Received: 11 May 2023 | Accepted: 10 July 2023

DOI: 10.1111/1365-2745.14204

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Consumers and nutrients alter colonization of an old field community independently and by distinct mechanisms

Robert W. Heckman[1,2]

[1]Department of Biology, University of North Carolina, Chapel Hill, North Carolina, USA

[2]USDA Forest Service, Rocky Mountain Research Station, Cedar City, Utah, USA

Correspondence
Robert W. Heckman
Email: robert.heckman@usda.gov

Funding information
National Science Foundation Division of Environmental Biology, Grant/Award Number: DEB-1311289; UNC's Alma Holland Beers Scholarship and WC Coker Fellowship; USDA Forest Service

Handling Editor: Anne Kempel

Abstract

1. As communities assemble, species establishment can be driven by multiple factors. Two such factors, nutrients and consumers, are predicted to interact, but few studies have explored whether this interaction results from synergistically altering the same biotic and abiotic mediators or complementarily altering different mediators.
2. To test this, I added seeds of multiple native species to old field communities in which I experimentally manipulated soil nutrients, leaf litter and consumers (insect herbivores and fungal pathogens). Using Bayesian hierarchical modelling, I evaluated the degree to which changes in light and water availability, fungal disease and insect herbivory, and community functional composition influenced seedling establishment and the richness of colonizing species and were driven by experimental treatments. I then examined whether nutrients, litter and consumers interactively determined the success of colonizing species with different resource allocation strategies.
3. Contrary to expectation, nutrient addition and consumer exclusion reduced, and litter removal increased, seedling establishment and colonizer richness independently and via different pathways. Also contrary to expectation, seedling resource allocation strategy did not interact with nutrient addition and consumer exclusion to alter establishment success. Rather, as community damage (foliar fungal disease + insect herbivory) increased, seedlings with high % leaf nitrogen (a proxy for an acquisitive resource allocation strategy) become increasingly disadvantaged relative to seedlings with low % leaf nitrogen (a proxy for a conservative resource allocation strategy).
4. *Synthesis*: These results indicate that seedling establishment is unlikely to be interactively impacted by nutrients and consumers (fungal pathogens + insect herbivores) because these two drivers act on different environmental pathways to influence community assembly.

KEYWORDS
community assembly, fertilization, insect herbivory, light availability, old fields, plant pathogens, seed addition, top-down, bottom-up

1 | INTRODUCTION

Establishing new populations is a critical aspect of community assembly that can be influenced by the independent and interactive effects of multiple factors. Two of these factors—nutrients and consumers—are ubiquitous drivers of community dynamics that are often predicted to interact (Heckman et al., 2016; Kempel et al., 2013). To date, most studies examining the interactive effects of nutrients and consumers on community assembly have focussed on mammalian herbivores (e.g. Borer et al., 2014; Eskelinen et al., 2022). Two other consumer groups—insect herbivores and fungal pathogens—are also key determinants of community structure (Agrawal & Maron, 2022; Allan et al., 2010; Kempel et al., 2015; La Pierre et al., 2015; Mitchell, 2003), but the effects of their interactions with nutrients are not as well understood. Nutrients and consumers can each influence community assembly via multiple, potentially synergistic or antagonistic pathways (Halliday et al., 2019; Harpole et al., 2017; Zirbel et al., 2017). This includes altering the availability of other resources (e.g. water and light; Borer et al., 2014; Rose et al., 2012), attributes of the plant community (Kempel et al., 2015; Wilfahrt et al., 2020) or competitive interactions among species (Seabloom et al., 2018). Although several studies have examined these paths independently, few have evaluated multiple paths by which nutrients and consumers can impact community assembly, regardless of consumer group identity. Ultimately, understanding how nutrients and consumers interact to influence seedling establishment will require identifying whether these drivers synergistically alter the same path or complementarily alter different paths.

Nutrient availability can influence seedling establishment in multiple ways. Nutrient addition often increases photosynthetic rate and above-ground plant productivity (Fay et al., 2015; Liang et al., 2020). As photosynthetic rate and productivity increase, more evapotranspiration may reduce soil water availability (Rose et al., 2012). Similarly, productive communities have large amounts of standing vegetation that can reduce light availability (Borer et al., 2014; DeMalach et al., 2017), which often leads to increased competition for light (Eskelinen et al., 2022; Hautier et al., 2009). Nutrient addition can also shift communities towards strategies that favour rapid acquisition of available resources (i.e. high tissue nutrient concentrations and metabolic rates; Cappelli et al., 2020; Cui et al., 2020), which may subsequently hinder seedling establishment (Davis et al., 2000). Together, these responses to nutrient addition may promote priority effects that can benefit larger, established residents and limit seedling establishment (Craine & Dybzinski, 2013; Tilman, 2004).

Like nutrients, consumers also influence colonization success in multiple ways. For instance, fungal pathogens and insect herbivores can reduce photosynthetic rates and standing plant biomass (Aldea et al., 2006; Allan et al., 2010; Coupe & Cahill, 2003; Mitchell, 2003; Seabloom et al., 2017), which can increase the availability of key resources like light and water (Heinen et al., 2022; Wilfahrt et al., 2020). The impacts of fungal pathogens and insect herbivores on community dynamics often depend on the characteristics of the consumers. When pathogens and herbivores preferentially impact dominant plants, they can promote colonization and increase community richness (Mordecai, 2011). This may result from reductions in the performance of resident individuals and the size of resident populations (Alexander, 2010; Katz, 2016). When pathogens and herbivores more strongly impact rare species, such as when generalists spill over from common plant species to rare ones, they can limit community diversity (Mordecai, 2011). Furthermore, high levels of disease and herbivory can promote conservative strategies among the resident community (i.e. low tissue nutrient concentrations and metabolic rates; Borer et al., 2015; Fine et al., 2004). Plants with conservative resource use strategies may be better defended against consumers, but less successful competitively (Pérez-Ramos et al., 2019).

In addition to their independent effects, nutrients can interact with herbivores and pathogens to alter colonization. First, high nutrient supply can shift community composition towards individuals and species with acquisitive traits, such as high growth rates, photosynthetic rates and foliar nutrient concentrations (Díaz et al., 2016; Reich, 2014). Due to physiological trade-offs, species with acquisitive phenotypes often allocate minimally to defence against herbivores and pathogens (Endara & Coley, 2011; Heckman et al., 2019; Züst & Agrawal, 2017). This leads to predictable changes in community composition: species that benefit from nutrient-rich environments may be most impacted by herbivores and pathogens and are likely to benefit most from their exclusion (Halliday et al., 2019; Heckman et al., 2019; Liu et al., 2017). Second, nutrient addition can increase plant tissue quality (e.g. higher foliar nitrogen concentrations) irrespective of changes in community composition, leading to higher rates of herbivory and disease on species within a community (Mattson, 1980; Veresoglou et al., 2013). As a result, impacts of fungal pathogens and insect herbivores are often greater in nutrient-rich habitats than in nutrient-poor habitats (Hahn & Maron, 2016; Mattson, 1980). Third, nutrient addition can alter the physical structure of communities. When standing biomass is higher, for example, increased humidity within the canopy could benefit fungal pathogens (Cappelli et al., 2020). Finally, by jointly impacting plant production, nutrients and consumers can alter the availability of other resources—like water and light—that are critical for colonization.

