

RESEARCH ARTICLE

Nutrient enrichment increases invertebrate herbivory and pathogen damage in grasslands

Anne Ebeling¹  | Alex T. Strauss^{2,3} | Peter B. Adler⁴  | Carlos A. Arnillas⁵ | Isabel C. Barrio⁶ | Lori A. Biederman⁷ | Elizabeth T. Borer² | Miguel N. Bugalho⁸ | Maria C. Caldeira⁹ | Marc W. Cadotte¹⁰  | Pedro Daleo¹¹  | Nico Eisenhauer^{12,13} | Anu Eskelinen^{12,14,15} | Philip A. Fay¹⁶ | Jennifer Finn¹⁷  | Pamela Graff¹⁸  | Nicole Hagenah^{19,20} | Sylvia Haider^{21,12}  | Kimberly J. Komatsu²²  | Rebecca L. McCulley²³  | Charles E. Mitchell²⁴  | Joslin L. Moore²⁵  | Jesus Pascual¹¹ | Pablo L. Peri^{26,27} | Sally A. Power²⁸ | Suzanne M. Prober²⁹ | Anita C. Risch³⁰  | Christiane Roscher^{14,12}  | Mahesh Sankaran^{31,32}  | Eric W. Seabloom²  | Holger Schielzeth¹  | Martin Schütz³⁰ | Karina L. Speziale³³  | Michelle Tedder²⁰ | Risto Virtanen¹⁵  | Dana M. Blumenthal³⁴ 

¹Institute of Ecology and Evolution, University of Jena, Jena, Germany; ²Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, USA; ³Odum School of Ecology, University of Georgia, Athens, GA, USA; ⁴Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, USA; ⁵Department of Physical and Environmental Sciences, University of Toronto–Scarborough, Toronto, ON, Canada; ⁶Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Reykjavik, Iceland; ⁷Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA, USA; ⁸Centre for Applied Ecology (CEABN-INBIO), School of Agriculture, University of Lisbon, Lisbon, Portugal; ⁹Forest Research Centre, School of Agriculture, University of Lisbon, Lisbon, Portugal; ¹⁰Department of Biological Sciences, University of Toronto–Scarborough, Toronto, ON, Canada; ¹¹Instituto de Investigaciones Marinas y Costeras, CONICET–UNMDP, Mar del Plata, Argentina; ¹²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; ¹³Institute of Biology, Leipzig University, Leipzig, Germany; ¹⁴Department of Physiological Diversity, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany; ¹⁵Department of Ecology and Genetics, University of Oulu, Oulu, Finland; ¹⁶USDA-ARS Grassland Soil and Water Research Laboratory, Temple, TX, USA; ¹⁷Centre for the Environment, School of Biology and Environmental Science, Queensland University of Technology (QUT), Brisbane, QLD, Australia; ¹⁸Facultad de Agronomía, IFEVA-CONICET, Universidad de Buenos Aires, Buenos Aires, Argentina; ¹⁹Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa; ²⁰School of Life Sciences, University of KwaZulu-Natal, Scottsville, South Africa; ²¹Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany; ²²Smithsonian Environmental Research Center, Edgewater, MD, USA; ²³Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY, USA; ²⁴Department of Biology, The University of North Carolina at Chapel Hill, Chapel Hill, NC, USA; ²⁵School of Biological Sciences, Monash University, Clayton, Vic, Australia; ²⁶Instituto Nacional de Tecnología Agropecuaria, Río Gallegos, Santa Cruz, Argentina; ²⁷Universidad Nacional de la Patagonia Austral (UNPA-CONICET), Santa Cruz, Argentina; ²⁸Hawkesbury Institute for the Environment, Western Sydney University, Penrith, Australia; ²⁹CSIRO Land and Water, Wembley, Australia; ³⁰Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland; ³¹National Centre for Biological Sciences, TIFR, Bengaluru, India; ³²School of Biology, University of Leeds, Leeds, UK; ³³Laboratorio Ecotono, Iniboma (CONICET-UNCO), Bariloche, Argentina and ³⁴USDA-ARS, Rangeland Resources & Systems Research Unit, Fort Collins, CO, USA

Correspondence

Anne Ebeling
Email: anne.ebeling@uni-jena.de

Funding information

National Science Foundation, Grant/
Award Number: NSF-DEB-1042132 and

Abstract

1. Plant damage by invertebrate herbivores and pathogens influences the dynamics of grassland ecosystems, but anthropogenic changes in nitrogen and phosphorus availability can modify these relationships.

Anne Ebeling and A. T. Strauss contributed equally to this study.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

NSF-DEB-1234162; Institute on the Environment, Grant/Award Number: DG-0001-13

Handling Editor: Eric Allan

2. Using a globally distributed experiment, we describe leaf damage on 153 plant taxa from 27 grasslands worldwide, under ambient conditions and with experimentally elevated nitrogen and phosphorus.
3. Invertebrate damage significantly increased with nitrogen addition, especially in grasses and non-leguminous forbs. Pathogen damage increased with nitrogen in grasses and legumes but not forbs. Effects of phosphorus were generally weaker. Damage was higher in grasslands with more precipitation, but climatic conditions did not change effects of nutrients on leaf damage. On average, invertebrate damage was relatively higher on legumes and pathogen damage was relatively higher on grasses. Community-weighted mean damage reflected these functional group patterns, with no effects of N on community-weighted pathogen damage (due to opposing responses of grasses and forbs) but stronger effects of N on community-weighted invertebrate damage (due to consistent responses of grasses and forbs).
4. *Synthesis.* As human-induced inputs of nitrogen and phosphorus continue to increase, understanding their impacts on invertebrate and pathogen damage becomes increasingly important. Our results demonstrate that eutrophication frequently increases plant damage and that damage increases with precipitation across a wide array of grasslands. Invertebrate and pathogen damage in grasslands is likely to increase in the future, with potential consequences for plant, invertebrate and pathogen communities, as well as the transfer of energy and nutrients across trophic levels.

KEYWORDS

fungi, grasslands, insects, nitrogen, nutrient network, phosphorus, precipitation gradient, temperature gradient

1 | INTRODUCTION

Human-induced nitrogen (N) and phosphorus (P) enrichment are among the most significant global changes affecting the world's ecosystems and biodiversity (Steffen et al., 2015; Vitousek et al., 1997). In terrestrial ecosystems, nutrient enrichment (eutrophication) often reduces the diversity of plants and animals and alters species composition, favouring, for example, fast-growing over well-defended plants (Borer, Harpole, et al., 2014; Lind et al., 2013; Suding et al., 2005). Eutrophication can also alter trophic interactions, but these effects are much less well understood (Throop & Lerdau, 2004). Plants around the world face diverse and changing suites of herbivores and pathogens, with correspondingly variable effects on plants (Bigger & Marvier, 1998; Tscharrntke & Greiler, 1995). Spatial and temporal variability present challenges for understanding herbivory and pathogen infection in general and for predicting how both damage types will change with eutrophication. This lack of knowledge is particularly acute in grasslands, which cover approximately 40% of Earth's ice-free land (White et al., 2000), but which have been less well studied, relative to crops and forests (Getman-Pickering et al., 2020; Liu et al., 2020; Mitchell, 2003; Tscharrntke & Greiler, 1995).

Invertebrate herbivory and pathogen infection can have long-term effects on plant growth, community composition, nutrient

fluxes and multitrophic interactions (Bigger & Marvier, 1998; Kozlov & Zvereva, 2017; Maron & Crone, 2006; Metcalfe et al., 2014; Rheubottom et al., 2019; Schmitz, 2008). Even low levels of chronic leaf damage can influence communities and ecosystems. For example, invertebrate herbivory can alter foraging decisions by vertebrate herbivores, magnifying ecosystem-level effects (Barrio et al., 2013), and even low levels of pathogen damage can greatly reduce leaf-level photosynthesis (Strengbom & Reich, 2006). In turn, invertebrates and pathogens, and therefore their effects on plants, can be regulated by both abiotic and biotic factors, including climate (Roslin et al., 2017; Tscharrntke & Greiler, 1995), plant defences (Cronin et al., 2010; Stamp, 2003), plant productivity and diversity (Borer et al., 2012), host plant rarity (Kamiya et al., 2014; Root, 1973), nutritional quality (Awmack & Leather, 2002; Cebrian et al., 2009; Elser et al., 1996) and predation (Borer et al., 2006; Hairston et al., 1960). Especially in grasslands, eutrophication can strongly influence those biotic factors, thereby affecting the individual performance of plant enemies (e.g. insect herbivores; Throop & Lerdau, 2004). At the plant community level, the addition of nutrients often decreases plant diversity, increases plant productivity (Ceulemans et al., 2014; De Schrijver et al., 2011; Isbell et al., 2013; Midolo et al., 2019) and favours fast-growing, poorly defended species (Lind et al., 2013),

or particular functional groups, such as grasses (De Schrijver et al., 2011). Eutrophication can also shift growth relative to defence in individual plants (Stamp, 2003) or increase soil pathogens relative to mutualists (Lekberg et al., 2021).

