

RESEARCH ARTICLE

Plant-herbivore interactions depend on plant richness, plant and soil history

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Abstract

1. Insect herbivores play a central role in grassland ecosystems. They depend on plants for their nutrition and exert feedback effects on plant communities. Although such reciprocal relationships are well recognized, how they are shaped by plant community diversity and history remains largely unexplored.
2. In a full-factorial mesocosm experiment in which plant species richness (1, 2, 3 and 6 species mixtures), soil and plant history conditions were manipulated, we used *Spodoptera exigua* (Hübner, 1808) caterpillars to inflict damage on *Plantago lanceolata* L. plants. We used herbivore performance, plant performance and various plant traits to investigate two main questions: (I) the interactive effects of plant traits, plant diversity and plant and soil history on herbivore performance, and (II) the impact of herbivory on plant traits and performance, considering varying plant diversity and plant and soil history.
3. Here, we found reciprocal effects between plants and herbivores that varied with plant species richness, plant history and soil history. Specifically, herbivores performed better on more nutritious plants, with the strength of this effect depending on both plant and soil history, while they performed worse with increasing plant species richness. However, the latter effect was not observed in a subsequent trial conducted a few weeks later. Additionally, herbivory reduced plant height in monocultures, altered nutritional quality and physical defences compared to undamaged controls depending on plant history, and increased chemical defence compounds.
4. Our study demonstrates that bidirectional interactions between plants and arthropods are key to understanding community-level responses, as the strength and direction of these reciprocal effects depend on plant and soil history as well

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as plant richness. This context dependence drives community dynamics and has important implications for ecosystem functioning, species coexistence and co-evolutionary processes.

KEYWORDS

above-ground arthropods, ecosystem functions, herbivory, *Plantago lanceolata*, plant–consumer feedback effects, Plant–soil feedback effects, *Spodoptera exigua*, trophic interactions

1 | INTRODUCTION

Herbivores play a crucial role in ecosystem dynamics by influencing plant communities, nutrient cycling and energy flow (Belovsky & Slade, 2000; Maron & Crone, 2006; Nitschke et al., 2014). While the effects of large herbivores on plant performance are well documented (e.g. Mortensen et al., 2018; Pringle et al., 2023), arthropod herbivores also significantly impact plant communities through reciprocal processes between plants and herbivores (Kozlov & Zvereva, 2017). The balance between these processes determines the extent of plant–herbivore interactions within different environmental contexts, influencing the abundance and distribution of both herbivores and plants (Hunter et al., 1997). Despite their importance, reciprocal interactions remain less studied, particularly in relation to plant diversity and community history (but see Heinze et al., 2019). Specifically, plant diversity and plant community history alter the physical, chemical and nutritional traits of plants, leading to changes in plant–consumer interactions based on community composition and the time available for co-development of plants and soils. Understanding these dynamics is crucial for unravelling the coevolutionary arms race between plants and their insect herbivores, where plants develop defences and herbivores evolve counter-adaptations (Ehrlich & Raven, 1964; Maron et al., 2019).

Plant effects on herbivores are key drivers of herbivore ecology, population dynamics and consumer interactions (Awmack & Leather, 2002; Hemmi & Jormalainen, 2002; Meyer, 2008). These effects are primarily driven by resource availability, particularly their quality (Awmack & Leather, 2002). Nutritional quality serves as a key indicator of resource availability for herbivores and is influenced by plant traits, including chemical and morphological defence mechanisms, which in turn affect plant physiology and growth. While plants with ample nutrient supply can grow rapidly, enhancing their competitive advantage, they may also become more susceptible to herbivores due to growth–defence trade-offs (Lind et al., 2013; Valdovinos et al., 2023). Herbivores can convert nutrient-rich plant material more efficiently into herbivore biomass, accelerating herbivore development by reducing the time herbivores spend on foraging, ingesting and processing food (Hemmi & Jormalainen, 2002). Consequently, nutritious plants attract herbivores and can sustain and promote the growth of larger herbivore populations (Meyer, 2008). Conversely, plants with limited nutrient supply can reduce individual and population growth rates in herbivores, driven by intensified foraging efforts (compensatory feeding) and increased

energy demands (Awmack & Leather, 2002; Crawley, 1989; Hemmi & Jormalainen, 2002; Wetzel et al., 2016). While low nutritional value can contribute to a plant's defence against herbivores by making them less attractive as a food source, plants also employ an array of chemical and physical defences to protect themselves from herbivory. Among their physical strategies, plants have evolved mechanical defences that minimize or prevent tissue damage, such as sharp structures (thorns or spines), thick or toughened tissues and protective surface features like hairs or trichomes (Barton, 2016). Chemical defences include an array of compounds, such as alkaloids, terpenoids, phenolics and glucosinolates, that plants produce to deter or harm herbivores and pathogens (Mithöfer & Boland, 2012). In response, herbivores may either avoid these plants altogether or mitigate the effects of toxins (Lefcheck et al., 2013) and even use them for their own protection against predators (Karban & Agrawal, 2002). Plant traits (e.g. nutritional value, defence traits) are not static but are shaped by the surrounding biotic and abiotic conditions, which in turn are influenced by factors like plant diversity (Felix et al., 2023; Gubsch et al., 2011; Lipowsky et al., 2015; Mraja et al., 2011) and plant community history (Dietrich et al., 2022; Zuppinger-Dingley et al., 2014).

Numerous studies have documented effects of plant diversity on herbivore abundance (Bröcher et al., 2024; Ebeling et al., 2025; Ebeling, Hines, et al., 2018; Ebeling, Meyer, et al., 2014), community composition (Ebeling, Rzanny, et al., 2018) and fitness (Ebeling et al., 2013; Unsicker et al., 2010) with consequences on rates of herbivory (Ebeling, Hines, et al., 2018; Meyer et al., 2017) and energy flows in the ecosystem (Barnes et al., 2020; Buzhdygan et al., 2020). Effects of plant diversity were often linked to changes in plant traits (Ehrlich & Raven, 1964; Maron et al., 2019). For instance, increasing plant diversity often exacerbates competition among neighbouring plants (Bachmann et al., 2018), which can reduce plant defences as resources are redirected towards growth (growth–defence trade-off; Lind et al., 2013; Viola et al., 2010). As a result, plants may become more vulnerable to herbivores due to decreased defences and increased nutritional value (Bassi et al., 2025). However, more diverse plant communities can also reduce herbivore damage, as chemical defences from one species may protect neighbouring plants or act synergistically with the chemical defences of other species (Hay et al., 1994; Kigathi et al., 2019). Furthermore, as plant communities grow together over time and develop a shared community history, plants can maximize their resource use by increasing complementarity via niche differentiation and character displacement, reducing

the cost of competition and freeing up resources for plant defence (Zupping-Dingley et al., 2014). The effect of plant community history may interact with plant diversity; for example, complementarity among plants that coexisted over longer periods tends to be more pronounced in species-rich communities than in low-diversity ones, leading to stronger trait differentiation and enhanced resource allocation for herbivore defence (Eisenhauer et al., 2019; Zupping-Dingley et al., 2014). However, plant diversity and community history shape not only the effects of plants on herbivores but also the influence of herbivores on plants.

Herbivores can induce shifts in plant communities and ecosystem functioning through various mechanisms (Barton, 2016; Maron & Crone, 2006), such as altering plant traits. For example, herbivory directly reduces the amount of photosynthetic tissue or reproductive organs by consuming plant parts, such as leaves, stems, flowers and seeds, or alters metabolite concentrations by inducing the production of phytohormones and defence compounds (i.e. induced chemical defence; Karban & Myers, 1989). In addition to physiological effects, herbivory can trigger morphological changes in plants, such as altering leaf shapes and promoting the development of mechanical defences (Barton, 2016). Herbivore-induced changes in plant traits can be rapid, such as the emission of plant volatiles, or develop more gradually, like morphological adaptations (Karbon & Myers, 1989). Both the direct loss of tissue and the biosynthesis of defence compounds are energy demanding for the plant, ultimately reducing plant performance (Maron & Crone, 2006).

