SOIL NUTRIENT ADDITIONS SHIFT ORTHOPTERAN HERBIVORY AND INVERTEBRATE COMMUNITY COMPOSITION

by

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THESIS ABSTRACT

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Anthropogenic alterations to global pools of nitrogen and phosphorus are driving declines in plant diversity across grasslands. As such, concern over biodiversity loss has precipitated a host of studies investigating how vertebrate herbivores affect the functioning of these nutrient enriched plant communities. However, there remains a dearth of empirical work cataloging (1) how *invertebrate* herbivores affect these communities, and (2) how invertebrate trophic structure responds to such communities. Here, I asked how long-term nitrogen (N) and phosphorus (P) enrichment affects Orthopteran herbivory and invertebrate community composition in a mountain meadow. First, I measured herbivory of two focal species—*Bromus carinatus*, a grass, and *Lupinus latifolius*, a legume—belonging to functional groups I hypothesized would increase and decrease, respectively, with nutrient enrichment. Then, I investigated whether nutrient induced changes in plant functional groups and habitat volume would change invertebrate trophic group abundances, including pollen/nectar-feeding herbivores, leaf-chewing herbivores, and parasitoids. I found that with both N and P additions, herbivory of *B. carinatus* increased, while herbivory of *L. latifolius* decreased, but only with N addition. Despite N quite drastically altering the plant community, it only changed one invertebrate

trophic group surveyed, increasing nectar/pollen-feeding herbivore abundance. By increasing grass abundance, P increased both (non-Orthopteran) leaf-chewing herbivore and parasitoid abundances. These findings suggest that (1) in systems with an abundant grasshopper community, plant community response(s) to soil nutrient enrichment is likely influenced by its herbivory, and (2) in diverse, natural systems, invertebrate community response to global change is complex because trophic groups may respond differently to plant community change.

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"Perhaps it brings to mind people who, to put it another way, entered the world of insects and were, in turn, entered by it, who at times were swallowed up by it and who at other times found their bearings inside it, such that the normal scale of existence—the standard hierarchies of being… was no longer a basis for either action or meaning, and such that the enormities of the circumstances that bound their lives could assume another proportion and a different place in their world, such that the world itself could become immeasurably larger and unconfining."

~ Hugh Raffles

For Gianna

&

Emilia P. Nartshuk, Chloropidae goddess

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I. INTRODUCTION

Increases in limiting soil nutrient availability can significantly alter food webs (Gruner et al., 2008; Lemoine et al., 2014; Prather et al., 2021). In grassland systems undergoing chronic soil nutrient enrichment, plant diversity typically declines as interspecific competition becomes primarily driven by competition for light access (Harpole & Tilman, 2007). As a result, resource-conservative species (i.e., forbs and legumes) are lost, resource-acquisitive species (i.e., grasses) are gained, and previously established species are subsequently excluded (Rajaniemi, 2002; Hautier, 2009; Borer et al., 2014; Harpole et al., 2016; Seabloom et al., 2021; Muehleisen et al., In review). Aboveground plant (habitat) volume and foliar nutrients often increase as well (Harpole et al., 2016; Zhao et al., 2017; Borer et al., 2020). Importantly, by increasing light availability, large mammalian herbivores can mitigate this diversity loss (Borer et al., 2014; Anderson et al., 2018; Sitters et al., 2020). However, despite evidence indicating that invertebrate herbivores can also, at times, exert significant pressure on plant communities, their responses to changing soil nutrients, apart from a few studies, have been overlooked in natural systems (Crawley, 1989; Belovsky & Slade, 2000; Haddad et al., 2000; Stein et al., 2010; Agrawal et al., 2012; La Pierre & Smith, 2016; Koerner et al., 2018; Andrew et al., 2022; Ebeling et al., 2022). Further, whole invertebrate communities—the composition of which oftentimes shifts in response to changing plant community composition and habitat volume—have also been understudied (Root, 1973; Koricheva et al., 2000; Haddad et al., 2009; Moreira et al., 2016). Understanding the relative effects of (1) invertebrate herbivory on nutrient enriched plant communities, and (2) nutrient enrichment on invertebrate community composition, will improve our

understanding of how the interaction of top-down and bottom-up processes effects primary producers and how food webs are restructured (or not) by a chronic global change driver.

Increased availability of limiting soil nutrients such as nitrogen (N) and phosphorus (P) may alter herbivore pressure on plant communities through multiple, not necessarily mutually exclusive, pathways. First, by changing plant community composition, nutrients modify host plant availability and distribution; this change may influence specialist herbivore recruitment as individuals track their hosts and generalist herbivore behavior as individuals respond to changing availability of multiple, palatable hosts, each offering different nutritional benefits (Crawley, 1989; Koricheva et al., 2000; Otway et al., 2005). Further, as limiting dietary N is often important for herbivore survival, developmental rate, growth rate, and reproduction, individuals may differentiate and preferentially feed upon higher quality, N enriched plants; as a result, they may also consume less to meet their nutritional needs (White, 1984; Fox et al., 1990; Prudic et al., 2005; Chen et al., 2004; Chen et al., 2008; Chen & Ruberson, 2008; Chen et al., 2010; Loaiza et al., 2010). Complicating this, however, is that some plant species, given greater access to limiting nutrients, may increase their tolerance to herbivory (Cronin et al. 2010). Finally, because habitat complexity influences invertebrate thermoregulation, mating behavior, and predator abundance and distribution, substantive change(s) to habitat may also alter herbivore pressure via shifting their abundances, behaviors, and/or feeding rates (Pimentel, 1961; Root, 1973; Price et al., 1980; Andow, 1991; Bernays, 1998; Siemann, 1998; Frazier et al., 2006; Pincebourde & Casas, 2019). Total, community level herbivory will therefore depend upon the balance between (1) the

number of herbivores supported by the plant community, and (2) per capita consumption, both of which are influenced by various, mediating factors (e.g., predation risk, plant defense mechanisms, intraspecific interactions).

Invertebrate trophic structure may change in response to nutrient enrichment. Moreover, it is likely that the response of one trophic group is contingent upon the response(s) of another (Root, 1973; Kareiva, 1983). For one, all herbivorous trophic groups may respond to predator and parasitoid pressure. Nectar/pollen-eating herbivores may also respond to plant community composition as they track floral resources (Wackers et al., 2007; Bluthgen & Klein, 2011; Galliot et al., 2017; Kaluza et al., 2017). Leaf-chewing, sap-sucking, and gall-forming herbivores may respond to plant community composition, foliar nutrients, and/or habitat volume as they track host plants and/or seek habitat prime for thermoregulation, predator avoidance, etc. (Pitt, 1999; Haddad et al., 2000; Ritchie, 2000; Adler & Bronstein, 2004; Otway et al., 2005; Lemoine et al., 2014; Lind et al., 2017). Predator and parasitoid abundances are often contingent upon prey and host availability, respectively, in addition to other benefits that may be associated with habitat. For example, in the case of spiders, vegetational complexity is often important for the construction of webs and for thermoregulation (Jones & Reichert, 2008; Mcnett & Rypstra, 2008). As they track hosts, parasitoids are likely responding to plant volatiles, produced in response to herbivore pressure, or constitutively (in the absence of herbivory) (Russell, 1989; Godfray, 1994; Waschke et al., 2013). Thus, predators and parasitoids may respond to prey/host abundance(s), plant community composition, and/or habitat volume (Root, 1973; Andow, 1991; Van der Putten et al., 2001; Langellotto & Denno, 2004; Randlkofer et al., 2010; Prather &

Kaspari, 2019; Welti et al., 2020; Prather et al., 2021). Cataloging how each guild responds to nutrient enriched plant communities is critical (1) for understanding the determinants of food web structure in natural systems, and (2) for understanding how/when plant diversity loss propagates through food webs (Haddad et al. 2009).

To test these cascading and interactive effects, mountain meadows are an ideal system. First, these systems are of high conservation value, so understanding their nutrient-plant-invertebrate interactions are important for informing conservation and restoration into the future. In the Pacific Northwest, the few and relatively small mountain meadows persisting today—comprising less than 5% of Oregon's western Cascades—contribute disproportionately to the diversity of the region's mostly forested landscape (Pfeiffer, 2012). Second, they can support an unusually high level of invertebrate herbivore activity (Ebeling et al., 2022). For example, in a study of invertebrate leaf damage in 27 grasslands around the globe, leaf-chewing invertebrates in the Bunchgrass Ridge meadow complex, the focal study system of this work, consumed at least two-fold more leaf tissue than leaf-chewers in any of the other 26 sites globally distributed sites (Ebeling et al., 2022). That these abundant and impactful invertebrate herbivores—and the invertebrate community as a whole—have been overlooked in a system of high conservation value warrants attention. Further, given the impressive amount of leaf tissue invertebrate herbivores have been observed consuming in these meadows, they likely play a key role in ecosystem functioning (Belovsky & Slade, 2000; Hartley & Jones, 2008; Weisser & Siemann, 2013; Nitschke et al., 2015; Belovsky & Slade, 2018).

Here, I explore how top-down (Orthopteran herbivory) and bottom-up (increased soil N and P availability) processes interact to influence a mountain meadow plant community, and how nutrient-induced changes to the plant community affect invertebrate community composition. Because I anticipated appreciable change in plant community composition and habitat volume, I hypothesized that herbivore pressure and invertebrate trophic group abundances would change significantly. Using a grass and a legume as focal species to investigate herbivory by abundant generalists, Orthoptera (Acrididae & Tettigonidae), I started with baseline hypotheses informed by likely changes in plant functional group abundances: because N would likely increase grass and decrease legume abundances, it would increase per capita herbivory of grasses and decrease per capita herbivory of legumes; since P would likely increase grasses while having no significant effect on legume abundance, per capita herbivory of grasses would increase and per capita herbivory of legumes would either decrease as more grass is consumed or not change (Tognetti et al., 2021). Per capita herbivory, however, will not only depend on changes in host plant availability, but also on changes in foliar nutrients and habitat volume. Net herbivory will depend on per capita herbivory and Orthoptera density. For the invertebrate community, since there are no prior data cataloging invertebrates at the meadow studied here, I only anticipated that there would be a shift in relative herbivore, predator, and parasitoid trophic groups given anticipated plant community change. I tested these hypotheses in a mountain meadow at Bunchgrass Ridge, located in the Cascade Range of western Oregon.

II. METHODS

Study Area

Bunchgrass Ridge is a gently sloping, high elevation plateau (~1350 m) in the Cascade Range of western Oregon (44°17'N, 121°57'W). Flanked by two lateral moraines on its northern and southern edges, it was sculpted by glaciers during the Pleistocene (Halpern et al., 2005). Soil profiles across the site capture traces of glacially derived cobbles, stones, and boulders in the deep (>170 cm), well-drained, and fine to very fine sandy loam. Soils also indicate that meadow vegetation has been present at Bunchgrass for centuries—possibly millennia (Halpern et al., 2005). Climate is characterized by warm, dry summers and cool, wet winters. Given the elevation, precipitation (>1000 cm) is generally in the form of snowfall, the snowpack of which can persist into late May (Halpern et al., 2005). Despite the significant volume of snowpack, soil moisture throughout summer months is often low (Pfeiffer, 2012).