Previous studies of eutrophication effects on invertebrate herbivores and leaf damage suggest that several of these biotic factors are involved. For example, N addition to tallgrass prairie led to increased numbers of insects, but decreased insect species richness, in part due to decreases in plant species richness (Haddad et al., 2000). More broadly, N addition consistently increased arthropod abundance, size and overall biomass across 13 temperate grasslands, likely due to increases in plant quality (lower C:N), structural complexity (more thatch) and live biomass (Lind et al., 2017). However, invertebrate herbivory might not increase with greater plant quality or arthropod biomass because of compensatory decreases in the per capita feeding rate of individual herbivores (La Pierre & Smith, 2016).

Effects of eutrophication on pathogens also involve multiple, partly conflicting mechanisms. Pathogen infection can increase as a result of increased leaf N concentrations supporting the nutritional demands of the pathogens ('nitrogen disease hypothesis'; Huber & Watson, 1974; Mitchell et al., 2003; Strengbom & Reich, 2006). Insects are limited by nitrogen, and some pathogens also depend on insects for dispersal (i.e. transmission) (Cronin et al., 2010), which could explain the greater diversity of viral pathogens found on species from N-rich habitats (Blumenthal et al., 2009). At the community level, pathogens are likely to be influenced by eutrophication-induced reductions in plant diversity (Liu et al., 2016), or changes in the relative abundance of susceptible versus resistant hosts (Halliday et al., 2019; Liu et al., 2017).

For both invertebrates and pathogens, responses to P are less well understood than responses to N (La Pierre & Smith, 2016; Lind et al., 2017; Loaiza et al., 2008), despite the fact that P in host plants is an essential nutrient required by invertebrate herbivores (Joern & Laws, 2013). In sum, while we know that nutrient addition often increases invertebrate herbivory and pathogen infection (Cappelli et al., 2020; Heckman et al., 2016, 2019; Veresoglou et al., 2013), we lack studies which compare these effects across plant species, functional groups, different nutrients such as N versus P, or study sites with variable climate (but see Lekberg et al., 2021 for below-ground).

Climate can influence invertebrate herbivores and pathogens directly, or via changes in their host plants and the surrounding community (Bale et al., 2002). For example, lower temperature can reduce the reproductive rate of invertebrate herbivores, and/or limit plant defence as a response to stress (Andrade et al., 2020). Previous studies have shown that colder climates appear to reduce herbivory (Kozlov et al., 2015; Metcalfe et al., 2014; Rheubottom et al., 2019) and the diversity and severity of some types of pathogens, such as rust fungi (Burdon et al., 2006; Liu et al., 2019). Reduced precipitation could favour stress-tolerant, well-defended plant species (Stamp, 2003). In temperate zones, for example, invertebrate damage on woody species has been found to be lower in dry than in wet regions (Kozlov et al., 2015), and European plants from dry habitats host fewer species of fungal pathogens than those from mesic

habitats (Blumenthal et al., 2009). Conversely, in some instances, drought-induced water stress can limit defence investment by plants (Andrade et al., 2020). In general, however, there is considerable uncertainty about how invertebrate herbivores and pathogens and their effects on plants respond to macro-scale variation in climate. Uncertainty is even greater for the potential interaction between climate effects and eutrophication. For example, increases in leaf damage following nutrient addition could be greater in warmer sites, because the negative effect of eutrophication on plant species richness becomes stronger at warmer sites (Midolo et al., 2019).

Despite the richness of examples and mechanisms, it is this interaction between drivers and the generality of patterns between eutrophication, climate and plant damage that remain unclear. Many studies have been conducted on individual plant species, selected sites with particular environmental conditions or using different methodological approaches. Standardized methods across a range of conditions are needed to gain generalizable insights into global ecological patterns (Anstett et al., 2016; Borer, Harpole, et al., 2014). Here we test how experimental eutrophication and global gradients in temperature and precipitation influence leaf damage by invertebrate herbivores and pathogens on 153 plant taxa, across 27 grassland sites in 10 countries and five continents. Using a standardized protocol, we conducted a factorial N and P addition experiment and measured leaf damage on dominant plant species. We used these data to calculate complementary measures of damage: mean leaf damage of single plant species within plots, and community-weighted leaf damage at the plot scale. Whereas weighted damage at the plot scale indicates how strongly a whole plant community is affected by leaf damage, information about leaf damage at the species level allows us to assess differences among taxa and functional groups, and may predict long-term compositional changes. With this approach, we asked the following questions:

1. How do local N and P addition influence community-level herbivory and pathogen leaf damage in grasslands? We predicted that invertebrate and pathogen damage would increase with N and/or P addition due to (a) community turnover from slow-growing, well-defended species towards fast-growing, poorly defended plant species and/or (b) lower C:N or C:P ratios of the leaf tissue, and therefore greater herbivore growth efficiency or aggregation within plots.
2. Does site climate (mean annual temperature and precipitation) influence leaf damage or modulate effects of N and P on leaf damage at the community level? We predicted that warmer, wetter sites would have higher levels of both damage types and allow for stronger effects of N and P addition.
3. Are herbivory and pathogen leaf damage of individual plant functional groups (grasses, forbs and legumes) affected differently by local N addition, P addition and climatic gradients (temperature and precipitation)? For example, we predicted that N addition would increase damage more strongly for grasses than legumes, since legumes are less likely to be N-limited.

2 | MATERIALS AND METHODS

2.1 | Nutrient network

The study was carried out in 27 grassland sites belonging to the Nutrient Network (www.nutnet.org), a globally distributed experiment. The sites cover a broad geographical range (10 countries across 5 continents; Figure 1), a large gradient in climatic conditions and a variety of grassland types (Table S1). At each site, study plots were placed within a relatively homogeneous $\sim 1,000\text{-m}^2$ vegetation patch, which represented the regional flora. Seven nutrient addition treatments were established (Nitrogen, Phosphorus, Potassium with micronutrients) in a full factorial, randomized block design (Borer, Harpole, et al., 2014). For our study, we used a subset of treatments only, namely Control (no nutrient addition), Nitrogen (N addition), Phosphorus (P addition) and Nitrogen + Phosphorus (NP addition). Both nutrients are added annually at a rate of 10 g/m^2 , in a form that is readily available for plants (time-released urea and triple-super phosphate). Each treatment is replicated three times at each site on plots of $5 \times 5\text{ m}$ size. Plots within a site were established within the same year. However, sites were established in different years, so at the time of data collection treatments had already been maintained for 1–10 years. For each site, we extracted data on mean annual precipitation (MAP) and mean annual temperature (MAT) from WorldClim Version 1 (Hijmans et al., 2005; Table S1).

2.2 | Estimation of leaf damage

Between 2014 and 2016, we measured leaf damage on the most common plant species at each site (median: 6 species; range 2–11

species per site) on 12 plots at each site (four treatments, three replicates per treatment) during the time of peak biomass (one measurement per site). We selected species based on their abundance across and within plots (available in all treatments and in at least 10 of the 12 plots, where possible, common within plots). If many species met these criteria, we choose a subset that covered the three plant functional groups grasses, forbs and legumes. Since legumes are often absent from fertilized plots, a total of only 11 legume species were recorded in our study. Across all sites, data collection resulted in leaf damage data for 153 taxa, belonging to 111 genera (details in Table S2). The 153 taxa covered three plant functional groups, namely grasses (60 taxa; 39 genera), legumes (11 taxa; 9 genera) and non-leguminous forbs (82 taxa; 63 genera). In all, 22 of the 153 taxa were measured at more than a single site (maximum at three sites).

For each species, we assessed damage on one fully expanded leaf from each of five individual plants per plot (if available). We strived to sample individuals from different parts of the plots, avoiding clusters of individuals as much as possible. In addition, individual plants and leaves were sampled randomly with respect to the response of interest. For plants with stems, we chose leaves approximately half-way up the stem, and for plants without stems, we chose fully expanded, mid-aged leaves. For each leaf, we visually estimated the area damaged by invertebrates (chewing and mining) and pathogens (rust, powdery mildew other pathogens), using four categories (A = 0%, B = 1%–5%, C = 6%–25%, D = >25%). For our analysis, we converted categories to numeric values that represent the midpoint of each range (A = 0%, B = 3%, C = 15%, D = 63%; Castagneyrol et al., 2012). We also estimated community-level indices of total invertebrate and pathogen damage for each plot, calculated as the mean damage scores (mean percentage of individual leaf damage

