Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography A Journal of Macroecology

META-ANALYSIS

Global Patterns and Drivers of Soil Extracellular Enzyme Activities in Response to Plant Invasion: A Meta-Analysis

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Received: 29 November 2024 | **Revised:** 12 June 2025 | **Accepted:** 19 June 2025

Handling Editor: Xiaofeng Xu

Funding: This work was supported by National Natural Science Foundation of China (32471672 and 32071598), Natural Science Foundation of Fujian Province (2024J01274 and 2020J01503), Minjiang River Estuary Wetland National Nature Reserve Administrative Office (MJHKSD20230202), Australian Research Council (DP2401012143) and Macquarie University's Faculty of Science and Engineering.

Keywords: extracellular enzyme activity | invasion duration | mycorrhizal association | nutrient availability | plant invasion | soil microorganisms

ABSTRACT

Aim: Plant invasion is a major global environmental challenge. While invasive plants can potentially enhance soil nutrient availability by stimulating soil extracellular enzyme activities, empirical studies have yielded conflicting results. A comprehensive understanding of global patterns and underlying drivers is therefore essential for inferring generalities.
Location: Global.
Time Period: 2000–2025.
Major Taxa Studied: Invasive plants and soil microorganisms.
Methods: We conducted a meta-analysis on 635 observations from 117 studies worldwide, investigating the effect of plant invasion on 11 soil carbon (C)-, nitrogen (N)- and phosphorus (P)-acquiring enzyme activities. We also analysed how environmental drivers and ecosystem types modulated these responses.
Results: Plant invasion significantly increased hydrolytic C-, N- and P-acquiring enzyme activities by 18% (11%–27%), 29% (22%–37%), and 32% (24%–41%), respectively, while it had no significant effects on oxidative enzyme activities. These enzymatic responses were primarily driven by elevated dissolved organic carbon and soil moisture content, coupled with decreased fungal/bacterial ratios under invasion. The most pronounced enzymatic responses occurred in neutral and alkaline soils during the early stages of invasion and when invasive plants formed mycorrhizal associations. Different ecosystem types displayed distinct

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enzymatic responses to plant invasion: grasslands showed elevated N-acquiring enzyme activities, wetlands exhibited enhanced P-acquiring enzyme activities, croplands demonstrated increases across all hydrolytic enzyme classes, while woodlands displayed modest enzymatic responses to invasion compared to other ecosystem types.

Main Conclusions: We found that (i) plant invasion consistently increased hydrolytic enzyme activities while it had negligible effects on the activities of oxidative enzymes; (ii) enzymatic responses to invasion were modulated by ambient soil pH, invader mycorrhizal status and invasion duration; and (iii) invasive plants enhanced soil nutrient availability across ecosystem types through different impacts on enzyme activities. These findings provided mechanistic insights into plant invasion success and advanced our predictive capacity for invasion impacts on biogeochemical processes.

1 | Introduction

Plant invasion is a major global environmental challenge with significant impacts on biodiversity, ecosystem services, and human welfare (IPBES 2023). Globally, over 13,000 naturalised plant species have established wild populations, with approximately 3000 classified as invasive species (van Kleunen et al. 2015). These invasive species threaten 20% of Earth's terrestrial habitats and have caused economic losses exceeding 8.9 billion USD in the past five decades (Diagne et al. 2021). Understanding the mechanisms driving invasion success is crucial for managing invasion (Early et al. 2016; Seebens et al. 2021).

Emerging evidence has revealed that invasive plants can reshape belowground nutrient cycling by modulating extracellular enzyme activities (EEAs) of soil microorganisms (Allison et al. 2006; Negesse et al. 2025; Sardans et al. 2017; Xu et al. 2022). Soil extracellular enzymes—critical for organic matter decomposition and nutrient release (Sinsabaugh and Follstad Shah 2012)—serve as vital indicators for assessing invasion-induced impacts on biogeochemical processes (Zhou and Staver 2019). However, empirical studies have reported conflicting results on these impacts (Allison et al. 2006; Fan et al. 2010; Ho and Chambers 2019; Thompson et al. 2018; Zhang et al. 2020). A quantitative synthesis is therefore necessary to resolve these inconsistencies and identify general patterns.

One potential explanation for these inconsistencies is the functional divergence between hydrolytic and oxidative enzymes and their differential responses to invasion-driven changes. Hydrolytic enzymes (e.g., β-glucosidase, urease, phosphatase) predominantly mediate the decomposition of simple organic compounds (Freeman et al. 2001; Stark et al. 2014), while oxidative enzymes (e.g., phenol oxidase, peroxidase) primarily degrade recalcitrant polymers, such as lignin (Cui et al. 2018; Sinsabaugh et al. 2008). Critically, plant invasions fundamentally alter these two functional soil enzyme activities by (i) changing substrate availability through enhanced root exudation and litter inputs, which may favour hydrolytic enzymes due to their specialisation in processing labile organic compounds (Liao et al. 2008), (ii) shifting microbial communities from slow-growing taxa (e.g., fungi) to fast-growing (e.g., bacteria) species through increased soil nitrogen (N) availability, potentially enhancing bacterial-derived hydrolytic enzymes while suppressing fungal-derived oxidative enzymes (Sardans et al. 2017; Torres et al. 2021; Zhang and van Kleunen 2019); and (iii) changing soil moisture content through altered hydrological processes (e.g., infiltration, retention, plant uptake, and transpiration), with moisture-sensitive hydrolytic enzymes likely showing stronger responses compared to oxidative enzymes that are less moisture-dependent (Ehrenfeld 2003; Xu et al. 2022). These mechanistic differences suggest that invasion impacts on soil enzyme activities are likely to be function-specific, potentially explaining the conflicting patterns observed across studies.

Environmental factors also can moderate soil enzymatic responses to plant invasion. First, invader traits, such as symbiotic associations (e.g., arbuscular vs. ectomycorrhizal fungi), N fixation ability, and plant form can influence soil enzyme activities via distinct impacts on microbial community composition as well as differences in the quantity and quality of substrate they produce (Liang et al. 2020; Pyšek and Richardson 2007). Second, ambient soil properties may regulate invasion effects on soil enzyme activities through complex interactions among bulk density, moisture content, texture, and soil pH (Xu et al. 2022). Third, climatic factors, such as temperature and precipitation, can moderate invasion impact by influencing both plant physiological processes and microbial metabolism (Zhou and Staver 2019). Fourth, the duration of invasions can influence enzymatic responses as substrate availability changes over time and soil microbial communities progressively adapt to these altered conditions (D'Antonio and Flory 2017). The complex interplay among these environmental variables also likely explains the variability in soil enzymatic responses to plant invasion.

Ecosystem types can shape soil enzymatic responses to plant invasion. For instance, grasslands, predominantly distributed across moisture-limited regions, are characterised by low N availability and reduced decomposition rates due to low moisture conditions (Berdugo et al. 2023). Wetland soils, despite their abundant organic matter reserves, possess distinctive redox environments that influence microbial functions, particularly through metal-mediated phosphorus (P) sorption/desorption (Sundareshwar et al. 2003). Croplands, characterised by high productivity, frequent fertiliser addition and organic matter removal through agricultural practices, may exhibit substantially different enzymatic patterns (Lal 2004; Vitousek et al. 2009). Woodlands, with their intricate vertical stratification and extensively developed belowground root networks, likely develop their own distinctive enzymatic responses (Poorter et al. 2010; Umaña et al. 2020). Ecosystem-specific nutrient availabilities, coupled with their distinctive biogeochemical properties, thus could create diverse ecological contexts that potentially mediate the magnitude and direction of plant invasion impacts on soil enzyme activities.