Studies have reported inconsistent effects of plant diversity on herbivore performance (Ebeling et al., 2013; Specht et al., 2008; Unsicker et al., 2010), but the role of plant community history in influencing herbivore performance remains largely unexplored. Here, we consider community history as the combined effect of plant and soil history. This encompasses the long-term ecological conditions and interactions within a plant community, including past plant species composition and soil characteristics, which together shape current plant traits and ecosystem dynamics (Thakur et al., 2021). Community history can shift a general plant response to herbivory towards a more specific one, allowing plants to more cost-effectively manage herbivore threats in their environment (Bassi et al., 2024). Again, these effects may interact with plant diversity, as extended co-occurrence in diverse communities can promote trait differentiation and resource-use complementarity, influencing plant–herbivore interactions (Zupping-Dingley et al., 2014). These reciprocal interactions between plants and herbivores can form feedback loops, where the responses of one organism affect the fitness and functioning of the other, ultimately shaping community dynamics and broader ecosystem processes ('plant–herbivore–feedback'; Eisenhauer et al., 2019; McNaughton, 1983).

Understanding the dynamics and mechanisms of reciprocal effects between plants and herbivores presents a challenge in the field. This is because key variables driving these interactions, such as chemical plant traits, are sensitive to environmental fluctuations. Additionally, crucial variables, like root traits, often require destructive sampling, and it is challenging to manipulate plant

community history independently from soil community history in a field setting (Vogel et al., 2019). To overcome these limitations, we take advantage of a mesocosm experiment in a highly controlled Ecotron that uses a fully crossed design for plant and soil history treatments, decoupling the individual and joint effects of plant community history and soil community history, respectively, along a plant diversity gradient (Eisenhauer et al., 2019; Madaj et al., 2025). To study plant–herbivore interactions, we used individuals of ribwort plantain (*P. lanceolata*) and caterpillars of the beet armyworm (*Spodoptera exigua*) as a model system. This choice was based on previous research showing that *P. lanceolata* is sensitive to changes in plant communities (Mraja et al., 2011) and that feeding by *S. exigua*, a generalist herbivore commonly used in ecological studies, induces plant defence responses (Biere et al., 2004; Reudler et al., 2011; Wang et al., 2014). With this unique experiment, we test how plant traits (leaf dry matter content [LDMC], nitrogen concentration, C:N ratio, amino acid-, iridoid glycoside- [aucubin and catalpol], verbascoside concentration, leaf toughness, leaf thickness and trichome density) affect herbivore performance (weight change, consumed biomass and conversion efficiency) and how herbivory changes plant traits and plant performance (plant height, number of leaves and number of flowers). While reciprocal effects between plants and herbivores are well established, our study is novel in exploring how these interactions are shaped by plant richness, plant history and soil history (Figure 1). We test the following hypotheses:

- Higher plant quality and lower chemical and physical defences increase herbivore performance and those traits shift depending on the surrounding community's diversity, plant and soil history.
- Herbivory lowers plant fitness and triggers chemical and morphological defence responses in plants. Additionally, plant diversity, plant history, and soil history can influence plant responses to herbivory, leading to more nuanced and context-dependent defences in plants from diverse or long-established communities.

2 | MATERIALS AND METHODS

2.1 | JenaTron experiment

We used the iDiv Ecotron facility (Bad Lauchstädt, Germany), a research platform of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig and the Helmholtz Centre for Environmental Research (UFZ; Schmidt et al., 2021), to establish the 'JenaTron Experiment' (hereafter JenaTron, Madaj et al., 2025). The experimental setup of the JenaTron is embedded and strongly influenced by the long-term grassland biodiversity experiment Jena Experiment (Roscher et al., 2004; Weisser et al., 2017), and uses the same plant species pool, site-specific soil and plants (see Madaj et al., 2025 for a detailed description). Within the JenaTron, we established 24 experimental units (hereafter EcoUnits) with controlled environmental conditions, such as irrigation and light regimes

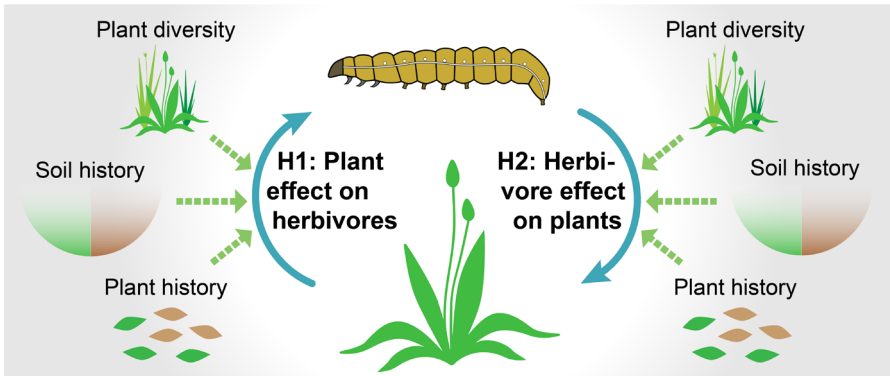


FIGURE 1 Conceptual framework illustrating the hypothesized reciprocal relationships between plants and herbivores, and the moderating roles of plant richness, plant and soil history. H1: We hypothesize that herbivore performance improves with higher plant quality and lower chemical and physical defences, and that these plant traits are influenced by the surrounding community's diversity as well as plant and soil history. H2: We hypothesize that herbivory reduces plant fitness and induces both chemical and morphological defence responses. These responses are expected to vary depending on plant diversity, plant history, and soil history, resulting in more nuanced and context-dependent defences in plants from diverse or long-established communities. Blue arrows represent direct relationships (e.g. from plants to herbivores, or herbivory to plants), while green dotted arrows indicate hypothesized context dependencies. Green and brown symbols represent treatments *with* (green) or *without* (brown) plant or soil history, respectively.

(Method S1). These EcoUnits were used to create plant communities with varying levels of plant species richness (1, 2, 3 and 6 species mixtures), hereafter referred to as 'plant richness'. We used a species pool consisting of six common and regionally typical grassland plant species: three dicots (*Leucanthemum vulgare* agg., *Plantago lanceolata* L. and *Ranunculus acris* L.) and three monocots (*Anthoxanthum odoratum* L., *Dactylis glomerata* L. and *Holcus lanatus* L.). Ten out of the 24 EcoUnits contained *P. lanceolata* and were used for the present study with one monoculture, three 2-species mixtures, four 3-species mixtures and two 6-species mixtures (Table S1). We planted the same number of individuals ($n=55$) per EcoUnit with standardized positions and equal densities among plant species. Each EcoUnit was divided into four isolated subunits, all containing the same plant community composition but differing in their plant and soil histories (Figure 2a; Eisenhauer et al., 2019). This created four distinct combinations: *without* plant and *without* soil history, *without* plant but *with* soil history, *with* plant *without* soil history and *with* both plant and soil history. *With* plant history was achieved by using plot-specific seeds collected in 2019 from plants that had been growing in the field site of the Jena Experiment since 2010 (plots from the Trait-Based Experiment; see Ebeling, Pompe, et al., 2014 for details). *Without* plant history was achieved by using the original seed material used to establish the experimental plots in the field in 2010, sourced from a regional seed producer (Rieger-Hofmann GmbH, Blaufelden, Germany). *With* soil history was achieved by excavating intact plot-specific soil monoliths (each 0.5 m in diameter and 0.8 m soil depth) from the field site of the Jena Experiment (plots from the Trait-based Experiment). *Without* soil history was achieved by excavating soil from bare ground plots from the field site of the Jena Experiment, that is, plots where all plants were removed two or three times a year (Roscher et al., 2004; Weisser et al., 2017) and therefore are standardized without any plant community-specific soil history (Eisenhauer et al., 2019). To simulate the typical mowing

regime of temperate grasslands and achieve comparable conditions to the management of the Jena Experiment, the plant biomass was cut 3 cm above the ground at peak biomass 5 months after initial sowing (Figure 2b).

