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RESEARCH ARTICLE

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Summer precipitation limits plant species richness but not overall productivity in a temperate mesic old-field meadow

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Abstract

Question: Water availability is a primary regulator of plant productivity and species richness in arid and semi-arid ecosystems, but its influence in other habitats is much less clear partly because experimental manipulations of water are relatively rare. How important is soil moisture availability relative to other key environmental factors in determining plant species biomass and diversity in temperate mesic grasslands?

Location: An old-field meadow in southeastern Ontario, Canada.

Methods: We established a long-term factorial field experiment to investigate how variation in soil water (achieved by rainout shelters and water additions), nutrients (NPK fertilizer additions), and above-ground herbivory (deer fence exclosures), interact as regulators of plant production, species richness, and species composition. Above-ground biomass for each species was determined in replicate plots (1 m^2, n = 10) after five years of treatment applications.

Results: The rainout shelters reduced community shoot biomass by 35% relative to ambient (control) plots, with no influence of the fertiliser. To our surprise, however, the fertiliser enhanced community biomass in the ambient and water addition plots to a similar extent. Species richness and Shannon diversity were increased by water addition, but reduced by the rainout shelters and by fertilisation. Total species richness across all replicate plots was 60% higher in the water addition treatment, and almost halved in the water-reduced treatment. In contrast to the above, the exclosures had negligible impacts on these community variables.

Conclusions: Together, these results suggest that in old-field meadow grasslands: (a) shoot productivity is primarily limited by soil nutrient supply except under drought conditions when water availability becomes the primary constraint; (b) the two main soil resources for plants — water and nutrients — affect productivity and species richness/composition in fundamentally different ways; and (c) future increases in summer soil aridity and anthropogenic nitrogen deposition may interact to reduce vegetation productivity and diversity in temperate mesic ecosystems.

KEYWORDS
climate change, diversity, grassland, herbivory, nutrients, production, species composition, species richness, water

1 | INTRODUCTION

Climate change has become one of the most pressing environmental issues for the 21st century (IPCC 2015). By modifying weather circulation patterns and hydrologic processes, climate change is expected to have a major impact on global precipitation regimes (Easterling et al., 2000; Houghton et al., 2001; Seneviratne, Lüthi, Litschi, & Schär, 2006). On a worldwide scale, we can expect increased inter- and intra-annual variability in precipitation; with certain regions experiencing either decreased or increased mean annual inputs (Zhang et al., 2007). From an ecological perspective, this prediction raises both concern and curiosity because water availability can be an important determinant of plant productivity in many terrestrial ecosystems (Churkina & Running, 1998). Extensive research in recent years has consequently used water manipulations to explore how changing precipitation regimes might alter plant community structure and ecosystem functioning (Beier et al., 2012; DeMalach, Zaady, & Kadmon, 2017; Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011; Zeppel, Wilks, & Lewis, 2014). These studies used a wide variety of experimental designs (e.g., some with just added water, just reduced water, or both, and some also included nutrient fertilizer treatments), variable durations of treatment applications (one year vs. multi-year), and sites from a wide range of climatic zones, soil types, and vegetation successional stages — including forest, shrubland, grassland, tundra, desert and agricultural fields. Not surprisingly, therefore, it is difficult to make meaningful comparisons of results between studies, and to draw overall conclusions (Beier et al., 2012; DeMalach et al., 2017; Hoover, Wilcox, & Young, 2018; Knapp et al., 2017; Wu et al., 2011).

By the end of this century, the mean annual precipitation of the temperate mesic climatic region of the Great Lakes basin in North America is predicted to rise by 10–20% even though summer precipitation may decrease by up to 50% (Kling et al., 2003). When coupled with the predictions of increased temperature and associated evapotranspiration, this precipitation decrease may cause summer soil moisture to decline by up to 30% (Kling et al., 2003). At the same time, the vegetation in this region is likely to be affected by soil nutrient loading, specifically from phosphorus- and nitrogen-containing fertilizer, manure, biosolids, and atmospheric nitrogen deposition (Chambers et al., 2001). In addition, densities of the most abundant large herbivore in this region — white-tailed deer — have more than doubled since European settlement (Gill, 1990), and continue to have severe effects on herbaceous and woody species populations in eastern North American forests (Horsley, Stout, & deCalesta, 2003; Macmillan & Aarssen, 2017) — although effects on old-field vegetation are largely unstudied. Most previous field-scale water manipulation studies have focussed on the herbaceous vegetation of arid, semi-arid, or summer-arid grasslands (e.g., prairie, alpine, steppe, mediterranean) (Hoover et al., 2018). By contrast, studies of temperate mesic grasslands and old-field meadows are relatively rare, and none of them (to our knowledge) combine multi-year application of both water addition and reduction treatments, together with soil nutrient manipulation as well as large herbivore exclosure treatments. Addressing these unstudied effects, therefore, defines the central motive and novel contribution of our study.

Here we report the results of a five-year field experiment of factorial manipulations of soil water availability (achieved by rainout shelters and water additions), nutrient availability (NPK fertilizer additions), and above-ground herbivory (deer fence exclosures) to determine the relative importance of these factors on plant production, species richness, and community composition in an old-field meadow in the temperate mesic climatic region of southeastern Ontario, Canada. Specifically, we asked: is peak annual above-ground biomass of temperate-mesic herbaceous vegetation limited more by soil nutrients or by summer soil moisture availability? We predicted — consistent with results of previous studies (Borer, Grace, Harpole, MacDougall, & Seabloom, 2017) — a soil nutrient limitation effect, but we had no clearly established basis for predicting a water limitation effect for this mesic temperate habitat (although it would seem unsurprising to find one). Similarly, we asked: Do soil nutrient availability and summer soil moisture availability have similar (or possibly interacting) effects on community species richness and composition? Again, we predicted — consistent with results of previous nutrient fertilization experiments (Borer et al., 2014) — that higher nutrient levels would be associated with reduced species richness and altered composition (in favour of more productive species), but we had no basis for predicting whether water availability would have similar effects in this study system. Finally, we asked: Do large natural herbivores (particularly white-tailed deer or rabbits) significantly influence peak shoot biomass or species richness/composition in mesic temperate old-field meadows in our study region — and if so, is this effect modulated by effects of soil nutrient or summer water availability, or vice versa?

2 | METHODS

2.1 | Study site

This study was conducted on Queen's University Biological Station (QUBS) property in an old-field meadow known locally as the Bracken Tract (44°38′N, 76°20′ W), situated near Newboro, ON, Canada. Mean annual precipitation and mean annual temperature (1981–2010) are 950 mm and 7.8°C, respectively (ECCC, 2017). Precipitation is relatively uniform throughout the year with the highest levels historically (1981–2010) during the fall and the lowest during late winter and mid-summer (ECCC, 2017). The study field (~150 m × 200 m) is surrounded by a mix of shrubland and mature woodland, and was last tilled and sown (with an unknown forage seed mix) sometime in the early 1990s, and since then has been used for periodic light cattle grazing and occasional hay harvests until 2010 (F. Phelan, pers comm.). A survey of the field in 2010 recorded 63 resident species (Appendix S1). A four-foot high barbed wire fence was installed around the field's perimeter in 2010 to prevent possible grazing by livestock, but without affecting accessibility by large wild herbivores, the most important in the region being white-tailed deer (Macmillan & Aarssen, 2017).

