Herbivore population differences rival geographic and biophysical variation in structuring ecosystem function

Running title: Herbivore populations restructure ecosystems

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Abstract

Geographic variation in ecosystem function is often attributed to differences in climate and soil properties, with biophysical constraints assumed to dictate spatial patterns in nutrient cycling, carbon storage, and plant productivity. However, biotic interactions, particularly herbivory, also vary geographically and can generate feedbacks that influence ecosystem processes. Using a replicated three-year field experiment, we tested how population-level functional differences in a widespread arthropod herbivore mediate geographic variation in ecosystem function. Structural equation modeling revealed that herbivores exerted strong direct effects on plant biomass, soil carbon, and nitrogen mineralization, often surpassing the influence of historical conditions and geographic variation in climate. Moreover, functionally distinct herbivore populations had divergent effects on nutrient cycling and plant diversity, demonstrating that population-level differences introduce novel pathways of influence on ecosystem function. These findings challenge ecosystem models that prioritize abiotic constraints and highlight the need to incorporate consumer-driven feedbacks into ecological frameworks.

Introduction

Geographic variation in ecosystem function has been widely attributed to spatial differences in biophysical factors, particularly climate variables such as temperature and precipitation, and legacy states such as soil properties and nutrient availability (Berg *et al.* 1993; Chapin *et al.* 2011; Reichstein *et al.* 2014; Schlesinger 2005). These factors shape broad-scale patterns in nutrient cycling, carbon storage, and primary production, leading to predictable ecosystem differences across climatic and edaphic gradients. However, ecosystem function is also influenced by biotic interactions, particularly those between herbivores and plants, which also vary geographically in response to local environmental conditions (Barley *et al.* 2021; Lynn & Fridley 2019; Marczak *et al.* 2013; Massad *et al.* 2024). Herbivore-plant interactions are shaped by temperature, soil, and plant nutrient availability, generating feedback that structure nutrient cycling and ecosystem processes (Elser *et al.* 2000; Pennings *et al.* 2009; Schmitz 2017; Schmitz & Trussell 2016). Thus, while biophysical variation sets the stage for ecosystem function, spatial heterogeneity in biotic interactions is the play that may further drive regional variation in ecosystem dynamics.

Despite increasing recognition of biotic interactions as key drivers of ecosystem processes, the mechanisms shaping geographic variation in herbivore-plant interactions remain unresolved, particularly in the context of conflating or confounding influences from local biophysical constraints and broader geographic gradients (Lynn *et al.* 2023; Lynn & Fridley 2019; Maron *et al.* 2014; Massad *et al.* 2024; Pennings & Silliman 2005; Schmitz & Trussell 2016). Extensive research has shown that geographically structured soil properties influence herbivory by shaping plant defense traits (e.g., Lynn *et al.* 2023; Lynn & Fridley, 2019), and that herbivore impacts can vary depending on interactions between abiotic and biotic factors across environmental gradients

(Maron *et al.* 2014; Massad *et al.* 2024). Moreover, herbivory often correlates more closely with local resource availability and biophysical constraints than with latitude alone, demonstrating the importance of small-scale environmental heterogeneity (Pennings & Silliman 2005, Baker *et al. in review*). While this work has clarified how bottom-up drivers such as soil fertility and plant defenses shape geographic patterns in herbivory, comparatively less is known about how herbivores, in turn, generate top-down effects that influence ecosystem function across space. In particular, little attention has been given to whether spatial variation in herbivore traits—driven by local environmental conditions—can create systematic differences in how herbivores affect nutrient cycling and plant community composition. Addressing this gap requires integrating biophysical context with an understanding of trait variation within species.

Trait variation within a species can strongly influence individual-level impacts on ecosystem function (Govaert et al. 2024; Raffard et al. 2019; Des Roches et al. 2018, 2021; but see Pichon et al. 2022), yet this variation is often overlooked in studies of geographic ecosystem dynamics. If herbivore populations differ in functional traits, such as foraging behavior (Joern *et al.* 2012), nutrient excretion, or stress physiology (Rosenblatt *et al.* 2019; Sommer *et al.* 2023), then their ecosystem impacts may diverge in ways not readily predicted by climate or edaphic properties alone. Variation in trait expression can arise through local adaptation, where populations evolve traits suited to persistent local environmental conditions, or through phenotypic plasticity, where individuals modify traits in response to locally varying environmental conditions (Bradshaw & Holzapfel 2006; Reed *et al.* 2010; Sommer *et al.* 2024). This dynamic may have cascading effects on the extent to which local herbivore populations interact with plant communities and mediate ecosystem functions such as nutrient cycling. For instance, herbivores in resource-limited environments may exhibit compensatory feeding strategies, such as increasing their consumption

rates of carbon-rich plants, leading to greater production of frass and litter inputs with altered stoichiometry, which can accelerate decomposition and mineralization rates (Raubenheimer *et al.* 2009; Sitters *et al.* 2020). By contrast, herbivores in resource-rich environments may primarily alter plant competitive dynamics, shifting community composition without strongly changing litter quality or quantity, and thereby exerting weaker influence on soil nutrient processes. These divergent strategies align with broader ecological expectations of how populations regulate energy and nutrient demands under different environmental constraints. Thus, failing to account for herbivore population-level functional differences could obscure key drivers of geographic variation in ecosystem function and resilience to environmental change.

We report on findings from a three-year geographically replicated experiment in which local populations of a dominant herbivore species were reciprocally transplanted across five sites to quantify how population-level trait differences mediate variation in ecosystem function across their geographic range in the New England region of the eastern USA. The species (*Melanoplus femurrubrum*) is a widespread grasshopper in which local populations differ in their expression of plasticity in physiological and behavioral traits (Baker *et al. in review*; Parsons & Joern 2014; Rosenblatt *et al.* 2019; Sommer *et al.* 2025). We applied structural equation modeling (SEM) to quantify the relative contributions of among-population variation, local climate, and historical legacies as drivers of key ecosystem variables and functions, including plant biomass, soil nutrients, and nitrogen mineralization. Grasshopper populations originating from warmer sites, characterized by higher daily mean maximum temperatures during the growing season, drove different ecosystem outcomes than populations from cooler sites (Baker et al. *in review*). These differences were linked to variation in behavioral and physiological trait plasticity expressed under environmental stressors. Overall, our findings demonstrate that within-species variation in

98 herbivore traits can manifest spatially to play an important role in shaping geographic variation in
99 ecosystem function.

100 **Methods**

101 *Natural history background*

102 Our study was conducted within a 17,000 km² area of the New England region of the
103 northeastern USA. Within this region, old field ecosystems are localized openings in a largely
104 afforested landscape and are legacies of abandoned agriculture (Foster 1992). There is a wide range
105 of inter- and intra-annual climate variability and extremes among local old field sites across the
106 region (Oregon State University 2002; Rosenblatt *et al.* 2016, 2019). Vegetation in these old fields
107 is comprised predominantly of forbs (*Solidago rugosa, S. altissima, Aster spp,* and grasses (*Poa*
108 *pratenses, Phleum pratense, Bromus inermis, Agropyron repens,* and *Agrostis spp*; Beckerman
109 2002; Britton & Brown 1970; Schmitz 2008a). The old fields provide habitat for *Melanoplus*
110 *femurrubrum* (hereafter grasshoppers), a moderately sized (2 - 3 cm) generalist herbivore
111 (Beckerman 2002) that is widely distributed across North America (Helfer 1987). Extensive land
112 use and development have fragmented the grasshopper's habitat, creating separate populations
113 throughout its range (Bomar 2001; Parsons & Joern 2014; Rosenblatt *et al.* 2019). The populations
114 appear to be locally adapted to cope with the climatic conditions of the local ecosystems in which
115 they reside (Rosenblatt *et al.* 2016, 2019; Baker *et al. in review*). This grasshopper species is the
116 most abundant and persistently present phytophagous insect in the New England old fields
117 throughout summer and early fall, consuming both grasses and forbs. Its populations also have
118 discrete generations, in which female grasshoppers deposit eggs in the soil in the late fall before
119 frost kills all adults, eggs diapause over winter, and juveniles hatch early in the following summer
120 (Capinera 1987; Chapman & Joern 1991; Uvarov 1977). This combination of discrete, within-

121 population generations makes this grasshopper an ideal study species because it enables clear
122 attribution of ecosystem effects to population-level trait variation and allows us to examine how
123 herbivore functional roles interact with biophysical conditions to shape ecosystem functioning.
124 We focused on two functional groups of plants that are important drivers of ecosystem
125 functioning (Schmitz 2006, 2008a): grasses *Poa spp.* and *Phleum pratense;* and the forb goldenrod
126 *Solidago rugosa*. These plant functional groups compete asymmetrically, with goldenrod
127 competitively dominating grasses and other forb plant species in the absence of herbivory (Schmitz
128 2006). Grasses are nitrogen (N)-rich and are a preferred resource for grasshoppers to build protein
129 for development, growth and reproduction (Rothley *et al.* 1997). Goldenrod is rich in soluble
130 carbon (C), which is an essential dietary resource for carbohydrate energy to support metabolism
131 (Hawlena *et al.* 2012; Rothley *et al.* 1997).
132 This species of grasshopper exhibits both behavioral and physiological plasticity to navigate
133 local climate variation and environmental stressors. Behaviorally, grasshoppers balance the
134 benefits and risks of vertical movement within the vegetation canopy: ascending into the upper
135 canopy provides access to nitrogen-rich forage but also exposes them to higher temperatures and
136 predation risk, while retreating into the lower canopy reduces these stressors but limits access to
137 high-quality food (Barton & Schmitz 2009; Pitt 1999). Physiologically, grasshoppers adjust their
138 metabolism to maintain homeostasis in response to stress. Increased respiration rates under
139 predation risk heighten the demand for soluble carbohydrate carbon, leading grasshoppers to shift
140 their diet toward goldenrod, a rich source of soluble C (Schmitz et al. 2016; Hawlena & Schmitz
141 2010).
142 This balance of behavioral and physiological plasticity is not uniform across populations.
143 Instead, the degree to which each strategy is enlisted varies with the local climate experienced by

