., 2015; Chaudhari et al., 2013; Angers and Simard, 1986), a key driver of enzymatic activity, further emphasizing the negative correlation between BD and enzyme activity. Seasonal shifts in enzyme correlations with reduction from the dry to wet season suggest changes in microbial resource allocation strategies, consistent with observations by Merino et al. (2016) regarding microbial adaptations to environmental fluctuations and nutrient demands in wet conditions.

The multiple linear regression analysis reveals dynamic seasonal shifts in soil-enzyme interactions, highlighting the complex nature of these relationships (Lee et al., 2021; Weintraub et al., 2013). The decreased R^2 values for βG and β-NAG in the wet season suggest that these carbon and nitrogen-cycling enzymes may be more sensitive to changes in soil moisture and associated environmental conditions. This aligns with the findings by Steinweg et al. (2012), who observed that soil moisture can significantly affect hydrolytic enzyme activities. Conversely, the increased R^2 values AP and AS in the wet season indicate that phosphorus and sulfur-cycling enzymes may be more strongly regulated by moisture-related factors. This could be due to increased substrate availability or changes in microbial community composition under wetter conditions, as suggested by Burns et al. (2013). The HEDI values showed strong associations with a broader range of soil properties in the dry season, where substrate availability and microbial activity were key drivers (Sistla and Schimel, 2013) but became more streamlined to fewer predictors in the wet season, where soil hydrology played a dominant role (Sistla and Schimel, 2013; Weintraub et al., 2013). This shift indicates that dominant controlling factors for overall enzyme activity may change between seasons, reflecting alterations in substrate availability, microbial community dynamics, or physicochemical soil properties (Wallenstein and Burns, 2011).

5 Conclusion

The investigation into the variations of hydrolytic enzyme activities between dry and wet conditions across different land covers has provided significant insights into the underlying mechanisms driving SOM decomposition in various land covers during wet and dry season. The study underlines the complex interaction between soil biogeochemical properties, vegetation types, moisture levels, and enzymatic activity, highlighting their collective impact on the dynamics of SOM decomposition. The higher βG activities observed during the wet season in A-Flatwoods and C-Shrub ecosystems emphasize the importance of adequate water storage and substrate availability in facilitating SOM decomposition under hydrologically favourable conditions. Similarly, the consistently elevated β-NAG activities across A-Upland Forests, B-Range Areas, and C-Shrub ecosystems indicate that optimal moisture levels and sufficient substrates are critical drivers of microbial activity and SOM decomposition. The increased AP activity in C-Shrub ecosystems during the dry season reflects the adaptive role of shrubs in maintaining soil moisture and promoting microbial processes under arid conditions. Conversely, the minimal seasonal variation in AS activity suggests its relative insensitivity to environmental fluctuations, highlighting its potential as a stable indicator of soil enzymatic functionality. Moreover, among ecosystems, B-Wetlands demonstrated consistently low enzymatic activity in wet season due to water saturation hindering oxygen diffusion and microbial activity. In contrast, upland forests and shrub ecosystems showed higher enzyme activities due to favourable conditions such as adequate substrate availability and well-aerated soils. The HEDI further highlighted these patterns, with variability across ecosystems reflecting the interplay of vegetation, soil type, and moisture conditions.

The correlations and regression analyses provide a deeper understanding of how soil properties such as OM, SP, and AC consistently correlate positively with enzyme activity, reflecting their central roles in enhancing substrate supply and promoting microbial growth. Similarly, CEC and MWHC foster an environment conducive to enzymatic functions by improving nutrient retention and water availability. On the other hand, high BD and waterlogging in wetland or canal ecosystems restrict oxygen diffusion and reduce enzymatic activity, inhibiting SOM turnover. This variability indicates the adaptive strategies of microbial communities in response to changing environmental conditions, particularly in maintaining the balance between the decomposition of labile and stable SOM. The variability in HEDI values, serving as a proxy for soil enzymatic processes governing SOM decomposition, across land covers and seasons provides critical insights into ecological functioning within this subtropical preserve. These findings emphasize the necessity of tailored conservation strategies to enhance ecosystem resilience and functionality. For instance, in wetland systems, managing hydroperiods to reduce waterlogging can improve oxygen diffusion and enzymatic activity. In shrub ecosystems, preserving native vegetation supports adaptive processes during dry seasons by maintaining soil moisture. Similarly, in upland forests, optimizing substrate availability through organic matter inputs sustains βG and β-NAG driven decomposition. HEDI offers a novel, integrative index that combines the activity of key hydrolytic enzymes involved in SOM breakdown, enabling a more holistic understanding of microbial decomposition potential. Unlike traditional approaches that assess enzymes individually, HEDI provides a composite measure that reflects microbial functioning across diverse ecosystems and seasons. Moreover, integrating HEDI into a monitoring framework and accounting for the complex interactions among soil properties, vegetation, and moisture can help track early shifts in soil functionality and enable the design of conservation practices that can maintain the crucial balance between labile and stable carbon turnover in SOM.

Moreover, the land covers in this study were not evenly distributed across the five major ecosystems; however, the sampling design still allowed us to capture representative variability within and across land cover types. While the current sampling density revealed meaningful patterns in enzyme activity and SOM dynamics, future studies with more balanced representation and increased sampling intensity alongside consideration of additional environmental could further strengthen these insights. Importantly, the findings of this study offer a transferable framework for understanding SOM decomposition and soil functioning in other subtropical or ecologically similar landscapes, supporting informed soil management and conservation strategies beyond the DeLuca Preserve.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

SM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft. NM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – review and editing. AR: Formal Analysis, Investigation, Methodology, Writing – review and editing. NM-I: Conceptualization, Investigation, Methodology, Writing – review and editing. SS: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review and editing. AB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review and editing. WM-H: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review and editing. JB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

The authors declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2025.1564047/full#supplementary-material

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