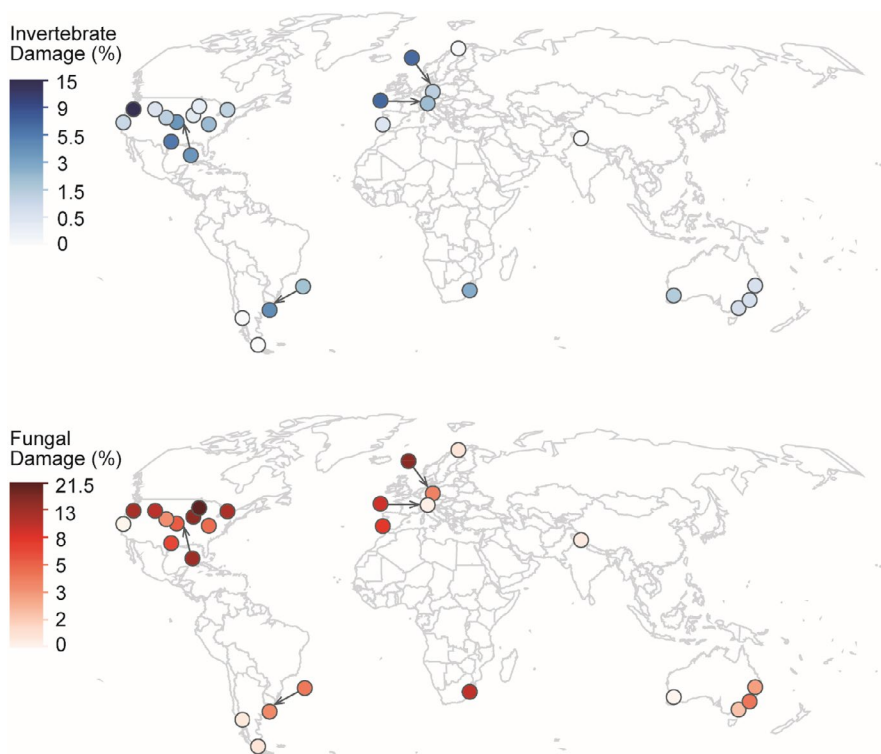


FIGURE 1 Invertebrate (a) and pathogen (b) leaf area damage (%) at 27 experimental sites of the Nutrient Network. Damage values shown here are community-level index of total leaf damage (%) (abundance-weighted means of sampled species) averaged across control plots within sites. To prevent points from lying on top of each other, we have moved them with arrows

within a taxa), weighted by the percent cover of each plant taxon in the plot (see below). This community-level metric included damage assessment on taxa that contributed to a majority of the surface area covered by living plants at most plots (median 63% of relative cover among plots). Plant coverage of target species did not differ significantly between treatments (Figures S1 and S2).

2.3 | Plant cover estimation

We estimated species-specific plant cover at the time of peak biomass within one permanently marked 1 m² subplot within each plot at all sites. We estimated cover to the nearest 1% for each species rooted within the plot. For plant taxa that were assessed for damage but not recorded during plant cover estimation in the designated subplot, we assigned a cover value of 0.01%.

2.4 | Statistical analyses

2.4.1 | Models testing for the effect of local nutrient application on community-level leaf damage under varying climatic conditions (Questions 1 and 2)

We conducted all analyses and calculations using the statistical program R, version 4.0.1 (R Core Team, 2020). Using all plots, we fit linear mixed-effects models (function `glmmTMB`; `GLMMTMB` package; Brooks et al., 2017) to explain variation in community-level indices of total damage (ln +1 transformed) by invertebrates or by pathogens. We included N, P, MAT, MAP and their interactions as explanatory variables, and site as a random term. As climate variables were not evenly distributed across the gradient, we scaled them around their means before analyses (variable mean = 0; Schielzeth, 2010). To test whether the duration of nutrient application might strengthen N and P effects on leaf damage, we added treatment year and two-way interactions between treatment year and N and P to an additional model. There was no significant effect of treatment year on invertebrate (treatment year: $p = 0.632$) or pathogen damage (treatment year: $p = 0.632$), and no significant interactions between treatment year and N or P (invertebrates N: treatment year: $p = 0.632$; invertebrates P: treatment year: $p = 0.628$; pathogens N: treatment year: $p = 0.632$; pathogens P: treatment year: $p = 0.628$). Given the absence of significant effects and the fact that we controlled for variation between sites with a random effect (which also covers treatment duration), we present the analysis without an additional fixed effect for treatment duration.

2.4.2 | Models testing for the response of plant functional groups to local nutrient application and varying climatic conditions (Question 3)

Using all plots, we fitted linear mixed-effects models (function `glmmTMB`; `GLMMTMB` package; Brooks et al., 2017) to ask how damage

on individual leaves (ln +1 transformed) varied with nutrient application. We included N, P, functional group and all possible interactions as fixed effects. We grouped the plant species into the three levels grasses, legumes and non-leguminous forbs (fixed effect 'functional group'), and set grasses as the intercept in the model since they are the dominant functional group in grasslands. Consequently, main effects of nutrients can be interpreted as effects on grasses in the control treatments, while interactions between nutrients and other functional groups indicate their deviations from the response of grasses. Site, taxon and the site-plot-taxon combination were specified as random effects, to account for pseudo-replication on the site and plot level (model output Table S5).

Using control plots only, we asked how damage on individual leaves (ln +1 transformed) differed with site climatic conditions. We fitted linear mixed-effects models (function `glmmTMB`; `GLMMTMB` package; Brooks et al., 2017) with MAT, MAP, plant functional group, and the interactions between functional groups and the climate variables as fixed effects. Again, we set grasses as the intercept. Site, taxon and the site-plot-taxon combination were specified as random effects (model output Table S7).

To show the response to nutrient addition (Figure 5) and climate (Figure 6) with appropriate standard errors for each functional group and to test whether these differ significantly from zero, we extracted the functional group means (model output Table S6; Figure 5) and functional group slopes (model output Table S8; Figure 6) by removing the main effects intercept and the main effect of functional groups. This approach reparametrizes the model with separate intercepts for each functional group and group-specific slopes (rather than contrasts for slopes) as described in Schielzeth (2010).

3 | RESULTS

3.1 | The effect of local nutrient application on community-level leaf damage under varying climatic conditions (Questions 1 and 2)

At the community level, accounting for variation in plant species abundance, pathogens damaged more than twice as much leaf area as did invertebrates (invertebrate damage: $2.5\% \pm 0.6$ SE; pathogen damage: $5.2\% \pm 1.3$ SE). We found strong differences between sites that were not attributed to MAP or MAT (Figure 1, random effect variance in Table S3). Nearly 42% (invertebrate damage) and 62% (pathogen damage) of the total variation in percent damage were explained by differences among sites.

3.1.1 | Invertebrate damage

Despite large variation, N addition significantly increased community-level invertebrate leaf damage by 28% across the 27 sites. Community-level invertebrate leaf damage was unaffected by P addition, and N and P addition acted additively (i.e. N \times P interaction

was not significant; Table S3; Figure 2). An increase in site-level MAP, but not MAT, was associated with greater invertebrate damage. However, N and P effects on community-level leaf damage were unaffected by site-level MAT or MAP (i.e. no significant interactions between climate and fertilization on damage: Table S3). In control plots, community-level total damage ranged from 0% (Potrok Aike, Argentina) to 14.9% (Bunchgrass, USA; Figure 1; Table S4). We found the most widespread damage in Fruebuel (Switzerland), where 78% of all plant individuals were affected by invertebrate herbivory.

3.1.2 | Pathogen damage

Community leaf damage caused by pathogens was unaffected by N or P addition (Table S3; Figure 2), irrespective of variation in MAT and MAP (but see different responses among functional groups below). Furthermore, community-level damage by pathogens increased marginally with site-level MAP, but not

MAT (Table S3; Figure 3). In control plots, values ranged from 0.04% (McLaughlin, USA) to 20.5% (Cedar Creek, USA; Figure 1; Table S4). We found the most widespread pathogen damage in Chiquaqua Bottoms (US), where 100% of all plant individuals showed pathogen damage.

3.2 | The response of single plant functional groups to local nutrient application and varying climatic conditions (Question 3)

At the functional group level, we found the highest average invertebrate leaf damage in legumes ($11.2\% \pm 2.0$ SE), followed by forbs ($3.3\% \pm 0.3$ SE) and grasses ($2.8\% \pm 0.4$ SE). The opposite pattern was found for pathogen leaf area damage, which was highest in grasses ($6.6\% \pm 0.7$ SE), followed by forbs ($5.8\% \pm 0.7$ SE) and legumes ($5.1\% \pm 1.6$ SE). Across all taxa (mean leaf damage of single species), average invertebrate leaf damage ($3.6\% \pm 0.28$ SE) was lower