144 grasshopper populations across the New England region (Rosenblatt *et al.* 2016, 2019; Baker *et*
145 *al. in review*). In response to environmental warming, populations occurring in warm sites elevated
146 their respiration rates and consistently occupied the same vertical stratum of the grassland canopy
147 throughout the day, potentially because a higher evolved thermal optimum allows them to cope
148 with warming without behavioral alterations. This combination of heightened metabolic demand
149 and stable canopy use was accompanied by a shift in diet toward soluble carbon-rich *Solidago*
150 (Baker *et al. in review*). We term this integrative expression of trait plasticity a climate "resistor"
151 strategy. In contrast, environmental warming caused populations occurring in cool sites to decrease
152 their respiration rates and elevate their canopy height, presumably to enhance the likelihood of
153 reaching their thermal optimum and increasing their access to N-rich forage (Baker *et al. in*
154 *review*), a strategy we term "reactor". Together, these trait differences reflect population-level
155 responses to regional climate variation and underscore how they may shape ecosystem function
156 under shifting environmental conditions.

157 Grasshopper populations engaging in resistor or reactor strategies stand to have
158 fundamentally different impacts on the plant community and ecosystem function (Figure S1). A
159 diet shift by resistors to increase carbohydrate C consumption is expected to reduce goldenrod
160 abundance, thereby weakening its competitive dominance and allowing other plants, such as
161 grasses, to increase in biomass (Schmitz 2006). Such herbivory-driven changes in plant species
162 interactions should cascade to alter the C:N ratios of plant tissue and litter, which can influence
163 soil microbial respiration and carbon and nitrogen mineralization and ultimately soil C and N
164 content (Hawlena *et al.* 2012; Hawlena & Schmitz 2010; Schmitz 2006). Alternatively, reactors
165 that merely feed higher in the canopy without undertaking a diet shift should have weaker
166 cascading impacts on these properties of the plant community and soil and ecosystem function.

Experimental design

Our three-year field experiment tested the predictions for the effects of resistor and reactor strategies using grasshopper populations from five old fields sampled across the broader region (Figure 1). Sites were chosen based on similarity in management, soil properties, hydrology, and plant community composition, while also capturing a spatial mosaic in mean daily maximum temperatures. This thermal mosaic was identified in a companion study (Baker *et al. in review*), which analyzed nine years of remotely sensed climate data (800 m^2 resolution; PRISM Climate Group 2022) and conducted field-based assessments of grasshopper trait plasticity across eight populations. Two of the five sites in our study were designated as common gardens for transplanting populations based on their relative differences in historical climate conditions (warm vs cool sites) that would lead to resistor and reactor strategies of their local grasshopper populations.

In Year 1, we established replicate, experimental mesocosms to isolate the effect of herbivores on ecosystem function (Schmitz 2004, 2010; Schmitz *et al.* 2010; Sommer & Schmitz 2020). We used cylindrical mesocosms (0.25 m^2 area × 1 m high) constructed from vinyl-coated garden wire and wrapped with aluminum insect screening. Each of the five field sites had two treatments (vegetation-only vs. local herbivores with vegetation) that were replicated eight times (Figure 1). We further established mesocosms at the two common garden sites to which we transplanted grasshoppers from the five other populations (Figure 1). Consequently, the entire experiment included 144 mesocosms. All treatments and populations were randomly assigned to mesocosm cages.

At the beginning of the growing season (June), mesocosm cages were sunk 10 cm into the soil in each field location, with each mesocosm enclosing natural vegetation. Mesocosm cages

were arrayed at least 1 m apart but situated to capture similar initial percent cover in the two primary functional groups—goldenrod and grass—and to minimize differences in varying biophysical conditions (e.g., slope, aspect or soil moisture) among mesocosms. Once mesocosms were established, we removed any resident arthropods and sealed the top with insect screening. Mesocosms were undisturbed for the growing season to allow ecosystem processes to recover from the initial disturbance caused by cage installation. At the end of the growing season (October) we measured baseline ecosystem conditions and functioning (described below) in all mesocosms. Shortly after the first frost, all mesocosms were "winterized" by removing the insect screen tops to permit entry of snowfall. This process of clearing the mesocosms of non-target species, monitoring, and removing the insect screen tops was maintained for all three years of the experiment.

We confirmed similarities in the initial biophysical conditions of the five sites by analyzing soil samples taken from each field for bulk density, pH, and texture. Bulk density was measured using soil cores collected from 10 random locations adjacent to the mesocosms. Soil cores were extracted using a 5 cm × 10 cm AMS Bulk Density Soil Sampler and returned to the lab for processing. In the lab, each core was sieved to 2 mm. Material < 2 mm was dried at 65°C for 48 hours and weighed. Material > 2 mm was measured for volume displacement. Bulk density was then calculated as the total dry mass of soil (including < 2 mm and > 2 mm fractions) divided by the total core volume, accounting for the volume of larger materials measured by displacement. Soil samples for pH and texture analyses were likewise taken from adjacent locations using the same soil corer. pH was determined potentiometrically in a slurry system using an electronic pH meter (Sims & Eckert 2011), while texture was assessed through a standard particle size analysis (Folk 1966). These soil properties are stable on short timescales and in the absence of human

activity (Pahlavan-Rad & Akbarimoghaddam 2018; Xia *et al.* 2020) and were therefore not measured again in subsequent years.

In late June of Year 2, we caught third-instar grasshoppers with sweep nets at their native sites. We stocked grasshoppers into the mesocosms at the same densities across all field sites, reflecting the average field density for the species across the region (Rosenblatt *et al.* 2019). For a given grasshopper population, this meant stocking five individuals in each cage at the homesite and transplanting another five into each cage at the common garden site(s). One week after stocking, we replaced any grasshoppers that experienced mortality due to handling stress. After initial setup, mesocosms were left undisturbed to allow biotic interactions and ecosystem processes to proceed naturally. During the growing season, we performed non-invasive monitoring by tapping the mesocosm walls to confirm grasshopper presence and by observing signs of grasshopper activity, including plant defoliation and frass accumulation. At the end of the growing season, mesocosms were winterized following the same procedure as Year 1.

In late June of Year 3, we again caught third-instar grasshoppers from their native populations, stocked them into their respective home site and transplant site mesocosms, and allowed them to progress with external monitoring for the growing season as in Year 2. At the end of the growing season (October) we again measured ecosystem properties and functioning. We deliberately did not measure ecosystem properties and functions in Year 2 to avoid altering longer-term ecosystem functioning that would have arisen from disrupting litterfall and microbial decomposition, and soil biophysical properties by interim vegetation clipping and soil sampling (Schmitz 2008b).

Ecosystem properties and function measurements

We chose ecosystem properties and function variables based on previous insights about key old field ecosystem variables that are impacted by grasshoppers (Figure S1; Hawlena et al. 2012; Hawlena & Schmitz 2010; Schmitz 2006, 2008a; Sommer & Schmitz 2020; Sommer et al *in review*; Strickland et al. 2013) combined with our *a priori* predictions of resistor and reactor effects explained above. With our goal of disentangling geographic variation, historical conditions, and the effects of herbivory, we also included initial assessments of soil organic matter in each mesocosm.

At the end of the growing season in Years 1 and 3, we took samples of soil, litter, plant tissue, and plant percent cover from inside each mesocosm. We took three soil cores (2 cm × 10 cm depth) from inside the mesocosm and placed them together into a plastic bag to homogenize the samples. All bags were immediately placed on ice and transferred to a refrigerator in the laboratory on the Yale University campus before being sieved to 4 mm for further processing (described below). Litter was sampled in three different locations within each mesocosm by taking material from the surface of the soil. Samples for plant foliar nutrient assessments of goldenrod and grass were obtained from 10 randomly selected goldenrod leaves and 10 grass clippings (including stem and inflorescence material, if present) across multiple individuals in each mesocosm. Each mesocosm's goldenrod and grass plant material was placed into separate coin envelopes before being dried for 48 h at 60C. Each plant sample was pulverized in a ball mill, packed in tin capsules and analyzed for C and N using an ECS 4010 Elemental Analyzer (Costech Analytical Technologies Inc.; Valencia, CA) connected to a Delta Plus Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific; Waltham, MA).

Plant species percent cover in each mesocosm was estimated by a single experienced observer to ensure consistency. Plant species were assessed for their spatial extent in a mesocosm

and then normalized to 100%, excluding bare ground. We then calculated the Shannon-Wiener diversity index for each mesocosm using species-specific normalized percentage cover estimates. We indirectly estimated herbivory effects on the aboveground biomass of plant functional groups to minimally perturb the mesocosm by creating allometric relationships relating percent cover to biomass (sensu Schmitz 2003). These allometric relationships were developed from 0.25 m^2 plots outside the mesocosms, with the proviso that the plots were first selected to target the entire possible range of percent cover for grasses and goldenrod, before being clipped, dried at 60ºC for 48 hours and weighed.