2.2 | Replication statement

Explanatory variables	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Plant diversity	EcoUnit	EcoUnit	10
Community history	Subunit	Subunit	40 (10 EcoUnits $\times$ 4 subunits)
Measures of herbivore response	Subunit	Three plants per subunit (each exposed plant received two caterpillars)	40 (10 EcoUnits $\times$ 4 subunits; herbivores only on exposed plants)
Measures of herbivore response	Subunit $\times$ herbivory treatment	Three treatment and three control plants per subunit	80 (10 EcoUnits $\times$ 4 subunits $\times$ 2 herbivory treatments)

2.3 | Measurements of herbivory performance

We obtained *S. exigua* eggs from Entocare (Wageningen, Netherlands) and reared caterpillars on an agar-based diet at 25°C with a 16:8 light cycle. Second-instar caterpillars, starved for 24 h, were weighed and placed in clip cages (4 cm diameter, 2 cm depth) on three randomly

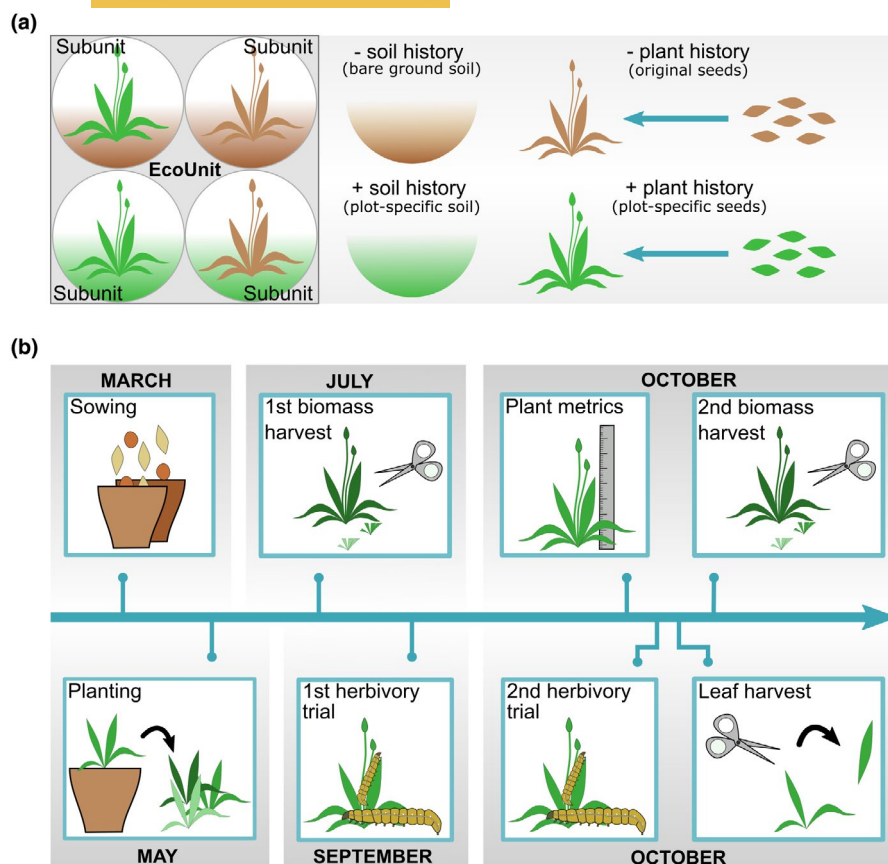


FIGURE 2 Schematic representation illustrating (a) the experimental timeline and (b) the design of a single EcoUnit, including the manipulation of community history. In (a), the timeline outlines key experimental steps in chronological order, indicating the months in which each task was completed. In (b), the EcoUnit design is shown, divided into four subunits, each representing a unique combination of plant and soil history. Specifically, each subunit contains either plants grown from plot-specific seeds (*with* plant history) or plants grown from original seeds (*without* plant history), as well as plot-specific soil (*with* soil history) or soil from bare ground plots (*without* soil history).

assigned *P. lanceolata* plants per subunit, two cages per plant. Each cage contained one caterpillar and two leaf tips (4 cm exposed). The same number of control plants had empty clip cages. After 48 h, caterpillars were reweighed (excluding dead ones). All plants were exposed to herbivory twice: the first trial to induce long-term, and the second trial, 6 weeks later, to induce short-term plant responses. Caterpillar weight change ($\text{mass}_{\text{after}} - \text{mass}_{\text{before}}^{-1}$), and additionally, for the second trial, the amount of plant biomass consumed (g) and conversion efficiency ($\text{mass}_{\text{gained}} - \text{mass}_{\text{consumed}}^{-1}$) were calculated (for more details see Method S2). For statistical analyses, we used average values for each EcoUnit $\times$ subunit combination ($n=40$) of the three plants per subunit that were exposed to herbivores. No ethical approval was required for this study in accordance with institutional and national guidelines.

2.4 | Measurements of plant performance and plant traits

During the second trial (6 weeks after the first trial), we recorded maximum plant height, number of leaves and number of flowers for exposed and control individuals (Method S3). We imaged caterpillar-fed leaves to estimate consumed and remaining leaf area using ImageJ (v.1.53a; Schneider et al., 2012). Leaves were harvested, flash-frozen and stored at -80°C for defence compounds (aucubin, catalpol and verbascoside) and amino acid analysis via LC-MS/MS (Method S3, Method S4, Table S2). Carbon and nitrogen concentrations (mg N g^{-1}) were determined using an elemental analyser

for 24 samples and predicted for 56 samples using Bagging-CARS-PLSR models (Richter & Bassi, 2023; Figure S1, Method S3). LMA (g m^{-2}), LDMC (g g^{-1}), leaf toughness (N), leaf thickness (mm) and hair density (hairs mm^{-2}) were measured following standard protocols (Perez-Harguindeguy et al., 2013; Method S3).

2.5 | Statistical analysis

Statistical analyses were performed in R version 4.1.2 (R Core Team, 2024). We grouped the leaf traits by applying a principal component analysis (PCA) on all plant traits (LDMC, nitrogen concentration, C:N ratio, concentration of essential amino acids, aucubin concentration, catalpol concentration, verbascoside concentration, thickness, toughness, hair density; 'prcomp'-function, 'vegan' package, Oksanen et al., 2013). One missing value for the three traits each (nitrogen concentration, carbon concentration and hair density) was imputed using the average of the corresponding values from control and exposed plants, respectively. In the PCA, we rotated the axes to maximize the sum of variances of the loadings ('varimax'-function, 'vegan' package, Oksanen et al., 2013) and inverted all axes to be biologically meaningful by multiplying the scores and loading with -1 .