Nutrients and consumers can alter another important determinant of seedling establishment—leaf litter. Because the abundance of leaf litter often increases with plant community productivity (Foster & Gross, 1998), factors that increase biomass production,

like nutrient addition or consumer exclusion, can promote litter accumulation. The build-up of leaf litter may exacerbate the size-asymmetric advantage in light competition that larger resident plants have against smaller colonizers (Foster & Gross, 1998), which may be especially important early in the growing season when the plant canopy is sparser. Beyond impacting light availability, litter can increase soil water availability by reducing evaporation from exposed soil (Deutsch et al., 2010), increase fungal disease by increasing the prevalence of overwintering fungal spores (Roy et al., 2014) and increase insect herbivory by providing habitat for herbivorous insects (Karban et al., 2012). Litter can also alter community functional composition by promoting acquisitive strategies that enhance competition for light (Letts et al., 2015).

Some determinants of establishment success may impact all potential colonizers similarly, while others may be determined by the characteristics of colonizing species. Drastically reducing the availability of a critical resource, like light or soil water, should reduce establishment by all but the most drought- or shade-tolerant species. This could lead to reductions in both the total number of seedlings that establish and their species richness (Borer et al., 2014). On the contrary, specialist herbivores or pathogens may prevent one or a few related species from establishing, while having no impact on other species (Mordecai, 2011). Thus, specialist consumers may impact colonizer richness more than the total number of established seedlings. Seedling functional strategies may also impact establishment. When consumers are present, conservative strategies among colonizing species may be advantageous because these plants will be better defended against herbivores and pathogens; the absence of consumers may promote more acquisitive colonizer strategies because these plants may be able to grow more quickly to take advantage of available resources (Blumenthal, 2006).

In this three-year study, I factorially manipulated (1) soil nutrient supply, (2) leaf litter presence and (3) consumer access (fungal pathogens + insect herbivores) to herbaceous old field communities. In the second and third years, I added seeds of 11 native species to each community and measured changes in five community attributes important for seedling success—water and light availability, community functional composition and disease and herbivory—in order to test: (1) whether nutrients, leaf litter and consumers interact to influence total seedling establishment and the richness of colonizing species, (2) whether these interactions are mediated by the same abiotic or biotic community attributes (Table S1), and (3) whether nutrients, leaf litter and consumers differentially impact the success of colonizing species with different resource allocation strategies.

2 | METHODS

2.1 | Study site

I performed this study in the Duke Forest Teaching and Research Laboratory (Orange Co., NC; research registration number R1112-314) in an old field that was abandoned in 1996. Since 1996, annual mowing has maintained herbaceous dominance by perennial species, including three dominant exotic species—*Lespedeza cuneata*, *Lonicera japonica* and *Schedonorus arundinaceus*, which constitute two-thirds of community cover (Heckman et al., 2016)—as well as several native species typical of North Carolina old fields (Oosting 1942).

2.2 | Experimental design

This study used a split-plot experimental design. I factorially manipulated (1) soil nutrient supply and (2) access by two important consumer groups—fungal pathogens and insect herbivores—to communities for 3 years at the whole-plot level. At the subplot level, I manipulated leaf litter for 2 years. This yielded a study that comprised 40 plots (2 nutrient supply levels × 2 consumer access levels × 10 replicate blocks). Each plot included two leaf litter removal subplots, for a total of 80 subplots within these 40 plots.

In May 2012, I established 40 2-m × 2-m plots separated by 1-m aisles and began the nutrient supply and consumer access treatments. I manipulated soil nutrient supply at two levels (fertilized with 10 g m^{-2} $year^{-1}$ N, P and K vs. not fertilized). This level of fertilization successfully alleviated nutrient limitation to communities of similar composition at this site (Fay et al., 2015). I manipulated consumer (fungal pathogen and insect herbivore) access to plots at two levels (sprayed with fungicide and insecticide vs. not sprayed). To do this, I sprayed all above-ground biomass within a plot every 2–3 weeks throughout the main growing season (April–October) with nonsystemic, broad-spectrum biocides. Repeated biocide application was necessary to protect newly produced tissue and to counter biocide degradation caused by rain and light. Neither the fungicide (mancozeb, Dithane® DF, Dow AgroSciences, Indianapolis, IN) nor the insecticide (es-fenvalerate, Asana® XL, Dupont, Wilmington, DE) affected the growth of species common at this site under greenhouse conditions, including many of the species present in this study (Heckman et al., 2016). Previous research indicates that the fungicide does not affect mycorrhizal fungi when applied at recommended rates (Parker & Gilbert, 2007).

This site was dominated by perennial grasses that can produce thick (5–15 cm) litter layers. Within each 2-m × 2-m plot, I manipulated leaf litter in one of two randomly selected 0.5-m^2 subplots within the central 1 m^2 of the plot at two levels (raked to remove all standing dead biomass and leaf litter on the ground vs. unraked). I first applied this treatment early in the second year of the study (February 2013) and repeated it early in the third year (March 2014).

2.3 | Seed addition

Early in the second year and third years of this study—February 2013 and March 2014—I removed litter from plots and then immediately added seeds of 11 native species to each plot at a rate of 1 g seed m^{-2} ground area $species^{-1}$ $year^{-1}$ (see Table S2 for details). This seed

addition rate accounts for the general increase in colonization ability with increasing seed size (Turnbull et al., 1999). For one extremely large-seeded species, *Tripsacum dactyloides*, I added a greater mass (4 g seed m^{-2} $year^{-1}$) of seeds because 1 g seed m^{-2} would have been insufficient to account for potentially low germination (see Table S2 for seed masses). Adding seeds in the second and third years of the study allowed more time for the consumer and nutrient treatments to influence community composition. I measured seedling success late in the second and third years of the study—late August 2013 and September 2014—as the number of established seedlings in each 0.5-m^2 subplot (seedling establishment) and the number of species of established seedlings (colonizer richness).