We performed several *ex-situ* soil measurements in the lab to capture state and function variables known to be relevant in this system; specifically, soil %C, soil %N, nitrogen mineralization, microbial biomass, and soil organic matter. After soils were homogenized and sieved to 4 mm, they were returned to a refrigerator for subsampling and further processing. All soil measurements were completed or converted into a shelf-stable form within 2.5 months of field sampling. Soil subsamples for C and N content analysis were passed through a 2 mm sieve, oven dried at 60ºC for 48 hours, then pulverized in a ball mill, packed into tin capsules and analyzed in the same manner as the plant and litter material, described above.

We calculated the dry-weight equivalent for each mesocosm's soil in terms of gravimetric moisture content (GWC) and water-holding capacity (WHC). GWC was determined by drying duplicate 5 g subsamples at 105°C for 24 hours to constant mass and calculating moisture loss. WHC was measured by saturating duplicate subsamples of sieved soil in a funnel lined with wet filter paper (Whatman #1), allowing them to drain for 2 hours, and then drying the drained soil at 105°C for 24 hours. The dry weights from these measurements were further used to determine soil adjustments to 65% WHC for nitrogen mineralization and microbial biomass incubations.

Nitrogen mineralization was measured using a 30-day incubation approach with KCl extraction. Soil was subsampled for Day 1 and Day 30 incubations, with a dry-weight equivalent of 6 g. For Day 1 extractions, the soil was extracted in 25 mL of 2M KCl. The soil-KCl mixture was initially mixed by hand, shaken on a shaker-table for 30 minutes, and then refrigerated overnight to settle. The chilled supernatant was then separated and stored at 4°C until analysis for colorimetric assays as described below. For Day 30 incubations, the dry-weight equivalent of 6 g soil was incubated at 20°C in uncovered tubes placed in sealed bags with moist paper towels to maintain ~65% WHC. Moisture was adjusted weekly based on WHC. On Day 30, the soil was extracted with 25 mL of 2M KCl following the same procedure as Day 1.

Ammonium and nitrate were quantified via colorimetric assays in separate extracts. Ammonium was analyzed using the salicylate-nitroprusside method (Sims *et al.* 1995), in which NH_4^+ reacts with hypochlorite and salicylate in an alkaline medium to form a blue indophenol compound, measured at 660 nm. Nitrate was analyzed via the VCl_3/Griess method (Hood-Nowotny *et al.* 2010), where NO_3^- is reduced to NO_2^- in a VCl_3 acidic medium and reacts with Griess reagents to form a chromophore, measured at 540 nm. N-mineralization rates were calculated as the changes in ammonium (NH_4^+) and nitrate (NO_3^-) concentrations over time (difference between the final and initial concentrations in mg/mL), multiplied by the bulk density (g/cm^3), and scaling by the soil depth (cm) for units of mg N/cm^2 per month.

Soil microbial biomass was estimated using a modified substrate-induced respiration (SIR) technique (Fierer & Schimel 2003). The equivalent of 4 g dry-weight soil was subsampled from the soil cores of each mesocosm, incubated overnight at 20 °C, slurried with a 4-mL autolyzed yeast solution by shaking for 1 h, and then capped with an air-tight lid modified for gas analysis (Bradford *et al.* 2008). Samples were then flushed with CO_2-free air, and after 4 h of incubation at

20°C, headspace CO_2 concentrations were measured using an Infra-Red Gas Analyzer (Li-COR model Li-7000). SIR was then estimated as mg CO_2-C/g dry soil/h, ensuring standardization across soil mass and moisture content.

Finally, soil organic matter was estimated for each mesocosm using a loss-on-ignition measurement. Subsamples were passed through a 2 mm sieve and dried at 105 °C before being placed into a 500 °C furnace for 12 h (Nelson & Sommers 1996). Soil organic matter is a key determinant of the physical, chemical, and biological processes in soil (Reeves 1997; Robertson *et al.* 2014; Romig *et al.* 1995), however, unlike the other ecosystem variables, we did not have any *a priori* hypotheses about the role of herbivory on soil organic matter. Therefore, it was only measured in the initial year 1 to quantify variability both within and across sites.

Analysis

We employed structural equation modeling (SEM) in R (v.4.4.1) to analyze the direct and indirect effects of grasshopper herbivory and plasticity on ecosystem properties and function variables. Due to the nested structure of the data, with measurements collected across five sites, we implemented a piecewise SEM approach using the piecewiseSEM package (v.2.3.0.1; Lefcheck et al. 2024; Lefcheck 2016). This approach enabled us to incorporate random effects via linear mixed-effects models (LMMs) using the lme4 package (v.1.1-35.5; Bates et al. 2015), ensuring that site-specific variability was accounted for as a random effect. Specifically, each LMM was constructed with site as a random effect, categorical treatment (vegetation-only; “resistor” herbivores; “reactor” herbivores) as a fixed effect, the baseline Year 1 measurement as a fixed effect, and additional ecosystem variables as fixed effects, where applicable, based on insights from previous old-field experiments (Hawlena *et al.* 2012; Hawlena & Schmitz 2010; Schmitz 2003, 2006, 2008a; Strickland *et al.* 2013) and assessments of soil ecosystem dynamics (Bradford

et al. 2008, 2013; Fernández-Martínez *et al.* 2020; Grandy *et al.* 2009; Smith & Bradford 2003). Rather than model the change in ecosystem variables across years, the baseline Year 1 measurements taken prior to treatment application were included as fixed effects to enable comparisons between the historic ecosystem state and other predictors. We evaluated model fit for all LMMs using diagnostics from the DHARMa (v.0.4.6; Hartig 2024) and car (v3.1-3; Weisberg 2019) packages, including assessments of residual normality, homoscedasticity, leverage, multicollinearity (via variance inflation factors), and model stability. For models that did not meet all assumptions of residual normality, we used non-parametric bootstrapping (via the boot package, v.1.3-30; Angelo Canty & Ripley 2024; Davison & Hinkey 1997) as a diagnostic tool to assess the robustness of fixed effect estimates and 95% confidence intervals. The results of these bootstrapped models were not used in the SEM itself; instead, they confirmed that the original models were stable and reliable. We also used the VarCorr function in lme4 to assess the importance of site as a random effect; where site variability was zero (or near-zero) and model fit significantly improved, we removed site as a random effect, using a simple linear model instead. Of the 12 LMMs, 3 met this criterion for simplification.

The SEM framework was structured to capture both direct and indirect pathways of exogenous categorical treatment variables on key response variables. We did not include any latent variables, as our ecosystem measurements were robust with respect to existing hypotheses. We evaluated the SEM model fit through global goodness-of-fit statistics, specifically Chi-squared and Fisher's C, to confirm that our SEM captured the data structure sufficiently. We used directed separation tests to identify theoretically plausible pathways missing from the initial model. When the significant pathways identified by these tests aligned with ecosystem theory, they were added to the respective LMMs, following the same LMM assessment as outlined above. Afterward, the

new paths were incorporated into the SEM. In the final model, the statistical significance of individual predictors was determined based on p-values in the path-specific coefficient summaries. We also examined marginal and conditional R-squared values from each LMM to assess the variance explained by fixed predictors alone (marginal R-squared) versus total variance, including random effects (conditional R-squared). Additionally, individual R-squared values from the SEM were compared with those from the LMM models, enabling us to disentangle the influence of fixed effects from site-level variability across treatments. Although a single SEM was used to evaluate all treatment effects, we present separate visualizations (Figures 2 and 3) to aid interpretability. These figures reflect subset contrasts extracted from the full model's path estimates, not distinct SEMs. All data, alongside direct comparisons between two common gardens, can be visualized in a supplemental Shiny app (https://nathaliesommer.shinyapps.io/herbivore-populations-structure-ecosystems/).

Results

Bulk density, pH, and texture measurements taken during Year 1 site establishment confirmed comparable soil characteristics across fields. Soil texture ranged between sandy loam and loam (sand: 59.94% ± 10.17; silt: 34.02% ± 9.63; clay: 6.10% ± 2.39), with an average bulk density of 0.69 g/cm^3 ± 0.16 and a pH of 5.02 ± 0.36. These results indicate that initial biophysical conditions were relatively consistent among sites, minimizing potential confounding effects of baseline soil heterogeneity on experimental outcomes (Figure S2 and S3).

Directed separation tests for the SEM supported the inclusion of additional pathways in seven of the twelve LMMs, predominantly from baseline Year 1 variables. The SEM demonstrated good overall fit, with a non-significant Chi-squared test (Chi^2 = 187.597, df = 187, p = 0.474),

indicating that the predicted covariance matrix closely aligned with observed data. Fisher's C was significant ($C = 781.807$, $df = 350$, $p < 0.001$), as expected in a complex ecological model. Despite this, individual R^2 values from the SEM closely matched conditional R^2 values from the linear mixed models (LMMs), confirming the model's robustness in capturing both direct and indirect effects, as well as site-level variability.