2.2 | Experimental design

In 2010, 240 field plots were set up in 16 parallel rows (separated by 8 m), with 15 plots (separated by 7 m) per row, that were grouped into 10 equal-sized blocks (24 plots per block). Each plot is 1.95 m in diameter (2.95 m^2), delineating the circular treatment area that was centered over a 1 m × 1 m sampling/harvest area. The plots were randomly assigned to one of 12 treatments representing a factorial combination of 3 watering levels (soil moisture: ambient, reduced, and supplemented) × 2 soil nutrient levels (control and fertilised) × 2 herbivore exclosure levels (control and fenced), with two replicates per treatment designated within each block (i.e., n = 20 replicates per treatment in total; only half of the plots harvested for this study).

The three soil moisture levels were: reduced (using rainout shelters); control (receiving only ambient precipitation); and increased (through regular watering to double ambient precipitation — see details below). Rainout shelters consisted of a 2 m × 2 m peaked wood frame covered with clear polyethylene plastic (0.006 inches thick), positioned 1.85 m above the ground and centered over the circular treatment area (Appendix S2). The plastic was installed near the end of May and maintained in place until early September each year from 2011 to 2015. The water addition treatment was applied weekly each year (beginning in 2011), from the beginning of June to the end of August, using water from a nearby pond that was chemically similar to the region's natural precipitation (data not shown). This water was pumped into a transportable watering tank and delivered individually to each plot through a hand-held hose and spray nozzle at the rate 50 litres per whole plot treatment area (i.e., 17 L/m^2) per week (Appendix S2). The latter rate approximates the average local rainfall received during the three-month (June–August) period across the years 2000–2010 based on climate data from Environment Canada's Kingston Pumping weather station for 2000–2007 and Kingston Climate weather station for 2009–2010 (Appendix S3). Accordingly, the total water (added plus natural ambient precipitation) received by the water addition treatment plots was approximately double that normally (on average) received by ambient precipitation only. Analyses of simultaneous light intensity and air and soil temperature recordings in the rainout shelters and nearby controls indicated that effects of the shelter apparatus on plot microclimate were minimal (Appendix S4).

The nutrient addition plots received 71.4 g/m^2 of 14:13:13 NPK slow-release (to restrict leachate and run-off losses) fertilizer (Nutricote 14-13-13 Type 100; Plant Products, Arysta Life Science America, New York, NY, USA) near the end of May in each year beginning in 2010. These additions are equivalent to ~10 g N, P_2O_5 and K_2O per m^2 — annual fertilisation levels that are widely used to remove any potential limitation by those nutrients of plant growth.

For the large herbivore exclosure treatment, permanent wire fencing (122 cm high with 10 cm × 5 cm opening grid) — effective for excluding white-tailed deer, rabbits, and groundhogs in particular, but also raccoons, porcupines, and skunks (less commonly found locally in old-field meadows) — was installed around the perimeter of the 2.95 m^2 circular treatment areas containing the plots (Appendix S2). Including the exclosure treatment therefore enabled not only a novel test of the direct impact (if any) of these mammals on the plant community biomass, but also allowed control for an important potential confound in the interpretation of our water and nutrient manipulation treatments. In other words, the latter — which we fully expected to stimulate plant growth — might in turn be expected to affect the extent to which resident herbivores (particularly deer and rabbits) may be attracted to graze on these particular plots (and thus limit the standing plant biomass recorded).

2.3 | Data collection

2.3.1 | Plot biomass and species composition

From July 20 to 27, 2015 (when the plant community was likely at peak biomass — i.e., just before leaf senescence — see seasonal photos in Appendix S2), 10 replicate plots of each of the 12 treatments (one replicate chosen randomly from each of the 10 blocks) were selected for harvest of standing above-ground biomass (both live and dead). Each selected 1 m × 1 m plot was partitioned into four equal quadrants (0.25 m^2 each) and all vegetation within each quadrant was cut at ground level (Appendix S2) and placed into a separate plastic bag and stored at −2°C for later lab processing. The plant material of two of the plastic bags (from diagonally opposite quadrants, selected randomly) was transferred to a paper bag, oven-dried at 70°C for a minimum of 48 hours to achieve constant mass, and then weighed to determine total harvested plant dry mass per 0.5 m^2. The remaining two bags from each plot were sorted to separate the live biomass by species (Appendix S5), and also to quantify standing dead biomass. This standing dead biomass was likely composed primarily of senesced plant shoot material produced during the current year but some material from previous years may also have been present. All sorted material was then oven-dried as described above to determine total harvested dry mass per species (and total standing dead dry mass) per 0.5 m^2. The relative biomass of each species was determined by dividing a species' total harvested dry shoot mass (i.e., for all above-ground structures) by the summed total harvested dry shoot mass of all species within a sampled plot. Total "live" (only) above-ground plant dry mass for the entire 1 m^2 harvest plot was determined by correcting the pooled dry mass of all four 0.25 m^2 sections according to the relative standing dead measurements (i.e., the proportion of each plot's total biomass that was standing dead) available from the two sorted quadrats. Total "live" (only) above-ground plant dry mass is hereafter referred to as simply "plot biomass".

2.3.2 | Plot Volumetric Water Content (VWC)

In order to assess the effect of the water manipulation treatments on soil moisture, volumetric water content (VWC — %; Campbell

Scientific [Logan, UT] HydroSense with 12 cm probes) was recorded in the experiment's 120 unharvested plots immediately before each of the 12 weekly watering events (and hence 7 days after the previous weekly watering) during the 2016 summer season. (We were unable to conduct these measurements in 2015.) In order to assess shorter-term temporal dynamics, VWC was also measured one hour after the 28 July watering event, 5 days later, and prior to watering on 4 August 2016. Each plot's VWC measurement is the average of four readings (taken from NE, NW, SW, and SE plot corners).

2.3.3 | Covariates

In 2016, several additional pre-existing sources of environmental variation were measured that could also affect plot-level variation in soil moisture availability, and hence plot productivity and species composition: plot elevation, soil depth, and soil texture. Elevation (metres above mean sea level) measurements were recorded at each plot centre using standard land surveying instrumentation. Soil depth was recorded as the median of four soil depth probe measurements taken along the perimeter of each central 1 m^2 plot sampling area. Soil texture composition was determined using particle size analysis (method based on Gee & Bauder, 1986). The average soil texture composition across all experimental plots was 45.5% ± 8.5 (SD) sand, 39.5% ± 11.8 silt, and 15.0% ± 3.9 clay. Analyses of variance (ANOVA) revealed that each covariate was independent of the experimental treatments — i.e., there was no significant variation among the treatments in either plot soil depth, elevation, percent clay, sand, or silt content.