In 2021, thirty-six plant species were detected within the study area (Table S1). Dominant species include, in order of decreasing dominance, *Carex pensylvanica* (sedge), *Phlox diffusa* (forb), *Festuca idahoensis* (grass), *Lupinus latifolius* (legume), and *Bromus carinatus* (grass). Dominant invertebrate families collected within the study area include, in decreasing order, Cicadellidae, Chloropidae, and Melyridae. Orthoptera families include Acrididae (grasshoppers) and Tettigoniidae (katydids), with *Melanoplus* spp. (Acrididae) being the most abundant genus.

As a Special Habitat Area for wildlife (Butruille, 1990) and a high priority target for restoration (Friesen et al., 2006), the Bunchgrass meadow complex is notable for its contribution to biodiversity both locally and regionally (Pfeiffer, 2012). In addition to

supporting plants that cannot survive under the forest canopy, these small meadow patches promote an array of wildlife—such as deer, elk, gophers, birds, butterflies, bees, and other insects—benefitting from its resources (Butruille, 1990). However, due to ongoing conifer encroachment, its diversity is currently precarious (Halpern et al., 2010; Rice et al., 2012). Previous work at the site includes an extensive account of plant-pollinator interactions, concluding that flower and pollinator abundance and richness are reduced in small and isolated meadows (Pfeiffer, 2012). Thus, conifer encroachment endangers both pollinators and their floral resources at Bunchgrass. Other work details the role of the endemic western pocket gopher (*Thomomys mazama*) in shaping meadow dynamics; importantly, through its mounding activity, *T. mazama* creates patches of hyper-localized disturbance in which forbs and other disturbance-reliant plant species can establish (Case et al., 2013). Though beyond the scope of this project, it is quite possible that their mounding activity influences plant-invertebrate interactions in the meadow studied here (Ostrow et al., 2002).

Experiment Establishment & Design

In 2008, the Nutrient Network (NutNet) initiated a Long-Term Experimental Research project at Bunchgrass Ridge (Borer et al., 2013). Within one of its meadows, they established three replicated treatment blocks, each containing eight different nutrient enrichment treatments (3 blocks x 8 nutrient treatments = 24 experimental plots). Experimental plots measure 5 x 5 m, each subdivided into 4 2.5 x 2.5 m subplots. Treatments consist of the factorial combinations of nitrogen (N), phosphorous (P), and potassium and macronutrients (K), in addition to a control (Figure S1). They are

maintained via the annual application of N, P, and K, while the micronutrient mix was applied once at the start of the study to prevent toxicity of largely immobile micronutrients. Nutrient addition rates are the following: 10 g N m-2 yr-1 as timed-release urea, 10 g P m-2 yr-1 as triple superphosphate, 10 g K m-2 yr-1 as potassium sulfate and 100 g m-2 of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn). NutNet's annual plant community sampling is conducted within the same "core" subplot. For this study, all within-plot methods outlined below were conducted in either two or three of the four subplots within a plot (Figure S1).

Plant Community Surveys

Since its establishment, NutNet has monitored plant community response to soil nutrient additions at Bunchgrass by measuring percent cover. Annually at peak biomass (approximately July 15-31) and within the same 1-m^2 area of the core subplot, all plants are identified to species. Each plant species, bare ground, and litter are visually estimated to the nearest 1%. In 2021, I measured cover in two additional subplots to comprehensively capture the heterogeneity existing across plots; this was important since single subplots were not representative of the entire plot and since multiple surveys were conducted across multiple subplots—not just the core. Mean percent cover (abundance) across the three subplots was used in analyses.

To further describe the plant community, I took photos throughout the season to quantify habitat volume (Waite, 2017). Initially, photos were to be used in conjunction with biomass data collected via biomass strips; however, strips did not accurately reflect

plot-wide biomass since certain species (e.g., *L. latifolius*), though large and often abundant in a plot, would be missed in 0.2 m^2 strips due to either their small stems, their patchy distribution across space, or a combination of the two. Using a 55.88×71.12-cm white posterboard as a backdrop, one photo was taken at the same point within a plot weekly for five weeks. Photos were taken at a standardized height off the ground (0.3-m) and distance from the board (1-m). They were then edited and analyzed with ImageJ's Fiji processing package (Schindelin et al., 2012). The board area (3,974-cm^2) was converted into black (plant material) and white (background). From these images, percent plant material within the 3,974-cm^2 area was quantified. Subsequently, photos were divided five height classes and habitat volume was quantified for each; these values were then regrouped into two height classes, representing lower and upper "canopies," for analyses (0-23.71 cm and 23.72-71.12 cm; Figure S2).

Foliar C:N Analysis

Since Orthopteran herbivores work to fulfill a range of dietary needs, I measured soil nutrient enrichment's effects on foliar nutrients for two focal plant species: *Bromus carinatus*, a grass, and *Lupinus latifolius,* a legume. These species were chosen because of their relatively high abundances across plots and their memberships to different functional groups (as a grass, *B. carinatus* is more N-poor than the legume *L. latifolius*) expected to change in abundance with nutrient enrichment. Foliar nutrients were measured via leaf tissue carbon to nitrogen ratios (C:N).

To measure C:N, the middle-most leaf for 30 mature individuals of each species (or as near to 30 as available) were collected from each plot at peak biomass (July 29,

2021). If there were less than 30 individuals for a species, more than one leaf was collected from individual plants. Samples were stored for later analyses. In the laboratory, leaves were dried at 60°C for 48 hours. Each 30-leaf sample (n = 55) was homogenized using a mortar and pestle and a ball mill. Once the consistency of a fine powder, percent carbon and nitrogen were measured via dry combustion on an Elementar vario MACRO cube with the help of Oregon State University's Soil Health Lab. These values were used to calculate C:N.

Orthoptera Survey

To measure Orthoptera density within experimental plots, eight 0.1-m^2 metal rings were evenly distributed across half the plot. For five weeks (July 8 - August 4), the number of individuals in each ring was counted by tapping in rings with a pole while avoiding the disturbance of other rings. Counts in a plot's eight rings were used to estimate density (number/m^2) across the entirety of each 25-m^2 experimental plot (Onsager & Henry 1977; Delgado et al.1999; Torrusio et al. 2002). These weekly surveys took place during peak activity under standardized weather conditions(13:00 to 14:00 h).

Leaf Tissue Removal Survey

For the same focal species used in foliar C:N analysis outlined above (*B. carinatus* and *L. latifolius*), and following the same leaf collection protocol, a leaf tissue removal survey was conducted to quantify Orthopteran herbivory. In the laboratory, proportion of tissue removed was visually quantified for all leaves and categorized into one of six bins: 0%, 1-5%, 6-25%, 26-50%, 51-75%, and 76-100%. I assumed minimal

effects from tissue lost to greenfall and holes chewed by herbivores that may have expanded in size as the leaf grew. Plot-level leaf tissue removal (LTR) for each focal species was calculated by multiplying mean percent leaf tissue removed by the species plot-level abundance. Further, assuming that the majority of leaf tissue was removed by Orthoptera, I calculated focal species' LTR per capita by dividing plot-level LTR by plot-level Orthoptera density (number/25 m^2).

Invertebrate Community Survey

To capture invertebrate trophic group abundances not limited to Orthoptera, sweep samples (30-cm diameter nets) were collected weekly for four weeks (July 8-29) under standardized weather conditions. Eight total sweeps were taken from the center of the same two subplots between 13:00 and 14:00 h. Samples were frozen the same day of collection to be sorted and identified to family later in the laboratory (Table S2; Borror & White, 1970). Families were further classified by trophic group (detritivore, herbivore, parasitoid, predator) and herbivorous families by herbivory type (gall, leaf, mine, pollen/nectar, suck, other). Total abundance over the four weeks of collection was used in analyses. Importantly, this collection method regularly missed Orthoptera; as such, they were excluded from leaf-chewing herbivore totals. Thus, leaf-chewing herbivores refers to non-Orthopteran leaf chewers.

Statistical Analyses

All analyses were conducted using the statistical program R, version 2022.09.01+372 (R Core Team, 2021). For testing relationships of interest, generalized

linear mixed-effects models were fit to explain variation induced by soil nutrient enrichment across variables of interest. lme4 was used for C:N, 2021 plant species cover, LTR and LTR per capita, parasitoid and predator abundances, and long-term plant functional group cover (function lmer, lme4 package). glmmTMB was used for Orthoptera abundance (distribution = negative binomial), habitat volume (total and lower height class distribution = negative binomial; upper height class distribution = Poisson), and herbivore abundances (distribution = Poisson) (function glmmTMB, glmmTMB package, Brooks et al., 2017). When analyzing plant functional group abundance, *P. diffusa*, a dominant forb, and other forbs were treated separately since *P. diffusa* is functionally different than other forbs at Bunchgrass (chewing and sucking herbivores do not eat it; and structurally, its effect on habitat differs significantly). In models, N and P were included as explanatory variables and block was included as a random term. Across all analyses, there were two instances in which there was an interaction between N and P: (other) forb abundance (negative) and nectar/pollen-feeding herbivores (positive). Since both N and P significantly reduced (other) forb cover independently, they were treated independently in all subsequent analyses. For data collected over multiple weeks, models that did and did not include week as a random effect were tested. Week was only included in habitat volume models; it was not included for Orthoptera and invertebrate trophic group models because their total abundances over the field season were the primary interest. Since gall-forming and leaf-mining herbivore abundances were low throughout the season, they were not included in trophic group analyses. C:N was analyzed independently for each focal species and at the "community" level, meaning that the mean change in C:N was taken across focal species *B. carinatus* and *L. latifolius*.

This community level metric was used in Orthopteran herbivory structural equation models (detailed below) because community level C:N best predicted Orthoptera density, as opposed to herbivory. Further, K was excluded as an explanatory variable in all analyses since only N and P were nutrients of interest in this study.

I used structural equation modeling (SEM) to analyze the indirect effects of soil nutrient enrichment on (1) Orthopteran herbivory via nutrients' direct effects on grass and legume abundances, habitat volume, C:N, and Orthoptera density, and (2) on invertebrate trophic groups via nutrients' direct effects on plant functional group abundances, and each plant functional groups' subsequent effect on habitat volume (function sem, lavaan package, Rosseel, 2012). For both sets of SEMs, I used the mean for total habitat volume over all weeks. For invertebrate trophic groups, legume abundance was not included because it remained uninfluenced by N and P. I used the sum of herbivores, predators, and parasitoids collected within a plot over all weeks. I did not include direct paths from soil nutrients to herbivores and secondary consumers because treatments consisted of applying nutrients directly to the soil such that invertebrates never consumed them directly. Paths from each plant functional group's abundance to secondary consumers were included in models, however, because it is possible that their independent contributions to habitat are important for predator and parasitoid abundances (e.g., constitutive volatiles that attract parasitoids; Blamires et al., 2007; McNett & Rypstra, 2008; Wäschke et al., 2013).