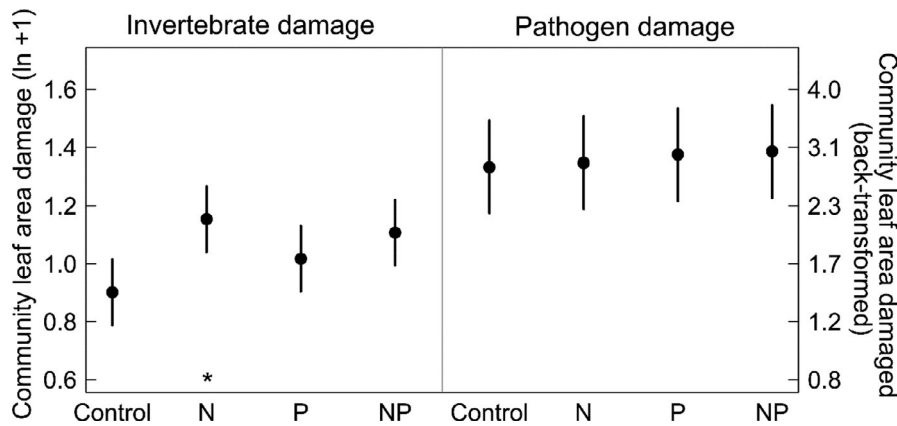


FIGURE 2 Community-level index of total leaf damage (%) in different nutrient addition treatments (N = nitrogen, P = phosphorus, NP = nitrogen and phosphorus). The left-hand y-axis shows log-transformed, and the right-hand y-axis back-transformed values of invertebrate and pathogen leaf damage. Relationships were analysed in mixed-effects models with invertebrate damage (left panel) and pathogen damage (right panel) as response variables, and site as a random effect. The figure shows model estimates (\pm SE) (shown in Table S3), and asterisks indicate significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

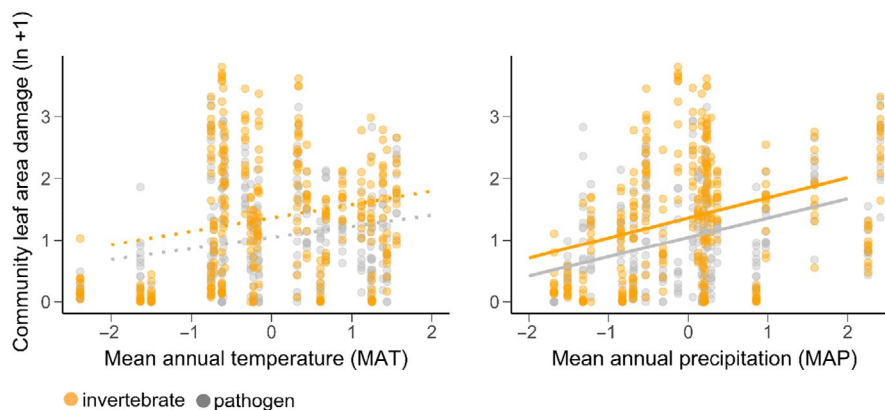


FIGURE 3 Community-level index of total leaf damage (%) versus the abiotic site conditions mean annual temperature (MAT), and mean annual precipitation (MAP). All explanatory variables are scaled to unit variance around the mean. Relationships were analysed in mixed-effects models with invertebrate damage (orange line) and pathogen damage (grey line) as response variables, and site as a random effect. Regression lines indicate the slope and significance of the relationship (solid line = significant and marginally significant effects; dashed line = no significance). Model estimates are shown in Table S3

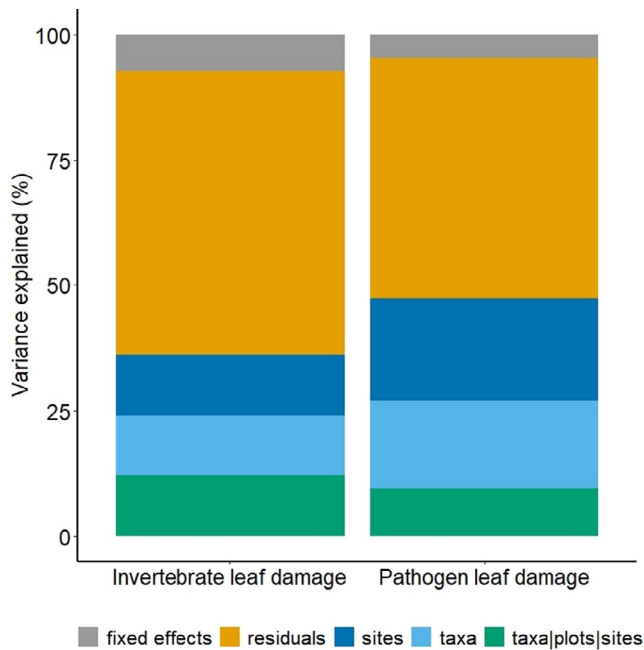


FIGURE 4 Variance decomposition of leaf damage by random effects, fixed effects and residuals from mixed-effects models using control plots only, with mean annual temperature, mean annual precipitation and functional group identity (plus interactions) as fixed effects, and site, taxon and taxon–plot–site ID as random effects. Model estimates and variances explained by each compartment are shown in Table S7

than pathogen damage ($6.1\% \pm 0.47$ SE). Overall, we found strong differences in leaf damage between taxa. Around 12% of the total variation in invertebrate damage and 18% of the variation in pathogen damage was explained by differences among taxa (Figure 4). In total, in control plots under ambient conditions, we observed no invertebrate damage for 13% of the taxa (20 out of 153 taxa), and no pathogen leaf damage for 11% of the taxa (19 out of 153). For roughly half of the taxa, more than 50% of the leaves scored showed some degree of invertebrate damage (62 of 153 taxa) or pathogen damage (78 of 153 taxa).

3.2.1 | Invertebrate damage

N addition significantly increased invertebrate leaf damage on grass and forb species, but not on legume species (Tables S5 and S6; Figure 5). Specifically, grass and forb species showed 27.3% (± 7.5 SE) and 28.2% (± 9.9 SE) greater damage, respectively, and legume species exhibited 7.4% (± 10.4 SE) lower leaf damage after N addition. P addition had a positive effect on damage in forbs, but not in grass and legumes species. In grasses, but not in forbs and legumes, the combined effect of N and P addition was significantly lower than expected if the single nutrient additions had an additive effect (negative estimate for the interaction term). Furthermore, grasses and legumes experienced a significant increase in damage severity with increasing MAP (only marginally

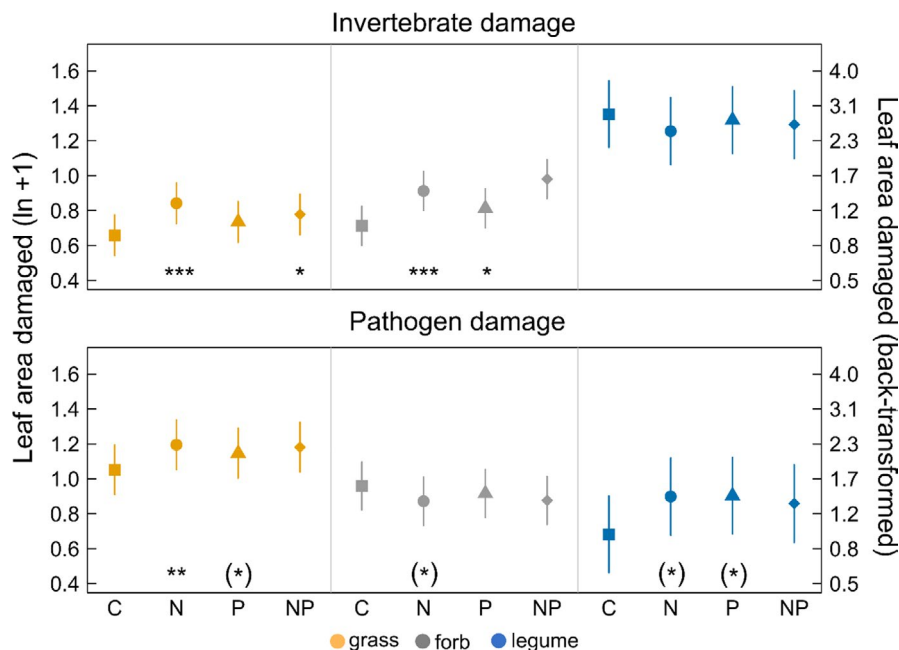


FIGURE 5 Damage on individual leaves (%) in different nutrient addition treatments (N = nitrogen, P = phosphorus, NP = nitrogen and phosphorus). The left-hand y-axis shows log-transformed, and the right-hand y-axis back-transformed values of invertebrate and pathogen leaf damage. Relationships were analysed in mixed-effects models with invertebrate damage (upper row) and pathogen damage (lower row) as response variables, site, taxon–plot–site ID and taxon as random effects, and N, P, functional group and all possible interactions as fixed effects. Different colours represent model estimates (\pm SE) of the different plant functional groups (shown in Table S5). Removing the intercept from the model allows extracting functional group means with appropriate standard errors, and thus testing for the significance of nutrient effects on each single functional group (shown in Table S6). Asterisks indicate significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; (*) $p < 0.1$

significant in grass species), but were unaffected by variation in site-level MAT (Tables S7 and S8; Figure 6). In contrast, leaf damage in forb species significantly increased with site-level MAT, but was unaffected by site-level MAP.

