Received: 4 August 2023 | Revised: 20 March 2024 | Accepted: 3 April 2024

DOI: 10.1111/avsc.12776

Applied Vegetation Science IAVS

RESEARCH ARTICLE

Impact of plant diversity and management intensity on magnitude and stability of productivity in North American grazing lands

Grégory Sonnier[1] | David J. Augustine[2] | Shishir Paudel[3] | Lauren M. Porensky[2] | Maria Silveira[4] | David Toledo[5] | Shefali Azad[1] | Raoul K. Boughton[1] | Dawn M. Browning[6] | Patrick E. Clark[7] | Philip A. Fay[8] | Nicole Kaplan[2] | Kate M. Thibault[9] | Hilary M. Swain[1] | Kristen S. Veum[10] | Elizabeth H. Boughton[1]

[1]Archbold Biological Station, Venus, Florida, USA

[2]USDA-ARS, Rangeland Resources and Systems Research Unit, Fort Collins, Colorado, USA

[3]Phipps Conservatory and Botanical Gardens, Pittsburgh, Pennsylvania, USA

[4]Range Cattle Research and Education Center, University of Florida, Ona, Florida, USA

[5]USDA-ARS Northern Great Plains Research Laboratory, Mandan, North Dakota, USA

[6]USDA-ARS Rangeland Management Research Unit, Las Cruces, New Mexico, USA

[7]USDA-ARS Northwest Watershed Research Center, Boise, Idaho, USA

[8]USDA-ARS Grassland, Soil, and Water Research Lab, Temple, Texas, USA

[9]National Ecological Observatory Network, Battelle, Boulder, Colorado, USA

[10]USDA-ARS, Cropping Systems and Water Quality Research, Columbia, Missouri, USA

Correspondence
Grégory Sonnier and Elizabeth H. Boughton, Archbold Biological Station, 123 Main Dr, Venus, FL 33960, USA.
Email: gsonnier@archbold-station.org and eboughton@archbold-station.org

Funding information
U.S. Department of Agriculture, Grant/Award Number: 58-0202-1-002

Co-ordinating Editor: Hannes Feilhauer

Abstract

Questions: Grasslands provide important provisioning services worldwide and their management has consequences for these services. Management intensification is a widespread land-use change and has accelerated across North America to meet rising demands on productivity, yet its impact on the relationship between plant diversity and productivity is still unclear. Here, we investigated the relationship between plant diversity and grassland productivity across nine ecoclimatic domains of the continental United States. We also tested the effect of management intensification on diversity and productivity in four case studies.

Methods: We acquired remotely sensed gross primary productivity data (GPP, 1986–2018) and plant diversity data measured at different spatial scales (1, 10, 100, 400 m^2), as well as climate variables including the Palmer drought index from two ecological networks. We used general linear mixed models to relate GPP to plant diversity across sites. For the case study analysis, we used linear mixed models to relate plant diversity to management intensity, and tested if the management intensity influenced the relationship between GPP (mean and temporal variation) and drought.

Results: Across all sites, we observed positive relationships among species richness, productivity, and the temporal stability of mean annual biomass production. These relationships were not affected by the scale at which species richness was observed. In three out of the four case studies, we observed that management effects on species richness were only significant at broader scales (i.e., ≥10 m^2) with no clear effect found at the commonly used 1-m^2 quadrat scale. In one case study, species-poor, intensively managed pastures presented the highest productivity but were more sensitive to dry conditions than less intensified pastures. However, in other case studies, we did not observe significant effects of management intensity on the magnitude or stability of productivity.

Conclusions: Generalization across studies may be difficult and require the development of intensification indices general enough to be applied across diverse management strategies in grazilands. Understanding how management intensification affects grassland productivity will inform the development of sustainable intensification strategies.

KEYWORDS
drought index, grassland management, grazing intensity, Gross Primary Productivity (GPP), Long-Term Agroecosystem Research Network (LTAR), National Ecological Observatory Network (NEON), rangeland, species–area relationship

1 | INTRODUCTION

Grazing lands, which encompass grasslands, prairies, steppes, savannas, pastures, and shrublands, provide critical ecosystem services including provisioning, supporting, regulating services, and cultural services (Gitay et al., 2001; Eastburn et al., 2017; Dubeux et al., 2022). Primary productivity is a key component of provisioning services in grazing lands (Coffin et al., 2021) with 17% of the world population dependent on grazing-land productivity for their well-being (WRI, 2000). Because anthropogenic changes are affecting grazing lands and the services they provide (Teague & Barnes, 2017; Sollenberger et al., 2019), numerous studies have explored how abiotic and biotic factors drive grazing-land productivity and its stability over time among and across biomes. It is well known that primary productivity is affected by both temperature (Myneni et al., 1998) and precipitation (Lauenroth & Sala, 1992; Knapp & Smith, 2001). However, the sensitivity of productivity to variation in precipitation or temperature differs between ecosystems (Huxman et al., 2004; Piao et al., 2014) and with management practices (Coffin et al., 2021).