2.4 | Community attributes

In 2013 and 2014, I measured several abiotic and biotic community attributes that could impact seedling success. Measurements differed between years and were more extensive in 2014 than in 2013. Specifically, in 2014, I measured soil water availability, light availability, community disease and herbivory, and community leaf N_{MASS}; in 2013, I measured light availability and community disease and herbivory. I first describe the measurements taken in 2014, then describe any differences from 2013 measurements (see Table S3 for details). During the 2014 growing season, I repeatedly measured the availability of water and light. Specifically, I measured soil water availability at 10-cm soil depth using a time-domain reflectometer (HydroSense Soil Water Content Measurement System, Campbell Scientific Australia) once per month (May–September 2014). Because there was no strong directional trend in soil water availability over the growing season, soil water availability of each subplot was the arithmetic mean of the five soil water measurements. I also measured light availability, the ratio of photosynthetically active radiation at two points at ground level to above the canopy × 100 (Borer et al., 2014). Light availability was measured monthly (March–September) within 2 h of solar noon on cloudless days (Accupar LP80 Ceptometer, Decagon Devices, Pullman, WA) and then integrated into a single value per subplot (auc() function in the R package MESS; Ekstrøm, 2016). Thus, light availability represented the average proportion of light (μmol PAR m^{-2} s^{-1} day^{-1}) available at ground level at solar noon over the 2014 field season. I also measured light availability at a single time point in September 2013, using the same approach (i.e. the ratio of ground level to above canopy light).

To assess community disease and herbivory, and community leaf N_{MASS}, I first visually quantified per cent cover of each plant species in each subplot in August. Because I evaluated cover for each species independently, the sum of cover values for each plot could exceed 100%.

I used different methods to assess foliar fungal disease and insect herbivory in communities in 2013 and 2014. In 2014, I maximized the number of host species surveyed in each subplot by haphazardly assessing damage on 20 leaves of the most abundant host species and each subsequent species, iterating until the summed cover of all sampled species was at least 80% of the subplot's total plant cover (Halliday et al., 2019). This sampling scheme is consistent with scheme recommendations for measuring other plot-scale community responses (Halbritter et al., 2020). In total, I surveyed fungal disease and insect herbivory on 23 species—12 grasses, 6 nonleguminous forbs, 3 woody vines, 1 tree and 1 leguminous forb. Following Heckman et al. (2016), Mitchell et al. (2002) and Mitchell (2003), I sampled leaves that varied in age, location within the subplot and degree of damage. For each sampled leaf, I recorded the per cent of the leaf's area that was damaged (by guilds of insect herbivore and fungal morphospecies) by referring to digitized images of known damage severity (James, 1971). I then calculated community disease and community herbivory.

$$\text{Community disease or herbivory} = \sum_{i=1}^{n} d_{i\ \text{subplot}} \left(\frac{c_{i\ \text{subplot}}}{c_{t\ \text{subplot}}} \right),$$

where $d_{i\ \text{subplot}}$ is mean per cent of leaf area damaged by fungal pathogens or insect herbivores for the *i*th species in the subplot, $c_{i\ \text{subplot}}$ is per cent cover of the *i*th species, and $c_{t\ \text{subplot}}$ is the total cover of species surveyed in the subplot (Mitchell et al., 2002).

In 2013, I surveyed disease and herbivory at the plot level rather than the subplot level. I surveyed fungal disease and insect herbivory on 18 species—8 grasses, 5 nonleguminous forbs, 3 woody vines, 1 tree and 1 leguminous forb.

To assess the resource allocation strategies of the resident community, I calculated community-weighted mean leaf % N (hereafter, community N_{MASS}) using the same species and calculation as community disease and herbivory in 2014. N_{MASS} has been shown to covary significantly with several other important functional traits (e.g. leaf mass per area, carbon assimilation and dark respiration; Díaz et al., 2016; Reich, 2014; Wright et al., 2004). From all species that constituted >80% of relative cover in each subplot, three young fully emerged leaves were harvested, dried at 60°C for 72 h and ground to a fine powder; leaf % N was quantified using a micro-Dumas combustion analyzer (Environmental Chemistry Lab, University of Georgia).

2.5 | Seedling traits

To assess the resource allocation strategies of the species added as seeds, I measured leaf % N on individuals of each species grown in the greenhouse at the University of North Carolina at Chapel Hill. All seeds were stratified in moist sand at 4°C for 1 month and then sowed into 0.94-L pots (Deepots, Stuewe and Sons, Corvallis, OR) containing a 50:50 mixture of potting medium (Fafard 3B, Sun Gro Horticulture, Agawam, MA, USA) and sterilized sand. At the two-leaf stage, each pot was thinned to a single individual and then randomly assigned to one of two groups: high nutrient supply, receiving the equivalent of 10 g NPK m^{-2}, and low nutrient supply, receiving the equivalent of 2 g NPK m^{-2}. I added slow-release forms of P and K once (triple super phosphate and potassium sulphate, respectively) and aqueous N in five biweekly applications of ammonium nitrate.

These two nutrient levels were intended to generate differences in nutrient limitation similar to what plants experienced in the field experiment; Heckman et al. (2019) also used these nutrient levels to achieve the same goal. To avoid limitation by micronutrients, both treatments received 100 g m^{-2} micronutrients (Micromax, The Scotts Company, Marysville, OH, USA). After 8 weeks in the greenhouse, I removed the youngest fully emerged leaf from each plant and processed them as described for community N_{MASS}. Four species could not be analysed due to poor germination (*Asclepias syriaca*, *Tripsacum dactyloides*) or limited growth (*Solidago pinetorum*, *Symphyotrichum pilosum*) in the greenhouse. Thus, I measured seedling % N on 70 plants (7 species × 2 nutrient supply levels × 5 replicates).

2.6 | Data analysis

In this study, I used Bayesian hierarchical models (brms package—Bürkner, 2017, Stan—Carpenter et al., 2017, R version 4.2.1—R Core Team, 2022), primarily with data collected in 2014, to address three questions. To answer the first question—whether nutrient supply, litter presence and consumer access interact to influence total seedling establishment and the richness of colonizing species—I examined treatment effects on seedling establishment (the number of seedlings in each subplot) and colonizer richness (species richness of colonizing seedlings) in September 2014. For each response, the full model included additive and pairwise interactive effects of nutrient addition, litter removal and consumer exclusion, a random effect of plot to account for the split-plot nature of the experiment, an observation-level random effect to account for overdispersion (Harrison, 2014) and Poisson errors with a log link (see Appendix A1 for complete model specification). The final simplified model omitted interactive treatment effects whose 90% credible intervals overlapped 0.

To evaluate the second question—whether interactive effects of nutrients, litter and consumers on seedling establishment and colonizer richness are mediated by the same community attributes—I used a multivariate hierarchical Bayesian model. This hierarchical model had a two-level structure, where each experimental treatment and two-way interactions between experimental treatments influenced five standardized (mean = 0; standard deviation = 1) community attributes—logit-transformed light availability, soil water availability, community N_{MASS}, logit-transformed community disease (foliar fungal disease) and logit-transformed community herbivory (foliar insect herbivory)—and those community attributes plus direct effects of nutrient supply and consumer access (to account for potentially missing mediators) could subsequently influence seedling establishment and colonizer richness (Table S1). For each response, I included plot as a random effect. The effects of experimental treatments on these community attributes were modelled with a Gaussian distribution and an identity link (i.e. linear mixed model); the effects of experimental treatments and community attributes on seedling establishment and colonizer richness were modelled with a Poisson distribution and a log link (i.e. Poisson generalized linear mixed model); correlations among community attributes and among seedling establishment and colonizer richness were also modelled. The full multivariate model included all main effects of, and two-way interactions among, treatments on community attributes. The final, simplified multivariate model omitted effects whose 90% credible intervals overlapped 0 (see Appendix A2 for full model specification).