3.2.2 | Pathogen damage

The experimental addition of N significantly increased pathogen leaf damage in grass species and marginally significantly increased it in legume species by 13.3% (± 4.7 SE) and 30.9% (± 20.6 SE), respectively (Tables S5 and S6; Figure 5). Similarly, compared to control plots, pathogen damage in grass and legume species was marginally significantly higher after experimental P addition, with an increase of 8.6% (± 4.8 SE) and 32.3% (± 19.1 SE), respectively. In contrast to grasses and legumes, pathogen leaf damage on forbs marginally significantly decreased with N addition. The effect of simultaneous N and P addition was not significantly different from what was predicted based on the single nutrient additions (i.e. N \times P interaction was not significant; Table S5 and S6; Figure 5). Whereas grasses and legumes were unaffected by climate variables, forbs showed a positive response to increasing MAP, but not MAT (Tables S7 and S8; Figure 6).

4 | DISCUSSION

Previous studies have shown widely varying effects of N and P fertilization on herbivory and pathogen infestation, ranging from positive (Borer, Seabloom, et al., 2014; Heckman et al., 2016; Veresoglou et al., 2013), to neutral (Borer, Seabloom, et al., 2014; Cappelli et al., 2020; Heckman et al., 2016, 2019; Lau et al., 2008), to negative (see references within Dordas, 2009). With our study, based on 153 species from 27 sites, we can now draw more general conclusions: (a) in temperate grasslands, N addition increases leaf damage by invertebrates at the community level by nearly one-third and especially for grasses and forbs, (b) N addition increases leaf damage by pathogens in grasses and legumes but not necessarily for forbs or at the community level, (c) there is no effect of increased P on the community-level leaf damage (see also Veresoglou et al., 2013) and (d) leaf damage increases with precipitation independently of nutrient effects.

4.1 | The effect of local nutrient application on community-level leaf damage

In contrast to our hypotheses and several previous studies (Borer et al., 2010; Cappelli et al., 2020; Heckman et al., 2019; Veresoglou

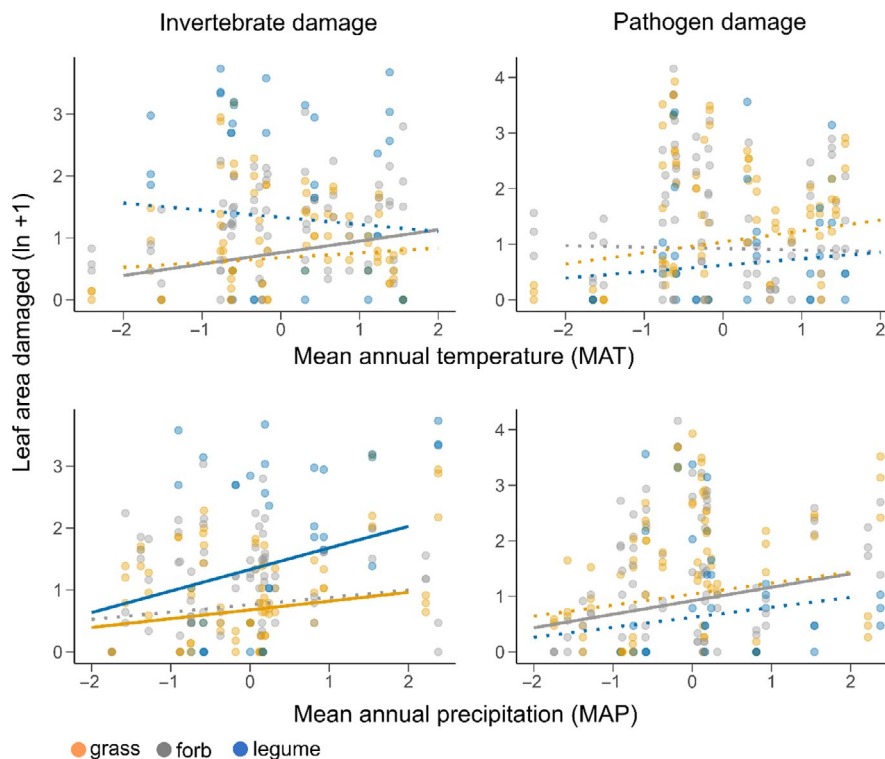


FIGURE 6 Damage on individual leaves (%) in control plots versus the climatic site conditions mean annual temperature (MAT) and mean annual precipitation (MAP). All explanatory variables are scaled to unit variance around the mean. Relationships were analysed in mixed-effects models with invertebrate damage (left panels) and pathogen damage (right panels) as response variables, site, taxon-plot-site ID and taxon as random effects, and MAT, MAP, functional group and all possible interactions as fixed effects (model estimates are given in Table S7). Differently coloured regression lines indicate the slope for each plant functional group. Points indicate average damage for a particular functional group within a site. Separate slopes for each functional group, extracted by removing the main effect slope from the model (shown in Table S8), indicate within-group climate effects that are significant (solid lines) or non-significant (dashed lines; $p > 0.05$)

et al., 2013), community-level pathogen infection in 27 grasslands was unaffected by addition of either N or P, and only N addition leads to greater invertebrate leaf damage.

A wide variety of mechanisms could drive the positive relationship between invertebrate leaf damage and N addition, ranging from N-induced changes in individual plants and enemies, to changes in plant population densities and community composition (Throop & Lerdau, 2004). N addition can alter plant traits, for example by increasing leaf nutrient content or specific leaf area, and decreasing concentrations of defence compounds such as lignin, silica and phenolics (Cappelli et al., 2020; Dordas, 2009; Firn et al., 2019; Heckman et al., 2016; Mitchell et al., 2010; Throop & Lerdau, 2004). Herbivores can also respond to changes in plant growth or quality via changes in individual performance, size, feeding rate, feeding strategy, aggregation within plots or susceptibility to their predators (Jonas & Joern, 2008; La Pierre & Smith, 2016; Lind et al., 2017; Throop & Lerdau, 2004). If increased individual enemy performance outpaces predation, this can lead to herbivore population growth (increase in abundance and biomass), and increasing damage (de Sassi et al., 2012; Jonas & Joern, 2008; Lind et al., 2017; Srivastava & Lawton, 1998). Because the plots in our study are smaller than the dispersal distance of many herbivores, behavioural responses and local dynamics of herbivores to changed nutrient environment can also be an important mechanism. Nonetheless, this shift in the interactions between consumers and their plant hosts demonstrates that this relationship is strongly contingent on the local nutrient environment. The N-induced alteration in plant species traits may act in concert with plant community changes, including reduced species numbers and evenness, increased productivity, and increased abundance of fast-growing, less defended species (Borer, Seabloom, et al., 2014; Soons et al., 2017).

4.2 | The effect of climatic conditions on community-level leaf damage and its interaction with nutrient effects

Studies of rainfall effects on pathogen infection and invertebrate herbivory have inconsistent results, and range from negative correlations (Andrade et al., 2020) to neutral (Rheubottom et al., 2019) and positive correlations (Kozlov et al., 2015; Strengbom et al., 2006). With our results, we can confirm the predicted positive relationship between precipitation and leaf damage in grassland communities. However, in contrast to the expected positive relationship between temperature and leaf damage and findings from previous studies (Burdon et al., 2006; Kozlov et al., 2015; Liu et al., 2019; Metcalfe et al., 2014; Rheubottom et al., 2019), community-level leaf damage was insensitive to site-level temperature. Although this seems surprising, similar patterns were found in other global studies as well. For example, in a synthetic review, only 37% of the published studies show higher rates of herbivory at lower latitudes in warmer areas (Moles et al., 2011), and herbivore leaf damage on a *Solidago* species did not change across a

broad climatic gradient spanning 10 degrees of latitude (Lynn & Fridley, 2019).

4.3 | The response of plant functional groups to local nutrient application and varying climatic conditions

Similar to findings from other studies (Rheubottom et al., 2019; Turcotte et al., 2014), we found the greatest herbivore damage in legumes and the least damage in grasses. This may be due to the fact that legumes, compared to grasses and forbs, have nutrient-rich leaves, as well as other traits that are typical of fast-growing species, such as high SLA and low levels of effective defence compounds, and are therefore more palatable to invertebrate herbivores (Firn et al., 2019; Lavorel & Garnier, 2002). Higher silicate concentrations in grasses, which increase leaf toughness, may also have protected grasses from chewing damage by invertebrates (Caldwell et al., 2016; Massey & Hartley, 2009; Schaller et al., 2016). Notably, we found the opposite pattern for pathogen damage, with grasses showing the greatest pathogen damage and legumes the least. One explanation might be the greater density of grasses in the plant communities compared to legumes and forbs, which could lead to more efficient density-dependent transmission for pathogens (Liu et al., 2020; Mitchell et al., 2003; Parker & Gilbert, 2018; Rottstock et al., 2014).

Those differences in plant traits and dominance between plant functional groups might explain distinct responses to nutrient addition and climatic conditions. For example, the increase in invertebrate damage with N addition in grasses and forbs but not legumes may reflect lower potential for increased palatability in legumes. Few previous studies have tested nutrient effects on enemy damage of individual functional groups. N addition was found to increase pathogen damage on grasses in Minnesota tallgrass prairie (Mitchell et al., 2003), but not in grass species common in West Coast grasslands (Borer et al., 2010).