In grazing lands, livestock producers often aim for both higher and more stable primary productivity for forage, and they use specific management techniques to achieve such goals (Sollenberger et al., 2019). These include seeding productive grasses or nitrogen-fixing legumes, broad application of fertilizers and/or lime, heavy irrigation, drainage, and altered grazing regimes, which, in various combinations, contribute to a management intensification gradient. Although management intensification increases the productivity of grazing lands and allows for higher stocking rates and densities, it does not consistently increase their resistance and resilience in the face of climate anomalies (Vogel et al., 2012; De Keersmaecker et al., 2014) and may affect other ecosystem services (Adewopo et al., 2014; Paudel et al., 2023). Furthermore, increases in grazing stocking rates and densities in both highly managed pastures and natural rangelands (i.e., grazing intensification) may lead to overgrazing and compromise ecosystem functions at both local and continental scales (Eldridge & Delgado-Baquerizo, 2017). These negative consequences of management and grazing intensification have led to calls for the development of sustainable intensification practices (Garnett et al., 2013; Kleinman et al., 2018; Spiegal et al., 2018). Considering that climate anomalies and extremes are expected to increase in both frequency and magnitude worldwide (Easterling et al., 2000; Griffiths & Bradley, 2007; Perkins-Kirkpatrick & Lewis, 2020) and that alternative management practices exist (e.g., prescribed fires, lower stocking rates, Fuhlendorf & Engle, 2004), the need to improve our understanding of the interplay among climate and management practices as drivers of productivity in grazing lands is crucial.

One mechanism by which management practices may affect productivity is through their impact on plant diversity via the well-studied diversity–productivity relationship. This relationship can take multiple forms, positive, negative, or unimodal (Mittelbach et al., 2001). There is growing evidence that plant diversity also promotes ecosystem resistance and resilience (Cardinale et al., 2012), and that specific management practices may disrupt these relationships (Bharath et al., 2020). Indeed, management intensification has been shown to reduce species and functional diversity, and to result in community homogenization and simplification (Flynn et al., 2009; Manning et al., 2015; Gossner et al., 2016; Koch et al., 2016; Carmona et al., 2020). However, most of these results are based on relatively small-scale experiments where plant species richness is manipulated and productivity is monitored through time with field-based productivity measurements (Tilman et al., 1996; Van Ruijven & Berendse, 2010; Vogel et al., 2012), limiting the scope of these studies. Overreliance on small scales is also present in studies investigating the effect of management and grazing intensity on plant diversity, especially in grassland ecosystems, where the 1-m^2 quadrat is often used for species surveys. To address this, one can investigate diversity patterns at multiple spatial scales and how species accumulate with the area sampled (i.e., the species–area relationship) as a proxy for species turnover (Ricotta et al., 2002; Koleff et al., 2003; Tittensor et al., 2007; Dembicz et al., 2021; Seabloom et al., 2021). For example, Seabloom et al. (2021), found that species loss due to nutrient addition increased with spatial scale in global grasslands. Thus, it becomes crucial to investigate the interplay between management intensity, plant diversity and productivity across spatial scales.

With the progress of remote sensing, productivity data are increasingly available for larger spatial scales and longer time periods (Robinson et al., 2018), thus better matching the scales at which management actions take place. Several metrics derived from

remote-sensed data have been proposed as proxies for productivity and tied to provisioning services, including, but not restricted to, the Normalized Difference Vegetation Index (NDVI; e.g., Pettorelli et al., 2005; Gu et al., 2013), GPP (e.g., Running et al., 2000), and Net Primary Productivity (NPP; e.g., Running et al., 2000). These three remote-sensing-derived metrics have been used extensively to test the diversity–productivity and the diversity–stability relationships (e.g., De Keersmaecker et al., 2014; McBride et al., 2014; Gillman et al., 2015; Burley et al., 2016; Brun et al., 2019; Wang et al., 2021). For example, Brun et al. (2019) used NDVI as a proxy for productivity and found that the relationship between productivity and species richness changed from a positive linear relationship at low land-use intensity to unimodal at high land-use intensity in French Alps grasslands. However, Burley et al. (2016) found weak association between α- and β-diversity and GPP, and no relationship between α- and β-diversity and stability in GPP in a continental analysis across Australia.