2.4 | Statistical analyses

2.4.1 | Plot VWC

The 2016 growing season VWC data were analysed using mixed-model analyses of covariance (ANCOVA) with Type II sums of squares. Each model included watering treatment, date of measurement and the two-way interaction between them as fixed factors. Plot elevation, soil depth, and one component of soil texture (i.e., percent clay, sand, or silt content) were included as covariates and the terms "block" and "plot" were included as random factors. Each soil texture component was tested in separate mixed-model ANCOVAs (results not shown) and the component with the highest significance (clay) was used in reported model analyses of the VWC data. This method of selecting a component of soil texture was applied to all subsequently described analyses that include a soil texture covariate. For the VWC and all similar analyses, pairwise differences among treatments were tested using LSMEANS with Tukey's HSD post-hoc tests. As well, the functions "lmer" (package lme4; Bates, Maechler, Bolker, & Walker, 2015), "Anova" (package car; Fox & Weisberg, 2011), and "lsmeans" (package lsmeans; Lenth, 2016) were, respectively, used to fit linear mixed models, and to perform ANCOVAs and post-hoc tests.

2.4.2 | Plot biomass relationships

Total shoot live biomass, the proportion of standing dead mass relative to live shoot biomass, and species' total and relative biomasses per plot were analysed in the same manner as the analyses of 2016 plot VWC except that the additional treatment (nutrients, and exclosures) and all interactions were included as fixed factors, and clay content was pre-selected as the soil texture covariate component on the basis of the VWC analysis described above, and "plot" was not included as a random factor.

2.4.3 | Species diversity relationships

Beta diversity, Shannon diversity, species richness, and Evar (Smith and Wilson's 1996 evenness) values were calculated on a 0.5 m^2 scale (based on biomass values recorded in the two sorted quadrants) for each plot to quantify treatment-induced changes in community composition. Shannon index and Evar index scores were analysed using mixed-model ANCOVAs in the same fashion as the analyses of plant biomass. Plot species richness was modelled using a generalized linear model (GLM) with a Poisson distribution, a log link and an estimated scale parameter (i.e., quasi-Poisson GLM) to account for under-dispersion (ϕ = 0.41). The quasi-Poisson GLM included the three experimental treatments as variates and all interactions as fixed factors. Plot elevation, soil depth, and sand content (the texture component selected according to the process described earlier) were included as covariates.

2.4.4 | Species composition relationships

Plant community divergence under the different experimental treatments was visualized using two-dimensional non-metric multidimensional scaling (NMDS) ordinations and computed using 1,000 random starts using the function "metaMDS" (package vegan; R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Species presence/absence ordinations for 2010 and 2015 used Bray–Curtis distances with untransformed data, while the 2015 species biomass ordination used Bray–Curtis distances with Wisconsin double standardized and square-root transformed data. Ellipses showing 95% confidence intervals of the means were overlain with the function "ordiellipse" (package vegan) to assist comparisons among treatments.

The extent of change in community composition among the experimental treatments was determined using Sorensen pair-wise total dissimilarity values — a monotonic transformation of beta diversity. Sorensen dissimilarity was partitioned into its two components — nestedness resultant dissimilarity (the nested loss or gain of species) and spatial turnover (the replacement of certain species by others — Simpson pair-wise dissimilarity) — using the function "beta.pair" (package betapart; Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). Total dissimilarity, nestedness resultant dissimilarity, and spatial turnover were then evaluated by Permutational Multivariate Analyses of Variance (PERMANOVA,

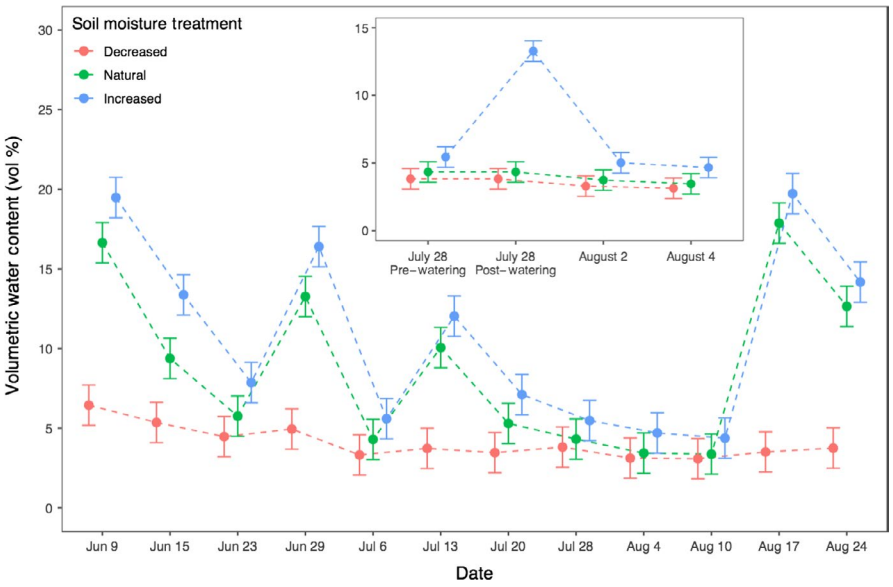

FIGURE 1 Effects of the watering treatments (decreased [n = 40], natural [n = 40], and increased [n = 40]) on weekly soil volumetric water content (vol %) to 12 cm depth across the 2016 growing season (June, July, August) and across a week of measurements (inset plot; July 28 pre/post watering, 2 August, 4 August). Data points are least-square means with 95% confidence intervals (CIs), and were recorded in random order across the treatments on the same day of each week, but are separated slightly along the x axis to facilitate visual comparisons of the treatments on each measurement day [Colour figure can be viewed at wileyonlinelibrary.com]

Anderson, 2001) with 10,000 permutations using the function "adonis" (package vegan).

3 | RESULTS

3.1 | Effects of the watering treatments on soil moisture

Soil volumetric water content (VWC) differed significantly among the reduced, ambient, and added water treatments ($F_{2,105}$ = 87.31, p < 0.0001), and the magnitudes of these differences depended on measurement date ($F_{11,1287}$ = 540.18, p < 0.0001; Appendix S6; Figure 1). In summary, averaging across the three summer months of measurement, the rainout shelters reduced mean plot VWC percentage by 5% (absolute), while the added watering treatment significantly increased VWC by at least 2% (Tukey HSD, p < 0.05). Note that the latter effect represents the minimum impact of this treatment because these soil moisture data were collected immediately prior to each watering event — i.e., 7 days after the previous watering event. To assess the temporal impact of the watering treatment through a full weekly cycle, we measured soil moisture at multiple times within a week (from 28th July to 4th August), and these data clearly show that the watering event immediately increased mean VWC threefold (i.e., by 8% absolute) within an hour after watering, but that this effect dissipated over subsequent days (Tukey HSD, p < 0.05; Appendix S6; Figure 1).