Herbivores, in general, played a statistically significant and ecologically meaningful role in shaping ecosystem responses, particularly by impacting the plant community and soil nutrients (Figure 2). Across models, herbivore treatments had strong direct effects on goldenrod biomass (average decrease from vegetation treatments: -6.018, $p < 0.001$), grass biomass (average increase from vegetation treatments: +6.851, $p < 0.001$), soil carbon (average decrease from vegetation treatments: -0.171, $p < 0.001$), and soil nitrogen (average decrease from vegetation treatments: -0.022, $p < 0.001$). Notably, for these response variables, the effect size of herbivores was greater than that of historical biophysical conditions or other predictors of ecosystem control such as initial vegetation biomass, and soil carbon and nitrogen content. Herbivory also had downstream impacts on foliar nutrients, with grass %C increasing (average increase from vegetation treatments: +0.314, $p < 0.01$) and goldenrod %N decreasing (average decrease from vegetation treatments: -0.176, $p < 0.05$).

The ecosystem impacts of grasshopper populations differed markedly between reactor and resistor strategies (Figure 3). Reactor herbivores exerted stronger reductions in goldenrod biomass (-7.362 vs -4.675) and slightly smaller reductions in soil carbon (-0.157 vs -0.185) than resistor herbivores. The grasshopper phenotypes had directionally different impacts on nitrogen mineralization rates, with resistor herbivores causing increased nitrogen mineralization rates (+1.323), and reactor herbivores causing reduced rates (-3.066). Indirect ecosystem effects also

varied between populations, with resistor grasshoppers decreasing plant diversity (-0.076) and reactor grasshoppers increasing plant diversity (0.156), following their different impacts on both goldenrod and grass biomass. These downstream differences reflect the distinct pathways through which the different herbivore plasticity strategies can influence ecosystem dynamics.

Historical condition and site-specific variation did not play predominant roles in ecosystem dynamics. Baseline Year 1 measurements were significant in six out of twelve response variables but did not have the largest effect size in any models (Figure S4). Historical conditions, more generally, were not the predominant variable in the SEM. Historical conditions only had the largest effect size in two paths for herbivory (grass foliar %C and plant diversity; Figure 2) and two paths for plasticity (grass foliar %C and goldenrod biomass; Figure 3). For example, grass foliar %C was most strongly influenced by historical soil %C (effect size: +1.0857, $p < 0.001$), which is consistent with ecosystem lag effects. Geographic differences were pronounced for some variables but not for others. Goldenrod biomass (marginal $R^2 = 0.13$; conditional $R^2 = 0.73$; SEM $R^2 = 0.73$) and litter nitrogen (marginal $R^2 = 0.04$; conditional $R^2 = 0.40$; SEM $R^2 = 0.40$) were mainly influenced by site-level effects, whereas site was removed as a random effect for the soil %C, grass foliar %C, and %N models due to no explained variability. Other variables reflected substantial but not predominant geographic heterogeneity, such as soil %N (marginal $R^2 = 0.30$; conditional $R^2 = 0.54$, SEM $R^2 = 0.59$), plant diversity (marginal $R^2 = 0.32$; conditional $R^2 = 0.75$), and grass biomass (marginal $R^2 = 0.18$; conditional $R^2 = 0.42$; SEM $R^2 = 0.42$). Overall, these findings underscore that while geographic variability and historical ecosystem properties shape ecosystem function, they do not supersede the effects of animal herbivory or its pathways of effect as determined at the herbivore population level.

Discussion

Our findings demonstrate that differences in local herbivore populations exert a dominant influence on ecosystem function, surpassing the direct effects of historical conditions and geographic variation in climate. Across models, herbivores directly altered plant biomass, soil carbon, and nitrogen availability, restructuring plant communities and modifying nutrient cycling pathways (Figure 2). While climate-driven geographic variation and historical legacies are widely recognized as key regulators of ecosystem function (Chapin *et al.* 2011; Reichstein *et al.* 2014; Schlesinger 2005), our results show that biotic interactions, particularly those mediated by herbivores, play an equal or even greater role in driving geographic variation in ecosystem processes (Bardgett & Wardle 2010; Miller *et al.* 2014; Pringle *et al.* 2023). Moreover, differences among herbivore populations introduced further variability in ecosystem function, leading to divergent effects on plant composition and nutrient cycling that exceeded the influence of historical conditions or geography (Figure 3).

Herbivore-driven effects on ecosystem function were not only strong but also propagated through feedback mechanisms that complicate traditional bottom-up models of plant-herbivore interactions. Geographic variation in herbivory is frequently attributed to differences in plant nutrient content, defense traits, and local abiotic constraints—factors that influence herbivore performance and consumption rates from the bottom up (Bradford *et al.* 2014; Lynn *et al.* 2023; Lynn & Fridley 2019; Marczak *et al.* 2013). This paradigm has helped illuminate how spatial variation in edaphic conditions can shape plant-herbivore dynamics, but it tends to cast herbivores as passive responders to their environment rather than active agents in structuring ecosystems. In contrast, our findings demonstrate that herbivores themselves can drive substantial top-down effects on biogeochemical cycles and community composition. By altering goldenrod dominance,

443 foliar nutrient content, and rates of nitrogen mineralization, we found herbivores restructured
444 plant-soil feedbacks in ways not readily explained by background environmental conditions alone
445 (Figure 2).

446 Divergent ecosystem impacts observed between herbivore populations further challenge
447 the assumption that herbivore effects are dictated primarily by climate or plant quality. Herbivore
448 populations from warmer sites increased nitrogen mineralization rates and reduced plant diversity,
449 while populations from cooler sites suppressed nitrogen mineralization and increased diversity.
450 These opposing effects occurred despite similar initial conditions across sites, suggesting that trait
451 differences among herbivore populations—shaped by environmental history but not reducible to
452 it—play a central role in mediating ecosystem outcomes. Our findings thus question the
453 conventional assumption that biophysical constraints primarily determine herbivore impacts on
454 plant communities (Bradford *et al.* 2014; Dostálek *et al.* 2020; Kuglerová *et al.* 2019; Lynn *et al.*
455 2023; Lynn & Fridley 2019; Marczak *et al.* 2013). Instead, our results align with emerging
456 evidence that herbivory impacts arise through dynamic feedbacks between consumers and
457 vegetation, with herbivores acting not only as recipients of environmental filtering but also as
458 agents of ecosystem restructuring (Barbero-Palacios *et al.* 2024; Maron *et al.* 2014; Massad *et al.*
459 2024; Pennings & Silliman 2005; Schmitz & Trussell 2016). By shifting competitive hierarchies
460 among plants and modifying nutrient flows, herbivores contribute to context-dependent patterns
461 in ecosystem function that are not easily predicted by climate or resource gradients alone. These
462 findings underscore the importance of integrating top-down consumer-driven processes into
463 ecosystem models and suggest that herbivore populations may amplify, dampen, or even reverse
464 the expected effects of environmental change on nutrient cycling and plant community
465 composition. While our design incorporated spatial replication and extended across three years,

466 the inference space remains limited by the discrete nature of mesocosms and time-point
467 measurements. Broader-scale, continuous monitoring would be valuable to assess how transient
468 or persistent these population-level effects are across heterogeneous landscapes.

469 Even within these constraints, the strength of the observed biotic feedbacks raises
470 important questions about how much such interactions can interact with, or even override, other
471 widely cited drivers of ecosystem variability, such as historical legacies. While historical legacies
472 are often considered dominant factors in shaping ecosystem trajectories, (Anderegg *et al.* 2015;
473 Kulmatiski *et al.* 2006), they did not emerge as dominant predictors of geographic variation in
474 ecosystem functioning in our study. Baseline Year 1 measurements, made prior to herbivore
475 manipulation, were statistically significant in six of the twelve models, yet in no case did historical
476 legacies explain the largest proportion of variation in ecosystem responses. Similarly, geographic
477 variability influenced some ecosystem variables, particularly goldenrod biomass and litter
478 nitrogen, but its effects were inconsistent and often weaker than those of herbivory and herbivore
479 population-level trait differences. Together, this suggests that while historical context may
480 establish the initial conditions, contemporary biotic interactions can exert stronger influences on
481 ecosystem function, particularly when consumers differ in their traits like behavior.

482 The distinct functional differences among herbivore populations underscore the
483 importance of considering population-level variation when evaluating ecosystem processes. In
484 population ecology, intraspecific variation is often characterized as continuous trait variation
485 among individuals within a species (Pichon *et al.* 2022; Des Roches *et al.* 2018), and such variation
486 can be incorporated into models using means and variances in parameters such as consumption
487 rates or metabolic costs. Conventional consumer-driven ecosystem models typically assume that
488 individual-level trait variation scales predictably to population-level effects (Evangelista *et al.*

2017; Govaert *et al.* 2024; Pichon *et al.* 2022; Raffard *et al.* 2019, 2023). However, our findings demonstrate that *population-level* trait differentiation may introduce qualitatively distinct functional effects that are not easily captured by simple continuous distributions. While discrete population-level categories are one way to represent these shifts, we recognize that structured continuous functions such as state-dependent trait distributions could also accommodate this complexity while preserving within-population variance. The divergent ecosystem impacts of the herbivore populations in our study suggest that models of consumer-driven ecosystem functioning may need to advance beyond trait means to explicitly account for state-dependent population-level variation in trait expression (Schmitz & Trussell 2016).