In this study, we used remotely sensed GPP because it is readily available at low resolution for the continental US and for a long period of time. We tested the impact of plant diversity and management intensity on the magnitude and stability of productivity in North American grazing lands at different spatial scales. First, we tested if plant diversity measured at different spatial scales was correlated with remotely sensed GPP and its variability over time. Considering the range of grasslands included in this study, we hypothesized a unimodal relationship between GPP and plant species diversity (Brun et al., 2019) and a positive linear relationship between temporal variation in GPP and plant species diversity. We also expected that these relationships would be stronger when plant diversity was measured at larger spatial scales, because these scales better align with the spatial resolution of the productivity estimates. We hypothesized that species turnover would be lower in high-productivity sites which would manifest by a negative relationship between the slope of the species–area relationship and productivity (Chiarucci et al., 2006). Second, we used four case studies to test if management intensity affected plant species richness measured at different spatial scales and how it affected the relationship between climate variability and GPP and its stability over time. We hypothesized stronger management intensity effects at larger scales. We also expected management intensification to increase GPP levels (Eldridge & Delgado-Baquerizo, 2017). Finally, we hypothesized that management intensification would decrease the stability in GPP in response to climate variability (De Keersmaecker et al., 2016).

2 | MATERIAL AND METHODS

2.1 | Plant diversity data

We acquired data on plant diversity from two ecological networks in North America (Appendix S1), the National Science Foundation's National Ecological Observatory Network (NEON; https://www.neonscience.org/), and the US Department of Agriculture's Long-Term Agroecosystem Research Network (LTAR; https://ltar.ars.usda.gov/). NEON is a continental-scale observatory designed to collect long-term open-access ecological data to better understand how US ecosystems are changing. The NEON data set includes data from 47 terrestrial field sites, of which we selected 14 NEON sites with herbaceous grassland or shrub vegetation that are grazed by livestock or wildlife (plant presence and percent cover [DP1.10058.001], RELEASE-2021 [https://doi.org/10.48443/abge-r811]; data set accessed from https://data.neonscience.org). The LTAR network is developing national strategies for the sustainable intensification of agriculture (Kleinman et al., 2018; Spiegal et al., 2018). It includes 18 different sites encompassing rangelands, croplands, and integrated systems of which we selected four rangeland sites. Altogether, the selected sites encompass nine ecoclimatic domains (Keller et al., 2008).

The mentioned two networks used the modified Whittaker plot method (Appendix S2) to measure plant diversity at multiple spatial scales (Stohlgren et al., 1995). For each Whittaker plot, observers recorded all vascular plant species present at subplots of 1 m^2 ($n = 8$), 10 m^2 ($n = 8$), 100 m^2 ($n = 4$), and 400-m^2 ($n = 1$) or 1000 m^2 at Northern Plains site. At the 1-m^2 scale, observers also recorded the percent cover of each vascular plant species. Based on these data sets, we obtained species richness (S) at each spatial scale.

2.2 | Climate data and remote-sensed gross primary productivity

We acquired climate data and GPP at each location using the Google Earth Engine. More specifically, we obtained GPP derived from Landsat Surface Reflectance data for the continental United States (Robinson et al., 2018). GPP is available at a 30-m resolution with a 16-day interval between each data point. We also used the Gridded Surface Meteorological data set (gridMET) to obtain daily temperature and precipitation at each plot location for the period 1988–2018 (Abatzoglou, 2013). GridMET data are available at a 4 km resolution, Whittaker plots within the same site may belong to the same grid. From gridMET, we obtained the Palmer Drought Severity Index (PDSI), also available at a 4 km resolution and produced thrice monthly (Abatzoglou et al., 2014). PDSI is calculated using precipitation and potential evapotranspiration data. A small PDSI value corresponds to dry conditions and a large PDSI value corresponds to wet conditions. We also acquired information on vegetation class at each plot as it can explain variation in productivity.

2.3 | Case study

We used data from four LTAR sites to assess the potential impact of management intensification on species richness at different scales and the impact of management intensification on the response of GPP (mean and coefficient of variation) to drought. At Archbold-University of Florida and Southern Plains, the management

intensification gradient resulted from a multifactorial change in land use, which encompasses seeding, fertilization, drainage, and contrasting grazing intensities. At Central Plains Experimental Range and Northern Plains, the management intensification gradient is primarily a grazing intensity gradient. Data were obtained directly from site leaders.