To test whether herbivore performance (weight change during the first and second trial, consumed biomass and conversion efficiency) changed with plant richness, plant- and soil history and to determine if these effects are mediated by principal components of plant leaf traits or the traits themselves (Question 1), we used structural

equation models (SEM; 'piecewiseSEM' package, Lefcheck, 2016). We used linear mixed-effect models to calculate each path ('lme4' package, Bates et al., 2015) and used the EcoUnit as a random term to account for the non-independence of the data collected in the subunits (see Section 2.2). In the starting model, we included the paths of plant richness, plant- and soil history and all possible interactions among them on the plant traits (e.g. nutrient-, chemical defence- and physical defence axes, or single trait values) and the paths of plant traits on herbivore performance. To improve the model fit, we included direct effects of plant richness, plant- and soil history on herbivore performance and covariation among variables based on the tests of directed separation. We fitted a single SEM with the three plant leaf trait principal components as mediators and one SEM for each single trait due to the strong correlation among plant traits.

To test how herbivory affected plants and how these effects varied with plant richness, plant and soil history (Question 2), we used SEMs to examine if these factors explained variation in plant leaf trait principal components or performance (height, leaf number and flower number), and if responses differed between exposed and control plants (see Section 2.2). We fitted plant richness, plant- and soil history, and herbivory and all possible interactions among them. Based on the tests of directed separation, we allowed covariation among endogenous variables. We tested the effect of plant richness, plant- and soil history, and herbivory also on each single plant trait, but as we just have a single response and neither mediators nor possible covariation, we only fitted the linear mixed-effects models. In addition to EcoUnit, we used subunit nested within the EcoUnit as a random effect to account for the spatial non-independence of the data on the level of subunits.

Model fit in the piecewise structural equation models was assessed using Fisher's *C* statistic, with $p > 0.05$ indicating that the model adequately captured the observed data.

3 | RESULTS

3.1 | Mapping of plant traits on PCA axes

The first three axes together explained 63.1% of variance in total trait space (axis 1 with 29.1%, axis 2 with 21.7% and axis 3 with 12.3%; Figure 3). Specifically, LDMC and the C:N ratio were negatively correlated, while nitrogen concentration and the concentration of essential amino acids were positively correlated with axis 1 (hereafter named 'nutrient axis'); the concentration of aucubin, catalpol and verbascoside positively correlated with axis 2 (hereafter named 'chemical defence axis'); and toughness, thickness and hair density positively correlated with axis 3 (hereafter named 'physical defence axis'). All traits had a loading larger than 0.25 on the respective component axis.

3.2 | Effects of plant traits, plant richness, and plant and soil history on herbivore performance

Herbivore performance was influenced by plant community richness and history, with effects varying between the two trials. In the first trial, herbivores gained less weight with increasing plant species richness, gaining only half as much weight when feeding on *P. lanceolata* from six-species communities compared to monocultures (Figure 4, Figure S2A, Table S3). Moreover, herbivores gained more weight when feeding on plants grown in communities with soil history (Figure S2A). In the second trial, the positive effect of soil history persisted, though it was clearly mediated by the nutrient axis, which could not be tested in the first trial (Figure 4, Figure S3A). Moreover, the effect of plant richness was no longer evident; instead, herbivores gained more weight when feeding on plants grown in communities with plant history (Figure 4,

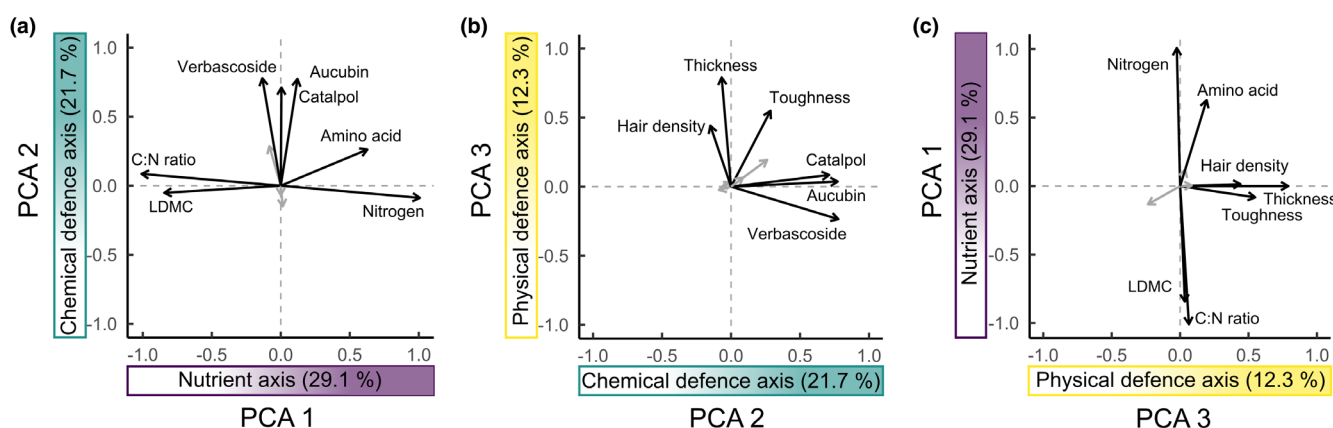


FIGURE 3 Principal component analysis of plant traits (LDMC, C:N ratio, nitrogen concentration, concentration of essential amino acids, aucubin concentration, catalpol concentration, verbascoside concentration, toughness, thickness and hair density). Panels show trait variation along PCA1–PCA2 (a), PCA2–PCA3 (b), and PCA3–PCA1 (c). Axes are rotated to maximize the sum of variances of the loadings. The variance explained by each axis is given in brackets. Black arrows indicate a loading higher than 0.25; grey arrows indicate a loading lower than 0.25. To increase visibility, only black arrows are labelled. The saturation level indicates low (white) and high (saturated) nutritional value (violet), chemical defence (teal) or physical defence (yellow).

Plant effects on herbivores

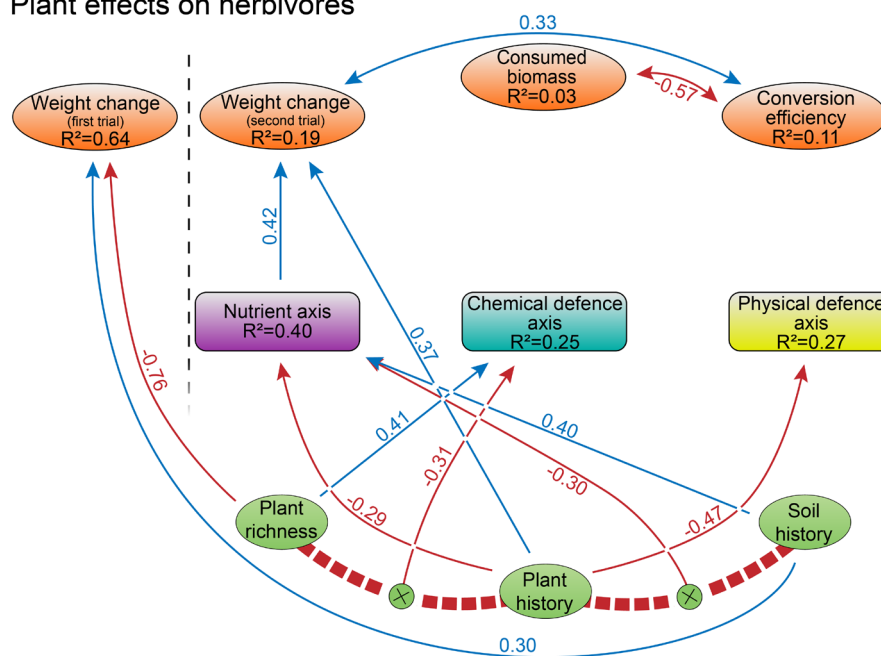


FIGURE 4 Structural equation model of plant richness, plant and soil history on herbivore performance with plant leaf traits principal components as mediators. The dashed vertical line separates herbivore weight gain between the first and second trials. Note that plant leaf traits were measured only once during the second trial; therefore, their effect on weight gain in the first trial is not tested in our model. Only significant paths are shown. Significant interactions among variables are indicated by dashed lines with their corresponding path. Blue paths indicate positive and red paths indicate negative relationships. The values on the paths are standardized estimates (mean = 0, SD = 1; see Table S3 for model summaries containing both original-scale and standardized estimates). Marginal R^2 are given for each corresponding endogenous variable.