Here we conducted a global meta-analysis encompassing 635 observations from 117 peer-reviewed studies across diverse ecosystems, examining the activities of 11 distinct soil enzymes. We hypothesised that: (i) hydrolytic and oxidative enzymes would exhibit differential responses to plant invasion, via invasion-induced changes in substrate availability, soil properties and microbial community composition; (ii) invasion effects would be modulated by invader traits, ambient soil properties, climatic factors, as well as invasion duration; and (iii) soil enzymatic responses to invasion would vary among ecosystem types, according to their distinct nutrient conditions. This meta-analysis represents the most extensive synthesis of soil enzymatic responses to plant invasion to date, incorporating a dataset approximately three-fold larger than previous compilations (Negesse et al. 2025; Xu et al. 2022; Zhou and Staver 2019). Our synthesis reveals how the interplay between enzyme classes, environmental variables and ecosystem types helps explain the inconsistent soil enzymatic responses previously documented across invaded systems, providing mechanistic insights into plant invasion success that enhance our predictive understanding of invasion impacts on biogeochemical processes.

2 | Materials and Methods

2.1 | Data Collection

We systematically searched the Web of Science database (www.webofscience.com), Google Scholar (scholar.google.com) and China National Knowledge Infrastructure (www.cnki.net) for peer-reviewed journal papers published until March 2025 using the keywords: (i) 'plant invasion' or 'plant encroachment' or 'invasive plant species' or 'alien plant species' or 'exotic plant species' and (ii) 'enzyme activity' or 'EEA' or 'hydrolase' or 'oxidase' or 'hydrolytic enzyme' or 'oxidative enzyme' or 'cellulase' or 'ligninase' or 'glucosidase' or 'cellobiohydrolase' or 'invertase' or 'xylosidase' or 'glucosaminidase' or 'aminopeptidase' or 'chitinase' or 'urease' or 'phosphatase' or 'phosphomonoesterase' or 'phenol oxidase' or 'peroxidase' or 'polyphenol oxidase'.

Studies were included in the meta-analysis if they met the following criteria: (i) they investigated paired invaded and uninvaded sites and provided complete statistical information (mean, sample size, and standard errors/deviations) for at least one soil C-, N- or P-acquiring enzyme activity; (ii) for studies with multiple sites, sampling points, or temporal measurements, each observation was treated as an independent case; (iii) for studies with multiple soil layers, only data from the topsoil layer (0–30 cm) was included to ensure comparability across studies; (iv) for field observations, measurements at invaded and uninvaded sites were conducted simultaneously or within short time intervals (e.g., 1 week) under similar environmental conditions to minimise confounding effects (Castro-Díez et al. 2014); and (v) for pot/mesocosm experiments, initial soil conditions were identical between invaded and uninvaded treatments.

Based on these criteria, our final dataset comprised 635 paired invaded and uninvaded observations of soil enzyme activities under plant invasion obtained from 117 peer-reviewed studies (Figure 1a), including 14 controlled pot/mesocosm experiments and 103 field observations (Table S1). The dataset included data on the activities of β-glucosidase (BG; $n = 279$), β-D-cellobiohydrolase (CBH; $n = 60$), xylanase (XYL; $n = 13$), invertase (INV; $n = 42$), N-acetyl-glucosaminidase (NAG; $n = 72$), urease (URE; $n = 360$), glycine aminopeptidase (GAP; $n = 28$), acid phosphomonoesterase (ACP; $n = 236$), alkaline phosphomonoesterase (ALP; $n = 219$), phenol oxidase (POX; $n = 116$) and peroxidase (PER; $n = 75$). The PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flowchart is provided in the Supporting Information (Figure S1).

2.2 | Data Extraction

Our meta-analysis included the following enzyme categories: (i) hydrolytic C-acquiring enzymes [e.g., BG, CBH, XYL, INV]; (ii) hydrolytic N-acquiring enzymes [e.g., NAG, URE, GAP]; (iii) hydrolytic P-acquiring enzymes [e.g., ACP and ALP]; and (iv) oxidative enzymes [e.g., POX and PER] (Table S2). For papers reporting multiple types of soil enzyme activities, their summed values were considered as the overall responses (Method S1). While specific substrates and protocols varied across studies, soil enzyme activities were generally assayed using colorimetric or fluorometric methods (Table S3), providing a basis for comparing soil enzyme activities.

We also extracted data on several explanatory variables, including soil properties [dissolved organic carbon (DOC), moisture content, pH, available N and P] and microbial characteristics (fungal and bacterial biomass, and fungal/bacterial ratios). Soil properties were measured using standard analytical techniques across studies, including high-temperature catalytic oxidation and spectrophotometric methods for DOC (Suzuki et al. 1992), gravimetric methods for moisture content (Gardner 1986), potentiometric methods (i.e., pH meters) for pH (Thomas 1996), Kjeldahl or colorimetric methods for available N (Bremner 1996) and colorimetric techniques (e.g., Bray-P1, Olsen methods) for available P (Olsen and Sommers 1982). Microbial biomass (bacteria and fungi) was predominantly assessed through phospholipid fatty acid analyses (PLFA) (Frostegård and Bååth 1996). To minimise methodological heterogeneity and ensure data comparability between studies, we excluded explanatory variables that were measured using techniques that were substantially different from the commonly accepted methods described above.

Environmental variables encompassed geographic location (latitude: 38° S to 54° N; longitude: 155° W to 145° E), climate variables [mean annual temperature (MAT): −4°C to 31°C; mean annual precipitation (MAP): 100–2750 mm; climate zone: equatorial, arid, warm temperate, and snow climates, following Köppen-Geiger climate classification (Kottek et al. 2006)], invader traits (plant growth form: woody and non-woody; mycorrhizal associations: arbuscular mycorrhizal, ectomycorrhizal and non-mycorrhizal; Soudzilovskaia et al. 2020; N-fixing capability: presence or absence; plants.usda.gov), invasion duration (short: < 5 years; medium: 5–20 years; long: > 20 years; Flory et al. 2017), and ambient soil pH (categorised as acidic: < 6.5, neutral: 6.5–7.4, and alkaline: > 7.5, following Soil Survey Division Staff 1993). Ecosystem types were classified following Jung et al. (2020), with some modifications: wetlands (including peatlands, riverine areas, mangroves, tidal marshes, mudflats and rice paddies); grasslands (areas predominantly covered by grasses and herbs with few or no trees); woodlands (forests and shrublands with substantial tree and shrub coverage); and croplands (agricultural lands and rural gardens).