- *Archbold Biological Station-University of Florida* (Arch-UF) is a partnership between Archbold Biological Station Buck Island Ranch and University of Florida Range Cattle Research & Education Center. This site consists of nine Whittaker plots (20 m × 20 m) located in subtropical pastures with three different management types: intensively managed pastures ($n = 3$), semi-natural pastures ($n = 3$), and native rangelands ($n = 3$). Intensively managed pastures (IMP) were heavily drained, heavily seeded with the productive, non-native forage grass *Paspalum notatum*, and fertilized annually or semi-annually with N, P, and K from the early 1970s to 1987 (56 kg ha^{-1} as NH_4SO_4 or NH_4NO_3 and 34–90 kg ha^{-1} of P_2O_5 and K_2O). Fertilization with P ended after 1987. Semi-natural pastures (SNP) were never fertilized, experienced little seeding of *Paspalum notatum*, and are less drained. Therefore, SNP retained a large proportion of their native species, including a large component of C4 grasses. Finally, native rangelands (NR) were also never fertilized, never seeded, and were undrained, with significant scrubby vegetation (*Serenoa repens*). Rotational grazing is implemented in each pasture type with higher cattle stocking rate in IMP compared to SNP and NR.
- *Southern Plains* (SP, El Reno, Oklahoma) site consists of six Whittaker plots (20 m × 20 m) located in a tall-grass prairie system with two different management types: IMP ($n = 3$), and NR ($n = 3$). IMP were a monoculture of an introduced warm-season grass, *Bothriochloa ischaemum*. The IMP were established in 2004 and were grazed with slightly greater stocking rate compared to NR (0.74 vs 0.58 Animal Unit Days ha^{-1}) and burned on a four-year cycle. The pastures were fertilized (89.7 kg ha^{-1} urea) annually and treated with picloram + 2,4-D, (Grazon® P + D; Dow AgroSciences, Midland, MI, USA) at a rate of 2338.60 mL ha^{-1} to suppress broad-leaved forbs. NR comprise a mixture of native warm-season C4 grasses. They have never been fertilized but weed suppression occurs as needed with Grazon® P + D (2338.60 mL ha^{-1}) followed by burning for woody-plant control on a four-year cycle.
- *Central Plains Experimental Range* (CPER, Nunn, Colorado) site consists of Whittaker plots (20 m × 20 m) located in native short-grass steppe with four different livestock grazing management regimes. Livestock at this site consists of yearling steers that graze from mid-May to early October each year. Grazing treatments consisted of season-long heavy grazing (HG, $n = 3$), season-long moderate grazing (MG, $n = 3$), adaptive rotational moderate grazing (ARG, $n = 3$), and season-long light grazing (LG). HG and LG treatments have been grazed at a stocking rate ca 50% above and below the MG treatment, respectively. The HG, MG, and LG treatments have been implemented every year since 1939; the ARG treatment began in 2014. During the first 50 years of these treatments, LG, MG, and HG were grazed at stocking rates of approximately 9.3, 12.5, and 18.6 AUD ha^{-1} respectively (Irisarri et al., 2016). In response to long-term increases in vegetation cover, livestock body weight, and livestock weight gains (Augustine et al., 2017; Raynor et al., 2021), stocking rates have increased in recent decades, with LG, MG, and HG stocking rates averaging 13.4, 19.0 and 27.0 AUD ha^{-1} during 2014–2021. ARG receives the same stocking rate as MG, but is managed with rotational grazing, which results in pulsed, intensive grazing for anywhere for a 20–40 days in some years, and complete rest (no grazing) in some years.
- *Northern Plains* (NP, Bismarck, North Dakota) site consists of 20 m × 50 m Whittaker plots located in grasslands with varying grazing levels. For this study, we separated treatments into the three categories HG with an approximate stocking rate of 92 AUD ha^{-1}, MG at an approximate stocking rate of 50 AUD ha^{-1}, and LG at an approximate stocking rate of 37 AUD ha^{-1}. HG and one MG pasture are part of a long-term grazing experiment that began in 1916 (Reeves et al., 2014). The other pastures are used and maintained as mixed-grass prairies. All pastures were historically composed of *Nassella viridula*, *Bouteloua gracilis*, *Hesperostipa comata*, *Pascopyrum smithii*, *Koeleria macrantha*, and sedges. However, since the mid-1980s, the region experienced invasion by *Bromus inermis* and *Poa pratensis*, two highly productive and palatable C3 grasses.