Although the reasons for the functional group differences we observed are speculative, they drive patterns at the community level. Specifically, invertebrate leaf damage in both dominant functional groups—grasses and forbs—increases after N addition, which is reflected at the level of the plant community (which also responds to N). In contrast, pathogen leaf damage increases with N in grasses but slightly decreases in forbs, and these effects cancel each other out at the community level (no response to N). Accordingly, the fact that we do not see effects of fertilization on the pathogen infection at the level of the entire plant community does not mean that individual species are not strongly affected. Finally, dominance by grasses means that their relatively high levels of pathogen damage are reflected at the community level, affecting 5.5% of total leaf area (range of 0.1%–21% across sites). This result supports previous work suggesting important roles for pathogens in grasslands (Allan et al., 2010; Strengbom & Reich, 2006).

However, despite using a global standardized approach, our study faces some limitations. For example, we are not able to

quantify or evaluate the temporal or spatial variability in herbivore and pathogen dynamics and whether our study design adequately captures this variation. Furthermore, we lack information on specific damage types and the resource specialization of the consumers. To get a more complete and mechanistic understanding on the relationship between climate, eutrophication and plant damage, additional work is needed.

5 | CONCLUSIONS

As humans continue to increase nitrogen and phosphorus supplies, it is becoming increasingly important to understand how increased nutrient inputs alter invertebrate and pathogen damage to grassland plant communities, and consequently the transfer of trophic energy through ecosystems. Using a standardized experiment at 27 globally distributed grasslands, we determined that precipitation and experimental nitrogen fertilization have proportionally strong, additive effects on the amount of leaf damage experienced by grassland plants. Overall, invertebrate and pathogen damage in grasslands are likely to increase in the future, especially at sites that get wetter, sites that are especially dominated by forbs (for invertebrate damage) or grasses (for pathogen damage), and sites that are heavily impacted by eutrophication.

ACKNOWLEDGEMENTS

This work was conducted using data from the NutNet collaborative experiment, funded at the site scale by individual researchers. Coordination and data management have been supported by funding to E.B. and E.S. from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programmes, and the Institute on the Environment (DG-0001-13). We thank Eric Lind and Ashley Asmus for support in data management and preparation. We further thank Dan LeCain for organizing and shipping equipment, required for the add-on study, and Julie Kray for creating Figure 1. At the Mt Caroline site, we thank Georg Wiehl for assistance with data collection, Denise and Malcolm French, and the Terrestrial Ecosystems Research Network (TERN) Great Western Woodlands Supersite for support. Furthermore, we thank Rui Alves for the logistic support on the establishment of the Companhia das Lezírias site. For the Indian site, we thank Yadugiri V. T. for assistance with data collection. This manuscript is an outcome of a workshop kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig (DFG FZT 118).

CONFLICT OF INTEREST

M.S. is an Associate Editor of Journal of Ecology, but took no part in the peer review and decision-making for this paper. The authors declare no other conflict of interest.

AUTHORS' CONTRIBUTIONS

A.E., A.T.S. and D.M.B. developed and framed the research question(s); A.Eb. and A.T.S. analysed the data; D.M.B., H.S. and J.F. contributed to the data analysis; A.Eb. wrote the manuscript with contributions from all other authors; A.C.R., A.Eb., A.Es., C.A.A., C.R., D.M.B., E.T.B., E.W.S., J.F., J.P., J.L.M., K.J.K., K.L.S., L.A.B., M.C.C., M.N.B., M.Sa., M.Sc., M.T., M.W.C., N.E., N.H., P.A.F., R.L.M., R.V., S.A.P., S.H. and S.M.P. contributed to the data collection; E.W.S. and E.T.B. are Nutrient Network coordinators.

DATA AVAILABILITY STATEMENT

Supporting data can be found in Dryad Digital Repository <https://doi.org/10.5061/dryad.gf1vhhmq5> (Ebeling & Blumenthal, 2021).

ORCID

Anne Ebeling  <https://orcid.org/0000-0002-3221-4017>
 Peter B. Adler  <https://orcid.org/0000-0002-4216-4009>
 Marc W. Cadotte  <https://orcid.org/0000-0002-5816-7693>
 Pedro Daleo  <https://orcid.org/0000-0001-9759-1203>
 Jennifer Firm  <https://orcid.org/0000-0001-6026-8912>
 Pamela Graff  <https://orcid.org/0000-0002-6042-2673>
 Sylvia Haider  <https://orcid.org/0000-0002-2966-0534>
 Kimberly J. Komatsu  <https://orcid.org/0000-0001-7056-4547>
 Rebecca L. McCulley  <https://orcid.org/0000-0002-2393-0599>
 Charles E. Mitchell  <https://orcid.org/0000-0002-1633-1993>
 Joslin L. Moore  <https://orcid.org/0000-0001-9809-5092>
 Anita C. Risch  <https://orcid.org/0000-0003-0531-8336>
 Christiane Roscher  <https://orcid.org/0000-0001-9301-7909>
 Mahesh Sankaran  <https://orcid.org/0000-0002-1661-6542>
 Eric W. Seabloom  <https://orcid.org/0000-0001-6780-9259>
 Holger Schielzeth  <https://orcid.org/0000-0002-9124-2261>
 Karina L. Speziale  <https://orcid.org/0000-0003-2224-2097>
 Risto Virtanen  <https://orcid.org/0000-0002-8295-8217>
 Dana M. Blumenthal  <https://orcid.org/0000-0001-7496-0766>

REFERENCES

- Allan, E., van Ruijven, J., & Crawley, M. J. (2010). Foliar fungal pathogens and grassland biodiversity. *Ecology*, *91*(9), 2572–2582. <https://doi.org/10.1890/09-0859.1>
- Andrade, J. F., Alvarado, F., Carlos Santos, J., & Santos, B. A. (2020). Rainfall reduction increases insect herbivory in tropical herb communities. *Journal of Vegetation Science*, *31*(3), 487–496. <https://doi.org/10.1111/jvs.12870>
- Anstett, D. N., Nunes, K. A., Baskett, C., & Kotanen, P. M. (2016). Sources of controversy surrounding latitudinal patterns in herbivory and defense. *Trends in Ecology & Evolution*, *31*(10), 789–802. <https://doi.org/10.1016/j.tree.2016.07.011>
- Awmack, C. S., & Leather, S. R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, *47*(1), 817–844. <https://doi.org/10.1146/annurev.ento.47.091201.145300>
- Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D., & Whittaker, J. B. (2002). Herbivory in global climate change research: Direct effects of rising