Figures S2b and S3). Furthermore, weight gain was positively associated with scores on the nutrient axis (Figure S3B), which had increased in plants grown in communities *without* plant history but *with* soil history (interaction between plant and soil history; Figure 4, Figures S4A and S5A–C). Thus, plant history exerted both positive direct effects and negative indirect effects on herbivore weight gain (Figure 4, Table S3). Specifically, plants with high scores on the nutrient axis had higher nitrogen- and amino acid concentrations, and lower LDMC and C:N ratios (Figure 5, Figure S6, Tables S4–S7). Plant richness and plant history also affected the chemical and physical defence axes (Figure 4, Figures S7–S9, Table S3), although most of these traits were not significantly related to herbivore performance (Figures S7–S9, Tables S8–S13). However, aucubin concentration had a significant positive effect on conversion efficiency (Figures S7D and S9A, Table S8). In the second trial, herbivores that gained more weight also showed higher conversion efficiency, and those with higher conversion efficiency generally consumed less plant biomass (Figure 4, Table S3).

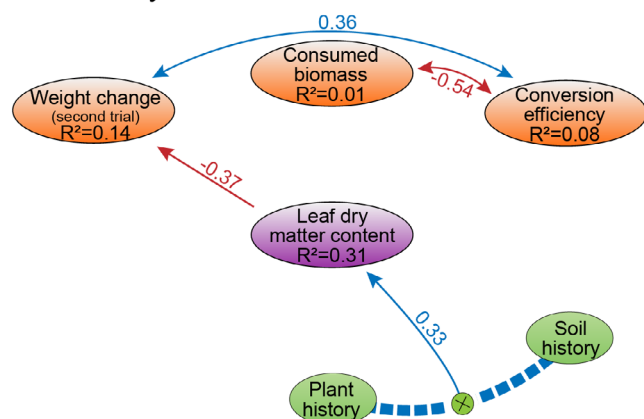
3.3 | Effects of herbivory on plants and interactions with plant richness, plant and soil history

Plants were significantly affected by herbivory, with responses varying across levels of plant species richness and history. Herbivory reduced plant height by 1 cm in species-poor

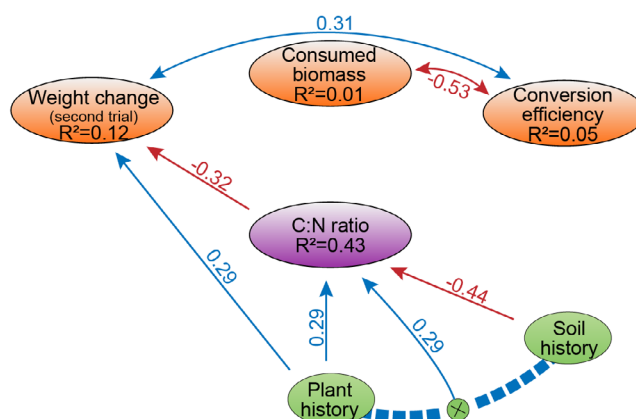
communities but increased it by 1 cm in species-rich communities, resulting in a plant diversity effect that was not observed in control treatments (Figure 6A, Figure S4C, Table S14). While the number of leaves and flowers was influenced by plant richness, plant history and soil history, these relationships did not differ between exposed and control plants (Figure 6A, Figures S4D,E and S10, Table S14). Exposed plants showed higher concentrations of chemical compounds (higher scores on the chemical defence axis) than control plants (Figure 6B, Figure S10E, Table S15). Moreover, in communities *without* plant history, herbivory led to an increase in plant quality (higher scores on the nutrient axis), whereas no such effect was observed in communities *with* plant history (Figure S4G, Table S15). A similar pattern was observed for the physical defence axis: exposed plants increased physical defence in communities *without* plant history but decreased it when growing in communities *with* plant history (Figure 6B, Figure S4I, Table S15). Specifically, herbivory increased the concentrations of aucubin, catalpol and verbascoside by up to 30%, depending on the compound (Figure S11E–G), and reduced LDMC (Figure 7, Figure S11A, Tables S16 and S20–S22). Notably, catalpol concentrations increased most strongly in exposed plants growing in communities *without* plant history, compared to those with history (Figure 7, Figure S12F, Table S21). Similarly, exposed plants in communities *without* plant history showed increased nitrogen concentrations and leaf thickness,

Nutrient axis

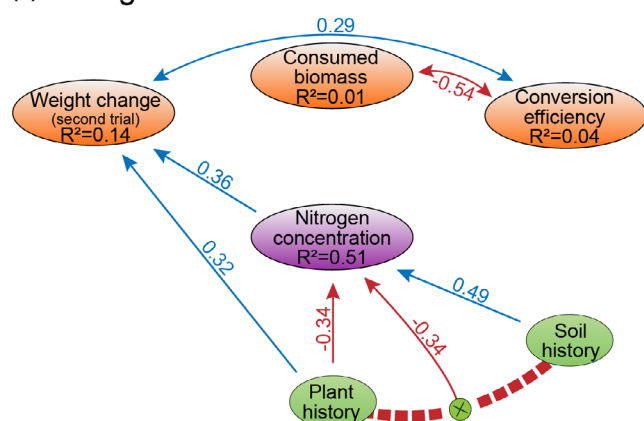
(a) Leaf dry matter content



(c) C:N ratio



(b) Nitrogen concentration



(d) Amino acid concentration

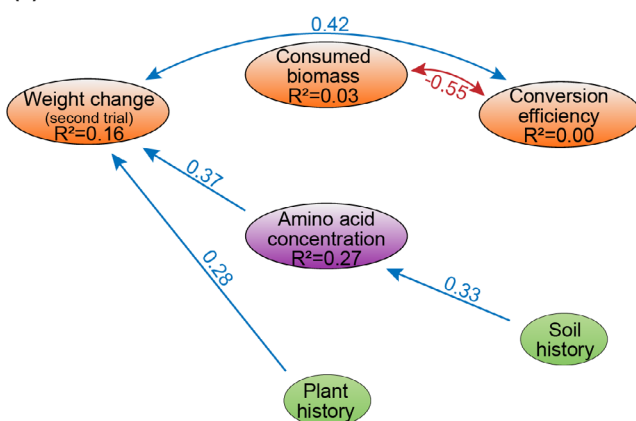


FIGURE 5 Structural equation models of plant richness, plant and soil history on herbivore performance with single plant traits, associated with the nutrient axis, as mediators: LDMC (a), nitrogen concentration (b), C:N ratio (c) and amino acid concentration (d). Only significant paths are shown. Significant interactions among variables are indicated by dashed lines with their corresponding path. Significant interactions of three variables are excluded to enhance readability. Blue paths indicate positive and red paths indicate negative relationships. The values on the paths are standardized estimates (mean=0, SD=1; see [Tables S4–S7](#) for model summaries containing both original-scale and standardized estimates). Marginal R^2 are given for each corresponding endogenous variable.

and decreased C:N ratios ([Figure 7](#), [Figure S12B,C,H](#), [Tables S17](#), [S18](#) and [S24](#)). Conversely, in communities with plant history, exposed plants decreased nitrogen concentrations and thickness and increased their C:N ratios.