2.4 | Statistical analysis

All analyses were performed in R (version 4.2.3) using the RStudio platform (RStudio Team, 2023) and tidyverse library (Wickham et al., 2019) for data manipulation formatting and plotting. We combined data from each site and each spatial scale to calculate species richness at 1, 10, 100 and 400 m^2 (or 1000 m^2 at NP). Prior to calculations, we checked for duplicated species across spatial scales, as they would inflate species richness calculations. Similarly, species identified only to the genus level were counted once across spatial scale unless the coding indicated two different species were present within the same Whittaker plot (e.g., *Cyperus* sp1, *Cyperus* sp2). We then built species–area relationship curves for each plot using the power law function $S = cA^z$, where S is species richness, A is the area, and c and z are constants. To estimate c and z, we used the equivalent log-transformed power law model $\log(S) = \log(c) + z \times \log(\text{Area})$. The y-intercept, $\log(c)$, is a measure of local diversity and the slope, z, is a measure of species turnover (Ricotta et al., 2002; Koleff et al., 2003). Most plots have multiple years of survey data. Thus, this process was repeated for each year and S (observed at each scale), the slope and the intercept were averaged over the years. We also averaged S observed at all scales. We also calculated the exponential of Shannon diversity (H') observed at the 1-m^2 scale based on available canopy cover data (Jost, 2007, 2010). We did not calculate H' at NP where we did not have canopy cover information.

To test our first set of hypotheses, we related mean annual GPP to *S* observed at each sampling scale separately and to the slope of the species–area relationship (SAR) using generalized linear mixed models in the 'lme4' package (Bates et al., 2015). Each model used the Gaussian family distribution, GPP as response variable, and site as random intercept. To test for non-linear relationships, we compared these models to models introducing a quadratic term for either *S* or slope of the SAR using likelihood ratio test. We repeated this to relate the coefficient of temporal variation in GPP (GPP_{cv}) to *S* observed at each sampling scale separately and to the slope of the SAR. For these models we also compared them to models introducing a quadratic term for either *S* or slope of the SAR using the likelihood ratio test. For both GPP and temporal variation in GPP, we also tested models, which included diversity metrics, vegetation class, and climate variables, and used the Akaike Information Criterion (AIC) to select the most parsimonious model. For all the analyses, we used diagnostic plots to check for normality of residuals, homoscedasticity and multicollinearity.

To test the effect of management intensity on diversity, we related *S* to management intensity using general linear models in each case study. We then proceeded with pairwise comparisons between levels using the package 'emmeans'. We repeated this analysis at each spatial scale and for the exponential of the Shannon diversity index. Finally, to determine how management intensity and drought affected productivity, we related GPP and its variation over time (GPP_{CV}) to management intensity and drought index (PDSI) using general linear models.

3 | RESULTS

3.1 | Relationship between species richness and Gross Primary Productivity magnitude and stability

We observed a six-fold variation in mean annual GPP across the data set with a minimum observed at Jornada Experimental Range and a maximum observed at Ar-UF. Species richness observed at 1 m^2 was positively related to GPP ($p < 0.001$), explaining 19.3% of the variation in mean annual GPP across the grassland data set (Figure 1a). We observed a comparable positive relationship at larger spatial