Both bottom-up and top-down SEMs were tested to ensure that moving from lower trophic levels to higher trophic levels (i.e., nutrients → plants → herbivores → secondary consumers) was more appropriate than the reverse (i.e., secondary consumers

→ herbivores → plants). I assumed as much because, given prior findings, the effects of soil nutrient enrichment likely override all top-down effects on soil nutrients (Borer et al., 2014; La Pierre et al., 2015; La Pierre, 2016). After comparing models with Akaike's information criteria (AICc), this assumption proved true; thus, I used the bottom-up model for analyses. In constructing path diagrams, I used $p < 0.15$ as a threshold for the inclusion of an indirect effect for Orthopteran herbivory SEMs and $p < 0.10$ for the invertebrate trophic group SEM. I chose to use $p < 0.15$ as a cutoff for Orthopteran herbivory SEMs because more complex, linear mixed-effects models found nutrients to have significant effects otherwise missed with a SEM cutoff of 0.05.

III. RESULTS

Nitrogen Addition Shifts Orthopteran Herbivory & Nectar/Pollen-Feeding Herbivore Abundance

In N enriched plots, while there was no significant difference in focal species' abundances (*B. carinatus*, $F_{19} = 1.452$, $p = 0.242$, beta = 0.35; *L. latifolius*, $F_{19} = 1.125$, $p = 0.302$, beta = -0.33; Figure 1A), grasses as a functional group increased ($F_{21} = 13.787$, $p = 0.001$, beta = 0.80; Figure S3A). As anticipated, C:N for both species decreased (*B. carinatus*, $F_{19} = 5.215$, $p = 0.034$, beta = -0.91; *L. latifolius*, $F_{19} = 6.4184$, $p = 0.020$, beta = -0.89; Figure 1B). Total habitat volume and habitat volume for the lower height class decreased while there was no significant change to the upper height class (total, estimate = -0.613, SE = 0.179, $p < 0.001$, beta = -0.61; lower, estimate = -0.423. SE = 0.126, $p < 0.001$, beta = -0.42; upper, estimate = -0.326, SE = 0.167, $p = 0.052$, beta = -0.33; Figure 1C). Further, Orthoptera density increased in N enriched plots (estimate = 0.767, SE = 0.365, $p = 0.036$, beta = 0.77; Figure 1D). Despite focal species' abundances not changing, plot-level herbivory (LTR) of (grass) *B. carinatus* and (legume) *L. latifolius* increased ($F_{18} = 4.898$, $p = 0.040$, $\beta = 0.74$) and decreased ($F_{19} = 7.546$, $p = 0.013$, beta = -0.83), respectively (Figure 2A). Per capita herbivory (LTR per capita), however, only decreased for *L. latifolius* (*B. carinatus*, $F_{18} = 3.241$, $p = 0.088$, beta = 0.58; *L. latifolius*, $F_{19} = 4.913$, $p = 0.039$, beta = -0.70; Figure 2B). Via structural equation modeling (CFI = 1.0, RMSEA < 0.001), it became apparent that plot-level herbivory of *B. carinatus* increased via an increase in total grass abundance (Figure 2C: pathway A→D) and, via decreases in C:N and habitat volume, an increase in Orthoptera density (Figure 2C: pathways C→I→J and B→G→J); plot-level herbivory of *L. latifolius* decreased via an

increase in grass abundance and a decrease in habitat volume (Figure 2C: pathways A→E and B→H).

Although N enrichment increased grass (F_{21} = 13.787, p = 0.001, beta = 0.80), decreased sedge (F_{19} = 19.483, p < 0.001, beta = -1.30), and decreased (other) forb (F_{18} = 10.465, p = 0.005, beta = -0.26) abundances, it only changed one invertebrate trophic group, pollen/nectar-feeding herbivores (Figure S3). In N enriched plots, their abundance declined (estimate = -0.805, SE = 0.242, p < 0.001, beta = 0.83). Unfortunately, because the SEM did not fit invertebrate community data well (RMSEA > 0.1), indirect pathways between N and pollen/nectar-feeding herbivores could not be parsed out. Species that contributed most to increased grass abundance include *A. occidentale, A. repens, B. carinatus*, and *F. idahoensis*; *C. pensylvanicus* is the only sedge within the meadow; and species that contributed most to decreased forb abundance include *A. millefolium, C. umbellata*, and *P. procerus* (Figure S4). The long-term record captured an increase in grasses (F_{278} = 10.092, p = 0.002, beta = 0.27) and a decrease in sedge (*C. pensylvanica*) over time (F_{285} = 10.257, p = 0.001, beta = -0.30), while there was no significant difference in legumes nor forbs, including *P. diffusa* (legumes, F_{268} = 3.368, p = 0.068, beta = -0.21; forbs, F_{235} = 0.949, p = 0.331, beta = -0.10; *P. diffusa*, F_{143} = 0.944, p = 0.333, beta = -0.13; Figure S5).

Phosphorus Addition Shifts Orthopteran Herbivory & Leaf-Chewing Herbivore and Parasitoid Abundances

In P enriched plots, *B. carinatus* increased in abundance (F_{19} = 23.503, p < 0.001, beta = 1.39) while *L. latifolius* did not change (F_{19} = 0.2480, p = 0.624, beta = -0.15; Figure 3A). Total habitat volume did not change, but habitat volume for the lower height

class increased (total, estimate = 0.209, SE = 0.178, p = 0.238, beta = 0.41; lower, estimate = 0.334, SE = 0.127, p = 0.008; upper, estimate = 0.320, SE = 0.169, p = 0.058, beta = 0.32; Figure 3B). Further, despite there being no change in Orthoptera density (Figure 3C), both plot-level (F_{18} = 11.950, p = 0.003, beta = 1.17) and per capita (F_{18} = 17.441, p < 0.001, beta = 1.33) herbivory of *B. carinatus* increased (Figure 4A-B). Herbivory of *L. latifolius* did not change (plot-level, F_{18} = 0.817, p = 0.377, beta = -0.29; per capita, F_{19} = 1.175, p – 0.292, beta = -0.33; Figure 4A). Structural equation modeling (CFI = 1.0, RMSEA < 0.001) indicated that the increase in grasses alone explained more herbivory of *B. carinatus* (Figure 4C: pathway A→B).

P enrichment increased grass (F_{21} = 47.303, p < 0.001, beta = 1.49), decreased *P. diffusa* (F_{18} = 10.982, p = 0.039, beta = -0.02), and decreased (other) forb abundances (F_{18} = 4.956, p = 0.004, beta = -1.01; Figure 5A). For invertebrate trophic groups, it increased leaf-chewing herbivore (estimate = 0.482, SE = 0.216, p = 0.025, beta = 0.48) and parasitoid (F_{19} = 6.869, p = 0.017, beta = 0.87) abundances (Figure 5B). Species contributing most to the increase in grasses include *A. repens*, *B. carinatus*, and *F. idahoensis*; and species contributing most to the decrease in forbs include *A. millefolium*, *C. umbellata*, and *P. procerus* (Figure S6). The structural equation model (CFI = 0.98, RMSEA = 0.058) indicated that leaf-chewing herbivores increased via an increase in grasses (Figure 5C: pathway B→E) and, through a decrease in *P. diffusa*, an increase in habitat volume (Figure 5C: pathway A→D→F); parasitoids increased via this change in leaf-chewing herbivores (Figure 5C: pathway [B→D]/[A→D→F]→I). Despite sap-sucking herbivores and predators not changing significantly with P enrichment (Figure 5B), there were links between phosphorus, *P. diffusa* abundance, sap-sucking herbivores,

and predators (Figure 5C: pathway A→C→H). Further, predator abundance was highly contingent upon nectar/pollen-feeding herbivore and sap-sucking herbivore abundances (Figure 5C: pathways G and H).

In the long-term record, I observed that long-term P enrichment has had a significant, positive effect on grasses ($F_{278} = 32.301$, $p < 0.001$, beta = 0.48), but it did not significantly change any other functional group (sedge, $F_{285} = 0.007$, $p = 0.931$, beta < 0.001; forbs, $F_{235} = 2.326$, $p = 0.129$, beta = -0.15; *P. diffusa*, $F_{143} = 1.066$, $p = 0.303$, beta = -0.15; legumes, $F_{268} = 2.545$, $p = 0.111$, beta = 0.19; Figure S5). Importantly, there appeared to be more sedge (*C. pensylvanica*) and *P. diffusa* in P enriched plots at the start of the experiment. Over time, this difference has been maintained, either naturally or via some stabilizing effect of P (Figure S5).

IV. DISCUSSION

I found that nutrient enrichment led to shifts in Orthopteran herbivory, with N and P influencing plant-Orthoptera interactions differently. Moreover, multiple mechanisms underly these shifts. In N enriched plots, the decrease in herbivory of *L. latifolius* was a function of individual Orthoptera eating less of the species (LTR per capita) due to increased grass abundance and decreased habitat volume (Figure 2B-C; pathways A→E and B→H). The relationship between habitat volume and Orthopteran herbivory of *L. latifolius* may be explained by the plants' physical stature; being relatively complex and dense, decreased vegetative volume around an individual could make dwelling in *L. latifolius* a relatively high predation risk for Orthoptera, especially since predator abundance did not change in N enriched plots (i.e., if predators prefer more complex structure, they may be present in higher numbers in *L. latifolius*) (Figure S3B; Holbrook & Schmitt 1988; Rothley et al. 1997; Pitt 1999; Danner & Joern, 2003). In contrast to *L. latifolius*, increased herbivory of *B. carinatus* was not explained by a change in per capita herbivory (LTR per capita). Rather, more *B. carinatus* was removed at the plot-level because more Orthoptera were present and more grass was available (Figure 2B-C: pathways A→D, B→G→J, and C→I→J). Decreased community-wide C:N—in addition to reduced habitat volume—did the work of attracting a higher density of Orthoptera into N-enriched plots. This implies that Orthoptera density is contingent upon the availability of limiting dietary N across palatable species and habitat quality and/or quantity (Mulkern, 1967).