To determine how general the answers to the first and second questions were across years, I repeated the analyses described above using data from the previous year, 2013. For the first question, I took the approach described above. For the second question, I modified the previously described approach in two ways. First, the 2013 multivariate model only included three of the five community attributes—logit-transformed light availability, logit-transformed community disease and logit-transformed community herbivory. Second, because community disease and herbivory were measured at the plot level in 2013 (rather than the subplot level, as in 2014), litter removal was not included as a predictor of community disease and herbivory. Model specifications are described in Appendix A3.

To assess the third question—whether nutrients, litter and consumers interact to differentially impact the success of colonizing species with different resource allocation strategies—I again used a multivariate hierarchical Bayesian model. To do this, I examined treatment effects on seedling establishment separately by species and how these treatment effects interacted with seedling % leaf N (hereafter, seedling N_{MASS}) measured from greenhouse-grown plants. This model included four community attributes—logit-transformed light availability, soil water availability, community N_{MASS} and logit-transformed community damage (foliar fungal disease + insect herbivory)—plus seedling N_{MASS}, which was averaged across multiple replicates of two nutrient levels from greenhouse measurements, and was treated as a species-level effect. Because this model addressed the ability of individual species' traits to predict species-level establishment success, it does not include colonizer richness as a response. This model also included random effects of plot and subplot nested within plot (to account for species-level differences). Because species-level seedling establishment was low, I used a zero-inflated Poisson model with a species-level random effect on the zero-inflated term (Appendix A4). This model included only 6 of the 11 species sown in this study. One species was removed because it was absent from all experimental plots (*Sorghastrum nutans*). Four other species had poor germination (*Asclepias syriaca*, *Tripsacum dactyloides*) or limited growth (*Solidago pinetorum*, *Symphyotrichum pilosum*) in the greenhouse, and thus, no values for seedling $N_{MASS.}$

The full prior specifications for these models are described in Appendix A. Briefly, I used weakly informative priors on all fixed and random effects (i.e. population-level and group-level parameters, respectively). Using more diffuse priors on the fixed effects did not qualitatively change the results. Each model was fit using four chains, each with 5000 Hamiltonian Monte Carlo iterations. Chains converged on a stationary distribution based

on trace plots and model diagnostics (Rhat = 1). Models adequately fit the data based on visual posterior predictive checks (pp_check() function). I also calculated marginal Bayesian R^2 to assess the proportion of variance explained by fixed effects (r2_bayes() function in performance R package; Gelman et al., 2019, Lüdecke et al., 2021).

3 | RESULTS

3.1 | Do nutrients, litter and consumers interact to influence seedling success?

The first prediction, that nutrient supply, litter presence and consumer access will interactively influence seedling establishment and colonizer richness, had little support. Contrary to expectations, none of the three treatments interactively altered seedling establishment or colonizer richness (all 90% credible intervals overlapped 0; Table S4). Rather, nutrient addition, litter removal and consumer exclusion each independently altered colonization. Specifically, nutrient addition reduced seedling establishment and colonizer richness by 97% and 95%, respectively; litter removal increased seedling establishment and colonizer richness by 158% and 84%, respectively; and consumer exclusion reduced these responses by 48% and 28%, respectively (Table S5, Figure 1a).

3.2 | Do interactive effects occur via the same community attributes?

The second prediction, that nutrients, litter and consumers would alter common mediators, also had limited support. All interactive effects of treatments on community attributes had credible intervals that substantially overlapped 0 (Table S6). Moreover, nutrient addition, litter removal and consumer exclusion each primarily influenced colonization via different mechanisms (Table S7, Figure 1b), which may explain the lack of support for the first prediction. After simplifying the model, the effects did not qualitatively differ from those in the full multivariate hierarchical model.

Nutrient addition reduced colonization through multiple mechanisms: directly and indirectly by reducing soil water and light availability and indirectly by increasing community N_{MASS}. Specifically,

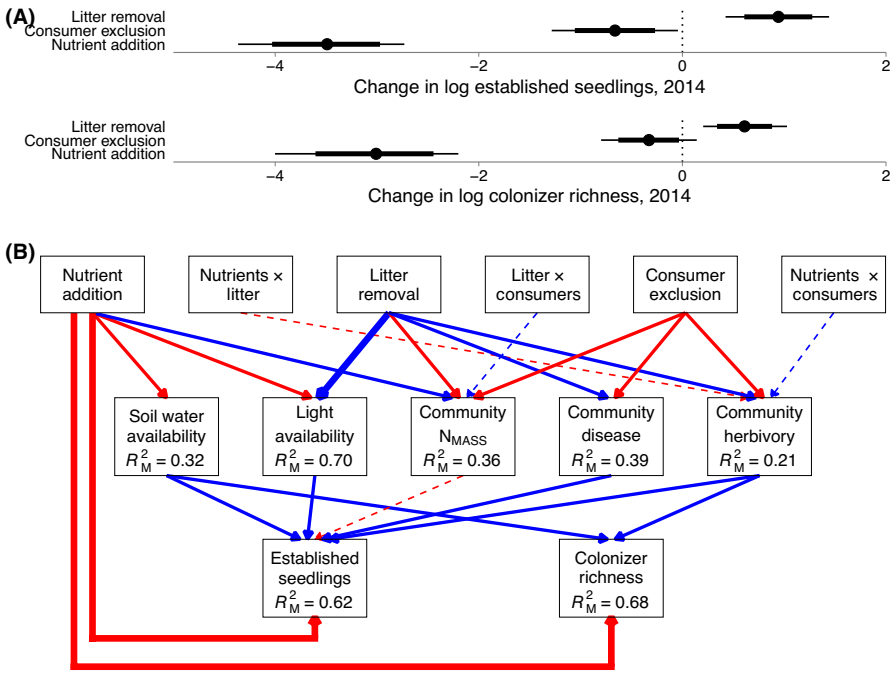

FIGURE 1 Direct and indirect effects of nutrient addition, litter removal and consumer exclusion on seedling success in 2014. (a) Point estimates and 80% and 95% credible intervals from a Bayesian hierarchical model showing treatment effects on seedling establishment and colonizer richness (see Table S5 for model estimates). (b) Results from a multivariate hierarchical Bayesian model used to examine the effects of nutrient addition, litter removal, consumer exclusion and their interactions on seedling performance mediated by soil water and light availability, community leaf N_{MASS}, community disease (foliar fungal disease) and community herbivory (foliar insect herbivory; see Table S7 for model estimates). Width and colour of arrows represent relative effect sizes (blue, positive; red, negative; solid wide, large effect (effect size > |1|), solid narrow, moderate effect (effect size < |1|), dashed, marginally significant). Effects on seedling success (seedling establishment and colonizer richness) were calculated from a Poisson generalized linear mixed model; all other effects were from linear mixed models. All community attributes were standardized (mean = 0, standard deviation = 1); community disease, community herbivory and light availability were logit-transformed first. R^2_M values are marginal Bayesian R^2 which only account for variance explained by fixed effects.