- temperature on insect herbivores. *Global Change Biology*, 8(1), 1–16. <https://doi.org/10.1046/j.1365-2486.2002.00451.x>
- Barrio, I. C., Hik, D. S., Peck, K., & Bueno, C. G. (2013). After the frass: Foraging pikas select patches previously grazed by caterpillars. *Biology Letters*, 9(3), 20130090. <https://doi.org/10.1098/rsbl.2013.0090>
- Bigger, D. S., & Marvier, M. A. (1998). How different would a world without herbivory be?: A search for generality in ecology. *Integrative Biology: Issues, News, and Reviews*, 1(2), 60–67. [https://doi.org/10.1002/\(SICI\)1520-6602\(1998\)1:2<60:AID-INBI4>3.0.CO;2-Z](https://doi.org/10.1002/(SICI)1520-6602(1998)1:2<60:AID-INBI4>3.0.CO;2-Z)
- Blumenthal, D., Mitchell, C. E., Pyšek, P., & Jarošík, V. (2009). Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences of the United States of America*, 106(19), 7899–7904. <https://doi.org/10.1073/pnas.0812607106>
- Borer, E. T., Halpern, B. S., & Seabloom, E. W. (2006). Asymmetry in community regulation: Effects of predators and productivity. *Ecology*, 87(11), 2813–2820. [https://doi.org/10.1890/0012-9658\(2006\)87\[2813:AICREO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2813:AICREO]2.0.CO;2)
- Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution*, 5(1), 65–73. <https://doi.org/10.1111/2041-210X.12125>
- Borer, E. T., Seabloom, E. W., Mitchell, C. E., & Cronin, J. P. (2014). Multiple nutrients and herbivores interact to govern diversity, productivity, composition, and infection in a successional grassland. *Oikos*, 123(2), 214–224. <https://doi.org/10.1111/j.1600-0706.2013.00680.x>
- Borer, E. T., Seabloom, E. W., Mitchell, C. E., & Power, A. G. (2010). Local context drives infection of grasses by vector-borne generalist viruses. *Ecology Letters*, 13(7), 810–818. <https://doi.org/10.1111/j.1461-0248.2010.01475.x>
- Borer, E. T., Seabloom, E. W., Tilman, D., & Novotny, V. (2012). Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters*, 15(12), 1457–1464. <https://doi.org/10.1111/ele.12006>
- Brooks, M. E., Kristensen, K., Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378. <https://doi.org/10.32614/RJ-2017-066>
- Burdon, J. J., Thrall, P. H., & Ericson, L. (2006). The current and future dynamics of disease in plant communities. *Annual Review of Phytopathology*, 44, 19–39. <https://doi.org/10.1146/annurev.phyto.43.040204.140238>
- Caldwell, E., Read, J., & Sanson, G. D. (2016). Which leaf mechanical traits correlate with insect herbivory among feeding guilds? *Annals of Botany*, 117, 349–361. <https://doi.org/10.1093/aob/mcv178>
- Cappelli, S. L., Pichon, N. A., Kempel, A., & Allan, E. (2020). Sick plants in grassland communities: A growth-defense trade-off is the main driver of fungal pathogen abundance. *Ecology Letters*, 23(9), 1349–1359. <https://doi.org/10.1111/ele.13537>
- Castagneyrol, B., Lagache, L., Giffard, B., Kremer, A., & Jactel, H. (2012). Genetic diversity increases insect herbivory on oak saplings. *PLoS ONE*, 7(8), e44247. <https://doi.org/10.1371/journal.pone.0044247>
- Cebrian, J., Shurin, J. B., Borer, E. T., Cardinale, B. J., Ngai, J. T., Smith, M. D., & Fagan, W. F. (2009). Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE*, 4(3), e4929. <https://doi.org/10.1371/journal.pone.0004929>
- Ceulemans, T., Stevens, C. J., Duchateau, L., Jacquemyn, H., Gowing, D. J. G., Merckx, R., Wallace, H., van Rooijen, N., Goethem, T., Bobbink, R., Dorland, E., Gaudnik, C., Alard, D., Corcket, E., Muller, S., Dise, N. B., Dupré, C., Diekmann, M., & Honnay, O. (2014). Soil phosphorus constrains biodiversity across European grasslands. *Global Change Biology*, 20(12), 3814–3822. <https://doi.org/10.1111/gcb.12650>
- Cronin, J. P., Welsh, M. E., Dekkers, M. G., Abercrombie, S. T., & Mitchell, C. E. (2010). Host physiological phenotype explains pathogen reservoir potential. *Ecology Letters*, 13(10), 1221–1232. <https://doi.org/10.1111/j.1461-0248.2010.01513.x>
- de Sassi, C., Lewis, O. T., & Tylianakis, J. M. (2012). Plant-mediated and nonadditive effects of two global change drivers on an insect herbivore community. *Ecology*, 93(8), 1892–1901. <https://doi.org/10.1890/11-1839.1>
- De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography*, 20(6), 803–816. <https://doi.org/10.1111/j.1466-8238.2011.00652.x>
- Dordas, C. (2009). Role of nutrients in controlling plant diseases in sustainable agriculture: A review. In E. Lichtfouse, M. Navarrete, P. Debaeke, S. Véronique, & C. Alberola (Eds.), *Sustainable agriculture* (pp. 443–460). Springer.
- Ebeling, A., & Blumenthal, D. M. (2021). Data from: Nutrient enrichment increases invertebrate herbivory and pathogen damage in grasslands [Dataset]. *Dryad*, <https://doi.org/10.5061/dryad.gf1vhhmq5>
- Elser, J. J., Dobberfuhl, D. R., MacKay, N. A., & Schampel, J. H. (1996). Organism size, life history, and N:P stoichiometry. *BioScience*, 46(9), 674–684. <https://doi.org/10.2307/1312897>
- Firn, J., McGree, J. M., Harvey, E., Flores-Moreno, H., Schütz, M., Buckley, Y. M., Borer, E. T., Seabloom, E. W., La Pierre, K. J., MacDougall, A. M., Prober, S. M., Stevens, C. J., Sullivan, L. L., Porter, E., Ladouceur, E., Allen, C., Moromizato, K. H., Morgan, J. W., Harpole, W. S., ... Risch, A. C. (2019). Leaf nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nature Ecology and Evolution*, 3(3), 400–406. <https://doi.org/10.1038/s41559-018-0790-1>
- Getman-Pickering, Z. L., Campbell, A., Aflitto, N., Grele, A., Davis, J. K., & Ugine, T. A. (2020). LeafByte: A mobile application that measures leaf area and herbivory quickly and accurately. *Methods in Ecology and Evolution*, 11(2), 215–221. <https://doi.org/10.1111/2041-210X.13340>
- Haddad, N. M., Haarstad, J., & Tilman, D. (2000). The effects of long-term nitrogen loading grassland insect communities. *Oecologia*, 124(1), 73–84. <https://doi.org/10.1007/s004420050026>
- Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94(879), 421–425. <https://doi.org/10.1086/282146>
- Halliday, F. W., Heckman, R. W., Wilfahrt, P. A., & Mitchell, C. E. (2019). Past is prologue: Host community assembly and the risk of infectious disease over time. *Ecology Letters*, 22(1), 138–148. <https://doi.org/10.1111/ele.13176>
- Heckman, R. W., Halliday, F. W., & Mitchell, C. E. (2019). A growth-defense trade-off is general across native and exotic grasses. *Oecologia*, 191(3), 609–620. <https://doi.org/10.1007/s00442-019-04507-9>
- Heckman, R. W., Wright, J. P., & Mitchell, C. E. (2016). Joint effects of nutrient addition and enemy exclusion on exotic plant success. *Ecology*, 97(12), 3337–3345. <https://doi.org/10.1002/ecy.1585>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Huber, D. M., & Watson, R. D. (1974). Nitrogen form and plant disease. *Annual Review of Phytopathology*, 12(1), 139–165. <https://doi.org/10.1146/annurev.py.12.090174.001035>
- Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 110(29), 11911–11916. <https://doi.org/10.1073/pnas.1310880110>