3.2 | Treatment effects on total plant shoot live biomass and standing dead relative mass

Both the watering and soil nutrient manipulations significantly affected plot total live above-ground biomass ($F_{2,95}$ = 36.70, p < 0.0001

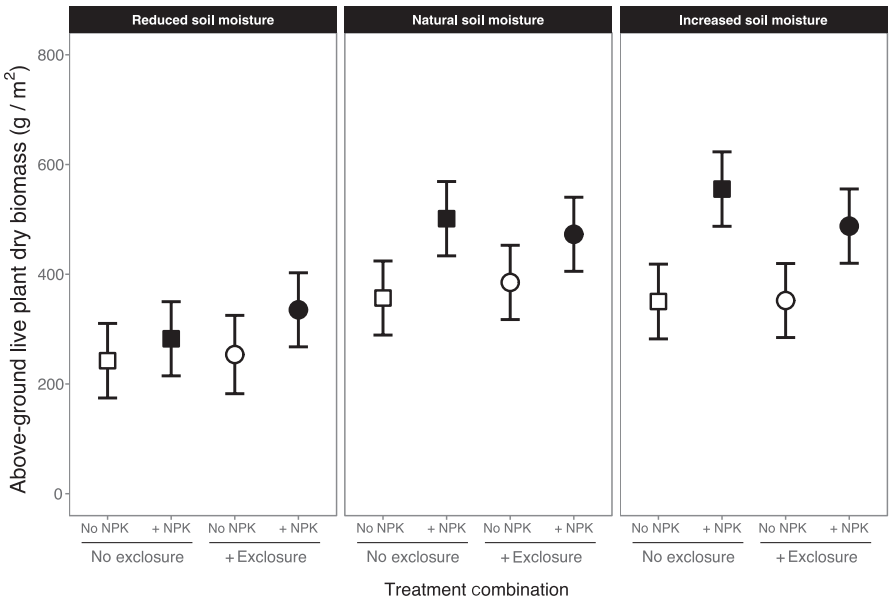

FIGURE 2 Effects of soil moisture (reduced, natural and increased), soil nutrients (natural levels [no NPK, white points] and increased [+NPK, black points]), and herbivore exclosure treatments (exclosure absent [no exclosure, square points] and exclosure present [+exclosure, circle points]) on total above-ground live plant dry mass (g/m^2). Data points are least square means (n = 10) with 95% confidence intervals (CIs)

TABLE 1 Diversity indices and total species pool sizes for the plant communities in each treatment group (Mean ± 1 *SE*)

Treatments	Shannon Index	Evar	Species richness	Species pool
Soil moisture				
Reduced (*n* = 39)	0.96 ± 0.044 a	0.19 ± 0.021 a	3.88 ± 0.20 a	10
Natural (*n* = 40)	1.19 ± 0.043 b	0.20 ± 0.021 a	5.45 ± 0.24 b	20
Increased (*n* = 40)	1.31 ± 0.043 c	0.19 ± 0.021 a	6.83 ± 0.27 c	32
Soil nutrients				
Natural (*n* = 59)	1.20 ± 0.038 a	0.21 ± 0.017 a	5.78 ± 0.21 a	30
Increased (*n* = 60)	1.10 ± 0.038 b	0.18 ± 0.017 a	4.76 ± 0.18 b	24
Exclosure				
Absent (*n* = 60)	1.18 ± 0.038 a	0.20 ± 0.017 a	5.52 ± 0.20 a	29
Present (*n* = 59)	1.12 ± 0.039 a	0.19 ± 0.017 a	4.99 ± 0.19 b	23

Note: Different letters denote significantly different treatment levels ($p < 0.05$) based upon ANCOVA (soil nutrients and exclosure treatments) or Tukey HSD post-hoc tests (soil moisture treatments). Complete ANCOVA results for Shannon Index, Evar (Smith and Wilson's (1996) evenness), and species richness can, respectively, be found in Appendix S15.

and $F_{1,95} = 44.88$, $p < 0.0001$, respectively; Appendix S7; Figure 2), and there was a significant interaction between the soil nutrient and soil moisture treatments ($F_{2,95} = 3.47$, $p = 0.035$; Appendix S7), indicating that the fertiliser enhanced community shoot biomass in the ambient and water addition plots (Tukey HSD, $p > 0.05$), but not in the reduced precipitation plots (Appendix S8). Plot biomass was decreased by 35% (~151 g/m^2) on average in the rainout shelters (Figure 2; Tukey HSD rainout versus ambient $p < 0.05$), but was not significantly affected by either the water additions (Tukey HSD, $p > 0.05$) or the herbivore exclosures ($F_{1,95} = 0.0009$, $p = 0.98$; Figure 2; Appendix S7).

Correspondingly, the rainout treatment also significantly increased the proportion of standing dead plant mass relative to live plant biomass from 19% to 26% (Tukey HSD, $p < 0.05$; Appendix S9). Standing dead relative biomass, however, was not significantly affected by the water addition or fertiliser treatments, or the presence of herbivore exclosures. Note that combining plot standing dead biomass with live plant biomass yielded the same statistical results as the analysis of shoot biomass alone (described above), except that there was no significant interaction between the watering and nutrients treatments (results not shown).

3.3 | Treatment effects on species diversity

Shannon diversity significantly decreased in response to the soil nutrient additions but was not affected by the herbivore exclosure treatment (Table 1). The rainout shelters significantly decreased Shannon diversity (Tukey HSD, $p < 0.05$) while the water addition treatment caused a significant increase ($p = 0.051$).

The species rank abundance curves for each treatment (Appendix S10) and the analysis of plot Evar scores (Table 1) indicated that community dominance structure was not altered by the experimental treatments (Appendix S10), implying that the differences in species richness reported above are likely the sole cause of the observed difference in Shannon Index. In comparison, species richness was significantly reduced by the nutrient additions (by an average of 1.02 species/0.5 m^2), and by the herbivore exclosures (0.53 species/0.5 m^2; Table 1; Figure 3). The soil moisture manipulations also altered species richness with post-hoc analyses revealing a significant decrease in the rainout treatment (1.57 species/0.5 m^2), and a significant increase in the added water treatment (1.38 species/0.5 m^2). Species total pool size (i.e., the number of species existing across replicate plots within a treatment category) differed significantly but moderately in response to the fertilisation and exclosure treatments, and was most strongly affected by the rainout shelters (which halved the total species pool), and by the water addition treatment, which increased it by 60% (Table 1; Appendix S10).