There are a few reasons as to why reduced habitat volume may have increased Orthoptera density in N enriched plots. At Bunchgrass, I observed Orthoptera inhabiting

bare ground, *P. diffusa*, (other) forbs, grasses, and legumes—sedges, however, were rarely occupied. Thus, Orthoptera could be responding in part to this decrease in sedge cover (Chambers & Samways, 1998). Further, as ectotherms, Orthoptera are often highly responsive to changes in temperature. Via decreased habitat volume, it is possible that ground-level temperatures and/or temperatures within the vegetative structure are higher and therefore more appealing to heat seeking Orthoptera (Forsman, 2000; Ahnesjo & Forsman 2006). Additionally, if predators prefer to dwell in more complex vegetation, less dense habitat may be preferable for predator avoidance (Pitt 1999). Further, this resultant increase in Orthoptera density may have led to greater herbivory of *B. carinatus* due to density-dependent behavioral change(s), which can be driven by either predator avoidance and/or an increase in intraspecific interactions (Greenfield & Shelly, 1985; Beckerman et al., 1997; Schmitz & Suttle, 2001). Since Orthoptera movement can increase with the frequency of both anti-predatory behavior and intraspecific interactions, greater movement within plots of higher grass abundance may lead to increased herbivory of *B. carinatus* as a function of more randomized movement (Joern, 1992).

With N enrichment, Orthoptera responded to nutrient enrichment similar to the way that vertebrate herbivores often respond: collectively, they consumed more of the functional group that is expected to increase—and in this case, *is* increasing (grasses)—and less of the functional group that is expected to decrease (legumes) (Figure 2A; Borer et al., 2014; Tognetti et al., 2021). However, it is important to note that Orthoptera themselves are likely contributing to nutrient cycling via their excrement, meaning that even as higher Orthoptera densities lead to more herbivory of grass and less herbivory of legume, the same increase in density may be accelerating the bottom-up effects of soil N

additions simultaneously (Belovsky & Slade, 2000). This makes it hard to say conclusively whether the *net* effect of Orthopteran herbivory is functionally equivalent to vertebrate herbivory or, from a biodiversity perspective, even positive. The relative stability of forbs and legumes over time may speak to Orthopteran mitigation of nutrient enrichment's anticipated effects, whereas fewer nectar/pollen-feeding herbivores may imply otherwise.

Orthopteran herbivores responded to P enrichment slightly differently. Plot-level (LTR) and per capita (LTR per capita) herbivory of *B. carinatus* increased (*L. latifolius* was unchanged), entirely as a function of increased grass abundance (Figure 4C: pathway A→B). When compared to N enriched plots, plot-level herbivory was likely higher and per capita herbivory significant because grass abundance increased by a much larger degree with P enrichment (Figures 5A, S3). Importantly, one limitation of this study is that foliar P was not measured; future work would benefit from its quantification as it is important for the production of RNA, an essential contributor to organism mass (Sutcliffe, 1970; Schade et al., 2003). However, similar studies to this one found its influence marginal, at least with adult Orthoptera (Loaiza et al., 2010).

In P enriched plots, increases in leaf-chewing herbivores and parasitoids were also observed. These changes are likely driven by increased host availability; (non-Orthopteran) leaf-chewing herbivores responded to grass abundance and parasitoids responded to leaf-chewing herbivore abundance (Figure 5C: pathways B→E, B→E→F[→I], and A→D→F[→I]; Nartshuk, 1984; Godfray, 1994). Leaf-chewing herbivores responded positively to habitat volume, possibly due to a preference for denser habitat (Figure 5C: pathway A→D→F; Nartshuk, 1984). Though P did not

significantly change nectar/pollen-feeding herbivores, sap-sucking herbivores, nor predators, the SEM model indicated that there was a strong relationship between these two herbivore types and predators. This finding, in addition to the observed relationship between leaf-chewing herbivores and parasitoids, supports explanations such as the resource concentration hypothesis which posit that predator and parasitoid abundances are highly contingent on prey availability (Figure 5C: pathways G and H; Root, 1973; Kareiva, 1983).

Because invertebrates could move freely between experimental plots, it is difficult to say with certainty how "chronic," homogeneous changes in soil nutrient availability, characteristic of N and P pollution, may influence the invertebrate community across the entirety of the meadow. However, because Orthoptera could move freely between plots, the results herein speak to how individuals may respond to naturally existing differences in patch quality across a diverse meadow complex (Heidorn & Joern, 1987; Olff & Ritchie, 1998; Agrawal et al., 2006). Thus, to gain more clarity regarding nutrient-plant-herbivore interactions across Bunchgrass, future experimental manipulation of Orthoptera density and Orthopteran predator pressure (both invertebrate and avian) could be conducted atop existing soil nutrient treatments in concert with the documentation of soil nutrient availability, plant community composition, Orthoptera density, and predator pressure across the complex. Ideally, this would be a long-term experiment so that the Orthoptera population's contribution (or not) to nutrient cycling can be quantified as well (Belovsky & Slade, 2000).

To further investigate the invertebrate community, similar complex-wide documentation of soil nutrients and plant community composition can be done in

conjunction with the same sweep sampling method used in this study. The observation that there were more leaf-chewing herbivores and parasitoids in high grass abundance plots (due to P) may suggest that they are more abundant in grassier patches across space, possibly due to strong grass-herbivore-parasitoid linkage (Stilmant et al., 2008).

Further, plant phenology, mountain hydrology, and Orthoptera emergence time may be changing in response to climate change (Forrest et al., 2010; Forrest & Thomson, 2011; Konstantina et al., 2015). Anecdotally, 2021 was an abnormally dry year such that cover data ideally would have been collected a week earlier. In 2022 (year two of data collection, not included here), snowpack persisted into June, while records indicate that it is usually gone by the end of May (Halpern et al. 2005). Further, adult Orthoptera were not observed until at least two weeks later in 2022 than in 2021. Investigations into how soil-plant-invertebrate interactions respond to such changes will be essential to understanding how these systems may be different in the future.

As demonstrated here, invertebrates readily respond to plant communities changed by chronic soil nutrient enrichment. Moreover, they respond along various axes, such as changes in functional group abundances, foliar nutrients, and habitat volume. That per capita and net herbivory changed in small experimental plots (25 m^2) within a diverse meadow complex is a testament to the amazing plasticity of Orthopteran herbivores. The same can be said of the parasitoids who responded to P enrichment, as they successfully navigated an odorous bouquet of volatiles to locate their hosts (leaf-chewing herbivores). As such, the patterns observed in this thesis demonstrate that when investigating chronic global change drivers, such as N and P pollution, nutrient-plant-invertebrate interactions should by no means be assumed marginal. Moreover, as plant

biodiversity continues to decline globally, it is essential to consider how invertebrates may respond, and how they may decelerate or accelerate the process.

APPENDICES

Primary Illustrations

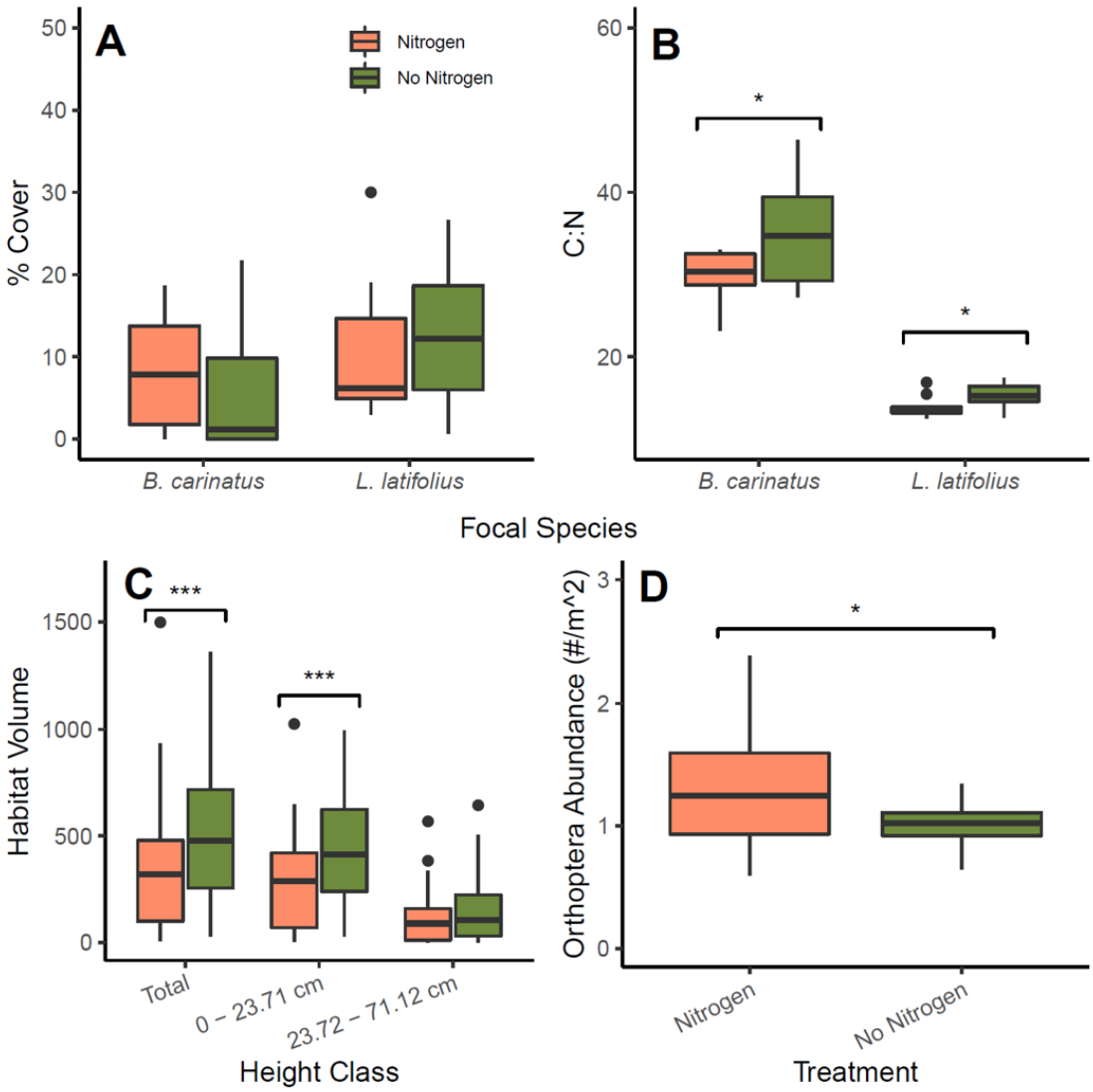

Figure 1. Focal species' percent cover (**A**), C:N (**B**), plant community habitat volume (**C**), and Orthoptera density (**D**) for nitrogen (N, NP, NK, NPK) and no-nitrogen plots. Habitat volume plot includes total volume and volume at 0-23.71 cm and 23.72-71.12 cm. Color designates nutrient presence: nitrogen (orange), no nitrogen (green). Significant difference is indicated by asterisk(s): * = $p < 0.05$; *** = $p < 0.001$.