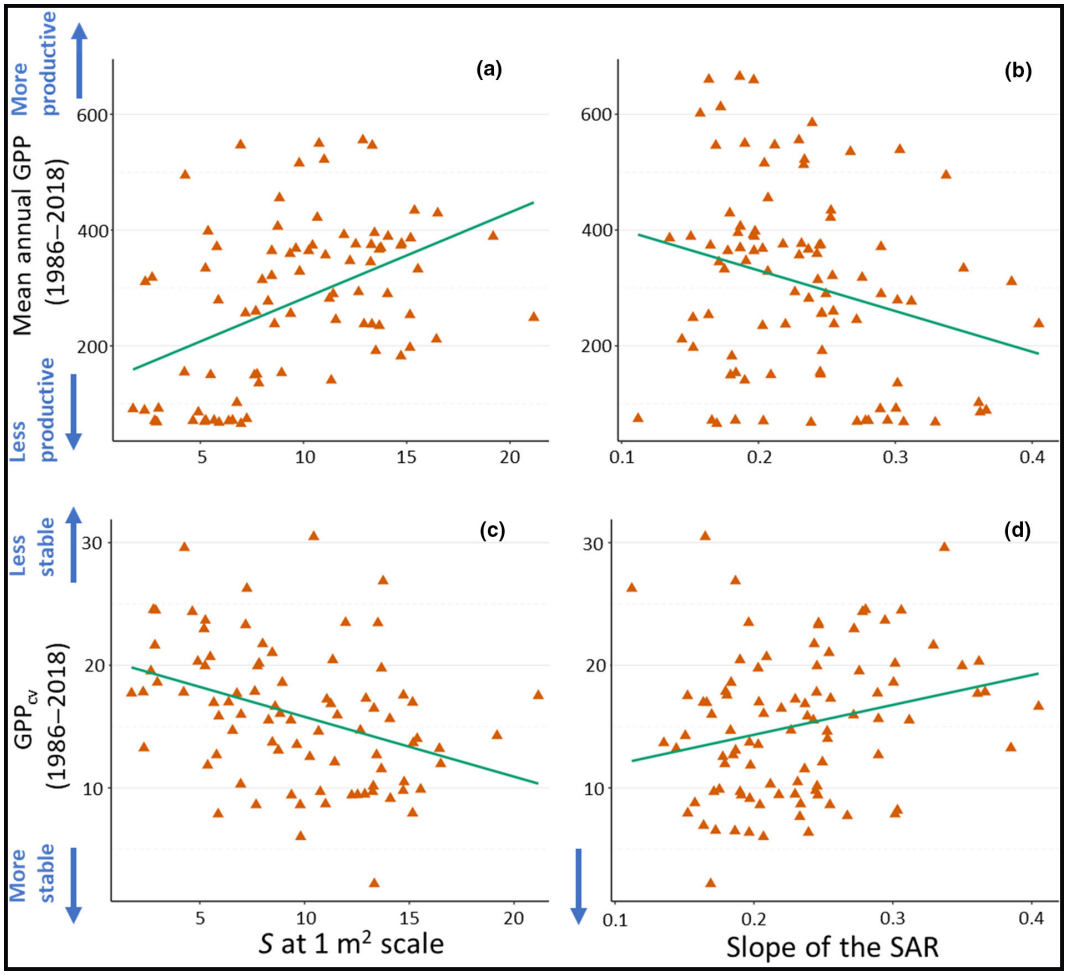

FIGURE 1 Panel showing the relationships between mean annual gross primary productivity (GPP) and species richness observed at 1 m^2 (a) and the slope of the species–area relationship (SAR) (b), and between coefficient of variation in GPP and species richness observed at 1 m^2 (c) and the slope of the SAR (d).

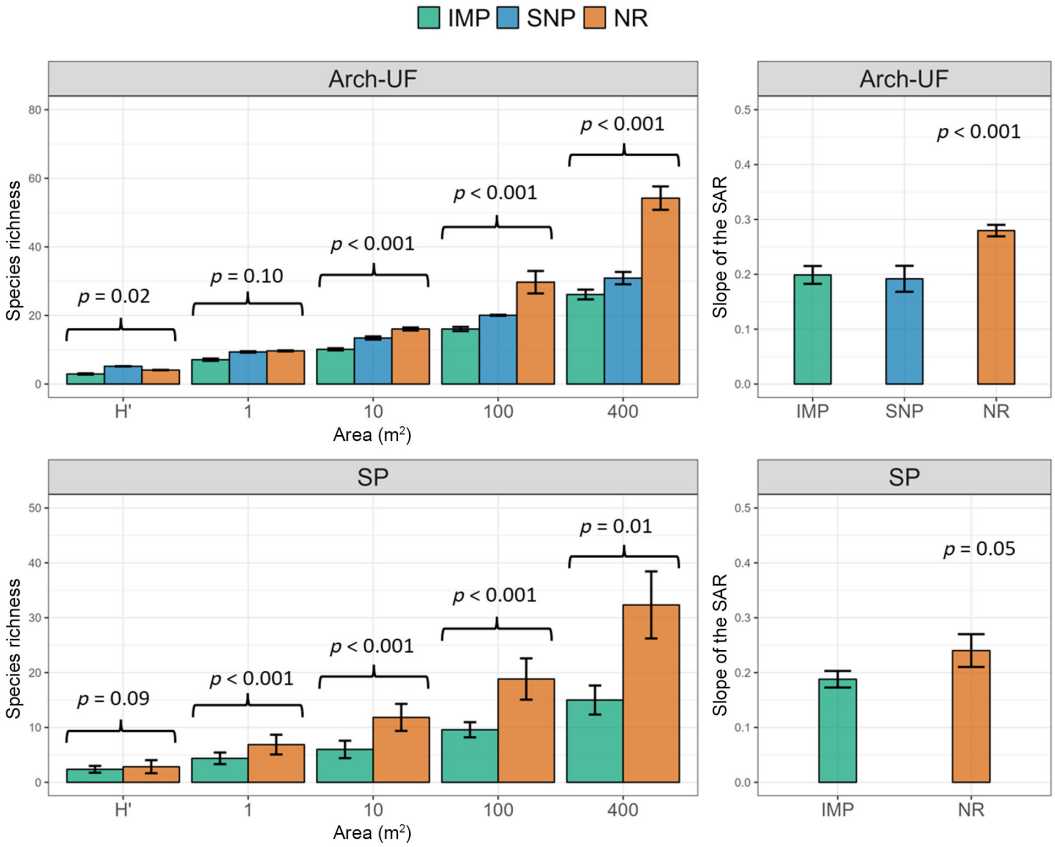

FIGURE 2 Species richness (mean ± SD) across scale at Arch-UF, and SP LTAR sites and in response to the different management practices applied at each site (IMP, Intensively Managed Pastures; NR, Native Range; SNP, Semi-Natural Pastures). H' is the exponential of Shannon diversity observed at the 1-m^2 scale calculated based on canopy cover data.