As regional climates shift, understanding how trait-based population differences influence ecosystem processes is critical for predicting ecosystem resilience and anticipating changes in the functional roles of consumers (Huang *et al.* 2017; Melles *et al.* 2011; Williams & Blois 2018). If populations exhibit unique trait-based effects on nutrient cycling and plant competition, then conservation efforts may need to shift from focusing solely on species-level diversity to explicitly considering population-level functional differences (Allendorf *et al.* 2010; Flanagan *et al.* 2018). The loss of functionally distinct populations due to habitat fragmentation or climate-driven range shifts could lead to disproportionate disruptions in ecosystem function. Conservation strategies might benefit from maintaining a portfolio of functionally diverse populations, ensuring that ecosystems retain the capacity to mediate nutrient cycling and plant competition under shifting environmental conditions. Protecting intraspecific diversity may further require targeting populations that contribute disproportionately to ecosystem resilience rather than assuming all populations within a species fulfill equivalent functional roles.

By resolving the relative contributions of biophysical constraints and consumer-driven interactions to geographic variation in ecosystem function, this study offers empirical insights into how to develop a predictive framework for mechanisms creating geographic variation in the ecosystem consequences of herbivore-plant dynamics, which is a need made increasingly urgent by ongoing global change. Herbivores, through their population-specific trait differences, emerge as central regulators of ecosystem function, rivaling or exceeding the influence of historical legacies and geographic variation in climate. These findings reinforce the need to incorporate consumer-driven processes into ecological models and conservation planning, particularly as environmental change reshapes population distributions and functional diversity. Future research should continue to explore how herbivore-driven processes interact with biophysical constraints to shape geographic variation in ecosystem function, with an emphasis on how population-level trait differences mediate ecosystem resilience in changing environments.

Figure captions

Figure 1. Our field experiment was conducted over three growing seasons to assess the effects of population-level variation in grasshoppers on ecosystem function across multiple sites in New England, USA. In Year 1, field mesocosms were established, and baseline ecosystem conditions were measured at each site (black circles with field labels corresponding to site-level data presented in Figures S1 and S2). In Year 2, grasshoppers were reciprocally transplanted between warm-origin (gold, "resistor" populations) and cool-origin populations (purple, "reactor" populations) with individuals stocked at their homesites (circles) and common gardens (stars). Throughout the second growing season, mesocosms were monitored and maintained to ensure population establishment. In Year 3, the transplant was repeated and final ecosystem measurements were taken to quantify the effects of different herbivore populations on plant biomass, soil nutrients, and nitrogen mineralization. The study design allowed for direct comparison of how functionally distinct grasshopper populations mediate ecosystem function under variable environmental conditions.

Figure 2. The path diagram illustrates the statistically significant ($p < 0.05$) direct and indirect effects of vegetation-only treatments and the average herbivory treatment on key ecosystem response variables. Arrow widths are scaled to represent effect sizes, with positive effects shown as solid lines and negative effects as dashed lines. The values next to each arrow indicate the effect size. To simplify the visualization, historical ecosystem variables (i.e., the Year 1 baseline metrics) are shown in gray, but were only included in the path diagram when their effect size was the largest for that respective model. A full path diagram with all significant paths regardless of the effect size can be found in Fig. S3. SEM results were visualized using the DiagrammeR package (v.1.0.11).

Figure 3. The path diagram illustrates the statistically significant ($p < 0.05$) direct and indirect effects of different forms of herbivore plasticity on key ecosystem response variables. All paths are derived from a single SEM model; however, the values shown here reflect the difference in effect size between the two herbivore treatments relative to vegetation-only controls (i.e., the net difference in effect size between the herbivore treatment and the vegetation treatment). As in Figure 2, arrow widths are scaled to represent effect sizes, with positive effects shown as solid lines, negative effects show as dashed lines, and the value next to each arrow indicates the effect size. Historical ecosystem variables (i.e., the Year 1 baseline metrics) were only included in the path diagram when their effect size was the largest for that respective model, shown in gray nodes and black arrows.

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References

Allendorf, F.W., Hohenlohe, P.A. & Luikart, G. (2010). Genomics and the future of conservation genetics. *Nat Rev Genet*, 11, 697–709.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., *et al.* (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science (1979)*, 349, 528–532.

Angelo Canty, B. & Ripley, D. (2024). boot: Bootstrap R (S-Plus) Functions.

Baker, M.S., Dobson, A.M., Sommer, N.R., Schmitz, O.J. & Trussell, G.C. (2025). Local thermal extremes shape the nature of herbivore plasticity that controls plant communities. *In review*.

Barbero-Palacios, L., Barrio, I.C., García Criado, M., Kater, I., Petit Bon, M., Kolari, T.H.M., *et al.* (2024). Herbivore diversity effects on Arctic tundra ecosystems: a systematic review. *Environ Evid*, 13, 1–21.

Bardgett, R.D. & Wardle, D.A. (2010). *Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change*. Oxford University Press.

Barley, J.M., Cheng, B.S., Sasaki, M., Gignoux-Wolfsohn, S., Hays, C.G., Putnam, A.B., *et al.* (2021). Limited plasticity in thermally tolerant ectotherm populations: Evidence for a trade-off. *Proceedings of the Royal Society B: Biological Sciences*, 288.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw*, 67, 1–48.

Beckerman, A.P. (2002). The distribution of Melanoplus femurrubrum: Fear and freezing in Connecticut. *Oikos*, 99, 131–140.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., Calvo Anta, R. DE, *et al.* (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, 20, 127–159.

Bomar, C.R. (2001). Comparison of grasshopper (Orthoptera: Acrididae) communities on remnant and reconstructed prairies in western Wisconsin. *J Orthoptera Res*, 10, 105–112.

Bonan, G.B., Hartman, M.D., Parton, W.J. & Wieder, W.R. (2013). Evaluating litter decomposition in earth system models with long-term litterbag experiments: An example using the Community Land Model version 4 (CLM4). *Glob Chang Biol*, 19, 957–974.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., *et al.* (2008). Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett*, 11, 1316–1327.

Bradford, M.A., Keiser, A.D., Davies, C.A., Mersmann, C.A. & Strickland, M.S. (2013). Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochemistry*.

Bradford, M.A., Warren, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., *et al.* (2014). Climate fails to predict wood decomposition at regional scales. *Nature Climate Change 2014 4:7*, 4, 625–630.

Bradshaw, W.E. & Holzapfel, C.M. (2006). Evolutionary Response to Rapid Climate Change. *Science (1979)*, 312, 1477–1478.

Britton, N.L. & Brown, A. (1970). *An illustrated flora of the northern United States and Canada*. Dover Publications.

Capinera, J.L. (1987). Population ecology of rangeland grasshoppers. In: *Integrated pest management on rangeland: a shortgrass prairie perspective* (ed. Capiner, J.L.). Westview Press.
Chapin, F.S.I., Mattson, P., Vitousek, P.M. & Chapin, M.C. (2011). *Principles of terrestrial ecosystem ecology*. 2nd edn. Springer, New York.
Chapman, R.F. & Joern, A. (1991). *Biology of grasshoppers*. John Wiley & Sons.
Davison, A.C. & Hinkey, D.V. (1997). *Bootstrap Methods and Their Applications*. Cambridge University Press, Cambridge.
Dostálek, T., Rokaya, M.B. & Münzbergová, Z. (2020). Plant palatability and trait responses to experimental warming. *Sci Rep*, 10.
Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., *et al.* (2000). Biological stoichiometry from genes to ecosystems. *Ecol Lett*, 3, 540–550.
Evangelista, C., Lecerf, A., Britton, J.R. & Cucherousset, J. (2017). Resource composition mediates the effects of intraspecific variability in nutrient recycling on ecosystem processes. *Oikos*, 126, 1439–1450.
Fernández-Martínez, M., Sardans, J., Musavi, T., Migliavacca, M., Iturrate-Garcia, M., Scholes, R.J., *et al.* (2020). The role of climate, foliar stoichiometry and plant diversity on ecosystem carbon balance. *Glob Chang Biol*, 26, 7067–7078.
Fierer, N. & Schimel, J.P. (2003). A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal*, 67, 798–805.
Flanagan, S.P., Forester, B.R., Latch, E.K., Aitken, S.N. & Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evol Appl*, 11, 1035–1052.
Folk, R.L. (1966). A review of grain-size parameters. *Sedimentology*, 6, 73–93.
Foster, D.R. (1992). Land-Use History (1730-1990) and Vegetation Dynamics in Central New England, USA. *Journal of Ecology*, 80, 753–771.
Govaert, L., Hendry, A.P., Fattahi, F. & Möst, M. (2024). Quantifying interspecific and intraspecific diversity effects on ecosystem functioning. *Ecology*, 105.
Grandy, A.S., Strickland, M.S., Lauber, C.L., Bradford, M.A. & Fierer, N. (2009). The influence of microbial communities, management, and soil texture on soil organic matter chemistry. *Geoderma*, 150, 278–286.
Hartig, F. (2024). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
Hawlena, D. & Schmitz, O.J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences*, 107, 15503–15507.
Hawlena, D., Strickland, M.S., Bradford, M.A. & Schmitz, O.J. (2012). Fear of Predation Slows Plant-Litter Decomposition. *Science (1979)*, 366, 1434–1438.
Helfer, J.R.. (1987). *How to know the grasshoppers, crickets, cockroaches, and their allies*. Dover Publications.
Hood-Nowotny, R., Umana, N.H.-N., Inselbacher, E., Oswald- Lachouani, P. & Wanek, W. (2010). Alternative Methods for Measuring Inorganic, Organic, and Total Dissolved Nitrogen in Soil. *Soil Science Society of America Journal*, 74, 1018–1027.