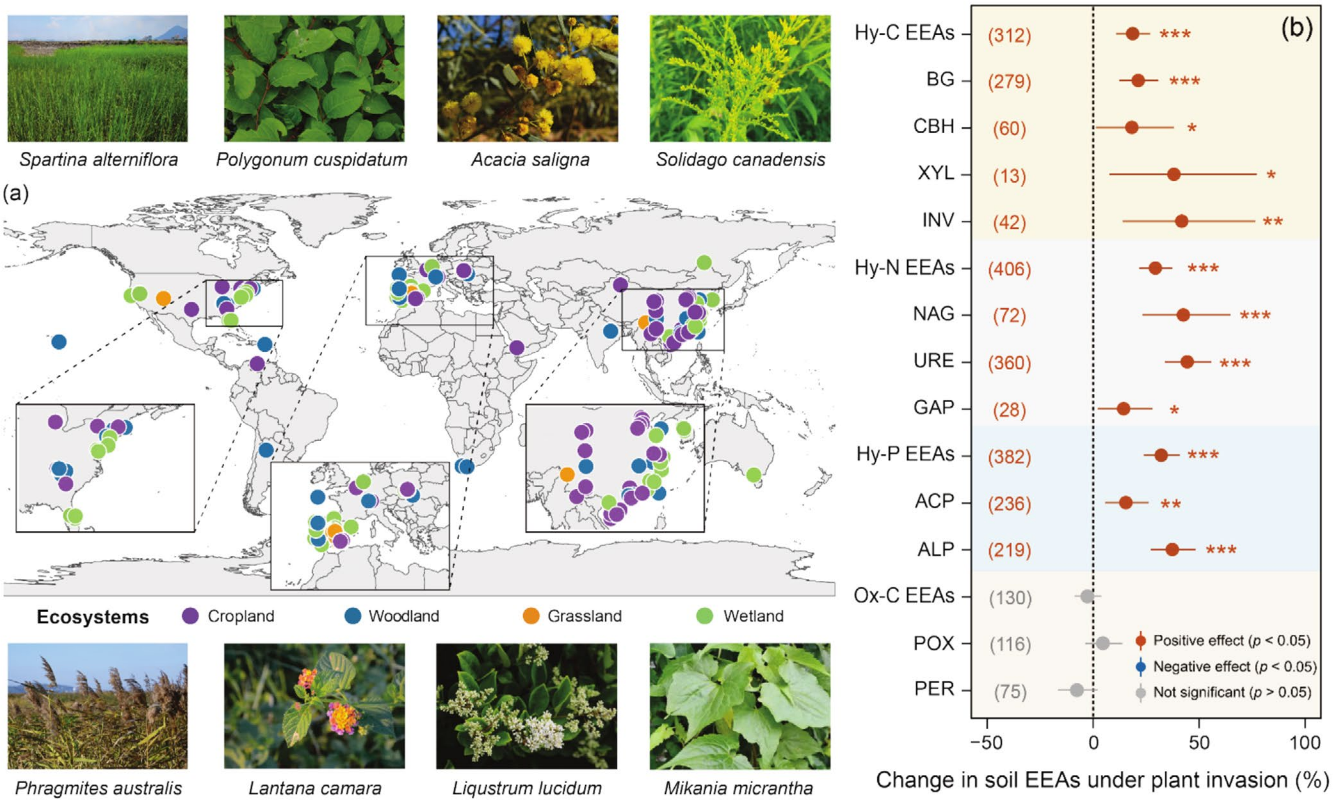

FIGURE 1 | Global distribution of plant invasion studies included in this meta-analysis (a) and percent changes in soil extracellular enzyme activities following plant invasion (b). In panel (a), dots of different colours represent different ecosystem types. The inset photographs showcase representative invasive plant species, used with permissions obtained from the respective photographers. Map boundaries shown do not necessarily reflect officially recognised national borders. In panel (b), error bars indicate 95% confidence intervals, with sample sizes for each enzyme displayed in parentheses. Statistical significance of effect sizes is denoted by asterisks (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$). ACP, acid phosphomonoesterase; ALP, alkaline phosphomonoesterase; BG, β-glucosidase; CBH, β-D-cellobiohydrolase; EEAs, extracellular enzyme activities; GAP, glycine aminopeptidase; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs; INV, invertase; NAG, N-acetyl-glucosaminidase; PER, peroxidase; POX, phenol oxidase; URE, urease; XYL, xylanase.

2.3 | Meta-Analysis

The natural log response ratio (lnRR) was used to analyse the effect of plant invasion on variables (Hedges et al. 1999), and was calculated using Equation (1):

$$\ln\mathrm{RR} = \ln\frac{X_e}{X_c} = \ln X_e - \ln X_c \quad (1)$$

where X_e and X_c were the mean values of a variable at the invaded and uninvaded sites, respectively. The variance (V) was calculated using Equation (2):

$$V = \frac{S_e^2}{n_e X_e^2} + \frac{S_c^2}{n_c X_c^2} \quad (2)$$

where S_e and S_c were the standard deviations of a variable at the invaded and uninvaded sites, respectively; n_e and n_c were the sample sizes of a variable at the invaded and uninvaded sites, respectively.

The weightings were applied to enhance the overall estimate's precision through minimising standard error and sampling variance. The effect size (weighted lnRR) was calculated as Equation (3):

$$\text{Effect size (weighted lnRR)} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}\ln\mathrm{RR}_{ij}}{\sum_{i=1}^{n}\sum_{j=1}^{k} w_{ij}} \quad (3)$$

where m was the total number of groups and k was the total number of sites in group i. If the bias-corrected 95% confidence interval (CI) of the effect size had no overlap with zero, the responses of variables to plant invasion were statistically significant, with the 95% CI calculated using Equation (4) (Hedges et al. 1999):

$$95\%\,\mathrm{CI} = 1.96 \times \mathrm{SE}\ (\text{Effect size}) \pm \text{Effect size} \quad (4)$$

The standard error (SE) of the effect size was estimated using Equation (5):

$$\mathrm{SE}\ (\text{Effect size}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}} \quad (5)$$

The weighted lnRR was converted to the percentage change in plant invasion effects on variables using Equation (6) (Rosenberg et al. 2000):

$$\text{Percentage change} = \left(e^{\text{Effect size}} - 1\right) \times 100\,\% \quad (6)$$

The meta-analysis was performed using the "*metafor*" R package with the restricted maximum likelihood "REML" method (Viechtbauer 2010). "Study ID" was included as a random factor in the meta-analysis, as multiple observations were derived from individual studies. Egger's regression tests were conducted to assess publication bias (Egger et al. 1997; Table S4). When publication bias was detected, the results were corrected using the trim-and-fill method (Duval and Tweedie 2000; Table S4).

Kernel density estimation (KDE) was used to generate smooth density curves for individual soil enzyme activities using the '*ggridges*' R package (Wilke 2024; Figure S2). The frequency distributions of the four functional enzyme classes were visualised using the '*ggplot2*' R package (Wickham 2016; Figure S3). For the four functional enzyme classes (Figure S3) and the three hydrolytic enzymes across different ecosystems (Figure 5a–c), we displayed individual observations with their 95% CIs using the '*caterpillars*' function from the '*orchard*' R package (Nakagawa et al. 2021).

Meta-regression analysis was performed to examine the relationships between plant invasion-induced changes in soil hydrolytic enzyme activities (i.e., C-, N- and P-acquiring enzymes) and the corresponding changes in explanatory variables (including DOC, moisture content, fungal/bacterial ratios) using the '*rma*' function from the '*metafor*' R package (Viechtbauer 2010) (Figure 2).