after accounting for covariates, nutrient addition directly reduced seedling establishment by 94% and colonizer richness by 92% (Table S7, Figure S2A,G, Figure 1b). This direct statistical effect likely indicates that an important covariate was not accounted for in this model. Nutrient addition also had strong effects on other resources. Nutrient addition reduced soil water availability by 15% (Figure S1A), which drove a 22% reduction in seedling establishment and a 28% decline in colonizer richness (Table S7, Figure S2B,H, Figure 1b). Similarly, nutrient addition reduced light availability by 34% (Figure S1B), which drove a 14% reduction in seedling establishment (Table S7, Figure S2C, Figure 1b). Moreover, nutrient addition increased community N_{MASS} by 17% (Figure S1C), which indirectly reduced seedling establishment by 24% (Table S7, Figure S2D, Figure 1b).

Litter removal's effect on seeding success was driven by two main factors. First, litter removal increased light availability by 230%, on average, throughout the growing season (Figure S1D), which increased seedling establishment by 70% (Table S7, Figure S2C, Figure 1b). Second, this effect was reinforced by a litter-removal-mediated increase in community disease and herbivory: Litter removal increased community disease by 40% on average (Figure S1F), leading to a 12% increase in seedling establishment (Table S7, Figure S2E, Figure 1b). Likewise, litter removal increased community herbivory by 235% (Figure S1G), which resulted in a 39% increase in seedling establishment and a 27% increase in colonizer richness (Table S7, Figure S2F, Figure 1b). Litter removal also reduced community N_{MASS} by 10% (Figure S1E), but this only reduced seedling establishment by 4% (Table S7, Figure S2D, Figure 1b).

Consumer exclusion reduced seedling success through multiple mechanisms that were largely distinct from those altered by nutrient addition. Unlike nutrient addition, and contrary to predictions, consumer exclusion did not alter light or soil water availability. Like nutrient addition, consumer exclusion altered community N_{MASS}, but the effects were in opposite directions—consumer exclusion reduced community N_{MASS} by 14% (Figure S1H), which increased seedling establishment by 2% (Table S7, Figure S2D, Figure 1b). Consumer exclusion, instead, reduced colonization primarily by altering community disease and herbivory, which were both unaffected by nutrient addition. Consumer exclusion reduced community disease by 66% (Figure S1I), on average, resulting in a 27% decline in seedling establishment (Table S7, Figure S2E, Figure 1b). Consumer exclusion also reduced community herbivory by 75% (Figure S1J), which resulted in a 20% reduction in seedling establishment and a 25% reduction in colonizer richness (Table S7, Figure S2F,I, Figure 1b). The large consumer-exclusion-driven reduction in community disease and herbivory indirectly harmed the colonizers, which apparently overwhelmed any positive effect that excluding pathogens and herbivores had on them. In support of this inference, there was no significant main effect of consumer exclusion on seedling establishment in the full multivariate hierarchical model after accounting for community disease and herbivory (Table S6).

3.3 | Are effects of nutrients, litter and consumers consistent between years?

Most results were consistent between years. None of the treatments interacted to alter seedling establishment or colonizer richness in 2013 (Table S4, Figure S3A). As in 2014, nutrient addition reduced seedling establishment and colonizer richness (88% and 62% reductions, respectively), litter removal increased seedling establishment and colonizer richness (328% and 103% increases, respectively), and consumer exclusion had no effect on colonizer richness (Table S5, Figure S3A). The most notable difference between years was that the effect of consumer exclusion switched directions—seedling establishment increased by 12% in 2013, but this effect was nonsignificant (Table S5, Figure S3A). Results from the 2013 multivariate hierarchical model are presented in Appendix B and Tables S8 and S9.

3.4 | Does seedling resource allocation strategy impact responses to nutrients, litter and consumers?

Contrary to the third prediction, seedling N_{MASS}, an indicator of seedling resource allocation strategy, only interacted marginally with the nutrient addition and litter removal treatments to alter establishment success (Table S10). However, seedling N_{MASS} interacted with both community N_{MASS} and community damage: as community damage increased, the interactive effects of community N_{MASS} and seedling N_{MASS} on seedling establishment became less pronounced (Table S11, Figure 2). This indicates that as community damage increases, acquisitive seedlings (indicated by high seedling N_{MASS}) become increasingly disadvantaged relative to conservative seedlings (indicated by low seedling N_{MASS}).

4 | DISCUSSION

Nutrient addition and consumer exclusion (fungal pathogens + insect herbivores) largely influenced seedling establishment and colonizer richness independently and via different mechanisms. Adding nutrients reduced seedling establishment indirectly by reducing light and soil water availability, while also directly reducing seedling establishment, which indicates the likely importance of an unmeasured environmental mediator. Exclusion of fungal pathogens and insect herbivores, on the contrary, primarily reduced seedling establishment and colonizer richness indirectly by reducing community disease and herbivory. The fact that nutrient addition reduced light availability—a critical resource for seedling establishment (Borer et al., 2014; DeMalach et al., 2017; Hautier et al., 2009)—while consumer exclusion did not, may also explain the lack of a nutrient addition × consumer exclusion interaction and the larger impacts of nutrients than consumers on seedling success. This lack of interaction is contrary to previous studies that found nutrients and mammalian herbivores interacted to influence community processes by

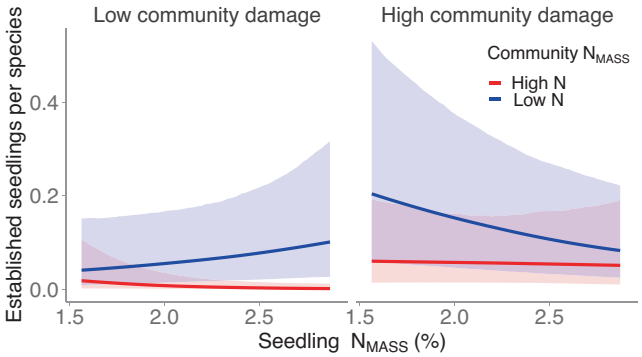

FIGURE 2 Results from a Bayesian hierarchical model used to examine the interactive effects of seedling N_{MASS}, community N_{MASS} and community damage (fungal disease + insect herbivory) on seedling establishment in September 2014 (see Table S11 for model estimates). For community damage and community N_{MASS}, high values are 1 standard deviation above the mean and low values are 1 standard deviation below the mean. Seedling leaf N_{MASS} was determined from eight-week-old plants grown under greenhouse conditions. Curves are derived from a zero-inflated Poisson generalized linear mixed model; confidence ribbons represent 90% credible intervals.

altering the availability of the same resource (e.g., Borer et al., 2014; Eskelinen et al., 2022). While the impacts of mammalian herbivores on community processes are well-studied, a recent meta-analysis lacked enough data to assess the impacts of insect herbivores on some community responses (Jia et al., 2018). Thus, similarities and differences in the impacts of mammalian herbivores and fungal pathogens and insect herbivores on community assembly warrant further study (e.g. Heckman et al., 2016; La Pierre et al., 2015). Together, these results demonstrate that multiple pathways influence seedling establishment, but that interactive effects might only occur in systems where nutrients and consumers leverage the same, critical mediator.