Huang, Q., Sauer, J.R. & Dubayah, R.O. (2017). Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors. *Glob Chang Biol*, 23, 3610–3622.

Joern, A., Provin, T. & Behmer, S.T. (2012). Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology*, 93, 1002–1015.

Kuglerová, M., Skuhrovec, J. & Münzbergová, Z. (2019). Relative importance of drought, soil quality, and plant species in determining the strength of plant–herbivore interactions. *Ecol Entomol*, 44, 665–677.

Kulmatiski, A., Beard, K.H. & Stark, J.M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, 43, 868–876.

Lefcheck, J., Byrnes, J. & Grace, J. (2024). Package 'piecewiseSEM''.'

Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol Evol*, 7, 573–579.

Lynn, J.S. & Fridley, J.D. (2019). Geographic patterns of plant-herbivore interactions are driven by soil fertility. *Journal of Plant Ecology*, 12, 653–661.

Lynn, J.S., Fridley, J.D. & Vandvik, V. (2023). More than what they eat: uncoupled biophysical constraints underlie geographic patterns of herbivory. *Ecography*.

Marczak, L.B., Wieogonekski, K., Denno, R.F. & Pennings, S.C. (2013). Importance of local vs. geographic variation in salt marsh plant quality for arthropod herbivore communities. *Journal of Ecology*, 101, 1169–1182.

Maron, J.L., Baer, K.C. & Angert, A.L. (2014). Disentangling the drivers of context-dependent plant-animal interactions. *Journal of Ecology*, 102, 1485–1496.

Massad, T.J., Rangel Nascimento, A., Fernando Campos Moreno, D., Simbaña, W., Garcia Lopez, H., Sulca, L., *et al.* (2024). Variation in the strength of local and regional determinants of herbivory across the Neotropics. *Oikos*, 2024.

Melles, S.J., Fortin, M.J., Lindsay, K. & Badzinski, D. (2011). Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Glob Chang Biol*, 17, 17–31.

Miller, J.R.B., Ament, J.M. & Schmitz, O.J. (2014). Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, 83, 214–222.

Nelson, D.W. & Sommers, L.E. (1996). Total carbon, organic carbon, and organic matter. In: *Methods of Soil Analysis* (eds. Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., et al.). Soil Science Society of America, Madison, WI, pp. 961–1010.

Oregon State University. (2002). PRISM Climate Group. *http://www.prism.oregonstate.edu*.

Pahlavan-Rad, M.R. & Akbarimoghaddam, A. (2018). Spatial variability of soil texture fractions and pH in a flood plain (case study from eastern Iran). *Catena (Amst)*, 160, 275–281.

Parsons, S.M.A. & Joern, A. (2014). Life history traits associated with body size covary along a latitudinal gradient in a generalist grasshopper. *Oecologia*, 174, 379–391.

Pennings, S.C., Ho, C.-K., Salgado, C.S., Więski, K., Davé, N., Kunza, A.E., *et al.* (2009). Latitudinal Variation in Herbivore Pressure in Atlantic Coast Salt Marshes, 90, 183–195.

Pennings, S.C. & Silliman, B.R. (2005). Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology*, 86, 2310–2319.

Pichon, N.A., Cappelli, S.L. & Allan, E. (2022). Intraspecific trait changes have large impacts on community functional composition but do not affect ecosystem function. *Journal of Ecology*, 110, 644–658.

Pringle, R.M., Abraham, J.O., Anderson, T.M., Coverdale, T.C., Davies, A.B., Dutton, C.L., *et al.* (2023). Impacts of large herbivores on terrestrial ecosystems. *Current Biology*, 33, R584–R610.

Raffard, A., Cucherousset, J., Santoul, F., Di Gesu, L. & Blanchet, S. (2023). Climate and intraspecific variation in a consumer species drive ecosystem multifunctionality. *Oikos*, 2023.

Raffard, A., Santoul, F., Cucherousset, J. & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biological Reviews*, 94, 648–661.

Raubenheimer, D., Simpson, S.J. & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Funct Ecol*, 23, 4–16.

Reed, T.E., Robin, S.W., Schindler, D.E., Hard, J.J. & Kinnison, M.T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3391–3400.

Reeves, D.W. (1997). The role of soil organic matter in maintaining soil quality in continuous cropping systems. *Soil Tillage Res*, 43, 131–167.

Reichstein, M., Bahn, M., Mahecha, M.D., Kattge, J. & Baldocchi, D.D. (2014). Linking plant and ecosystem functional biogeography. *Proc Natl Acad Sci U S A*, 111, 13697–13702.

Robertson, G.P., Gross, K.L., Hamilton, S.K., Landis, D.A., Schmidt, T.M., Snapp, S.S., *et al.* (2014). Farming for ecosystem services: An ecological approach to production agriculture. *Bioscience*, 64, 404–415.

Des Roches, S., Pendleton, L.H., Shapiro, B. & Palkovacs, E.P. (2021). Conserving intraspecific variation for nature's contributions to people. *Nature Ecology & Evolution 2021 5:5*, 5, 574–582.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., *et al.* (2018). The ecological importance of intraspecific variation. *Nat Ecol Evol*, 2, 57–64.

Romig, D.E., Garlynd, M.J., Harris, R.F. & McSweeney, K. (1995). How farmers assess soil health and quality. *Journal of Soil Water Conservation*, 50, 229–236.

Rosenblatt, A.E., Crowley, B.T. & Schmitz, O.J. (2016). Linking trophic interactions to plasticity in thermal sensitivity of geographically separated populations of a herbivore. *Evol Ecol*, 30, 649–661.

Rosenblatt, A.E., Wyatt, K.S. & Schmitz, O.J. (2019). Will like replace like? Linking thermal performance to ecological function across predator and herbivore populations. *Ecology*, 1000, 1–12.

Rothley, K.D., Schmitz, O.J. & Cohon, J.L. (1997). Foraging to balance conflicting demands: Novel insights from grasshoppers under predation risk. *Behavioral Ecology*, 8, 551–559.

Schimel, D., Stephens, B.B. & Fisher, J.B. (2015). Effect of increasing CO2 on the terrestrial carbon cycle. *Proc Natl Acad Sci U S A*, 112, 436–441.

Schlesinger, W. (2005). *Biogeochemistry*. Elsevier.

Schmitz, O.J. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett*, 6, 156–163.
Schmitz, O.J. (2004). From mesocosms to the field: the role and value of cage experiments in understanding top-down effects in ecosystems. In: *Insects and Ecosystem Function*. Springer-Verlag, Berlin, pp. 277–302.
Schmitz, O.J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, 87, 1432–1437.
Schmitz, O.J. (2008a). Effects of predator hunting mode on grassland ecosystem function. *Science (1979)*, 319, 952–954.
Schmitz, O.J. (2008b). Herbivory from individuals to ecosystems. *Annu Rev Ecol Evol Syst*, 39, 133–152.
Schmitz, O.J. (2010). *Resolving ecosystem complexity*. Princeton University Press, Princeton.
Schmitz, O.J. (2017). Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. *F1000Res*, 6, 1767.
Schmitz, O.J., Hawlena, D. & Trussell, G.C. (2010). Predator control of ecosystem nutrient dynamics. *Ecol Lett*, 13, 1199–1209.
Schmitz, O.J. & Trussell, G.C. (2016). Multiple stressors, state-dependence and predation risk — foraging trade-offs: toward a modern concept of trait-mediated indirect effects in communities and ecosystems. *Curr Opin Behav Sci*, 12, 6–11.
Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M., *et al.* (2018). Animals and the zoogeochemistry of the carbon cycle. *Science (1979)*, 362.
Sims, G.K., Ellsworth, T.R. & Mulvaney, R.L. (1995). Microscale determination of inorganic nitrogen in water and soil extracts. *Commun Soil Sci Plant Anal*, 26, 303–316.
Sims, T.J. & Eckert, D. (2011). Recommended soil pH and lime requirement tests. In: *Recommended soil testing procedures for the northeastern United States*. The Northeast Coordinating Committee for Soil Testing.
Sitters, J., Kimuyu, D.M., Young, T.P., Claeys, P. & Olde Venterink, H. (2020). Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. *Nat Sustain*, 3, 360–366.
Smith, V.C. & Bradford, M.A. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. *Applied Soil Ecology*, 24, 197–203.
Sommer, N.R., Alshwairikh, Y.A., Arietta, A.Z.A., Skelly, D.K. & Buchkowski, R.W. (2023). Prey metabolic responses to predators depend on predator hunting mode and prey antipredator defenses. *Oikos*, 2023, 1–11.
Sommer, N.R., Dobson, A.M., Baker, M.S., Trussell, G.C. & Schmitz, O.J. (2025). Ecosystem effects of predators are amplified across generations through prey behavioral plasticity. *In review*.
Sommer, N.R. & Schmitz, O.J. (2020). Differences in prey personality mediate trophic cascades. *Ecol Evol*, 10, 9538–9551.
Sommer, N.R., Schmitz, O.J. & Trussell, G.C. (2024). Adaptive phenotypic plasticity under global change. *Authorea*.

Strickland, M.S., Hawlena, D., Reese, A., Bradford, M.A. & Schmitz, O.J. (2013). Trophic cascade alters ecosystem carbon exchange. *Proc Natl Acad Sci U S A*, 110, 11035–11038.