scales (Appendix S3), with a similar amount of explained variation (R^2 = 18.8%, 16.8% and 21.9% respectively for spatial scales of 10, 100 and 400 m^2). We observed a weak but significant negative relationship between the slope of the SAR and mean annual GPP (R^2 = 5.6%, p = 0.01; Figure 1b). Several models explained a significant amount of the variation in mean annual GPP observed in our data set (Appendix S4). Out of these, the best model included the effect of vegetation class, precipitation, latitude, PDSI, and species richness at the 1-m^2 scale and explained 65% of the variation in our data set. Including the slope of the SAR did not increase the variance explained.

We observed a four-fold variation in the coefficient of variation of GPP (GPP_{CV}) across the data set with a maximum observed at Jornada Experimental Range and a minimum observed at Arch-UF. GPP_{CV} was negatively related to species richness observed at 1 m^2, but species richness only explained 13.1% of the variation in GPP_{CV} (Figure 1c). Similar relationships were observed at broader spatial scales with R^2 = 15.2%, 10.8% and 11.2%, respectively for 10, 100 and 400 m^2. GPP_{CV} was positively related to the slope of the SAR, but it only explained 5.1% of the variation in GPP_{CV} (Figure 1d). None of the models tested explained a large amount of the variation in GPP_{CV} (Appendix S5). Out of these, the most parsimonious model included only the effect of vegetation class and explained 10% of the variation in GPP_{CV}. Including the slope of the SAR or the species richness observed at the 1-m^2 scale did not increase the variance explained.

3.2 | Impact of management intensification at Arch-UF and SP

Species diversity varied between the pasture types at both Arch-UF and SP (Figure 2). We did not detect a significant effect of pasture management intensity on species richness measured at the 1-m^2 scale at Arch-UF. But at SP and at the 1-m^2 scale, we observed higher species richness in NR compared to IMP (Est = 2.5, t = 5.87, p < 0.001). As the spatial scale increased, the differences between treatments became clearer at both sites. At the largest scale (400 m^2), we observed significantly higher species richness in the NR compared to IMP at both Arch-UF (Est = 28.11, t = 12.27, p < 0.001) and SP (Est = 17.33, t = 4.51, p = 0.01). We also observed significantly higher H' in both SNP and NR compared to IMP at Arch-UF (Est = 2.25, t = 6.79, p < 0.001 and Est = 1.15, t = 3.43, p < 0.001, respectively) with the highest H' observed in SNP. Surprisingly this was not the case at the SP, where we observed no difference in H' between IMP and NR.

The slope of the species–area relationship was significantly higher in the NR compared to IMP in both Arch-UF (Est = 0.08,