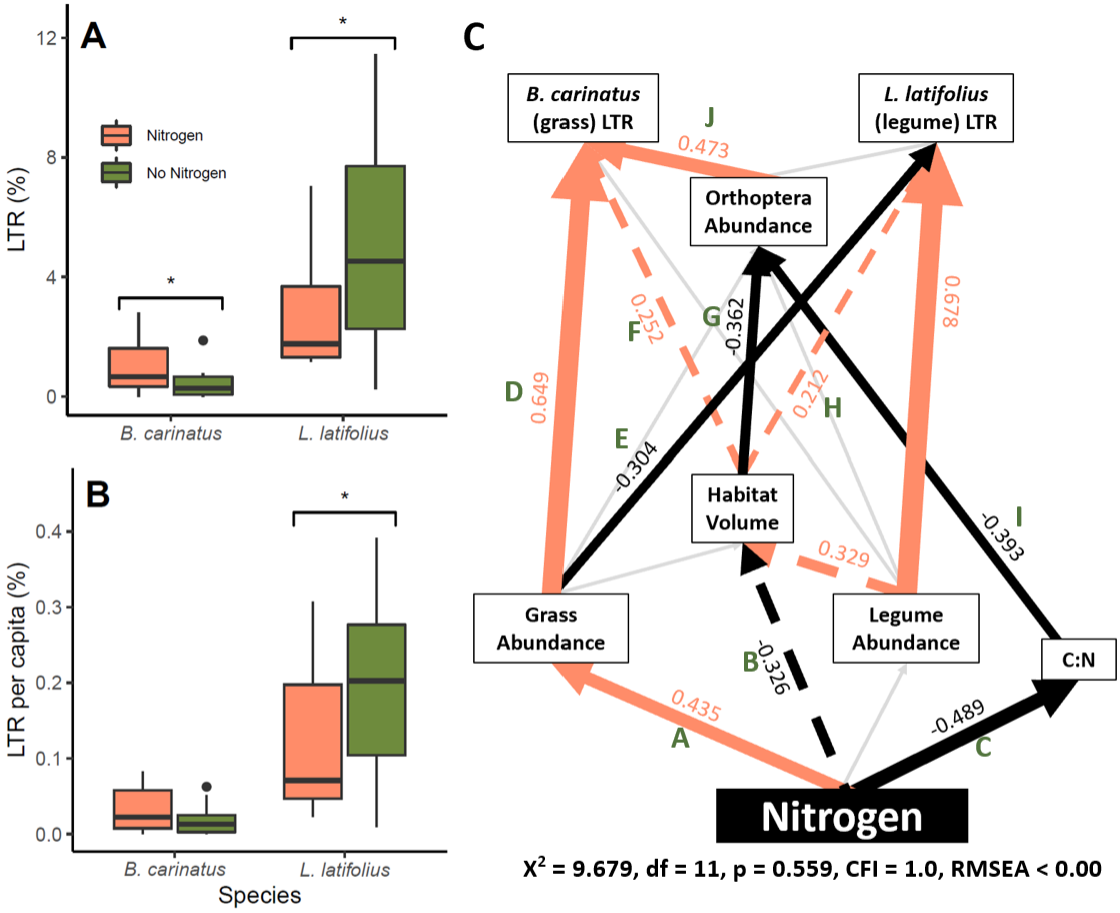

Figure 2. Focal species' leaf tissue removal (LTR) (**A**) and LTR per capita (**B**) for nitrogen (N, NP, NK, NPK) and no-nitrogen plots; and structural equation model tracing indirect pathways from nitrogen to LTR (**C**). In **A** and **B**, color designates nutrient presence: nitrogen (orange), no nitrogen (green). Significant difference is indicated by asterisk: * = $p < 0.05$. In **C**, color designates significance: positive (orange), negative (black), nonsignificant (grey). Green letters label pathways added for ease of explanation in results. Solid lines indicate significance at $p < 0.05$ and dashed lines at $p < 0.15$. Values associated with arrows are scaled estimates of coefficients; arrows are weighted to reflect magnitude.

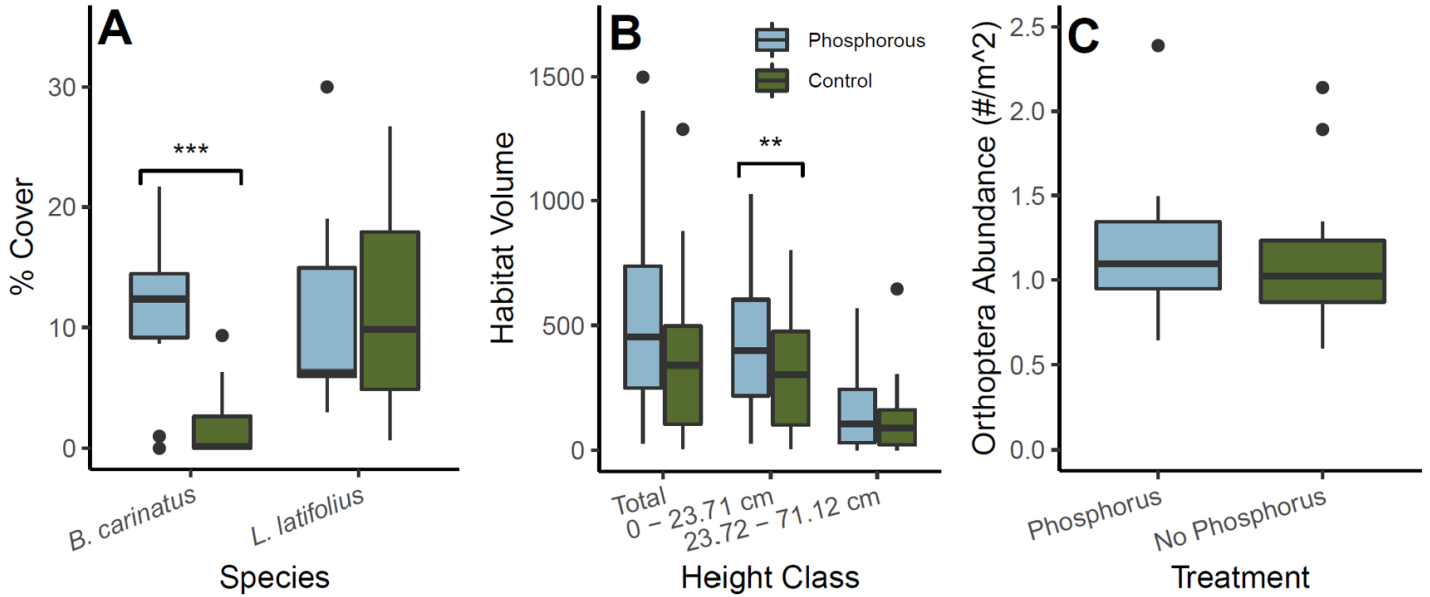

Figure 3. Focal species' percent cover (**A**), plant community habitat volume (**B**), and Orthoptera density (**C**) for phosphorus (P, NP, PK, NPK) and no-phosphorus plots. Habitat volume plot includes total volume and volume at 0-23.71 cm and 23.72-71.12 cm. Color designates nutrient presence: phosphorus (blue), no phosphorus (green). Significant difference is indicated by asterisk(s): ** = $p < 0.01$; *** = $p < 0.001$.

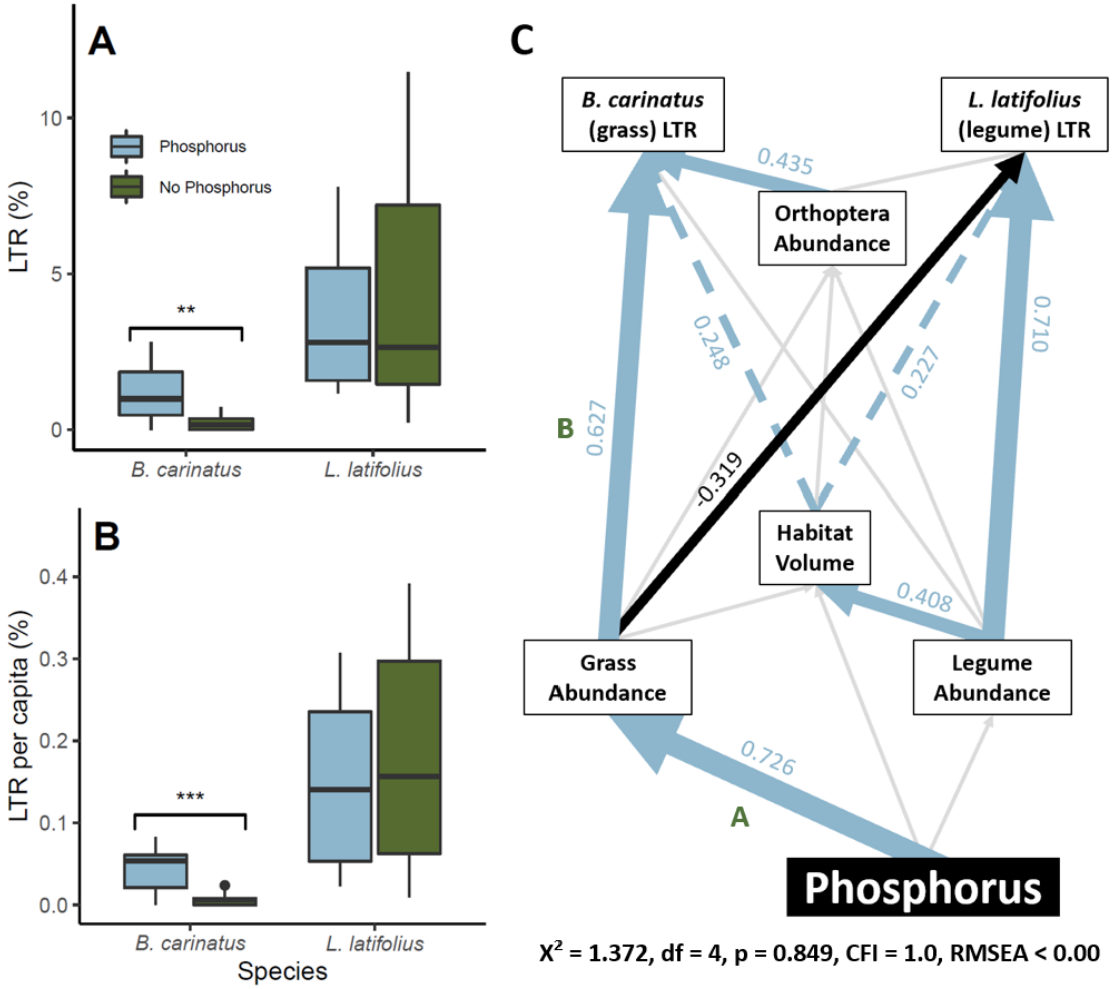

Figure 4. Focal species' leaf tissue removal (LTR) (**A**) and LTR per capita (**B**) for phosphorus (P, NP, PK, NPK) and no-phosphorus plots; and structural equation model tracing indirect pathways from phosphorus to LTR (**C**). In **A** and **B**, color designates nutrient presence: phosphorus (blue), no phosphorus (green). Significant difference is indicated by asterisk(s): ** = $p < 0.01$; *** = $p < 0.001$. In **C**, color designates significance: positive (blue), negative (black), nonsignificant (grey). Green letters label pathways added for ease of explanation in results. Solid lines indicate significance at $p < 0.05$ and dashed lines at $p < 0.15$. Values associated with arrows are scaled estimates of coefficients; arrows are weighted to reflect magnitude.