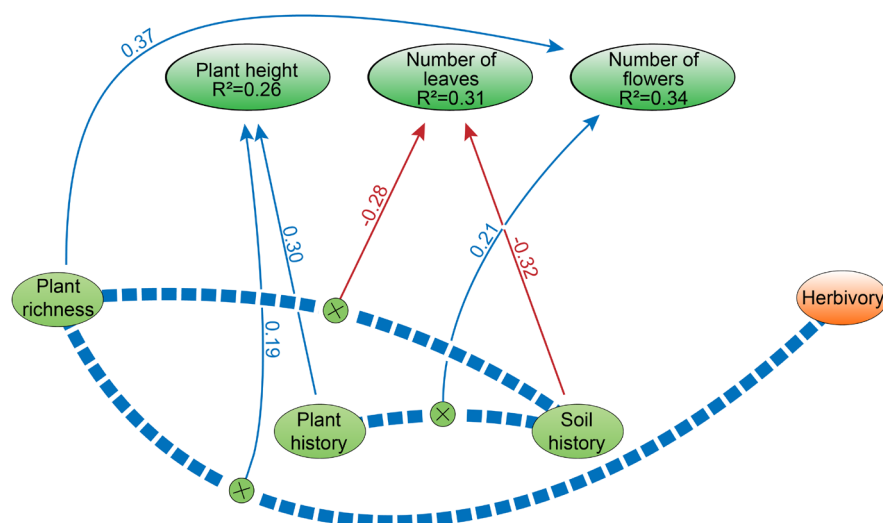
4 | DISCUSSION

Our study examines the reciprocal effects between arthropod herbivores and plants, considering the influence of plant diversity, along with plant and soil history. We found that both plant and soil history, along with plant species richness, affect the performance of herbivores (*S. exigua*). In addition, plant richness and both plant and soil history altered plant responses to herbivore exposure. Together, these findings indicate that plant–herbivore feedback loops are intricately shaped by plant diversity, plant history and soil history.

4.1 | Plant richness and community history changes plant effects on herbivores

The performance of *S. exigua* depended on traits of the consumed *P. lanceolata* individuals. Caterpillars of *S. exigua* performed better when feeding on *P. lanceolata* with higher nutritional quality, that is, lower leaf dry matter content (LDMC) and C:N ratios, and higher concentrations of essential amino acids and nitrogen. While caterpillars consumed the same amount of food regardless of the plant's nutritional quality, they gained weight more rapidly when consuming nutritious plants, owing to the increased conversion efficiency of nutrient-rich food into body mass. This pattern aligns with previous findings linking nutritional quality to herbivore performance (Awmack & Leather, 2002; Blumenthal et al., 2020). In contrast, physical defence traits and chemical defence compounds (e.g. aucubin, catalpol and verbascoside) did not reduce herbivore performance, contradicting other studies (Biere

(a) Herbivore effects on plant performance



(b) Herbivore effects on plant traits

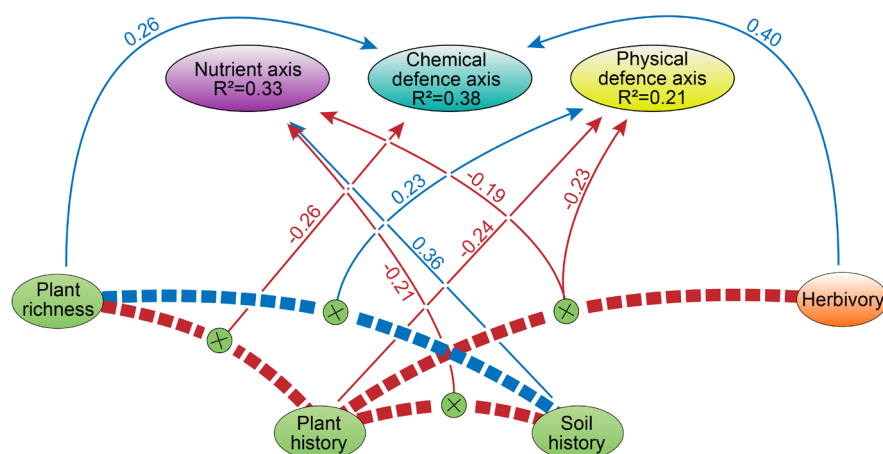


FIGURE 6 Structural equation model of plant richness, plant and soil history, and herbivory on (a) plant performance and (b) plant leaf traits principal components. Only significant paths are shown. Significant interactions among variables are indicated by dashed lines with their corresponding path. Significant interactions of three variables are excluded to enhance readability. Blue paths indicate positive and red paths indicate negative relationships. The values on the paths are standardized estimates (mean=0, SD=1; see [Tables S14](#) and [S15](#) for model summaries containing both original-scale and standardized estimates). Marginal R^2 is given for each corresponding endogenous variable.

et al., 2004; Reudler et al., 2011; Richards et al., 2012), where chemical defences did reduce herbivore performance. While a 24–72-h window is commonly used and often sufficient to detect induced defences in *P. lanceolata* (Fuchs & Bowers, 2004; Wang et al., 2015), this is not always the case (Fontana et al., 2009; Medina-van Berkum et al., 2024). That aucubin and catalpol act as feeding deterrents rather than as physiological inhibitors could also explain the absence of observable effects in our no-choice experiment (Biere et al., 2004). Similarly, physical barriers might also lose their effectivity when caterpillars are forced to feed on these plants. Unexpectedly, higher aucubin concentrations even improved conversion efficiency. Such an effect was previously shown only for a strict *Plantago* spp. specialist herbivore (*Junonia coenia*), which showed a hump-shaped relationship between concentrations of aucubin and catalpol and herbivore performance (Richards et al., 2012). Additionally, beneficial trait correlations or dose-dependent physiological effects might explain such patterns where a typical defence can be neutralized (Karban & Myers, 1989; Richards et al., 2012).

For effects of plant richness on herbivore performance, previous studies have found inconsistent results, particularly when herbivores were allowed to feed on multiple plant species (Ebeling et al., 2013; Specht et al., 2008; Unsicker et al., 2010). Here, we demonstrate that herbivores consuming only *P. lanceolata* grown in species-poor communities gained more weight than those consuming plants in species-rich communities; however, this effect was only observed in the first feeding trial. Two non-mutually exclusive mechanisms could explain the differences in herbivore performance between the two feeding trials. One possibility is herbivory-induced changes in plant traits following the first exposure (Zhu et al., 2018). However, effects of herbivory on defence traits cannot explain the change of plant species richness effects between trials, as only differences in plant height between herbivore-damaged and control plants interacted with plant richness. Further, because destructive trait measurements were only taken after the second trial, we cannot directly assess whether plants were chemically or morphologically different during the first trial. A second possibility is temporal changes in plant ontogeny and community development. The first