Uvarov, B. (1977). *Grasshoppers and locusts. A handbook of general acridology. Volume 2. Behaviour, ecology, biogeography, population dynamics.* Centre for Overseas Pest Research, London.

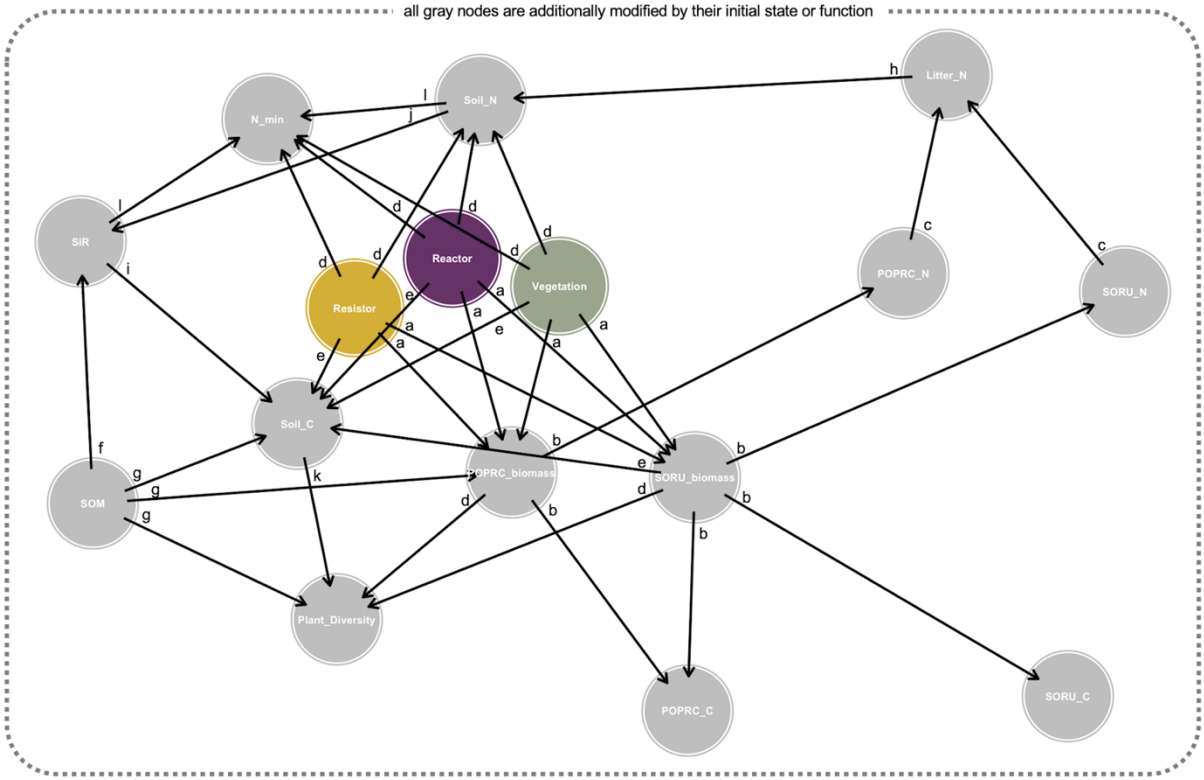
Weisberg, F.J.S. (2019). An R Companion to Applied Regression.

Williams, J.E. & Blois, J.L. (2018). Range shifts in response to past and future climate change: Can climate velocities and species' dispersal capabilities explain variation in mammalian range shifts? *J Biogeogr*, 45, 2175–2189.

Xia, Q., Rufty, T. & Shi, W. (2020). Soil microbial diversity and composition: Links to soil texture and associated properties. *Soil Biol Biochem*, 149, 107953.

Supporting Information for Sommer *et al.* Herbivore population differences rival geographic and biophysical variation in structuring ecosystem function

Figure S1. Directed acyclic graph of hypothesized pathways for herbivore and vegetation effects tested in the structural equation model. All paths were grounded in prior empirical work, signified by the letter from the originating node.



[a]Baker et al. in review; Rosenblatt et al. 2019; Schmitz 2003, 2008; [b]Hawlena & Schmitz 2010; Rothley et al. 1997; Schmitz et al. 2016; [c]Hawlena et al. 2012; Schmitz 2006; [d]Bradford et al. 2013; Schmitz 2006; [e]Fernández-Martínez et al. 2020; Schmitz 2006; Schmitz et al. 2017; Strickland et al.

2013; [f]Bradford et al. 2013; Grandy et al. 2009; [g]Grandy et al. 2009; Reeves 1997; [h]Smith & Bradford 2003; [i]Tao et al. 2023; [j]Dong et al. 2022; [k]Anacker et al. 2021; Chen et al. 2018; [l]Liu et al. 2016; Xu et al. 2024

Figure S2. Bulk density and pH across all five sites, measured in Year 1. Site abbreviations correspond to the map in Figure 1 (main text).

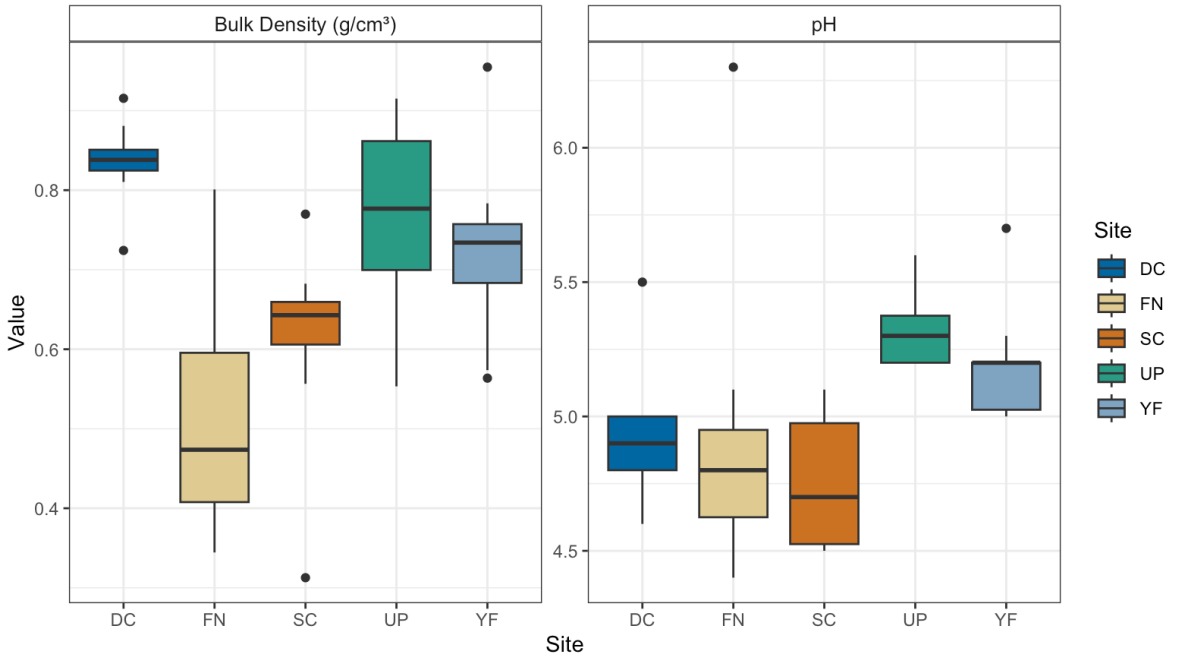


Figure S3. Soil texture components measured across all five sites in Year 1. Site abbreviations correspond to the map in Figure 1 (main text).