3.4 | Treatment effects on species composition

Prior to the onset of the experimental manipulations in 2010, the plots contained no significant variation in beta diversity components (total dissimilarity, nestedness resultant dissimilarity, or spatial turnover) in relation to their subsequent treatment assignments (Appendix S11). Accordingly, the NMDS ordination on the 2010 species presence/absence data (Appendix S11) indicated no significant differences in community composition among the treatments. However, the subsequent five years of watering and nutrient manipulations caused significant divergence in total dissimilarity (Appendix S12) and nestedness resultant dissimilarity (Appendix S12), but not spatial turnover (Appendix S12), while the herbivore exclosures had only a marginal effect ($p = 0.097$) on nestedness resultant dissimilarity (Appendix S12). Accordingly, both the species presence/absence (Figure 4) and species biomass NMDS ordinations of the 2015 data (Appendix S12) depict significant community composition divergence associated with the watering and nutrient manipulations but not the exclosures.

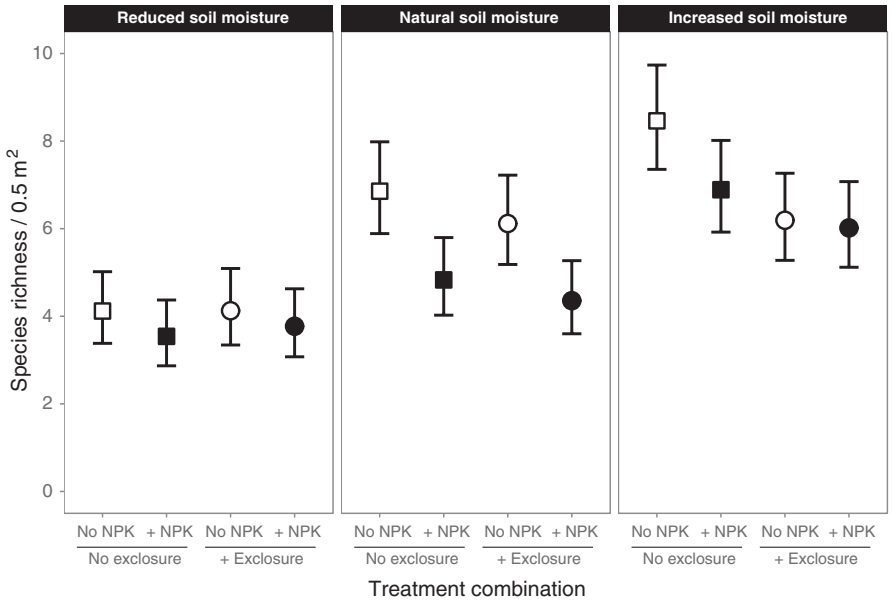

FIGURE 3 Effects of soil moisture (reduced, natural and increased), soil nutrients (natural levels [no NPK, white points] and increased [+NPK, black points]), and herbivore exclosure treatments (exclosure absent [no exclosure, square points] and exclosure present [+exclosure, circle points]) on plot species richness per 0.5 m^2. Data points are leas-square means (n = 10) with 95% CIs

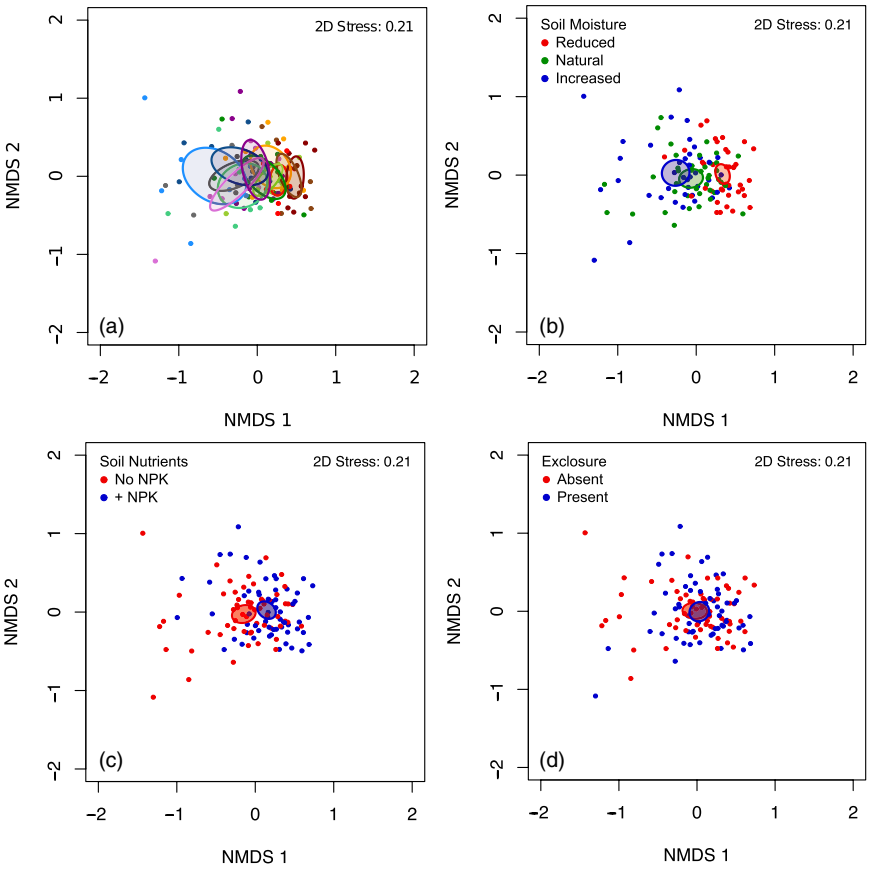

FIGURE 4 NMDS plots showing 2015 plant species composition similarity (Bray-Curtis, presence/absence species matrix) among plots assigned to: (a) all twelve treatment combinations, (b) three soil moisture treatments (decreased [n = 39], natural [n = 40], and increased [n = 40]), (c) two nutrients treatments (no NPK [n = 59] and + NPK [n = 60]), and (d) two herbivore exclosure treatments (exclosure absent [n = 60] versus present [n = 59]). Ellipses are 95% confidence intervals of the mean for each treatment level. Each dot (119 in total) represents a 1 m × 1 m plot [Colour figure can be viewed at wileyonlinelibrary.com]

3.5 | Treatment effects on productivity of individual species

Total and relative biomass were investigated for the nine species whose occurrence among all plots harvested in 2015 was sufficiently frequent for statistical analyses. These nine species and their respective total occurrences (out of 120 plots) are: *Bromus inermis* Leyss. (119), *Vicia cracca* L. (116), *Poa pratensis* L. (115), *Linaria vulgaris* Mill. (61), *Asclepias syriaca* L. (50), *Galium mollugo* L. (40), *Cerastium arvense* L. (32), *Hieracium* spp. (29), and *Carex livida* (Wahlenb.) Willd. (27). The graminoid *Bromus inermis* strongly dominated the total shoot biomass across all treatments, but nevertheless, the absolute

TABLE 2 Species' absolute (g/0.5 m^2) and relative (i.e., proportional) biomass across the experimental treatment groups and their associated *p*-values from mixed model ANCOVAs