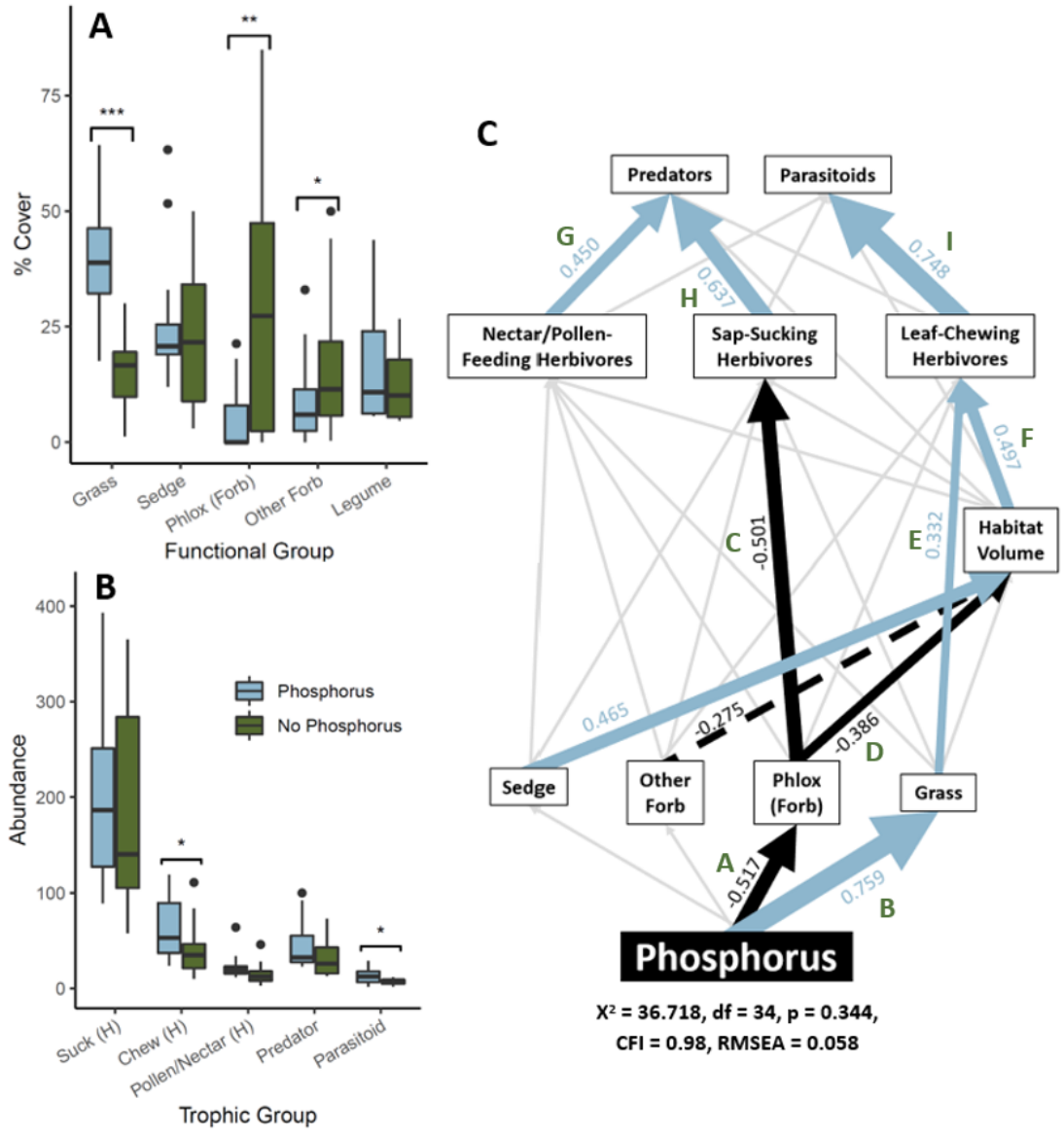

Figure 5. Plant functional group percent cover (**A**) and invertebrate trophic group abundances (**B**) for phosphorus (P, NP, PK, NPK) and no-phosphorus plots; and structural equation model tracing indirect pathways from phosphorus to trophic group abundances (**C**). In **A** and **B**, color designates nutrient presence: phosphorus (blue), no phosphorus (green). Significant difference is indicated by asterisk(s): * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. In **C**, color designates significance: positive (blue), negative (black), nonsignificant (grey). Green letters label pathways added for ease of explanation in results. Solid lines indicate significance at $p < 0.05$ and dashed lines at $p < 0.10$. Values associated with arrows are scaled estimates of coefficients; arrows are weighted to reflect magnitude.

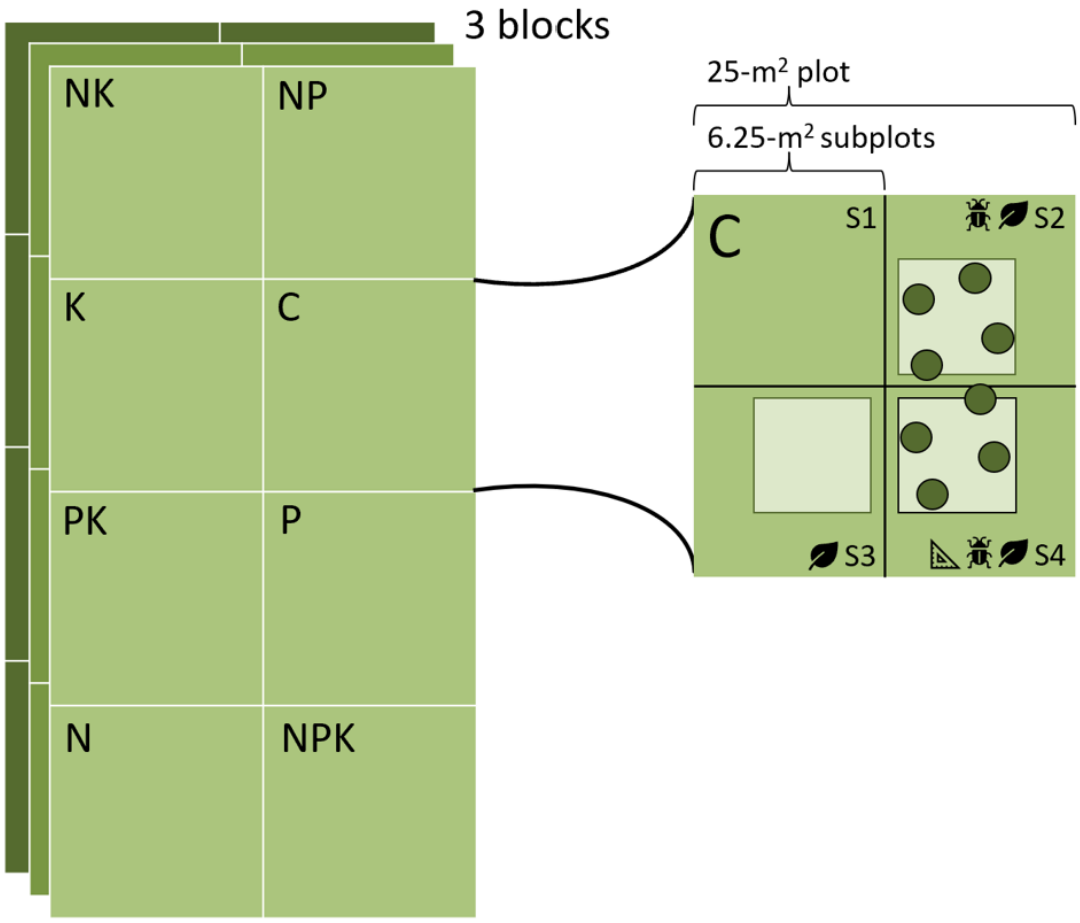

Figure S1. Experimental setup. Eight treatments × three blocks for a total of 24 plots (left). On the right: set-up within plots. Sublots S1, S2, S3, and S4 labeled. Light green boxes designate where cover was measured; dark green circles represent where rings for measuring orthoptera density could hypothetically be randomly placed; leaf icon indicates that leaf tissue removal and C:N ratio data was measured in the subplot; beetle icon indicates that sweep samples for measuring the invertebrate community were collected in the subplot; set square icon indicates subplot in which habitat volume was measured.

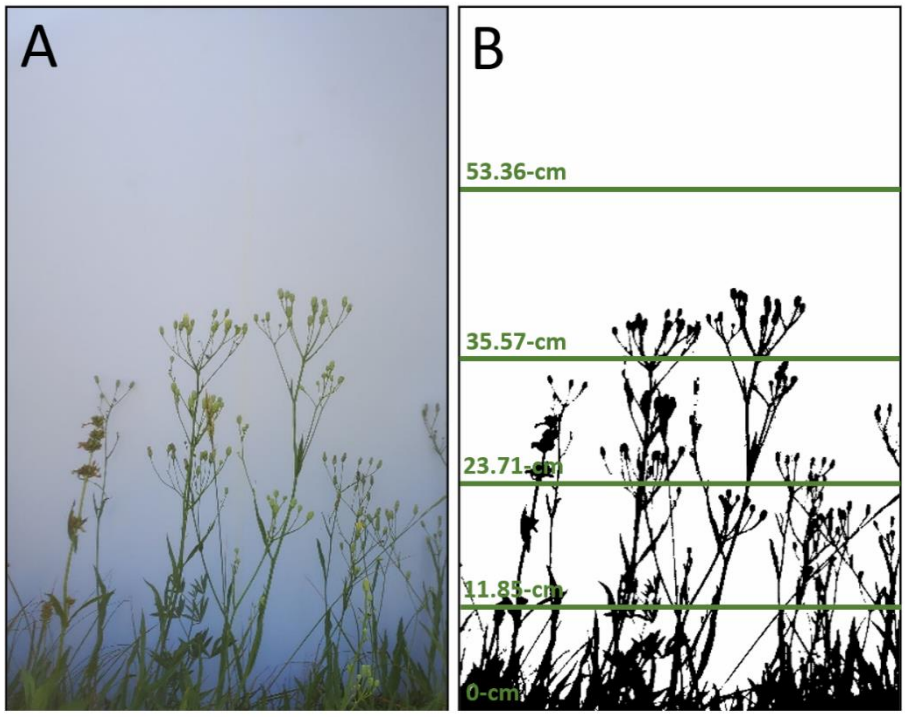

Figure S2. Photo (K-addition plot taken on July 10, 2021) used for habitat density analysis. **(A)** Photo before ImageJ processing. **(B)** Photo after processing where green lines differentiate regions for habitat analysis by height class.