4.1 | Nutrients, litter and consumers influence different mediators of seedling establishment

Nutrient addition reduced colonization in this study substantially and by several distinct mechanisms. First, and most importantly, nutrient addition reduced light availability, which is often an important mediator of the effects of eutrophication on plant diversity (Borer et al., 2014; Harpole et al., 2017; Hautier et al., 2009). This strong impact on light availability is consistent with other work from this system (Wilfahrt et al., 2020). Second, nutrient addition reduced soil water availability, probably because the greater primary production of fertilized plots promoted greater transpiration (Rose et al., 2012). Together, these indirect effects mediated by resource availability may have resulted from the resident community's ability to pre-emptively utilize the increased nutrient supply to reduce the availability of other resources (Hautier et al., 2009). Nutrient addition also promoted increasing community N_{MASS}, which is typical of quick-growing species (Díaz et al., 2016; Reich, 2014). Increasing the abundance of these quick-growing species may have exacerbated priority effects: during the early growing season, resident individuals with established root systems could have quickly utilized the recently applied nutrients to slow seedling establishment and out-compete small seedlings (Craine & Dybzinski, 2013; Schwinning & Weiner, 1998). Together, this suggests that nutrient addition simultaneously promotes quick-growing species and shifts competition from below-ground competition for nutrients to size-asymmetric light competition (DeMalach et al., 2017; Schwinning & Weiner, 1998), which marginally reduces seedling establishment in communities that can respond quickly. Finally, contrary to expectation, nutrient addition did not influence community disease or herbivory (Cappelli et al., 2020).

Nutrient addition also had a direct negative effect on colonization after accounting for environmental covariates. This may have occurred because an important covariate was unaccounted for. For example, the effect of community biomass may not be fully explained by other environmental variables. In another study at this site, light availability was a statistically significant predictor of, but explained relatively little variation in, community biomass ($p < 0.001$, $R^2_M = 0.08$; Borer et al., 2014; Fay et al., 2015). Additionally, this direct effect may have resulted from a mismatch between the spatial and temporal scales of light and soil water availability measurements and those most relevant for establishing seedlings. For instance, seedlings may have been influenced only by soil water availability in the top layer of soil or during periods of acute drought (Harrington, 1991; Padilla & Pugnaire, 2007), which may be missed by monthly measurements of slightly deeper soil water. Similarly, seedling establishment may depend more on light availability at a single developmental stage than on light integrated over the entire growing season (Hutchings & Booth, 1996). Thus, while nutrient addition detectably reduced light and soil water availability, which subsequently reduced seedling establishment, my measurements of these resources may not have fully captured their importance for seedling establishment.

Seedling establishment and colonizer richness both increased with community herbivory in 2014, while seedling establishment also increased with community disease. This suggests that consumers had large enough impacts on the resident community to influence competition with establishing seedlings. Because populations of resident species were denser than the establishing seedlings, consumers that regulate plant populations in a density-dependent manner would have larger impacts on resident species than on establishing seedlings (Connell, 1971; Gilbert, 2002; Janzen, 1970). This explanation is supported by other results from this system: excluding consumers from communities planted with native herbaceous species limited establishment by exotic herbs and native trees (Heckman et al., 2017, 2022). Thus, consumers may promote population growth when species are rare, but limit population growth as they increase in abundance (Mordecai, 2011).

The impact of consumers on seedling establishment was considerably larger in the final year of this study than in the previous

year. This may have resulted from a combination of factors. First, community fungal disease and insect herbivory in unsprayed plots were twice as high in 2014 as in 2013 (combined damage: 9.7% and 4.5%, respectively), which may have resulted in differences in consumer pressure on plant populations between years. Consumer pressure can vary annually for a number of reasons, including differences in temperature and precipitation (e.g. Liu et al., 2019; Scherber et al., 2013), which highlights a key consideration when interpreting consumer reduction studies: consumer exclusion only yields detectable changes in plant performance when ambient consumer pressure is sufficiently high. Second, effects of consumer exclusion on community composition may require several years to observe (Agrawal & Maron, 2022; Allan & Crawley, 2011; Komatsu et al., 2019; Wilfahrt et al., 2020), especially when consumer pressure is not consistently high. Thus, longer studies, which can incorporate years with varied environmental conditions, may be required to better understand the average impacts of fungal pathogens and insect herbivores on community processes.

Litter removal enhanced seedling success via several mechanisms. As predicted, the largest effect of litter removal was to increase light availability, which drastically increased seedling establishment (Foster & Gross, 1998). Similarly, litter removal reduced community N_{MASS}. Reduced competition for light in litter removal plots may have allowed plants with more conservative (i.e. low N_{MASS}) strategies to thrive (Letts et al., 2015), which marginally increased seedling establishment. Contrary to prediction, however, litter removal increased community disease and herbivory. This may have occurred because litter can intercept fungal spores before they land on live tissue or obscure growing leaves and stems from insect herbivores. In total, although the magnitude of effects differed considerably, all indirect effects of litter removal promoted increased seedling success.

4.2 | Effects of seedling resource allocation strategies on establishment success

Seedling resource allocation strategy was an important determinant of establishment success that was related to consumer pressure. Contrary to prediction, species with more acquisitive resource allocation strategies had low establishment success regardless of consumer pressure, which is consistent with some previous work (Kempel et al., 2013). For species with more conservative resource strategies (i.e. lower seedling N_{MASS}), establishment success increased with increasing consumer pressure (i.e. higher community damage). This suggests that the increased seedling establishment in unsprayed plots was driven primarily by responses from more conservative species, which are frequently well defended (Endara & Coley, 2011). Thus, consumers had stronger negative impacts on the resident community than on colonizer species (Mordecai, 2011), but only when the colonizers possessed traits that were advantageous in the presence of consumers. This has important implications for understanding community assembly: High consumer pressure may promote the establishment of species with more conservative resource allocation strategies, but reducing consumer pressure fails to promote greater establishment of acquisitive species.