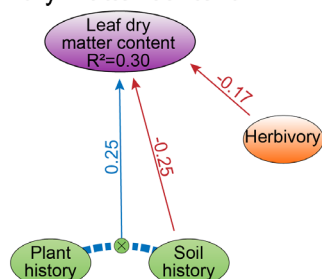
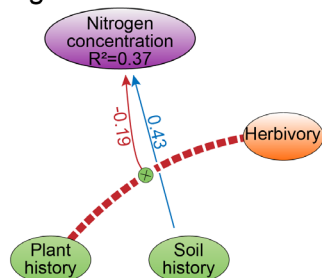
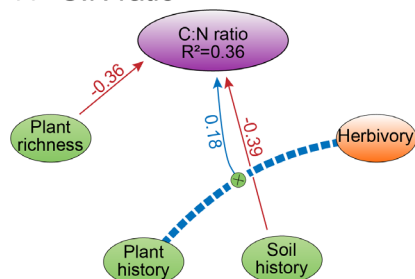
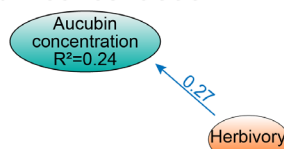
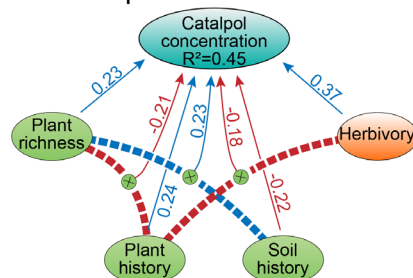
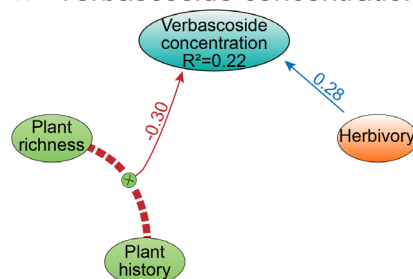
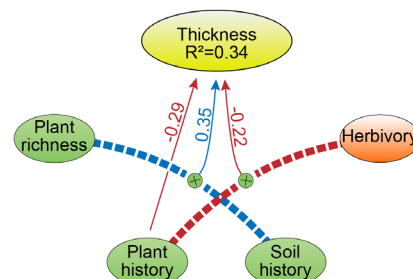
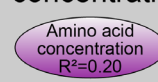
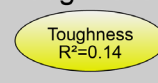
Nutrient axis**(a) Leaf dry matter content****(b) Nitrogen concentration****(c) C:N ratio****Chemical defence axis****(d) Aucubin concentration****(e) Catalpol concentration****(f) Verbascoside concentration****Physical defence axis****(g) Thickness****No herbivory effect on plant traits****(h) Amino acid concentration****(i) Toughness****(j) Hair density**

FIGURE 7 Effect of plant richness, plant and soil history on single plant traits. (a–c) and H, traits associated with the nutrient axis: LDMC (a), nitrogen concentration (b), C:N ratio (c) and amino acid concentration (h). (d–f), traits associated with the chemical defence axis: aucubin concentration (d), catalpol concentration (e) and verbascoside concentration (f). (g, i, j), traits associated with the physical defence axis: leaf thickness (g), leaf toughness (i) and hair density (j). Only significant effects are shown. Significant interactions among variables are indicated by dashed lines with their corresponding effect. Significant interactions of three variables are excluded to enhance readability. Blue paths indicate positive and red paths negative relationships. The values on the paths are standardized estimates (mean=0, SD=1; see [Tables S16–S25](#) for model summaries containing both original-scale and standardized estimates). Marginal R^2 is given for each corresponding model.

trial occurred shortly after plants had regrown following the biomass harvest, while the second took place at a later developmental stage, when plants had matured and possibly reallocated resources towards reproduction at the expense of defence (Quintero & Bowers, 2011). Such ontogenetic effects may be modulated by plant richness: In species-rich communities, stronger competition can lower light availability due to increased shading, which could alter trait expression (e.g. LDMC) and influence plant quality for herbivores (Bachmann et al., 2018). Interestingly, despite expectations of a growth-defence trade-off under resource limitation, *P. lanceolata* in high-diversity plots produced more flowers, had lower C:N ratios and exhibited increased catalpol concentrations. This suggests that richness may enhance both reproductive output and defence, complicating simple trade-off expectations.

Herbivore weight gain was influenced by both plant and soil history, with these effects largely mediated by changes in plant nutritional quality. Plant history decreased nutritional quality but still had a net positive effect on caterpillar performance, likely due to changes in unmeasured traits. For instance, structural plant traits such as root architecture (Loranger et al., 2012) and leaf size (Zhang et al., 2017) are known predictors of herbivore performance and can themselves be shaped by community selection (Zuppingier-Dingley et al., 2014). In contrast, the results on soil history suggest positive legacy effects of previous soil condition. Effects on herbivore performance were fully explained by soil history effects on plant nutritional quality. Although we did not record specific soil characteristics and our ability to fully explain soil history effects remains limited, our results suggest that soil nutrients, particularly nitrogen,

may be a crucial factor. These differences in nutrient availability with soil history may arise due to changes in the below-ground food web (Amyntas et al., 2024) or interaction with arbuscular mycorrhizal fungi (Albracht et al., 2024) and affect above-ground herbivores (Wang et al., 2014). Importantly, interactive effects between plant and soil history emerged, highlighting that plant history and soil history jointly shape plant traits, and that multiple, potentially opposing, trait-mediated pathways contribute to herbivore performance.

4.2 | Herbivore effects on plants change with plant richness and community history

Herbivory induced changes in individuals of *P. lanceolata*. Even though plants had only a few weeks to adjust to herbivory after the first exposure (Figure 2), plant height decreased in monocultures compared to controls, indicating that herbivory can suppress plant growth under certain conditions (Zhu et al., 2018). In monocultures, intense intraspecific competition for shared resources may limit nutrient availability, constraining regrowth following damage. In contrast, mixtures may buffer such effects through complementary resource use, facilitative interactions or more resilient soil communities (Thakur et al., 2021; Zuppinger-Dingley et al., 2014).

In response to herbivore exposure, *P. lanceolata* individuals showed elevated concentrations of all chemical defence compounds (aucubin, catalpol and verbascoside), similar to increases in aucubin and catalpol reported by others (Darrow & Bowers, 1999; Wang et al., 2015; Zhu et al., 2018; but see Fuchs & Bowers, 2004; Jarzomski et al., 2000). These compounds can be induced shortly after herbivore attack and remain elevated for weeks (Darrow & Bowers, 1999), potentially contributing to changes in plant effects on herbivores over repeated measurements (see Discussion: Section 4.1). While changes in chemical defences were independent from history treatments, history affected responses in other plant properties. In response to herbivore exposure, *P. lanceolata* individuals increased nutrient quality and physical defence in communities *without* plant history, while plants from communities *with* plant history showed no change in nutrient quality and even reduced physical defence. This pattern suggests that in communities *with* plant history, where plants have evolved or been selected under unique biotic pressures (including herbivory and plant–plant interactions), the defence strategy may have diverged markedly from those *without* plant history (Medina-van Berkum et al., 2025). Here, reduced physical defence and stable nutrient quality after herbivory could indicate a more adapted or cost-optimized response. For example, these plants might rely more on tolerance strategies (e.g. rapid recovery; Strauss & Agrawal, 1999) or indirect defences (e.g. attracting predators; Dicke & Baldwin, 2010), rather than investing in physical barriers (Lind et al., 2013; Viola et al., 2010). Importantly, in communities *without* plant history, the post-herbivory increase in nutrient quality could benefit herbivores by making the plants even more palatable or nutritious, potentially creating a feedback loop of continued herbivore pressure (Stolter, 2008). However, these nutrients are

also critical for the synthesis of chemical defences (Stamp, 2003). Conversely, in communities *with* plant history, the reduction in physical defence might seem counterintuitive, but if herbivory is predictable and mild, plants might allocate fewer resources to defence and more resources to growth or reproduction. Such a strategy could pay off under stable conditions (Lind et al., 2013; Viola et al., 2010). While we found no significant interactive effect of herbivory and plant history on plant performance, these shifts imply that evolutionary or selection history within plant communities does not just affect baseline traits, but also the plasticity of those traits under stress.