All possible combinations of the individual environmental variables were evaluated within a mixed-effects meta-regression using maximum likelihood estimation to identify the main drivers underlying enzymatic patterns (Terrer et al. 2016). Model selection was guided by the corrected Akaike information criterion (AICc) (Hurvich and Tsai 1991). The relative importance of each predictor was calculated as the sum of Akaike weights—the probability of a model being the most parsimonious—across all models in which the predictor appeared (Figure 3). The predictors featured in models with high Akaike weights were assigned greater weight, reflecting the overall support for each variable across all tested models. The importance threshold of 0.8 was established to distinguish critical predictors from non-essential ones (Terrer et al. 2016).

To test whether the impact of plant invasion on soil hydrolytic C-, N- and P-acquiring enzyme activities differed between subgroups of selected predictor variables (Figure 4), the significance of the between-group heterogeneity (Q_m) was assessed using chi-squared tests (Rosenberg et al. 2000; Table S5). Differences in hydrolytic enzyme activities within a specific ecosystem type were analysed using one-way analysis of variance (ANOVA) followed by Tukey's HSD post hoc test for multiple comparisons (Figure 5).

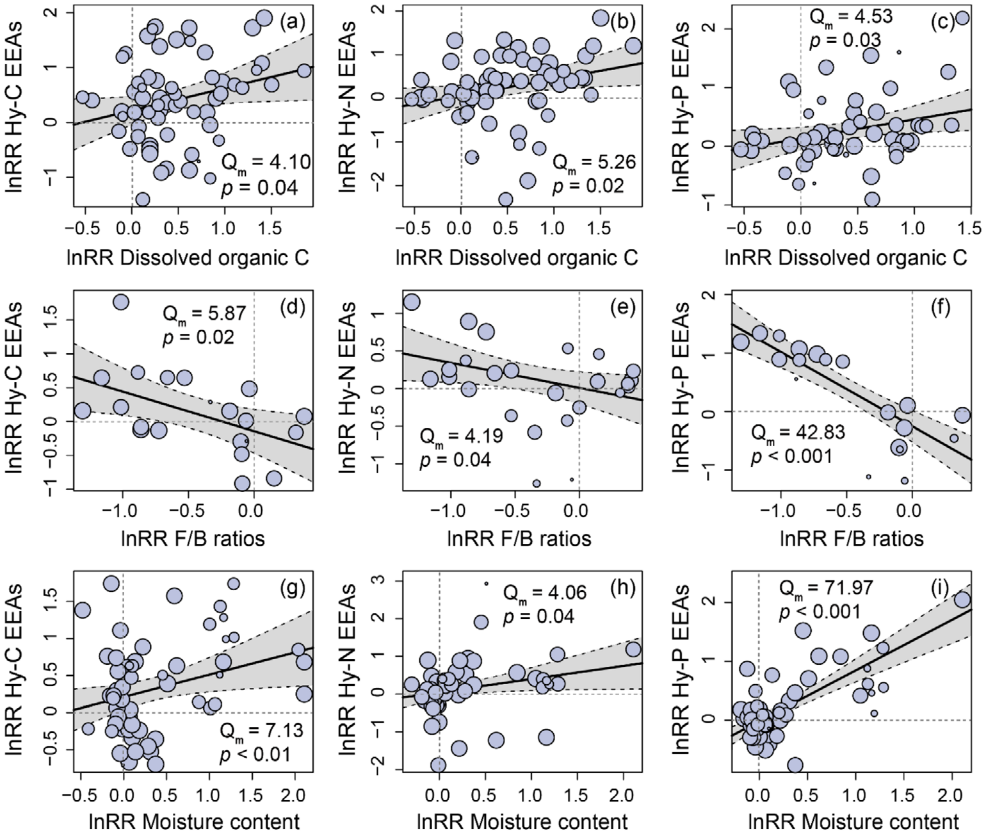

FIGURE 2 | Relationships between effect sizes (lnRR) of soil hydrolytic enzyme activities and corresponding changes in dissolved organic carbon (a–c), fungal/bacterial ratios (d–f), and soil moisture content (g–i). Shaded regions indicate 95% confidence intervals around regression lines. Q_m represents the moderator test value from meta-regression analysis, with accompanying p-values denoting statistical significance of relationships. DOC, dissolved organic carbon; EEAs, extracellular enzyme activities; F/B ratios, fungal/bacterial ratios; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs.

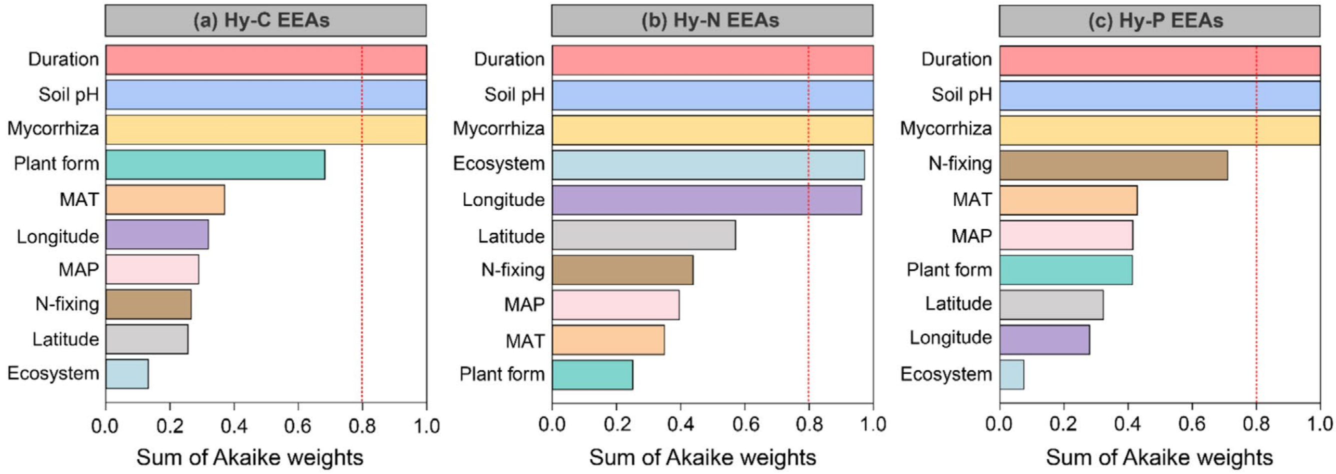

FIGURE 3 | Model-averaged ranked importance of the predictors of plant invasion effects on soil hydrolytic enzyme activities. Importance is estimated from the sum of Akaike weights based on model selection analysis using corrected Akaike's information criteria. A cutoff value is set at 0.8 to differentiate between important and non-essential predictors. Predictors: MAT (i.e., mean annual temperature); MAP (i.e., mean annual precipitation); Mycorrhizal association (i.e., arbuscular mycorrhizal, ectomycorrhizal, and non-mycorrhizal invaders); N-fixing (i.e., N-fixing and non-N-fixing invaders); plant form (i.e., woody and non-woody invaders); climate zone (i.e., equatorial, arid, warm temperate, and snow); ecosystem type (i.e., cropland, wetland, grassland, and woodland); soil pH (i.e., acidic, neutral, alkaline); and invasion duration (i.e., short, medium, and long). EEAs, extracellular enzyme activities; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs.