5 | CONCLUSIONS

By experimentally manipulating seed rain, this study explicitly evaluated the role of recruitment in community assembly, which may be key to understanding long-term community responses to nutrients and consumers. Specifically, these results show that nutrients, leaf litter, and fungal pathogens and insect herbivores influence colonization through multiple independent mechanisms rather than altering the same environmental pathways. These independent effects may have been driven by priority effects and differences in population size. Fungal pathogens and insect herbivores benefitted native seedlings in these communities in one year, suggesting that consumers regulate populations in a density-dependent manner (Gilbert, 2002; Mordecai, 2011). Increasing nutrient supply reduced seedling establishment, likely because larger, established individuals were able to pre-emptively use most of these nutrients to reduce the availability of light and water. Over time, nutrient addition may reduce community richness by increasing the abundance of quick-growing, strong light competitors (Borer et al., 2014; DeMalach et al., 2017; Hautier et al., 2009) and decreasing light availability to seedlings (Foster & Gross, 1998). Thus, only when nutrients and consumers alter the same critical mediators are their synergistic effects on community assembly mechanisms, such as seedling establishment, likely to arise.

AUTHOR CONTRIBUTIONS

Robert W. Heckman designed and performed the study, analysed the data and wrote the manuscript.

ACKNOWLEDGEMENTS

J. Bruno, J. Cronin, P. Fay, F. Halliday, C. Mitchell, R. Peet, M. Rua, J. Umbanhowar, M. Welsh, P. Wilfahrt, J. Wright and members of the Farrior lab group provided advice on this study. L. Fridie, F. Halliday, T. Hodges, A. Kinniburgh, J. Napier, E.A. Reece, M. Sandoval, S. Tolar and P. Wilfahrt helped with field and lab work. S. Kay helped with model specifications. This study was funded by a Doctoral Dissertation Improvement Grant (NSF-DEB-1311289). UNC's Alma Holland Beers Scholarship and WC Coker Fellowship provided summer funding. This study was supported in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions of this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy.

CONFLICT OF INTEREST STATEMENT

The author declares no competing interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14204.

DATA AVAILABILITY STATEMENT

Data associated with this study are available from the USDA Forest Service Research Data Archive: https://doi.org/10.2737/RDS-2023-0047 Heckman (2023).

ORCID

Robert W. Heckman https://orcid.org/0000-0002-2281-3091

REFERENCES

Agrawal, A. A., & Maron, J. L. (2022). Long-term impacts of insect herbivores on plant populations and communities. *Journal of Ecology*, *110*, 2800–2811.

Aldea, M., Hamilton, J. G., Resti, J. P., Zangerl, A. R., Berenbaum, M. R., Frank, T. D., & DeLucia, E. H. (2006). Comparison of photosynthetic damage from arthropod herbivory and pathogen infection in understory hardwood saplings. *Oecologia*, *149*, 221–232.

Alexander, H. M. (2010). Disease in natural plant populations, communities, and ecosystems: Insights into ecological and evolutionary processes. *Plant Disease*, *94*, 492–503.

Allan, E., & Crawley, M. J. (2011). Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecology Letters*, *14*, 1246–1253.

Allan, E., van Ruijven, J., & Crawley, M. J. (2010). Foliar fungal pathogens and grassland biodiversity. *Ecology*, *91*, 2572–2582.

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*, 887–895.

Borer, E. T., Lind, E. M., Ogdahl, E. J., Seabloom, E. W., Tilman, D., Montgomery, R. A., & Kinkel, L. L. (2015). Food-web composition and plant diversity control foliar nutrient content and stoichiometry. *Journal of Ecology*, *103*, 1432–1441.

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., … Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*, 517–520.

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *80*, 28.

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*, 1349–1359.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M. A., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, 32.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. D. Boer & G. R. Gradwell (Eds.), *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen. (pp. 298–312).

Coupe, M. D., & Cahill, J. F. (2003). Effects of insects on primary production in temperate herbaceous communities: A meta-analysis. *Ecological Entomology*, *28*, 511–521.

Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, *27*, 833–840.

Cui, E., Weng, E., Yan, E., & Xia, J. (2020). Robust leaf trait relationships across species under global environmental changes. *Nature Communications*, *11*, 2999.

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534.

DeMalach, N., Zaady, E., & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecology Letters*, *20*, 60–69.

Deutsch, E. S., Bork, E. W., & Willms, W. D. (2010). Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics. *Plant Ecology*, *209*, 135–145.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171.

Ekstrøm, C. (2016). *MESS: Miscellaneous esoteric statistical scripts*. R package version 0.4-3. http://CRAN.R-project.org/package=MESS

Endara, M. J., & Coley, P. D. (2011). The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology*, *25*, 389–398.

Eskelinen, A., Harpole, W. S., Jessen, M.-T., Virtanen, R., & Hautier, Y. (2022). Light competition drives herbivore and nutrient effects on plant diversity. *Nature*, *611*, 301–305.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., … Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, *1*, 15080.

Fine, P. V. A., Mesones, I., & Coley, P. D. (2004). Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, *305*, 663–665.

Foster, B. L., & Gross, K. L. (1998). Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology*, *79*, 2593–2602.

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. *The American Statistician*, *73*, 307–309.

Gilbert, G. S. (2002). Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology*, *40*, 13–43.

Hahn, P. G., & Maron, J. L. (2016). A framework for predicting intraspecific variation in plant defense. *Trends in Ecology & Evolution*, *31*, 646–656.

Halbritter, A. H., De Boeck, H. J., Eycott, A. E., Reinsch, S., Robinson, D. A., Vicca, S., Berauer, B., Christiansen, C. T., Estiarte, M., Grünzweig, J. M., Gya, R., Hansen, K., Jentsch, A., Lee, H., Linder, S., Marshall, J., Peñuelas, J., Kappel Schmidt, I., Stuart-Haëntjens, E., … Vandvik, V. (2020). The handbook for standardized field and laboratory measurements in terrestrial climate change experiments and observational studies (ClimEx). *Methods in Ecology and Evolution*, *11*, 22–37.

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*, 138–148.

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Hagenah, N., Kirkman, K., La Pierre, K. J., … Stevens, C. J. (2017). Out of the shadows: Multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Functional Ecology*, *31*, 1839–1846.

Harrington, G. N. (1991). Effects of soil moisture on shrub seedling survival in semi-arid grassland. *Ecology*, *72*, 1138–1149.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616.

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*, 636–638.

Heckman, R. W. (2023). Abiotic and biotic attributes of an old field community impacting colonization in response to nutrient addition, litter removal, and consumer exclusion. *Forest Service Research Data Archive*, https://doi.org/10.2737/RDS-2023-0047

Heckman, R. W., Halliday, F. W., & Mitchell, C. E. (2019). A growth–defense trade-off is general across native and exotic grasses. *Oecologia*, *191*, 609–620.

Heckman, R. W., Halliday, F. W., & Wilfahrt, P. A. (2022). Nutrients and consumers impact tree colonization differently from performance in a successional old field. *Oecologia*, *198*, 219–227.

Heckman, R. W., Halliday, F. W., Wilfahrt, P. A., & Mitchell, C. E. (2017). Effects of native diversity, soil nutrients, and natural enemies on exotic invasion in experimental plant communities. *Ecology*, *98*, 1409–1418.

Heckman, R. W., Wright, J. P., & Mitchell, C. E. (2016). Joint effects of nutrient addition and enemy exclusion on exotic plant success. *Ecology*, *97*, 3337–3345.