Table S1. Plant species and their functional group observed within study area in 2021.

Species	Functional Group
A. aurantiaca	Forb
A. ledophyllus	Forb
A. millefolium	Forb
A. occidentale	Grass
A. occidentalis	Forb
A. repens	Grass
A. scabra	Grass
B. carinatus	Grass
B. vulgaris	Grass
C. chrysophylla	Legume
C. occidentale	Forb
C. pensylvanica	Sedge
C. remotifolium	Forb
C. subalpinus	Forb
C. umbellata	Forb
D. intermedia	Grass
E. aliceae	Forb
E. glaucus	Grass
F. idahoensis	Grass
F. vesca	Forb
H. gracile	Forb
H. scouleri	Forb
I. chrysophylla	Forb
L. latifolius	Legume
L. nevadensis	Legume
L. triternatum	Forb
O. imbricatus	Forb
P. adsurgens	Forb
P. diffusa	Forb
P. douglasii	Forb
P. gracilis	Forb
P. hastata	Forb
P. pratensis	Grass
P. procerus	Forb

V. americana	Legume
V. nuttallii	Forb

Table S2. Trophic group classification of invertebrate families from sweep sample collection within experimental plots in 2021.

Order	Family	Trophic Group	Herbivore Type
Acari	Acari	predator	
Araneae	Araneidae	predator	
Araneae	Caponiidae	predator	
Araneae	Linyphiidae	predator	
Araneae	Lycosidae	predator	
Araneae	Philodromidae	predator	
Araneae	Salticidae	predator	
Araneae	Theridiidae	predator	
Coleoptera	Cantharidae	predator	
Coleoptera	Carabidae	predator	
Coleoptera	Cerambicidae	herbivore	other part
Coleoptera	Chrysomelidae	herbivore	leaf
Coleoptera	Coccinellidae	predator	
Coleoptera	Curculionidae	herbivore	other part
Coleoptera	Dascillidae	herbivore	leaf
Coleoptera	Melyridae	herbivore	pollen/nectar
Coleoptera	Mordellidae	herbivore	pollen/nectar
Coleoptera	Phalacridae	herbivore	leaf
Coleoptera	Tenebrionidae	herbivore	leaf
Coleoptera	Thyreocoridae	herbivore	leaf
Diptera	Agromyzidae	herbivore	mine
Diptera	Asilidae	predator	
Diptera	Bibionidae	herbivore	pollen/nectar
Diptera	Calliphoridae	herbivore	pollen/nectar
Diptera	Cecidomyiidae	herbivore	gall
Diptera	Ceratopogonidae	parasitoid	
Diptera	Chamaemyiidae	predator	
Diptera	Chloropidae	herbivore	leaf

Diptera	Dolchopodidae	predator	
Diptera	Lauxaniidae	detritivore	
Diptera	Muscidae	predator	
Diptera	Otitidae	detritivore	
Diptera	Phoridae	parasitoid	
Diptera	Pipunculidae	parasitoid	
Diptera	Platypezidae	fungus	
Diptera	Sarcophagidae	detritivore	
Diptera	Sphaeroceridae	detritivore	
Diptera	Stratiomyidae	detritivore	
Diptera	Tachinidae	parasitoid	
Diptera	Tephritidae	herbivore	other part
Hemiptera	Acanaloniidae	herbivore	suck
Hemiptera	Alydidae	herbivore	suck
Hemiptera	Anthocoridae	predator	
Hemiptera	Berytidae	herbivore	suck
Hemiptera	Cercopidae	herbivore	suck
Hemiptera	Cicadellidae	herbivore	suck
Hemiptera	Corimelaenidae	herbivore	suck
Hemiptera	Dictyopharidae	herbivore	suck
Hemiptera	Lygaeidae	herbivore	suck
Hemiptera	Membracidae	herbivore	suck
Hemiptera	Miridae	herbivore	suck
Hemiptera	Nabidae	predator	
Hemiptera	Pentatomidae	herbivore	suck
Hemiptera	Reduviidae	predator	
Hemiptera	Rhopalidae	herbivore	suck
Hymenoptera	Braconidae	parasitoid	
Hymenoptera	Diapriindae	parasitoid	
Hymenoptera	Dryinidae	parasitoid	
Hymenoptera	Eulophidae	parasitoid	
Hymenoptera	Eupelmidae	parasitoid	
Hymenoptera	Eurytomidae	herbivore	leaf
Hymenoptera	Formicidae	predator	
Hymenoptera	Halticidae	herbivore	pollen/nectar
Hymenoptera	Ichneumonidae	parasitoid	

Hymenoptera	Megachilidae	herbivore	pollen/nectar
Hymenoptera	Pompillidae	herbivore	pollen/nectar
Hymenoptera	Proctotrupidae	parasitoid	
Hymenoptera	Pteromalidae	parasitoid	
Hymenoptera	Scelionidae	parasitoid	
Hymenoptera	Tenthredinae	parasitoid	
Hymenoptera	Torymidae	parasitoid	
Lepidoptera	larvae	herbivore	leaf
Lepidoptera	Oecophoridae	herbivore	suck
Lepidoptera	Tortricidae	herbivore	suck
Orthoptera	Acrididae	herbivore	leaf
Orthoptera	Tettigonidae	herbivore	leaf
Raphidioptera	Raphidiidae	predator	
Thysanoptera	Phloeothripidae	herbivore	leaf
Thysanoptera	Thripidae	herbivore	leaf

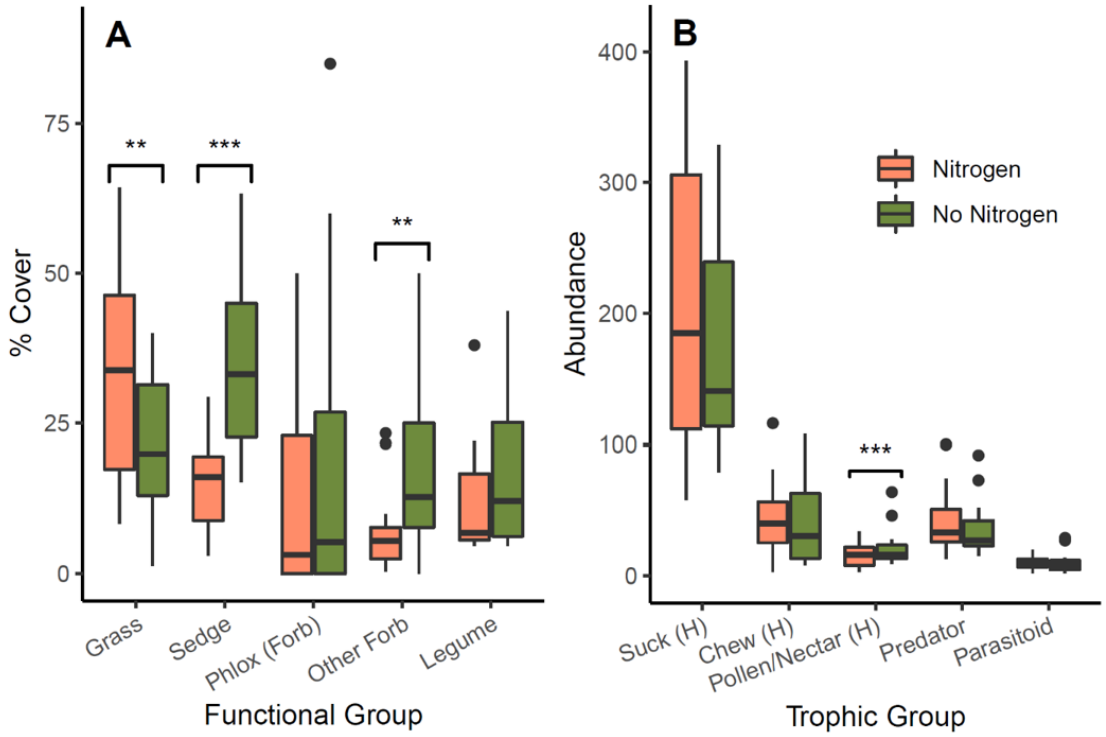

Figure S3. Plant functional group percent cover (**A**) and invertebrate trophic group abundances (**B**) for nitrogen (P, NP, PK, NPK) and no-nitrogen plots. Color designates nutrient presence: nitrogen (orange), no nitrogen (green). Significant difference is indicated by asterisk(s): * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