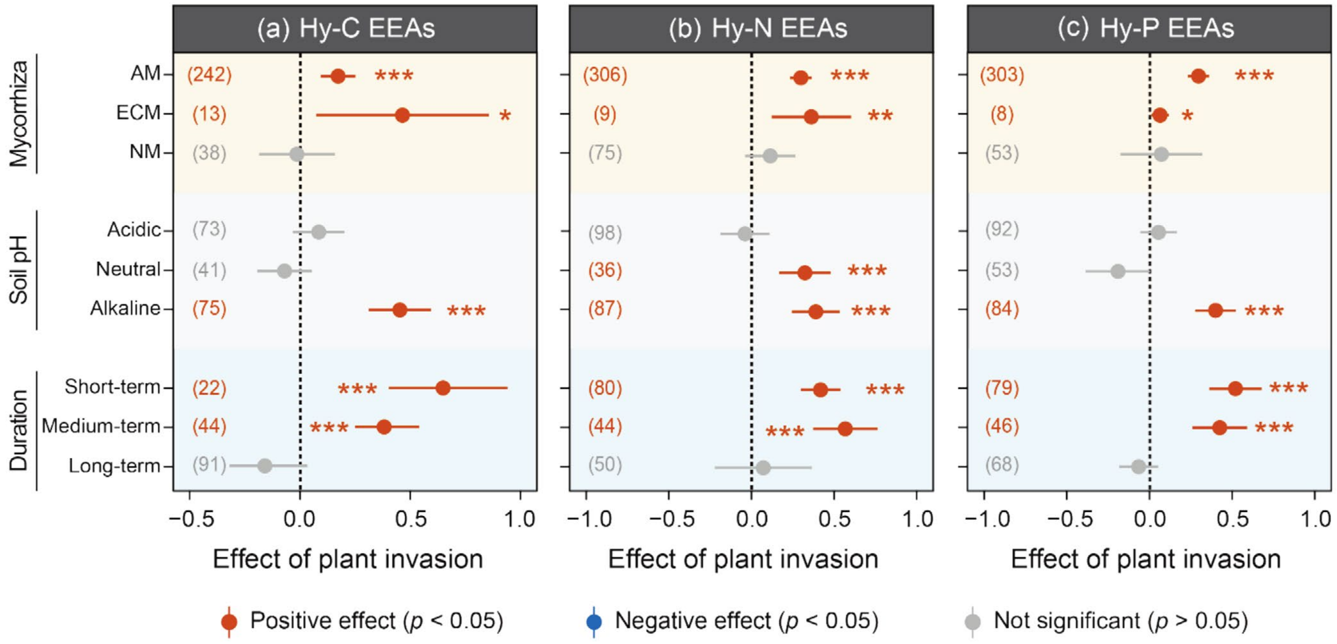

FIGURE 4 | Effects of plant invasion on soil hydrolytic enzyme activities based on mycorrhizal association types, soil pH, and invasion duration. Error bars represent 95% confidence intervals, and the sample size for each variable is shown in parentheses (a–c). Asterisks indicate significant effect sizes (***$p<0.001$; **$p<0.01$; *$p<0.05$). EEAs, extracellular enzyme activities; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs.

3 | Results

We found that plant invasion significantly increased soil hydrolytic enzyme activities while it exerted minimal effects on oxidative enzyme activities (Figure 1b). On average, plant invasion enhanced soil hydrolytic C-acquiring enzyme activities by 18% [95% CIs: 11%–27%]. Specifically, invasion increased the activities of β-glucosidase (BG) by 21% (12%–31%), cellobiohydrolase (CBH) by 18% (1%–38%), xylosidase (XYL) by 38% (8%–77%), and invertase (INV) by 42% (14%–76%). For hydrolytic N-acquiring enzymes, plant invasion increased overall activities by 29% (22%–37%), with notable increases in N-acetyl-glucosaminidase (NAG) by 43% (23%–65%), urease (URE) by 44% (34%–56%), and aminopeptidase (GAP) by 14% (2%–28%). Similarly, plant invasion enhanced hydrolytic P-acquiring enzyme activities by 32% (24%–41%), including a