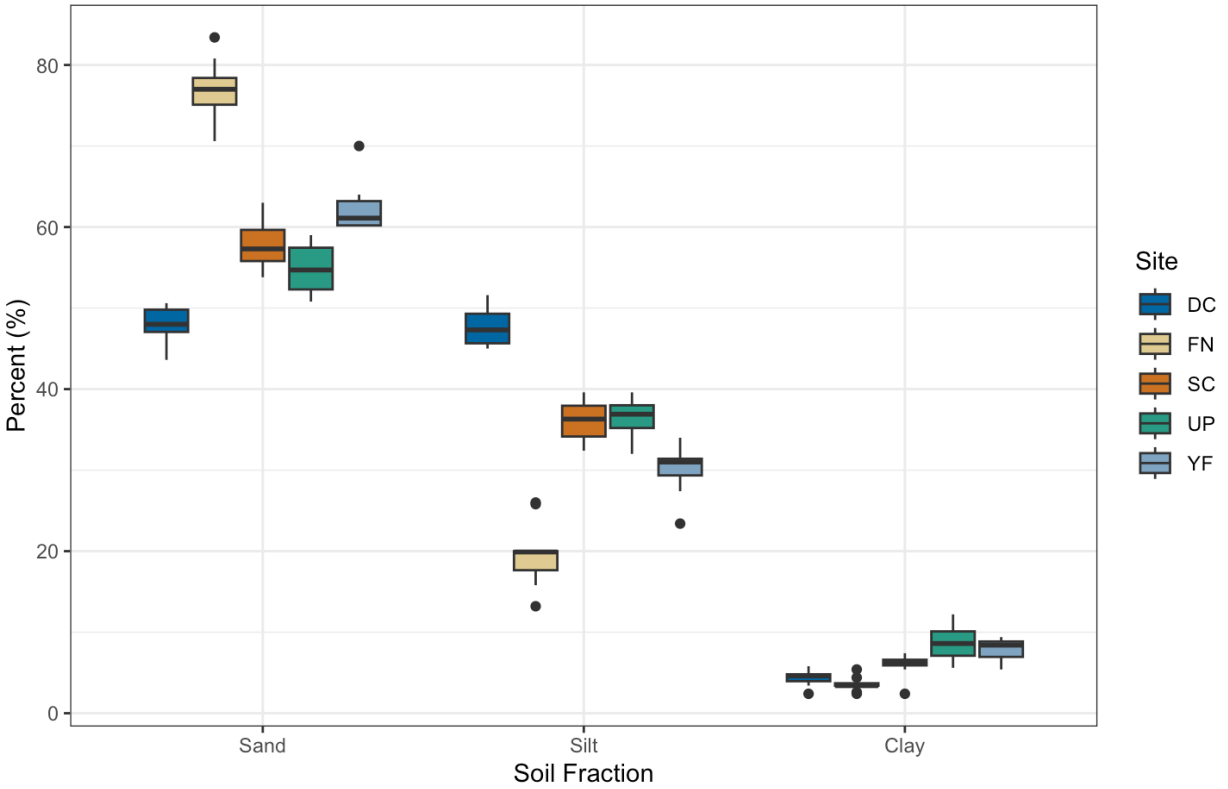
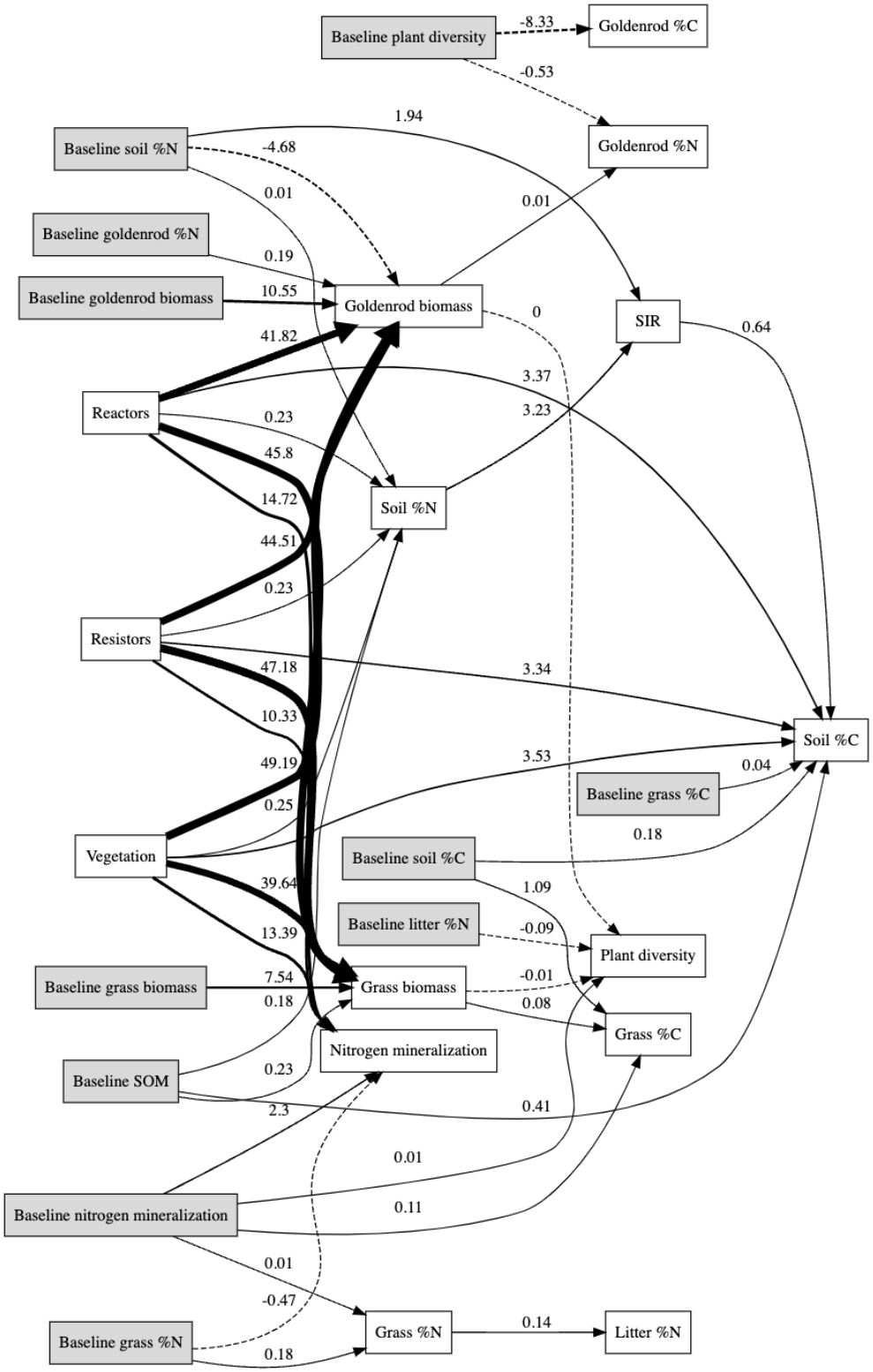


Figure S4. Full SEM; includes all statistically significant paths [$p < 0.05$])



References

Anacker, B.L., Seastedt, T.R., Halward, T.M. & Lezberg, A.L. (2021). Soil carbon and plant richness relationships differ among grassland types, disturbance history and plant functional groups. *Oecologia*, 196, 1153–1166.

Baker, M.S., Dobson, A.M., Sommer, N.R., Schmitz, O.J. & Trussell, G.C. (2025). Local thermal extremes shape the nature of herbivore plasticity that controls plant communities. *In review*.

Bradford, M.A., Keiser, A.D., Davies, C.A., Mersmann, C.A. & Strickland, M.S. (2013). Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochemistry*.

Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., *et al.* (2018). Plant diversity enhances productivity and soil carbon storage. *Proc Natl Acad Sci U S A*, 115, 4027–4032.

Dong, L., Berg, B., Gu, W., Wang, Z. & Sun, T. (2022). Effects of different forms of nitrogen addition on microbial extracellular enzyme activity in temperate grassland soil. *Ecol Process*, 11, 1–8.

Fernández-Martínez, M., Sardans, J., Musavi, T., Migliavacca, M., Iturrate-Garcia, M., Scholes, R.J., *et al.* (2020). The role of climate, foliar stoichiometry and plant diversity on ecosystem carbon balance. *Glob Chang Biol*, 26, 7067–7078.

Grandy, A.S., Strickland, M.S., Lauber, C.L., Bradford, M.A. & Fierer, N. (2009). The influence of microbial communities, management, and soil texture on soil organic matter chemistry. *Geoderma*, 150, 278–286.

Hawlena, D. & Schmitz, O.J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences*, 107, 15503–15507.

Hawlena, D., Strickland, M.S., Bradford, M.A. & Schmitz, O.J. (2012). Fear of Predation Slows Plant-Litter Decomposition. *Science (1979)*, 366, 1434–1438.

Liu, Q., Qiao, N., Xu, X., Xin, X., Han, J.Y., Tian, Y., *et al.* (2016). Nitrogen acquisition by plants and microorganisms in a temperate grassland. *Sci Rep*, 6, 1–10.

Reeves, D.W. (1997). The role of soil organic matter in maintaining soil quality in continuous cropping systems. *Soil Tillage Res*, 43, 131–167.

Rosenblatt, A.E., Wyatt, K.S. & Schmitz, O.J. (2019). Will like replace like? Linking thermal performance to ecological function across predator and herbivore populations. *Ecology*, 1000, 1–12.

Rothley, K.D., Schmitz, O.J. & Cohon, J.L. (1997). Foraging to balance conflicting demands: Novel insights from grasshoppers under predation risk. *Behavioral Ecology*, 8, 551–559.

Schmitz, O.J. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett*, 6, 156–163.

Schmitz, O.J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, 87, 1432–1437.

Schmitz, O.J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science (1979)*, 319, 952–954.

Schmitz, O.J., Buchkowski, R.W., Smith, J.R., Telthorst, M. & Rosenblatt, A.E. (2017). Predator community composition is linked to soil carbon retention across a human land use gradient. *Ecology*, 98, 1256–1265.

Schmitz, O.J., Rosenblatt, A.E. & Smylie, M. (2016). Temperature dependence of predation stress and the nutritional ecology of a generalist herbivore. *Ecology*, 97, 3119–3130.

Smith, V.C. & Bradford, M.A. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. *Applied Soil Ecology*, 24, 197–203.
Strickland, M.S., Hawlena, D., Reese, A., Bradford, M.A. & Schmitz, O.J. (2013). Trophic cascade alters ecosystem carbon exchange. *Proc Natl Acad Sci U S A*, 110, 11035–11038.
Tao, F., Huang, Y., Hungate, B.A., Manzoni, S., Frey, S.D., Schmidt, M.W.I., *et al.* (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, 618, 981–985.
Xu, J., Wang, Y., Zhang, Y., Li, Q., Du, B., Asitaiken, J.L.H.T., *et al.* (2024). Effect of nitrogen addition on soil net nitrogen mineralization in topsoil and subsoil regulated by soil microbial properties and mineral protection: Evidence from a long-term grassland experiment. *Science of The Total Environment*, 947, 174686.