- Joern, A., & Laws, A. N. (2013). Ecological mechanisms underlying arthropod species diversity in grasslands. *Annual Review of Entomology*, 58(1), 19–36. <https://doi.org/10.1146/annurev-ento-120811-153540>
- Jonas, J. L., & Joern, A. (2008). Host-plant quality alters grass/forb consumption by a mixed-feeding insect herbivore, *Melanoplus bivittatus* (Orthoptera: Acrididae). *Ecological Entomology*, 33(4), 546–554. <https://doi.org/10.1111/j.1365-2311.2008.01004.x>
- Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, 89(1), 123–134. <https://doi.org/10.1111/brv.12046>
- Kozlov, M. V., Lanta, V., Zverev, V., & Zvereva, E. L. (2015). Global patterns in background losses of woody plant foliage to insects. *Global Ecology and Biogeography*, 24(10), 1126–1135. <https://doi.org/10.1111/geb.12347>
- Kozlov, M. V., & Zvereva, E. L. (2017). Background insect herbivory: Impacts, patterns and methodology. In F. M. Cánovas, U. Lüttge, & R. Matyssek (Eds.), *Progress in botany* (Vol. 79, pp. 313–355). Springer International Publishing. https://doi.org/10.1007/124_2017_4
- La Pierre, K. J., & Smith, M. D. (2016). Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems. *Oecologia*, 180(2), 485–497. <https://doi.org/10.1007/s00442-015-3471-7>
- Lau, J. A., Strengbom, J., Stone, L. R., Reich, P. B., & Tiffin, P. (2008). Direct and indirect effects of CO₂, nitrogen, and community diversity on plant–enemy interactions. *Ecology*, 89(1), 226–236. <https://doi.org/10.1890/07-0423.1>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lekberg, Y., Arnillas, C. A., Borer, E. T., Bullington, L. S., Fierer, N., Kennedy, P. G., Leff, J. W., Luis, A. D., Seabloom, E. W., & Henning, J. A. (2021). Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. *Nature Communications*, 12(1), 3484. <https://doi.org/10.1038/s41467-021-23605-y>
- Lind, E. M., Borer, E., Seabloom, E., Adler, P., Bakker, J. D., Blumenthal, D. M., Crawley, M., Davies, K., Firn, J., Gruner, D. S., Stanley Harpole, W., Hautier, Y., Hillebrand, H., Knops, J., Melbourne, B., Mortensen, B., Risch, A. C., Schuetz, M., Stevens, C., & Wragg, P. D. (2013). Life-history constraints in grassland plant species: A growth-defence trade-off is the norm. *Ecology Letters*, 16(4), 513–521. <https://doi.org/10.1111/ele.12078>
- Lind, E. M., La Pierre, K. J., Seabloom, E. W., Alberti, J., Iribarne, O., Firn, J., Gruner, D. S., Kay, A. D., Pascal, J., Wright, J. P., Yang, L., & Borer, E. T. (2017). Increased grassland arthropod production with mammalian herbivory and eutrophication: A test of mediation pathways. *Ecology*, 98(12), 3022–3033. <https://doi.org/10.1002/ecy.2029>
- Liu, X., Chen, L., Liu, M., García-Guzmán, G., Gilbert, G. S., & Zhou, S. (2020). Dilution effect of plant diversity on infectious diseases: Latitudinal trend and biological context dependence. *Oikos*, 129(4), 457–465. <https://doi.org/10.1111/oik.07027>
- Liu, X., Lyu, S., Sun, D., Bradshaw, C. J. A., & Zhou, S. (2017). Species decline under nitrogen fertilization increases community-level competence of fungal diseases. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162621. <https://doi.org/10.1098/rspb.2016.2621>
- Liu, X., Lyu, S., Zhou, S., & Bradshaw, C. J. A. (2016). Warming and fertilization alter the dilution effect of host diversity on disease severity. *Ecology*, 97(7), 1680–1689. <https://doi.org/10.1890/15-1784.1>
- Liu, X., Ma, Z., Cadotte, M. W., Chen, F., He, J.-S., & Zhou, S. (2019). Warming affects foliar fungal diseases more than precipitation in a Tibetan alpine meadow. *New Phytologist*, 221(3), 1574–1584. <https://doi.org/10.1111/nph.15460>
- Loaiza, V., Jonas, J. L., & Joern, A. (2008). Does dietary P affect feeding and performance in the mixed-feeding grasshopper (Acrididae) *Melanoplus bivittatus*? *Environmental Entomology*, 37(2), 333–339. [https://doi.org/10.1603/0046-225X\(2008\)37\[333:DDPAF\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2008)37[333:DDPAF]2.0.CO;2)
- Lynn, J. S., & Fridley, J. D. (2019). Geographic patterns of plant-herbivore interactions are driven by soil fertility. *Journal of Plant Ecology*, 12(4), 653–661. <https://doi.org/10.1093/jpe/rtz002>
- Maron, J. L., & Crone, E. (2006). Herbivory: Effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences*, 273(1601), 2575–2584. <https://doi.org/10.1098/rspb.2006.3587>
- Massey, F. P., & Hartley, S. (2009). Physical defences wear you down: Progressive and irreversible impacts of silica on insect herbivores. *Journal of Animal Ecology*, 78, 281–291. <https://doi.org/10.1111/j.1365-2656.2007.0>
- Metcalfe, D. B., Asner, G. P., Martin, R. E., Silva Espejo, J. E., Huasco, W. H., Farfán Amézquita, F. F., Carranza-Jimenez, L., Galiano Cabrera, D. F., Baca, L. D., Sinca, F., Huaraca Quispe, L. P., Taype, I. A., Mora, L. E., Dávila, A. R., Solórzano, M. M., Puma Vilca, B. L., Laupa Román, J. M., Guerra Bustios, P. C., Revilla, N. S., ... Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, 17(3), 324–332. <https://doi.org/10.1111/ele.12233>
- Midolo, G., Alkemade, R., Schipper, A. M., Benítez-López, A., Perring, M. P., & De Vries, W. (2019). Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis. *Global Ecology and Biogeography*, 28(3), 398–413. <https://doi.org/10.1111/geb.12856>
- Mitchell, C. E. (2003). Trophic control of grassland production and biomass by pathogens. *Ecology Letters*, 6(2), 147–155. <https://doi.org/10.1046/j.1461-0248.2003.00408.x>
- Mitchell, C. E., Blumenthal, D., Jarošík, V., Puckett, E. E., & Pyšek, P. (2010). Controls on pathogen species richness in plants' introduced and native ranges: Roles of residence time, range size and host traits. *Ecology Letters*, 13(12), 1525–1535. <https://doi.org/10.1111/j.1461-0248.2010.01543.x>
- Mitchell, C. E., Reich, P. B., Tilman, D., & Groth, J. V. (2003). Effects of elevated CO₂, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology*, 9(3), 438–451. <https://doi.org/10.1046/j.1365-2486.2003.00602.x>
- Moles, A. T., Bonser, S. P., Poore, A. G. B., Wallis, I. R., & Foley, W. J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, 25(2), 380–388. <https://doi.org/10.1111/j.1365-2435.2010.01814.x>
- Parker, I. M., & Gilbert, G. S. (2018). Density-dependent disease, life-history trade-offs, and the effect of leaf pathogens on a suite of co-occurring close relatives. *Journal of Ecology*, 106(5), 1829–1838. <https://doi.org/10.1111/1365-2745.13024>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. [https://doi.org/10.1890/0012-9658\(2002\)083\[3097:CFHIWS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3097:CFHIWS]2.0.CO;2)
- Rheubottom, S. I., Barrio, I. C., Kozlov, M. V., Alatalo, J. M., Andersson, T., Asmus, A. L., Baubin, C., Brearley, F. Q., Egelkraut, D. D., Ehrich, D., Gauthier, G., Jónsdóttir, I. S., Konieczka, S., Lévesque, E., Olofsson, J., Prevéy, J. S., Slevan-Tremblay, G., Sokolov, A., Sokolova, N., ... Hik, D. S. (2019). Hiding in the background: Community-level patterns in invertebrate herbivory across the tundra biome. *Polar Biology*, 42(10), 1881–1897. <https://doi.org/10.1007/s00300-019-02568-3>
- Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs*, 43(1), 95–124. <https://doi.org/10.2307/1942161>

- Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C., Cameron, E. K., Dáttilo, W., Donoso, D. A., Drozd, P., Gray, C. L., Hik, D. S., Hill, S. J., Hopkins, T., Huang, S., ... Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356(6339), 742–744. <https://doi.org/10.1126/science.aaj1631>
- Rottstock, T., Joshi, J., Kummer, V., & Fischer, M. (2014). Higher plant diversity promotes higher diversity of fungal pathogens, while it decreases pathogen infection per plant. *Ecology*, 95(7), 1907–1917. <https://doi.org/10.1890/13-2317.1>
- Schaller, J., Roscher, C., Hillebrand, H., Weigelt, A., Oelmann, Y., Wilcke, W., Ebeling, A., & Weisser, W. W. (2016). Plant diversity and functional groups affect Si and Ca pools in aboveground biomass of grassland systems. *Oecologia*, 182(1), 277–286. <https://doi.org/10.1007/s00442-016-3647-9>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>
- Schmitz, O. J. (2008). Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 39(1), 133–152. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173418>
- Soons, M. B., Hefting, M. M., Dorland, E., Lamers, L. P. M., Versteeg, C., & Bobbink, R. (2017). Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. *Biological Conservation*, 212, 390–397. <https://doi.org/10.1016/j.biocon.2016.12.006>
- Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *The American Naturalist*, 152(4), 510–529. <https://doi.org/10.1086/286187>
- Stamp, N. (2003). Out of the quagmire of plant defense hypotheses. *Quarterly Review of Biology*, 78(1), 23–55. <https://doi.org/10.1086/367580>
- Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, 347, 1259855. <https://doi.org/10.1126/science.1259855>
- Strengbom, J., Englund, G., & Ericson, L. (2006). Experimental scale and precipitation modify effects of nitrogen addition on a plant pathogen. *Journal of Ecology*, 94(1), 227–233. <https://doi.org/10.1111/j.1365-2745.2005.01073.x>
- Strengbom, J., & Reich, P. B. (2006). Elevated CO₂ and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*. *Oecologia*, 149(3), 519–525. <https://doi.org/10.1007/s00442-006-0458-4>
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12), 4387–4392. <https://doi.org/10.1073/pnas.0408648102>
- Throop, H. L., & Lerdau, M. T. (2004). Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. *Ecosystems*, 7(2), 109–133. <https://doi.org/10.1007/s10021-003-0225-x>
- Tscharntke, T., & Greiler, H. J. (1995). Insect communities, grasses, and grasslands. *Annual Review of Entomology*, 40(1), 535–558. <https://doi.org/10.1146/annurev.en.40.010195.002535>
- Turcotte, M. M., Davies, T. J., Thomsen, C. J. M., & Johnson, M. T. J. (2014). Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. *Proceedings of the Royal Society B: Biological Sciences*, 281(May), 1–7. <https://doi.org/10.1098/rspb.2014.0555>
- Veresoglou, S. D., Barto, E. K., Menexes, G., & Rillig, M. C. (2013). Fertilization affects severity of disease caused by fungal plant pathogens. *Plant Pathology*, 62(5), 961–969. <https://doi.org/10.1111/ppa.12014>
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., Melillo, J. M., Lubchenko, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325), 494–499. <https://doi.org/10.1126/science.277.5325.494>
- White, R., Murray, S., & Rohweder, M. (2000). Grassland ecosystems. In *Pilot analysis of global ecosystems (PAGE)* (pp. 11–28). World Resources Institute. Retrieved from http://pdf.wri.org/page_grasslands.pdf

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Ebeling, A., Strauss, A. T., Adler, P. B., Arnillas, C. A., Barrio, I. C., Biederman, L. A., Borer, E. T., Bugalho, M. N., Caldeira, M. C., Cadotte, M. W., Daleo, P., Eisenhauer, N., Eskelinen, A., Fay, P. A., Firn, J., Graff, P., Hagenah, N., Haider, S., Komatsu, K. J., ... Blumenthal, D. M. (2022). Nutrient enrichment increases invertebrate herbivory and pathogen damage in grasslands. *Journal of Ecology*, 110, 327–339. <https://doi.org/10.1111/1365-2745.13801>