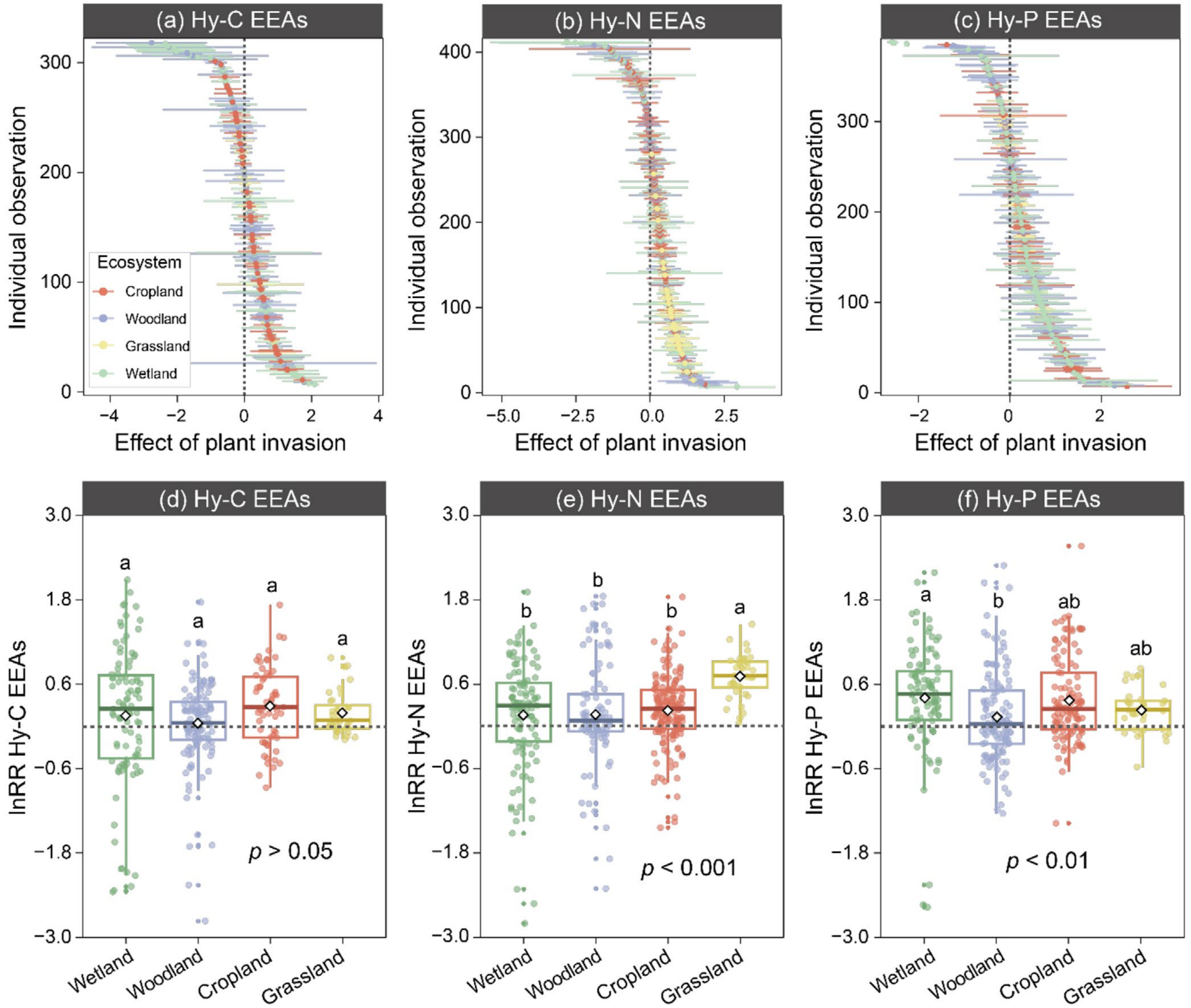

FIGURE 5 | Ecosystem-specific responses of soil hydrolytic enzyme activities to plant invasion across different ecosystem types. Panels (a–c) show the raw data, while panels (d–f) show the normalised data. Colours represent different ecosystem types. Effect sizes with 95% confidence intervals (95% CIs) of each sample are presented in increasing order. Each box plot represents the mean (diamond), median (bold horizontal line), interquartile range (25th–75th percentiles; box), and 5th–95th percentile range (whiskers). Differences in soil hydrolytic enzyme activities within each ecosystem were analysed using one-way analysis of variance (ANOVA) followed by Tukey's HSD post hoc test for multiple comparisons. Different letters above box plots indicate significant differences between ecosystem types ($p < 0.05$). The p-values shown in each panel represent the overall ANOVA significance level. Ecosystem types were classified following Jung et al. (2020), with some modifications: Wetlands (including peatlands, riverine areas, mangroves, tidal marshes, mudflats, and rice paddies); grasslands (areas predominantly covered by grasses and herbs with few or no trees); woodlands (forests and shrublands with substantial tree and shrub coverage); and croplands (agricultural lands and rural gardens). EEAs, extracellular enzyme activities; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs.

15% (6%–26%) increase in acid phosphatase (ACP) activity and a 37% (27%–48%) increase in alkaline phosphatase (ALP) activity. In contrast, plant invasion had no significant effect on oxidative enzyme activities [−3% (−9%–4%)], including phenol oxidase (POX) [5% (−4%–14%)] and peroxidase (PER) [−8% (−16%–2%)].

Plant invasion enhanced dissolved organic carbon (DOC) by 65% (46%–86%) and soil moisture content by 36% (22%–51%), while it decreased fungal/bacterial (F/B) ratios (Figure S4). The responses of soil hydrolytic C-, N- and P-acquiring enzyme activities were positively correlated with changes in DOC and moisture content but negatively correlated with changes in F/B ratios (Figure 2a–i). Conversely, soil oxidative enzyme activities showed no significant associations with alterations in DOC, moisture content, or F/B ratios (Figure S5a–c). We observed progressive depletion of DOC and water content but increasing F/B ratios with invasion duration (Figure S6).

Our model selection analysis identified invasion duration, ambient soil pH, mycorrhizal association, and ecosystem type as primary predictors of invasion effects on soil enzyme activities

(Figure 3a–c). Specifically, arbuscular mycorrhizal (AM)- and ectomycorrhizal (ECM)-associated invaders showed higher soil hydrolytic enzyme activities compared to non-mycorrhizal (NM)-associated invaders (Figure 4a–c). In alkaline and neutral soils, plant invasion substantially increased soil hydrolytic C-, N- and P-acquiring enzyme activities, whereas these effects were attenuated in acidic soils (Figure 4a–c). Additionally, plant invasion significantly enhanced soil hydrolytic enzyme activities during short- to medium-stage invasion (1–20 years), while effects became negligible during long-term invasion (> 20 years; Figure 4a–c).

Ecosystem types significantly influenced hydrolytic enzyme responses (Figure 5a–c), with grasslands exhibiting the strongest N-acquiring enzyme activities (Figure 5e) and wetlands showing the highest P-acquiring enzyme activities (Figure 5f). Croplands demonstrated notable increases across all C-, N- and P-acquiring enzyme activities, whereas woodlands showed consistently modest enzymatic responses to invasion compared to other ecosystem types (Figure 5d–f).

4 | Discussion

4.1 | Distinct Responses Between Hydrolytic and Oxidative Enzyme Activities

Supporting Hypothesis I, we found that plant invasion induced distinct responses in soil hydrolytic and oxidative enzyme activities. Specifically, invasion significantly increased hydrolytic enzyme activities but had no effect on oxidative enzyme activities (Figure 1b). These differential responses suggested that plant invasion fundamentally altered soil biogeochemical processes in ways that favour specific enzymatic pathways. Three key mechanisms likely underpinned these contrasting responses of hydrolytic and oxidative enzyme activities to plant invasion.

First, increased labile substrate availability could explain increases in hydrolytic enzyme activities under invasion. We identified strong positive correlations between changes in DOC and hydrolytic enzyme activities (Figure 2a–c), whereas no significant relationships were observed between DOC and oxidative enzyme activities (Figure S5a). The significantly higher DOC in invaded soils (Figure S4) aligned with inputs from highly productive invaders via enhanced root exudation and litter deposition (Ehrenfeld 2003; Liao et al. 2008). These substrate-rich conditions favoured hydrolytic enzymes specialised in processing labile organic compounds (Cui et al. 2018; Sinsabaugh and Follstad Shah 2010), while simultaneously suppressing microbial investment in energetically expensive oxidative enzymes (Allison et al. 2006; Calabrese et al. 2022).

Second, shifts in soil microbial community composition could drive the different enzyme production patterns. Plant invasion substantially reduced F/B ratios in invaded soils (Figure S4), reflecting a shift toward bacterial dominance. This microbial community restructuring likely reflected the competitive advantage of fast-growing, *r*-strategist bacteria over slower-growing, *K*-strategist fungi under nutrient-enriched conditions (Fierer et al. 2007). The enhanced nutrient availability, driven by invaders' characteristically high tissue N content, created conditions that favoured bacterial proliferation (Castro-Díez et al. 2014; Liao et al. 2008; Sardans et al. 2017). Since bacterial communities typically exhibited higher hydrolytic enzyme production than fungal communities (Sinsabaugh et al. 2008), this shift toward bacterial dominance could explain the enhanced hydrolytic enzyme activities observed under invasion.

Third, we observed that plant invasion enhanced soil moisture content (Figure S4) which may explain the differential effects of invasion on hydrolytic and oxidative enzyme activities. The observed increase in soil moisture content under invasion may arise from multiple mechanisms, such as enhanced root-mediated water retention, altered canopy structure affecting evaporation, or improved soil structure (via root activity and organic inputs), thereby increasing water retention capacity (e.g., Ehrenfeld 2003; Liao et al. 2008; Nunez-Mir and McCary 2024). Importantly, invasion-induced increases in soil moisture content were associated with elevated hydrolytic enzyme activities (Figure 2g–i). Mechanistically, this occurred because moisture conditions facilitated substrate diffusion and enzyme-substrate interactions (Xu et al. 2022). In contrast, we found oxidative enzyme activities to be suppressed under higher moisture content, likely because water-logged pores created anaerobic microsites that limited oxygen availability—a key requirement for these enzymes (Freeman et al. 2001; Yang et al. 2022).