	Absolute Biomass		Relative Biomass		Absolute Biomass		Relative Biomass		Absolute Biomass		Relative Biomass	
Treatment	**Mean ± *SE***	***p***	**Mean ± *SE***	***p***	**Mean ± *SE***	***p***	**Mean ± *SE***	***p***	**Mean ± *SE***	***p***	**Mean ± *SE***	***p***
	Bromus inermis				*Linaria vulgaris*				*Asclepias syriaca*			
Soil moisture												
Reduced	92.82 ± 7.52	0.059	0.70 ± 0.038	**0.0021**	21.70 ± 6.96	0.82	0.11 ± 0.028	0.32	8.11 ± 7.11	0.055	0.057 ± 0.028	0.31
Natural	113.93 ± 7.44		0.56 ± 0.037		18.12 ± 6.90		0.081 ± 0.028		29.19 ± 7.04		0.11 ± 0.028	
Increased	110.14 ± 7.44		0.52 ± 0.037		17.05 ± 6.90		0.066 ± 0.028		23.80 ± 7.04		0.091 ± 0.028	
Soil nutrients												
Natural	85.29 ± 6.45	**<0.001**	0.57 ± 0.031	0.20	14.26 ± 6.23	0.14	0.069 ± 0.025	0.17	11.36 ± 6.08	**0.016**	0.056 ± 0.025	**0.033**
Increased	125.97 ± 6.40		0.62 ± 0.031		23.66 ± 6.20		0.11 ± 0.025		29.38 ± 6.03		0.11 ± 0.025	
Exclosure												
Absent	106.31 ± 6.39	0.86	0.60 ± 0.031	0.65	19.07 ± 6.20	0.97	0.093 ± 0.025	0.65	13.85 ± 6.02	0.078	0.061 ± 0.025	0.082
Present	104.95 ± 6.44		0.58 ± 0.031		18.84 ± 6.22		0.081 ± 0.025		26.88 ± 6.06		0.11 ± 0.025	
	Poa pratensis				*Vicia cracca*				*Gallium mollugo*			
Soil moisture												
Reduced	2.44 ± 2.52	**<0.001**	0.026 ± 0.012	**<0.001**	6.42 ± 1.58	0.12	0.045 ± 0.0084	0.086	8.22 ± 3.00	0.17	0.056 ± 0.017	0.27
Natural	21.10 ± 2.49		0.11 ± 0.012		10.40 ± 1.56		0.051 ± 0.0083		3.56 ± 2.96		0.021 ± 0.017	
Increased	20.99 ± 2.49		0.10 ± 0.012		9.15 ± 1.56		0.047 ± 0.0083		11.51 ± 2.96		0.054 ± 0.017	
Soil nutrients												
Natural	16.83 ± 2.06	0.17	0.10 ± 0.010	**<0.001**	9.60 ± 1.35	0.24	0.058 ± 0.0071	**0.021**	8.98 ± 2.45	0.50	0.055 ± 0.014	0.30
Increased	12.86 ± 2.04		0.055 ± 0.010		7.71 ± 1.34		0.037 ± 0.0070		6.55 ± 2.43		0.033 ± 0.014	
Exclosure												
Absent	16.08 ± 2.03	0.41	0.085 ± 0.0099	0.38	9.81 ± 1.34	0.14	0.053 ± 0.0070	0.24	3.49 ± 2.42	**0.017**	0.020 ± 0.014	**0.017**
Present	13.61 ± 2.05		0.072 ± 0.010		7.50 ± 1.35		0.043 ± 0.0071		12.04 ± 2.45		0.068 ± 0.014	
	Carex spp.				*Hieracium* spp.				*Cerastium arvense*			
Soil moisture												
Reduced	0 ± 0.64	**0.0039**	0 ± 0.0056	**0.029**	0.039 ± 0.60	0.078	0.00027 ± 0.0045	0.11	0.0029 ± 0.53	**0.0034**	<0.0001 ± 0.0019	**0.0027**
Natural	0.53 ± 0.63		0.0024 ± 0.0055		1.46 ± 0.60		0.0078 ± 0.0045		0.39 ± 0.53		0.0020 ± 0.0019	
Increased	2.90 ± 0.63		0.020 ± 0.0055		1.81 ± 0.60		0.013 ± 0.0045		2.35 ± 0.53		0.0087 ± 0.0019	
Soil nutrients												
Natural	1.78 ± 0.52	0.082	0.012 ± 0.0046	0.15	1.89 ± 0.50	**0.024**	0.014 ± 0.0037	**0.015**	0.21 ± 0.44	**0.023**	0.0011 ± 0.0016	**0.028**
Increased	0.50 ± 0.52		0.0027 ± 0.0045		0.32 ± 0.50		0.00074 ± 0.0037		1.63 ± 0.44		0.0060 ± 0.0016	
Exclosure												
Absent	1.31 ± 0.52	0.65	0.0072 ± 0.0045	0.93	1.96 ± 0.50	**0.012**	0.013 ± 0.0037	**0.034**	1.53 ± 0.43	**0.040**	0.0056 ± 0.0016	0.055
Present	0.96 ± 0.52		0.0075 ± 0.0046		0.25 ± 0.50		0.0018 ± 0.0037		0.30 ± 0.44		0.0015 ± 0.0016	

Note: Data are means ± 1 *SE*, and bold fonts indicate significant *p*-values (<0.05). The nine included species had the greatest level of occurrence across all experimental plots and are ordered in this table according to their mean relative abundance across all sampled plots.

and/or relative biomasses of seven other of these nine species were significantly altered by the experimental manipulations (Table 2; Appendix S13). Specifically, the fertilizer additions enhanced the absolute biomasses of *Bromus inermis*, *Asclepias syriaca*, and *Cerastium arvense*; decreased the absolute biomass of *Hieracium* spp. and *Carex livida*; and decreased the relative biomass of *Vicia cracca* and *Poa pratensis*. The water addition treatment decreased the absolute and relative biomasses of *Cerastium arvense* and *Carex livida*. By contrast, the rainout shelters almost eliminated *Poa pratensis* (strong decreases in both its absolute and relative biomass), tended to decrease the absolute biomasses of both *Asclepias syriaca* and *Bromus inermis*, but the latter's overall dominance ultimately resulted in a significant increase in its relative biomass. Finally, the herbivore exclosures decreased the absolute biomass of *Cerastium arvense* and increased the absolute and relative biomass of *Galium mollugo*.

4 | DISCUSSION

4.1 | The relative importance of nutrients, water and herbivory on overall community productivity

Our factorial experimental design permitted us to investigate not just the individual effects of each treatment factor in isolation, but also their interactions. As we expected, the NPK fertilizer additions generally increased plot shoot live biomass (Figure 2) — a result consistent with several previous studies showing that nitrogen limitation (LeBauer & Treseder, 2008) and nutrient co-limitation of grassland productivity is common and globally distributed (Borer et al., 2017). However, the statistically significant interaction between the nutrient addition and water manipulation treatments indicates that the fertiliser's stimulatory effect on plant growth depended on water availability. Specifically, the fertiliser enhanced total live above-ground biomass in both the ambient and water addition plots (Tukey HSD, $p > 0.05$), but had negligible impact in the rainout plots (Figures 2,3).