5 | CONCLUSION

This study demonstrates that plant traits significantly influence herbivore performance, while herbivory, in turn, alters plant traits. Importantly, both directions are influenced by plant richness and community history, highlighting the role of long-term ecological processes in shaping plant–consumer interactions. Our research is pioneering in its exploration of plant–consumer dynamics and highlights the value of plant richness and legacy effects in grassland plant communities. Although limited by a small number of replicates and a focus on a single plant species interacting with a generalist herbivore, the patterns we observed are likely to extend to other generalist herbivores. Nevertheless, interactions involving specialist herbivores may differ substantially, as such herbivores and their host plants often display more specific, co-evolved responses. We emphasize the need to explore these reciprocal effects in other contexts, as the understanding of reciprocal dynamics between organisms is crucial for advancing our knowledge of ecosystem functioning, species coexistence, and coevolutionary processes.

AUTHOR CONTRIBUTIONS

Maximilian Bröcher, Sebastian T. Meyer and Anne Ebeling contributed to the study conception and design. Maximilian Bröcher, Sebastian T. Meyer, Sybille Unsicker and Pamela Medina-van Berkum conceptualized the herbivore experiment. Maximilian Bröcher and Pamela Medina-van Berkum reared the caterpillars. Anna-Maria Madaj, Anne Ebeling, Alexandra Weigelt, Nico Eisenhauer and Nicole M. van Dam established and coordinated the JenaTron-Experiment. Maximilian Bröcher, Leonardo Bassi and Pamela Medina-van Berkum collected the data. Maximilian Bröcher analysed the data with input from Sebastian T. Meyer and Anne Ebeling. Maximilian Bröcher, Sebastian T. Meyer, Anne Ebeling, Leonardo Bassi and Pamela Medina-van Berkum contributed to the interpretation of the results. Maximilian Bröcher led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data and R code are available from the Jena Experiment database (<https://jexis.idiv.de/>): <https://doi.org/10.25829/RQCW-TF92> (Bröcher et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of species mixtures of the JenaTron Experiment.

Table S2. Details of analysis of amino acids by LC-MS/MS [HPLC 1260 (Agilent Technologies)-QTRAP6500 (AB SCIEX)] in positive ionization mode.

Table S3. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance (Fisher's $C = 26.14$, $p = 0.887$, $df = 36$, $AIC = 189.9$).

Table S4. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the LDMC as mediator (Fisher's $C = 23.57$, $p = 0.262$, $df = 20$, $AIC = -414.5$).

Table S5. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the nitrogen concentration as mediator (Fisher's $C = 19.12$, $p = 0.384$, $df = 18$, $AIC = -99.7$).

Table S6. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the C:N ratio as mediator (Fisher's $C = 19.21$, $P = 0.379$, $df = 18$, $AIC = -8.4$).

Table S7. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the amino acid concentration as mediator (Fisher's $C = 15.93$, $p = 0.598$, $df = 18$, $AIC = 121.1$).

Table S8. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the aucubin concentration as mediator (Fisher's $C = 15.58$, $p = 0.418$, $df = 18$, $AIC = -39.1$).

Table S9. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the catalpol concentration as mediator (Fisher's $C = 18.56$, $p = 0.419$, $df = 18$, $AIC = -125.5$).

Table S10. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the verbascoside concentration as mediator (Fisher's $C = 18.72$, $p = 0.409$, $df = 18$, $AIC = -56.1$).

Table S11. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the leaf toughness as mediator (Fisher's $C = 19.55$, $p = 0.359$, $df = 18$, $AIC = -256.0$).

Table S12. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the leaf thickness as mediator (Fisher's $C = 13.50$, $p = 0.636$, $df = 16$, $AIC = -378.7$).

Table S13. Summary of the structural equation model for plant species richness, plant and soil history effects on herbivore performance with the hair density as mediator (Fisher's $C = 18.49$, $p = 0.555$, $df = 20$, $AIC = -181.8$).

Table S14. Summary of the structural equation model for plant species richness, plant and soil history, and herbivory effects on plant performance (Fisher's $C = 2.48$, $p = 0.871$, $df = 6$, $AIC = -1133.8$).

Table S15. Summary of the structural equation model for plant species richness, plant and soil history, and herbivory effects on plant leaf traits principal components (Fisher's $C = 4.76$, $p = 0.575$, $df = 6$, $AIC = 690.5$).

Table S16. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on LDMC.

Table S17. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on nitrogen concentration.

Table S18. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on C:N ratio.

Table S19. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on amino acid concentration.

Table S20. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on aucubin concentration.

Table S21. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on catalpol concentration.

Table S22. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on verbascoside concentration.

Table S23. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on leaf toughness.

Table S24. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on leaf thickness.

Table S25. Summary of linear mixed-effect models for plant species richness, plant and soil history, and herbivory effects on hair density.

Figure S1. Validation statistics showing the relationship between (A) observed and predicted carbon and (B) observed and predicted nitrogen concentrations with their respective coefficient of determination (R^2), root mean squared error (RMSE), and relative percent deviation (RPD).

Figure S2. Direct effects of plant richness, plant, and soil history on herbivore performance for (A) weight change in the first trial and (B) weight change in the second trial.

Figure S3. Direct effects of plant richness, plant, and soil history on plant leaf traits principal components and the effects of those on herbivore performance: (A–D) nutrient axis, (E–H) chemical defence axis, and (I–L) physical defence axis.

Figure S4. Effects from significant interactions of two predictors detected in structural equation models (Figures 4 and 6) on (A–B) plant traits mediating plant effects on herbivores, (C–E) plant performance parameters in response to herbivory, and (F–J) plant traits in response to herbivory (see Tables S3, S14, S15 for the model summaries).

Figure S5. Effects from significant interactions of two predictors detected in structural equation models (Figure 5, Figure S9) on (A–C) plant traits associated with the nutrient axis and (D) catalpol concentration (see Tables S4–S6, S9 for the model summaries).

Figure S6. Direct effects of plant richness, plant, and soil history on plant leaf traits associated with the nutrient axis and the effects of those on herbivore performance: (A–D) leaf dry matter content, (E–H) nitrogen concentration, (I–L) C:N ratio, and (M–P) amino acid concentration.

Figure S7. Direct effects of plant richness, plant, and soil history on plant leaf traits associated with the chemical defence axis and the effects of those on herbivore performance: (A–D) aucubin

concentration, (E–H) catalpol concentration, and (I–L) verbascoside concentration. The predictions were extracted from the structural equation models that test plant effects on herbivores (Figure S9; see Table S8–S10 for the model summaries).

Figure S8. Direct effects of plant richness, plant, and soil history on plant leaf traits associated with the physical defence axis and the effects of those on herbivore performance: (A–D) toughness, (E–H) thickness, and (I–L) hair density.

Figure S9. Structural equation models (SEMs) of plant richness, plant and soil history on herbivore performance with single plant leaf traits as mediators. A–C, SEMs that use traits associated to the chemical defence axis: aucubin concentration (A), catalpol concentration (B), and verbascoside concentration (C). D–F, SEMs that use traits associated to the physical defence axis: toughness (D), thickness (E), and hair density (F).

Figure S10. Direct effects of plant richness, plant, and soil history, and herbivory on plant performance (A–C) and on plant leaf traits principal components (D–F).

Figure S11. Direct effects of plant richness, plant, and soil history, and herbivory on plant leaf traits associated with the nutrient axis (A–D), chemical defence axis (E–G), and physical defence axis (H–J).

Figure S12. Effects from significant interactions of two predictors detected in structural equation models (Figure 7) on (A–C) plant traits associated with the nutrient axis, (D–F) catalpol concentration, and (G–H) thickness (see Tables S16–S18, S21, S24 for the model summaries).

Method S1. JenaTron environmental conditions.

Method S2. Measurements of herbivory performance.

Method S3. Measurements of plant performance and plant traits.

Method S4. Targeted defence compound and amino acid analysis.

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