4.2 | Environmental Controls on Soil Hydrolytic Enzyme Activities

Supporting Hypothesis II, we found that plant invasion significantly increased soil hydrolytic enzyme activities, but the extent of these increases was dependent on environmental variables, such as the invader's mycorrhizal status, ambient soil pH, and invasion duration (Figure 3a–c). Our results demonstrated that invasive plants with mycorrhizal associations (AM or ECM) significantly elevated soil hydrolytic enzyme activities compared to non-mycorrhizal invaders (Figure 4a–c). This finding aligned with the recognised role of mycorrhizae in enhancing nutrient availability during invasion (Sun et al. 2022; Tedersoo et al. 2020). This enhancement may operate through three complementary mechanisms. First, fungal partners directly secreted enzymes through their hyphae (Lindahl and Tunlid 2015). Second, mycorrhizal networks facilitated enhanced belowground carbon allocation from host plants (Choreño-Parra and Treseder 2024), creating substrate-rich conditions that fuel greater enzyme production (Liang et al. 2020). Third, the extensive extraradical mycelium expanded the spatial reach of enzymes, accessing nutrients in distant soil microsites beyond the range of non-mycorrhizal plants (Jiang et al. 2020; Smith and Read 2008). Collectively, these findings highlighted mycorrhizal symbiosis as a key pathway for invasive plants to enhance soil enzymatic processes and nutrient acquisition.

We found plant invasion elevated hydrolytic enzyme activities in neutral and alkaline soils but not in acidic soils (Figure 4a–c). While invasive plants consistently lowered soil pH via N-rich litter inputs stimulating H^+ release (Li et al. 2016), the net enzymatic response depended on initial soil conditions and buffering capacity. For instance, neutral and alkaline soils maintained sufficient buffering capacity to preserve pH conditions favourable for microbial function, even when litter inputs caused mild acidification (German et al. 2011). Conversely, acidic soils inherently operated under severe pH constraints (H^+ stress, Al^{3+} toxicity) that suppressed microbial metabolism and enzyme production (Luo et al. 2022; Sinsabaugh et al. 2008). Therefore, invasion-induced acidification would further intensify these limitations, overwhelming any potential stimulatory effect of increased substrate availability. Consequently, these findings revealed that the biogeochemical effects of plant invasion were not uniform but were strongly mediated by initial soil pH conditions and associated microbial constraints.

Soil hydrolytic enzyme activity was most pronounced during short- (< 5 years) and medium-term (5–20 years) invasions but declined significantly under long-term (> 20 years) invasions (Figure 4a–c). This temporal pattern corresponded with three key shifts: DOC depletion, increased F/B ratios, and reduced soil moisture content (Figure S6). These shifts suggested a two-phase mechanism governing invasion impacts. Initially, invasive plants stimulated hydrolytic enzyme production, facilitating rapid exploitation of labile substrates (Zhang and van Kleunen 2019; Zhou and Staver 2019). Over time (> 20 years), however, sustained invasion depleted readily available substrates (reflected by DOC depletion) and reduced moisture content (Figure S6). This substrate limitation, combined with moisture stress, likely reduced bacterial biomass (reflected by rising F/B ratios; Figure S6), consequently constraining hydrolytic enzyme activities in long-invaded soils (Lankau et al. 2009; Zhang et al. 2023).

4.3 | Ecosystem-Specific Soil Enzymatic Responses to Plant Invasion

Our findings revealed distinct enzymatic responses to plant invasion across different ecosystems (Figure 5a–c). Specifically, in N-limited grasslands, invasion significantly elevated N-acquiring enzyme activities (Figure 5e). This surge likely reflected a competitive strategy by invasive plants to overcome inherent N constraints, leveraging enzymatic N-acquisition as a key mechanism in these systems (Sardans et al. 2017; Yu et al. 2020). Conversely, wetlands exhibited the most pronounced increase in P-acquiring enzyme activities under invasion (Figure 5f). Given the prevalence of P limitation in these ecosystems, this enhanced enzymatic P-mining likely represented a critical adaptation by invaders to access organic P pools (Fan et al. 2023; Zhai et al. 2021). This adaptation was particularly important in mineral-rich wetlands where P was immobilised by iron and aluminium oxides (Sundareshwar et al. 2003; Chacón et al. 2005; Zhang et al. 2024). In contrast to natural ecosystems, invaded croplands showed elevated activities across all measured C-, N- and P-acquiring enzymes (Figure 5d–f). This broad enzymatic upregulation likely reflected intense competitive pressure from thriving crops. In agricultural systems, frequent fertilisation promotes vigorous crop growth, forcing invasive plants to upregulate all enzymatic pathways to effectively compete for nutrients against these well-fertilised native species (Dang et al. 2022; Golivets and Wallin 2018). Woodlands presented a markedly different pattern, with invasive species inducing only modest enzymatic changes compared to uninvaded sites (Figure 5d–f). This limited enzymatic response suggested that belowground nutrient competition may be less critical for invasive success in woodlands, where competition was likely dominated by aboveground resources like light and water (Poorter et al. 2010; Umaña et al. 2020). Overall, these ecosystem-specific enzymatic responses underscored that invasive plants differentially alter soil enzyme activities based on prevailing ecological contexts and soil nutrient constraints.

4.4 | Limitations and Future Research Directions

Our meta-analysis had several limitations that should inform future research directions. First, while many factors theoretically influenced enzymatic responses to plant invasion, the available literature contained insufficient data on key variables such as invasive plant traits (biomass, litter quality, root exudates) and detailed microbial community composition (Nunez-Mir and McCary 2024; Vilà et al. 2011). Future studies should systematically collect these mechanistic data to enable more robust interpretations of invasion impacts on soil enzyme dynamics (Luo et al. 2022).

Second, our analysis revealed only modest changes in oxidative enzyme activities following plant invasion, likely reflecting the short timescales of included studies (Dostál et al. 2013). Over extended timeframes, depletion of labile compounds and accumulation of recalcitrant materials would drive greater investment in oxidative enzymes (Calabrese et al. 2022; Wutzler et al. 2017). Multi-decadal studies are therefore needed to capture these long-term microbial adaptations.

Third, our ecosystem-specific patterns required experimental validation through manipulative studies that simultaneously measure soil enzyme activities, invader traits, and nutrient dynamics (He et al. 2025). For example, N manipulation in grasslands and P manipulation in wetlands could verify whether enzymatic nutrient acquisition drives invasion success (Jiang et al. 2024; Zhang and Suseela 2021). Moreover, multi-nutrient experiments in croplands and resource allocation studies in woodlands would test our proposed mechanisms (Alba et al. 2019; Craine and Dybzinski 2013). Such experiments would strengthen causal interpretations beyond our correlative evidence.

Finally, interactions between invasive species and other global change factors likely modify soil enzyme activities in complex ways. Agricultural intensification in croplands, increasing drought in grasslands, altered hydrology in wetlands and rising temperatures across ecosystems may amplify or diminish invasion impacts (Norby and Zak 2011; Ochoa-Hueso et al. 2018; Yang et al. 2022). These interactive effects remain largely unexplored, constraining our ability to predict enzymatic responses under projected environmental changes.