Given the mesic climate at our site, we were greatly surprised that the growth response to fertiliser was similar in both the ambient and in the water addition treatment plots because this conclusion suggests that shoot productivity in old-field meadow grasslands in our region is limited by soil nutrients alone (Figure 2). Furthermore, since total summer precipitation in the harvest year was close to the average over the previous 15 years for our study site (Appendix S3), the conclusion suggests that water availability is generally not limiting shoot productivity at our site — although more severe impacts of water limitation would of course be expected in a summer drought year (Carson & Pickett, 1990; Craine et al., 2012).

One potential explanation for the lack of a clear independent response to the added water treatment is that the loam soil (45% sand, 40% silt, on average) at our site did not retain the extra water sufficiently well to promote a plant growth response. Soil moisture was clearly substantially enhanced (ca. three-fold) immediately after our water additions, but this effect seems to have dissipated quickly — especially during the relatively hot and dry part of the growing season from mid-July to mid-August (Figure 1 and inset), resulting in negligible differences between *any* of the water treatments in that period. In fact, close examination of the entire soil water content data across the full summer indicates that the added water treatment plots tended to be significantly wetter than the ambient plots *only* during weeks of substantial rainfall (i.e., when the ambient plot soil moisture was already relatively high; Fig. 1). Overall, this observation, and comparison of the ambient and rainout shelter plot VWC data, suggest that when the soil was relatively dry at our site (e.g., the individual weeks leading up to 23rd June, 6th July, and July 20th–10th August), it had little capacity to retain (i.e., store) added water, presumably because the loam texture allowed any incoming water to quickly drain down through the soil profile.

This conclusion is supported by the statistical significance of soil depth and clay as covariates in the ANCOVAs of shoot biomass and volumetric water content, respectively, because these soil properties are likely to influence plot variation in the soil's capacity to retain water. First, soil depth across the harvested plots ranged from 18 cm to 82 cm (indicating considerable plot variation in total water holding capacity across the full soil profile), and plots with deeper soils tended to produce more shoot biomass (Appendix S7). Second, clay content — which is generally correlated with soil water retention capacity — was a statistically significant positive covariate in the analyses of both the weekly soil VWC data through the full 2016 growing season, as well as the within-week multiple measurements in late July that year (Appendix S6). Plot soil depth also had a similar, although marginal covariate effect on these two moisture datasets ($p = 0.11$ and $p = 0.065$, respectively). Together, these results suggest that soil moisture limitation on plant community shoot biomass in the ambient compared to the water addition plots did not occur at our site because the soil had a low water holding capacity when it was relatively dry. In other words, our experimental water additions may have failed to enhance soil moisture during those relatively dry periods when plant growth would have been most likely to be potentially water-limited. Accordingly, it is possible that more frequent watering (e.g., every second or third day — even of the same total amount — i.e., doubling total seasonal rainfall input) may have led us to conclude that water availability was in fact limiting shoot biomass in the ambient plots.

However, in contrast to the lack of a shoot biomass response, the water addition treatment clearly enhanced species richness compared to the ambient plots (discussed in detail below). The discrepancy in the responses of these two variables may be due to differences in temporal impact (i.e., biomass is largely dependent on current year conditions while richness may be cumulatively impacted by precipitation variability over the full five years of the manipulations). Alternatively, or in addition, the discrepancy may be caused by different responses of these variables to the effects of the added water treatment (i.e., biomass unresponsive to short periods of elevated moisture when the soil is already relatively wet, while richness is enhanced under those same conditions). Whatever the cause, perhaps the most interesting overall conclusion here is that the two main soil resources for plants in temperate mesic old-field vegetation — water and nutrients — affect productivity and species richness in fundamentally different ways.

The rainout shelters generally tended to reduce productivity (Figure 2), and significantly increased the proportion of standing dead plant tissue relative to total live shoot biomass (Appendix S9). These two results are consistent in suggesting that plant shoot mortality was enhanced in the drought-like conditions of the rainout shelter treatment. The larger proportion of standing dead relative biomass — that may have accumulated not just in the current year but over the full five years of the rainout shelter treatment application — may impose a direct limitation on the current year's production through physical effects of shoot crowding and shading. Furthermore, the reduced soil moisture treatment may also have indirectly decreased productivity by reducing the supply of nutrients to plants (Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009), which, evidently, are naturally limiting productivity at our field site. The potential importance of this mechanism is supported by preliminary nutrient analyses (Appendix S14) of each plot's total plant shoot tissue (standing dead and live biomass). Specifically, the NPK fertilisation consistently increased N concentrations, irrespective of the watering treatment (Appendix S14). However, for P — which is generally much less mobile in soils compared to N (Schlesinger, 1997) —fertilisation enhanced shoot P concentrations nearly twofold in the ambient and increased soil moisture plots, but had no effect under the rainout shelters (Appendix S14).

The effects of white-tailed deer on ecosystem properties such as productivity in old-field meadow grasslands have received little study and so are largely unknown (Russell, Zippin, & Fowler, 2001). Our data indicate that the exclosures did not alter plot biomass (Figure 2). Although we regularly observed signs of deer browsing on shrubs and trees inside the field that contained our experimental plots, we conclude that animal densities were too low for herbivory to significantly affect grassland productivity, and/or that the deer specifically avoided foraging on the grass species that dominated the plant community.

4.2 | The relative importance of nutrients, water and herbivory on species diversity and community composition

The experimental treatments altered community composition (Appendix S12; Figure 4) by causing nested gains or losses of species — i.e., the composition of the most species-poor community was a subset of the most species-rich. There was, conversely, no indication of treatment-induced changes in community evenness or species replacement. Specifically, the fertilizer additions, rainout shelters, and herbivore exclosures all reduced plot species richness and total species pool size. In contrast, the water additions increased mean species richness and total species pool size (Table 1). Furthermore, the magnitudes of these changes suggest that soil moisture is a stronger regulator of species richness than soil nutrients or herbivory. For example, the fertilizer additions reduced the total species pool count by six, while the reduced and increased soil moisture treatments caused a ten species decrease and 12 species increase, respectively (Table 1).

The higher productivity, yet lower species richness, associated with the nutrient addition treatment can be interpreted (as for previous studies) in terms of a nutrient acquisition/conservation tradeoff (Grime, 1979). Specifically, high availability of growth limiting resources may favour species with rapid growth rates (Laliberte, Shipley, Norton, & Scott, 2012), increasing the ratio of above-ground to below-ground biomass, and thereby decreasing light penetration and intensifying competition for light (Borer et al., 2014). Increased light competition and reduced environmental heterogeneity may then cause the random loss of rare species irrespective of their traits, or the loss of species of functional groups poorly adapted to high fertility and low light conditions (Suding et al., 2005). Accordingly, species richness may decline in response to nutrient addition even when the effect of light competition is controlled for (Borer et al., 2017).