Heinen, R., Thakur, M. P., Hiddes De Fries, J. R., Steinauer, K., Vandenbrande, S., Jongen, R., & Bezemer, T. M. (2022). Foliar herbivory on plants creates soil legacy effects that impact future insect herbivore growth via changes in plant community biomass allocation. *Functional Ecology*, *36*, 1047–1062.

Hutchings, M. J., & Booth, K. D. (1996). Studies of the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. *Journal of Applied Ecology*, *33*, 1182–1190.

James, C. (1971). *A manual of assessment keys for plant diseases*. American Phytopathological Society.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*, 501–528.

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., & Luskin, M. S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 6237–6242.

Karban, R., Grof-Tisza, P., & Holyoak, M. (2012). Facilitation of tiger moths by outbreaking tussock moths that share the same host plants. *Journal of Animal Ecology*, *81*, 1095–1102.

Katz, D. S. W. (2016). The effects of invertebrate herbivores on plant population growth: A meta-regression analysis. *Oecologia*, *182*, 43–53.

Kempel, A., Chrobock, T., Fischer, M., Rohr, R. P., & van Kleunen, M. (2013). Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 12727–12732.

Kempel, A., Razanajatovo, M., Stein, C., Unsicker, S. B., Auge, H., Weisser, W. W., Fischer, M., & Prati, D. (2015). Herbivore preference drives plant community composition. *Ecology*, *96*, 2923–2934.

Komatsu, K. J., Avolio, M. L., Lemoine, N. P., Isbell, F., Grman, E., Houseman, G. R., Koerner, S. E., Johnson, D. S., Wilcox, K. R., Alatalo, J. M., Anderson, J. P., Aerts, R., Baer, S. G., Baldwin, A. H., Bates, J., Beierkuhnlein, C., Belote, R. T., Blair, J., Bloor, J. M. G., … Zhang, Y. (2019). Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences*, *116*, 17867–17873.

La Pierre, K. J., Joern, A., & Smith, M. D. (2015). Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie community composition and forb biomass. *Oikos*, *124*, 842–850.

Letts, B., Lamb, E. G., Mischkolz, J. M., & Romo, J. T. (2015). Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. *Plant Ecology*, *216*, 357–370.

Liang, X., Zhang, T., Lu, X., Ellsworth, D. S., BassiriRad, H., You, C., Wang, D., He, P., Deng, Q., Liu, H., Mo, J., & Ye, Q. (2020). Global response patterns of plant photosynthesis to nitrogen addition: A meta-analysis. *Global Change Biology*, *26*, 3585–3600.

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.

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*, 1574–1584.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*, 3139.

Mattson, W. J. (1980). Herbivory in relation to plant-nitrogen content. *Annual Review of Ecology and Systematics*, *11*, 119–161.

Mitchell, C. E. (2003). Trophic control of grassland production and biomass by pathogens. *Ecology Letters*, *6*, 147–155.

Mitchell, C. E., Tilman, D., & Groth, J. V. (2002). Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. *Ecology*, *83*, 1713–1726.

Mordecai, E. A. (2011). Pathogen impacts on plant communities: Unifying theory, concepts, and empirical work. *Ecological Monographs*, *81*, 429–441.

Padilla, F. M., & Pugnaire, F. I. (2007). Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, *21*, 489–495.

Parker, I. M., & Gilbert, G. S. (2007). When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. *Ecology*, *88*, 1210–1224.

Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, *10*, 2555.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.

Rose, L., Coners, H., & Leuschner, C. (2012). Effects of fertilization and cutting frequency on the water balance of a temperate grassland. *Ecohydrology*, *5*, 64–72.

Roy, B. A., Hudson, K., Visser, M., & Johnson, B. R. (2014). Grassland fires may favor native over introduced plants by reducing pathogen loads. *Ecology*, *95*, 1897–1906.

Scherber, C., Gladbach, D. J., Stevnbak, K., Karsten, R. J., Schmidt, I. K., Michelsen, A., Albert, K. R., Larsen, K. S., Mikkelsen, T. N., Beier, C., & Christensen, S. (2013). Multi-factor climate change effects on insect herbivore performance. *Ecology and Evolution*, *3*, 1449–1460.

Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, *113*, 447–455.

Seabloom, E. W., Borer, E. T., & Kinkel, L. L. (2018). No evidence for trade-offs in plant responses to consumer food web manipulations. *Ecology*, *99*, 1953–1963.

Seabloom, E. W., Kinkel, L., Borer, E. T., Hautier, Y., Montgomery, R. A., & Tilman, D. (2017). Food webs obscure the strength of plant diversity effects on primary productivity. *Ecology Letters*, *20*, 502–512.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 10854–10861.

Turnbull, L. A., Rees, M., & Crawley, M. J. (1999). Seed mass and the competition/colonization trade-off: A sowing experiment. *Journal of Ecology*, *87*, 899–912.

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*, 961–969.

Wilfahrt, P. A., Halliday, F. W., & Heckman, R. W. (2020). Initial richness, consumer pressure, and soil resources jointly affect plant diversity and resource strategies during a successional field experiment. *Journal of Ecology*, *108*, 2352–2365.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827.

Zirbel, C. R., Bassett, T., Grman, E., & Brudvig, L. A. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology*, *54*, 1070–1079.

Züst, T., & Agrawal, A. A. (2017). Trade-offs between plant growth and defense against insect herbivory: An emerging mechanistic synthesis. *Annual Review of Plant Biology*, *68*, 513–534.

SUPPORTING INFORMATION

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

Appendix A. Specifications for hierarchical Bayesian models.

Appendix B. Supplementary results, 2013.

Table S1. Predicted relationships between treatments, community attributes, and seedling success.

Table S2. Native species added as seed in this study and their sources.

Table S3. Timeline and summary of treatments applied and responses measured.

Table S4. Parameter estimates, full interaction treatment models, 2013 and 2014.

Table S5. Parameter estimates, simplified treatment models, 2013 and 2014.

Table S6. Parameter estimates, full interaction multivariate hierarchical model, 2014.

Table S7. Parameter estimates, simplified multivariate hierarchical model, 2014.

Table S8. Parameter estimates, full interaction multivariate hierarchical model, 2013.

Table S9. Parameter estimates, simplified multivariate hierarchical model, 2013.

Table S10. Parameter estimates, full interaction species-level treatment model, 2014.

Table S11. Parameter estimates, simplified species-level multivariate hierarchical model, 2014.

Figure S1. Significant bivariate relationships, 2014.

Figure S2. Significant bivariate relationships, 2014.

Figure S3. Effects of treatments and community attributes on establishment and richness, 2013.

Figure S4. Significant bivariate relationships, 2013.

How to cite this article: Heckman, R. W. (2023). Consumers and nutrients alter colonization of an old field community independently and by distinct mechanisms. *Journal of Ecology*, *111*, 2507–2518. https://doi.org/10.1111/1365-2745.14204