5 | Conclusion

Through a global meta-analysis, we revealed distinct patterns and key drivers of soil enzymatic responses to plant invasion (Figure 6). First, plant invasion consistently enhanced hydrolytic enzymes globally while it had minimal effects on oxidative enzymes. This pattern primarily resulted from increased labile substrate availability, shifts toward bacterial-dominated communities, and elevated soil moisture content in invaded soils. Second, mycorrhizal associations of invaders, ambient soil pH, and invasion duration emerged as primary modulators of hydrolytic responses, with

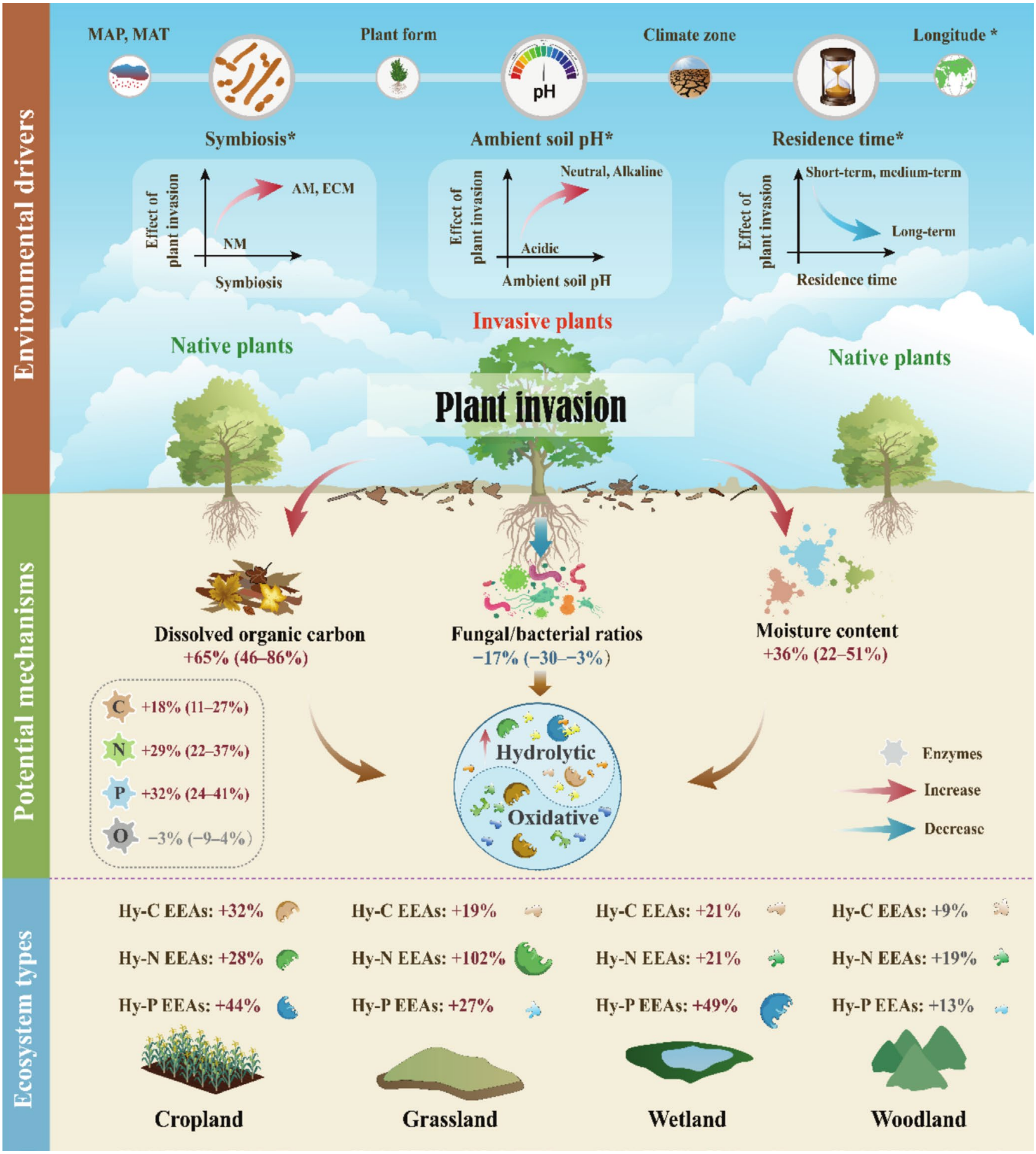

FIGURE 6 | A conceptual diagram illustrating the mechanisms through which invasive plants influence soil extracellular enzyme activities. Invasive plants enhance dissolved organic carbon (DOC) and soil moisture content while reducing fungal/bacterial (F/B) ratios. This leads to increased hydrolytic enzyme activities without significantly affecting oxidative enzyme activities. The magnitude of these effects is modulated by several key factors, including the invasive plants' mycorrhizal associations, ambient soil pH, invasion duration, and ecosystem types. The most pronounced enzymatic responses occurred in neutral and alkaline soils, under invasions of short to medium duration, and when mycorrhizal-associated invaders were involved. Different ecosystem types exhibit characteristic enzymatic response patterns: Grasslands show pronounced increases in N-acquiring enzymes, wetlands display elevated P-acquiring enzymes, croplands demonstrate enhanced levels of all C-, N- and P-acquiring enzymes, while woodlands show comparatively lower enzymatic responses. The numbers show the percentage change in soil extracellular enzyme activities following plant invasion. Numbers in parentheses represent 95% confidence intervals. Red values indicate significant increases, blue values indicate significant decreases and grey values denote non-significant changes. EEAs, extracellular enzyme activities; Hy-C EEAs, hydrolytic C-acquiring EEAs; Hy-N EEAs, hydrolytic N-acquiring EEAs; Hy-P EEAs, hydrolytic P-acquiring EEAs.

the strongest effects in neutral and alkaline soils, during short- to medium-term invasions, and with mycorrhizal-associated invaders. Third, ecosystem-specific patterns in hydrolytic enzymes included enhanced N-acquiring enzymes in grasslands, P-acquiring enzymes in wetlands, elevated C-, N- and P-acquiring enzymes in croplands, but minimal responses in woodlands. Our synthesis demonstrated how complex interactions among enzyme types, environmental factors, and ecosystem characteristics govern soil enzymatic responses to plant invasions globally. These mechanistic insights advanced our understanding of invasion success and provided a predictive framework for assessing invasion impacts on belowground biogeochemical processes.

Author Contributions

M.L. designed research; X.C., D.H. and T.F. collected the data; X.C., M.L., Y.L. and L.S. analysed the data; M.L., X.C., J.C., J.J.L.R., M.v.K., K.J.v.G., L.F., Y.q.L., J.C., Y.Z. and R.L.S. wrote and reviewed the paper.

Acknowledgements

This work was sponsored by grants from the National Natural Science Foundation of China (32471672; 32071598), the Natural Science Foundation of Fujian Province (2024J01274; 2020J01503), and the Minjiang River Estuary Wetland National Nature Reserve Administrative Office (MJHKSD20230202). Dr. Le Roux acknowledges funding received from the Australian Research Council (DP2401012143) and Macquarie University's Faculty of Science and Engineering (Outside Studies Program Fellowship).

Disclosure

Declaration of generative AI and AI-assisted technologies in the writing process: During the preparation of this work, the authors used ChatGPT in order to polish and refine the language of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and took full responsibility for the content of the publication.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code used in this study have been deposited in Figshare (https://doi.org/10.6084/m9.figshare.29383139) and are publicly available to ensure complete transparency and reproducibility of our findings.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.