In contrast to the rainout shelter-induced decrease in species richness, our water addition treatment did not alter productivity, yet increased species richness. A recent meta-analysis of 41 grassland experiments (involving a wide range of climatic and soil environments) reported no statistically significant effect of water addition on species richness (DeMalach et al., 2017). However, two other experiments in temperate-mesic old-field vegetation also found that species richness was increased by water addition (Sternberg, Brown, Masters, & Clarke, 1999; Stevens, Shirk, & Steiner, 2006). Added water may lower the risk of summer desiccation, thereby reducing mortality rate generally (especially for seedlings), and thus retaining at least some resident plants of relatively rare species (that might otherwise be lost completely from a drier plot) — species that, evidently (in the present study), contributed negligibly to total plot biomass. The increased soil moisture availability may also decrease below-ground competition without increasing above-ground biomass and consequent competition for light. Accordingly, with less intense total resource competition, competitive exclusion of rare species by competitively dominant species may be less likely. Overall, these findings indicate that the relationship between overall community productivity and diversity along a soil nutrient gradient may differ from the corresponding relationship along a soil moisture gradient — even though production along both gradients in our study at least tended to correlate positively with increasing levels of each of these resources.

The exclosure treatment significantly reduced species number (primarily in the ambient and water-added plots), suggesting that natural large animal herbivory promoted species richness (Table 1, Figure 3). The absence of a corresponding effect on productivity (Table 1, Figure 2) suggests that white-tailed deer may selectively target the dominant species, thereby benefitting the more marginal species by counteracting competitive exclusion (Smith et al., 2016). Alternatively, herbivory may have been negligible, and there may have been adverse effects on species richness due to the noticeable build-up and persistence of previous years' standing dead material around the inside edges of at least some of the fences compared to unfenced plots (Appendix S2).

4.3 | The relative importance of nutrients, water and herbivory on individual species' responses

The community structure across all experimental treatment combinations is characterized by low evenness and the consistent dominance of one plant species, *Bromus inermis*, whose average relative biomass was 59%. *Bromus inermis* is one of North America's most important agricultural grass species and is extensively used in pasture and hay fields (Carlson and Newall, 1985), but it is also of great concern as an invasive plant of natural old-field and grassland communities (Fink & Wilson, 2011; Goldberg, 1987). *Bromus inermis* often coexists with another grass — *Poa pratensis*, which had an average relative biomass of 8% at our site. *Poa pratensis* and *Bromus inermis* together account for 10% of the United States' Great Plains' total plant species cover and, respectively, 56% and 37% of its exotic species cover (Cully, Cully, & Hiebert, 2003).

Our factorial experiment allows us to investigate the impacts of changes in available soil moisture and nutrients on the relative proportions of *Bromus inermis* and *Poa pratensis* when the two species are in direct competition with each other in a natural setting. The results clearly show that decreased soil moisture and increased soil nutrient availability enhanced the relative proportion of *Bromus inermis* but weakens that of *Poa pratensis* (Table 2). Specifically, NPK fertilizer additions caused a 48% increase in *Bromus inermis*'s absolute biomass but almost halved *Poa pratensis*'s relative (i.e., proportional) biomass. Furthermore, the rainout shelters almost eliminated *Poa pratensis* — strongly decreasing both its absolute and relative biomass by 88% and 8.4%, respectively — and tended to significantly decrease the biomass of *Bromus inermis* although its relative biomass was increased (by 14% on average).

This treatment-induced variation in relative biomass may be a consequence of differing abilities of the two species to tolerate abiotic stress. *Poa pratensis* is widely considered to have poor heat and drought tolerance (Jiang & Huang, 2000). By comparison, *Bromus inermis* has long been valued as a forage and pasture crop because of its relatively superior drought tolerance (Malte, 1915), and it was used extensively in revegetation efforts following the Dust Bowl of the 1930s (Thomson, 1937) where its strong capacities for below-ground resource competition and suppressing the establishment of competing grass and broad-leaved seedlings even after the removal of its shoots (Gerry & Wilson, 1995) would have been advantageous.

Our results indicate that the decreased summer precipitation that is expected in this region as a result of future climate change (Kling et al., 2003), as well as the ongoing nutrient enrichment of soils due to fertilisation and/or pollution, will likely enhance the relative proportions of *Bromus inermis* at the expense of *Poa pratensis* in invaded mesic temperate grasslands. Likewise, increased frequencies of summer drought may further promote the agricultural usage of *Bromus inermis* and, consequently, inadvertently augment its spread into grasslands and old-field meadows. Accordingly, future efforts to conserve southeastern Ontario's native grassland species will likely need to increasingly direct efforts towards controlling *Bromus inermis*.

5 | CONCLUSIONS

Our results suggest that the two main soil resources for plants in temperate mesic old-field vegetation — water and nutrients — affect productivity and species richness in fundamentally different ways. Specifically, we found that: (a) peak annual biomass was limited by nutrient supply alone when soil moisture was at ambient or elevated levels, and by soil water availability alone under simulated drought conditions (i.e., mean growing season soil moisture at ~50% of ambient normal levels); and (b) naturally occurring species richness at our field site was strongly positively influenced by soil moisture, with total species richness increased 60% by water additions, and halved under rainout shelters. Accordingly, we predict that more frequent and extensive drought years in the future would not just tend to lower hay production from old-field meadows, but would also substantially reduce its species richness, and increase the relative proportion of the invasive grass, *Bromus inermis*.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Queen's University digital repository — QSpace: http://hdl.handle.net/1974/26320

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SUPPORTING INFORMATION

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

Appendix S1. List of 63 species recorded within the full 240 experimental plots at the Bracken field site across the 2010 growing season (prior to treatments)

Appendix S2. Images of field experiment at various times during the growing season

Appendix S3. Historical total summer (June, July, and August) precipitation (2000–2015) recorded by Environment Canada near the study site

Appendix S4. Assessment of the effects of the rainout shelter treatment on plot microclimates

Appendix S5. List of 33 species recorded at the Bracken field site within the 120 plots harvested in 2015

Appendix S6. Mixed-model ANCOVA results for the effects of the watering treatments on soil volumetric water content

Appendix S7. Mixed-model ANCOVA for total plot above-ground live plant dry biomass

Appendix S8. Soil moisture treatment × soil nutrients treatment interaction plot for the analyses of above-ground live plant biomass

Appendix S9. Plot standing dead material in proportion to total live shoot biomass

Appendix S10. Species pools and species proportional abundances in each experimental treatment group

Appendix S11. Analyses of 2010 plant species composition

Appendix S12. Analyses of 2015 plant species composition

Appendix S13. Post-hoc Tukey HSD tests of soil moisture treatment inter-group comparisons on the absolute (g/0.5 m^2) and relative biomass of species where mixed-model ANCOVA identified soil moisture as a significant factor (Table 2)

Appendix S14. Plant shoot tissue nitrogen (N) and phosphorus (P) analyse

Appendix S15. Statistical results of the analyses of the experimental treatment effects on Shannon Index, Evar, and species richness

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