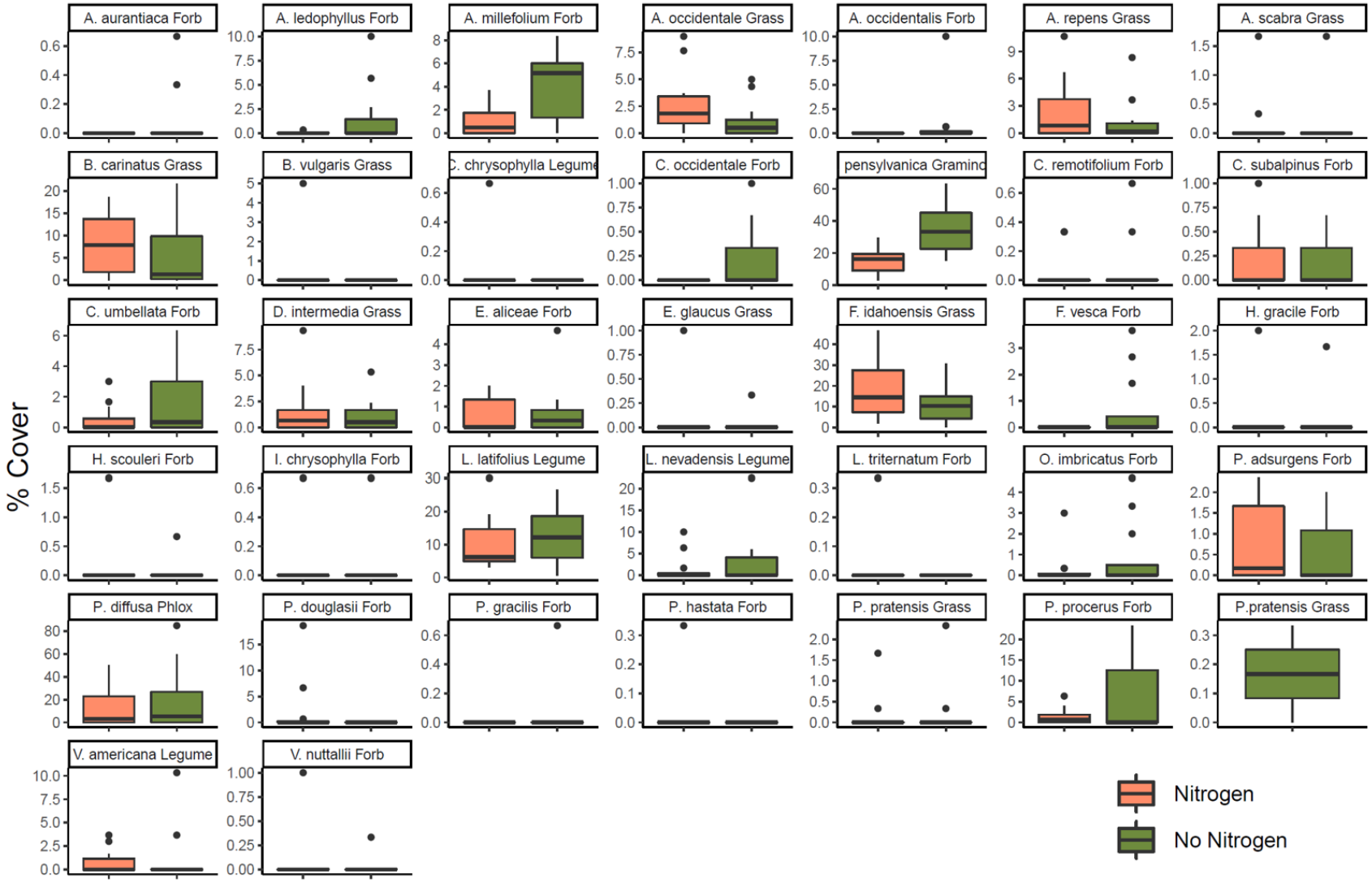

Figure S4. Percent cover of all species present within study area for nitrogen (N, NP, NK, NPK) and no-nitrogen plots in 2021. Next to each species name is its functional group. Color designates nutrient presence: nitrogen (orange), no nitrogen (green).

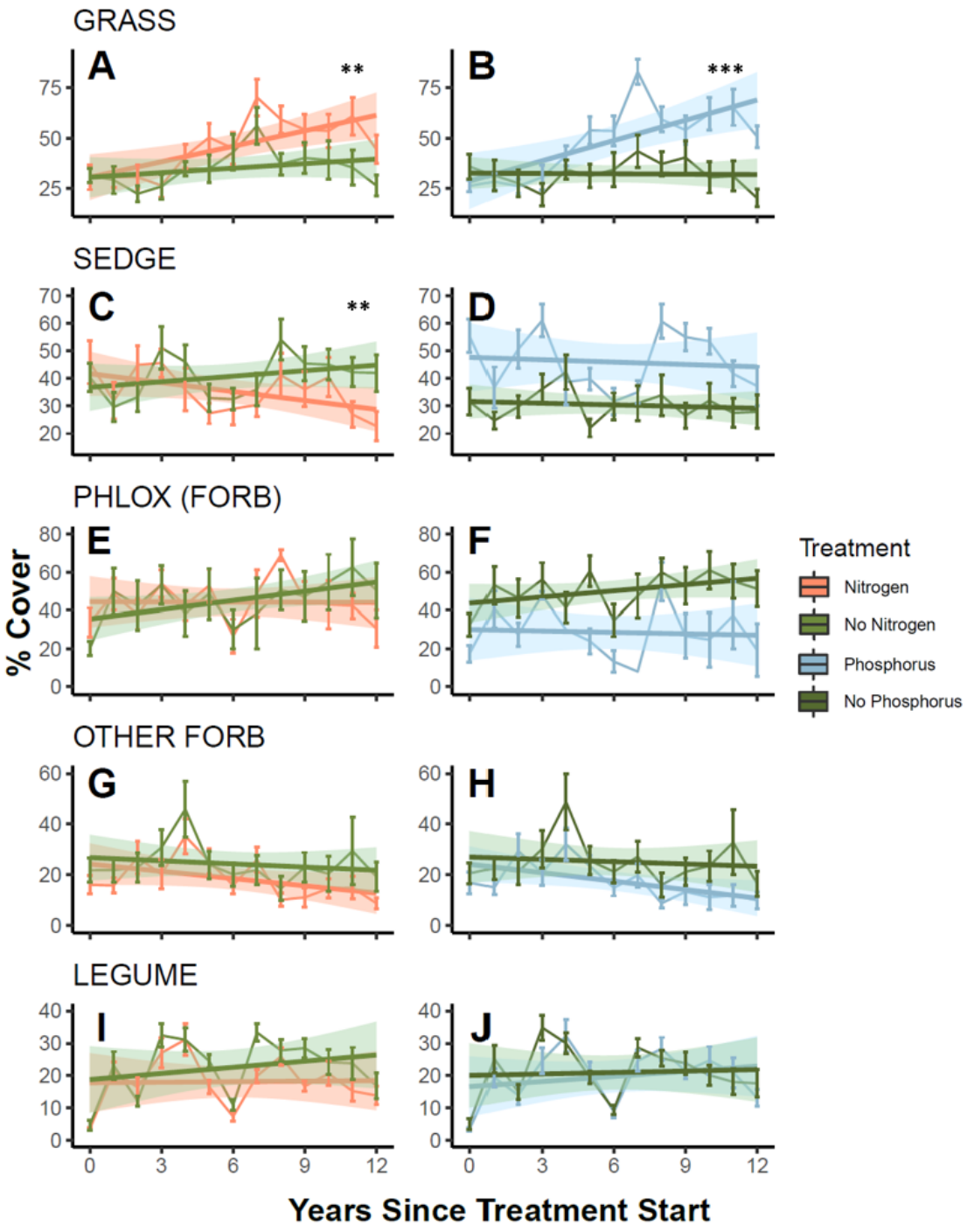

Figure S5. Grass (**A**, **B**), sedge (**C**, **D**), phlox (forb) (**E**, **F**), other forb (**G**, **H**), and legume (**I**, **J**) percent cover over time for N-containing (N, NP, NK, NPK) (**A**, **C**, **E**, **G**, **I**) and P-containing (P, NP, PK, NPK) (**B**, **D**, **F**, **H**, **J**) plots compared to no-nitrogen and no-phosphorus plots, respectively. Data collected from the same (1) core subplot within a plot. Color designates nutrient presence: nitrogen (orange), no nitrogen (light green), phosphorus (blue), no phosphorus (dark green). Shaded areas are 85% confidence intervals. Significant change over time due to N or P addition is indicated by asterisk(s): ** = $p < 0.01$; *** = $p < 0.001$.

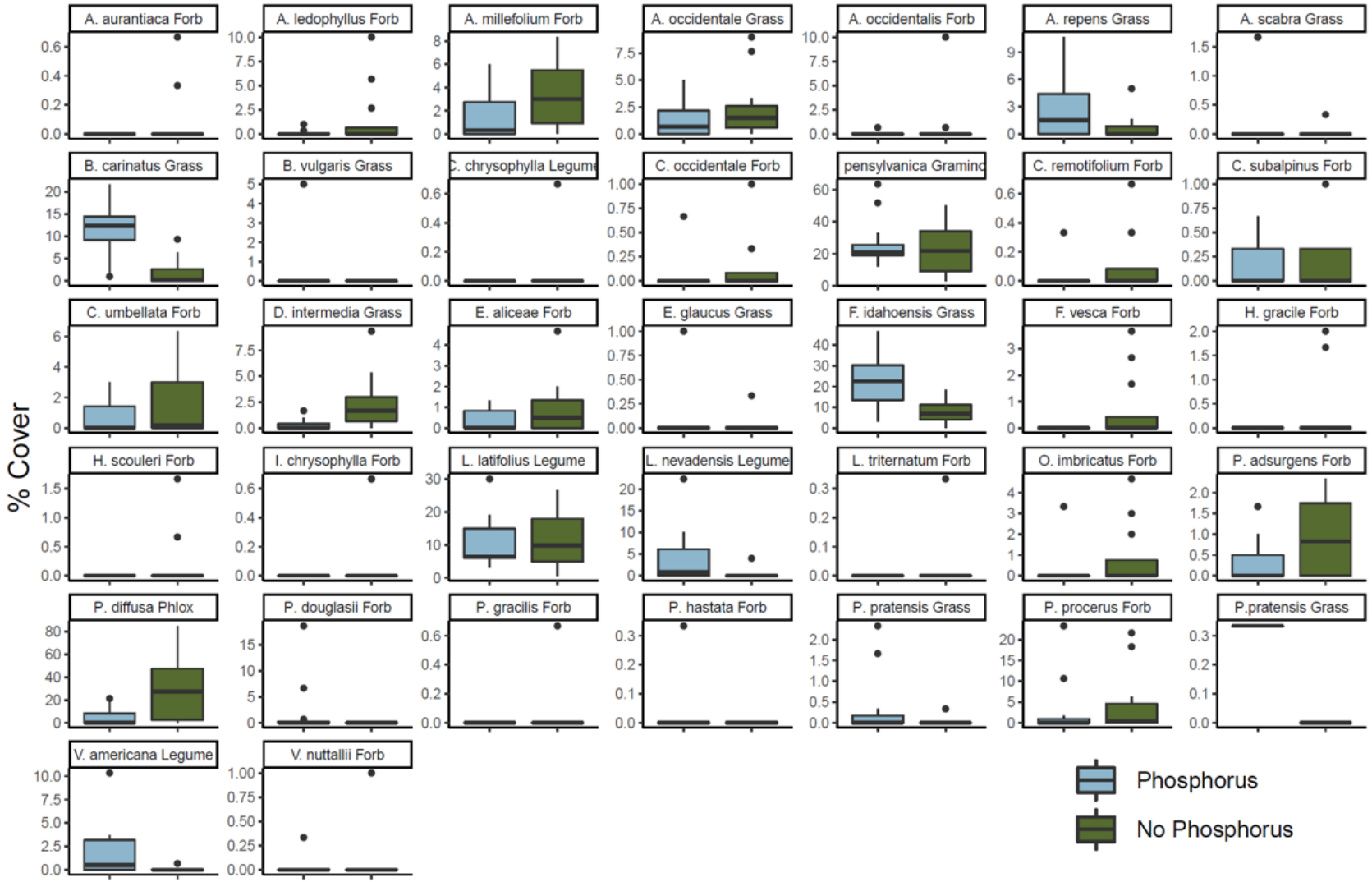

Figure S6. Percent cover of all species present within study area for phosphorus (P, NP, PK, NPK) and no-phosphorus plots in 2021. Next to each species name is its functional group. Color designates nutrient presence: phosphorus (blue), no phosphorus (green).

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