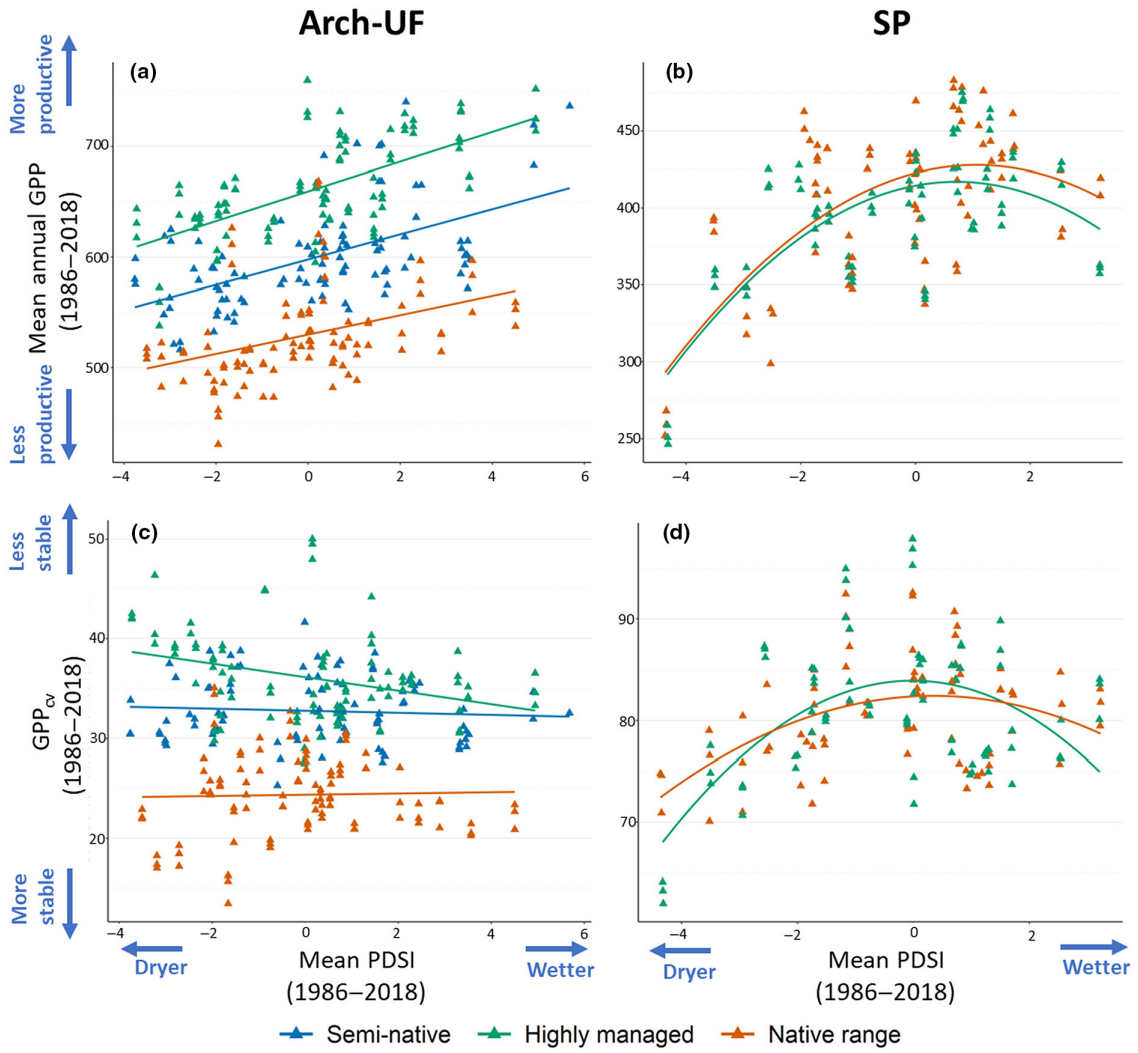

FIGURE 3 Response of annual gross primary productivity (GPP) to drought (PDSI) and pasture management at Arch-UF (a) and Southern Plains (b). Coefficient of variation in GPP as a response to drought and pasture management at Arch-UF (c) and Southern Plains (d).

$t=4.05$, $p<0.001$) and SP (Est=0.05, $t=2.70$, $p=0.05$). At Arch-UF, the slope of the species–area relationship was not different between IMP and SNP ($z=0.19\pm0.05$ vs $z=0.18\pm0.03$, respectively).

At Arch-UF, GPP was significantly different between pasture types, with the highest GPP observed in IMP, followed by SNP and NR (Figure 3a,c). GPP increased with Palmer drought index, with drier years resulting in lower GPP and wetter years resulting in higher GPP. IMP, SNP and NR productivity responded similarly to drought (Pasture type×PDSI, $p>0.05$). The coefficient of variation in GPP varied between management types with higher variation in IMP followed by SNP and NR. Variation in GPP was not affected by PDSI in SNP and NR, but in IMP variation in GPP decreased in wetter years.

At the SP, we did not detect any impact of pasture management intensity on GPP or its variation over time. Mean annual GPP significantly increased with PDSI, with wetter years resulting in higher GPP (Figure 3b,d).

3.3 | Impact of management intensification at CPER and NP

Species richness at the 1-m^2 scale did not vary significantly between grazing intensities in both CPER ($F_{2,69}=0.18$, $p=0.83$) and NP ($F_{2,45}=1.99$, $p=0.15$) despite a tendency for lower species richness in the HG treatment at NP (Figure 4). Similarly, the slope of the species–area relationship was not significantly different between grazing intensity regimes in both CPER ($F_{2,6}=1.67$, $p=0.26$) and NP ($F_{2,45}=0.21$, $p=0.81$). However, and similar to the previous case studies, at the largest scale, we observed significantly higher species richness in the ARG treatment compared to the HG treatment at CPER (Est=7.78, $t=3.14$ $p=0.01$) and higher species richness in the LG compared to the HG treatment at NP (Est=12.86, $t=2.36$, $p=0.05$).

At both CPER and NP, GPP significantly increased with the Palmer drought index, with wetter years resulting in higher mean annual GPP (Figure 5a,b). We also observed a higher coefficient of

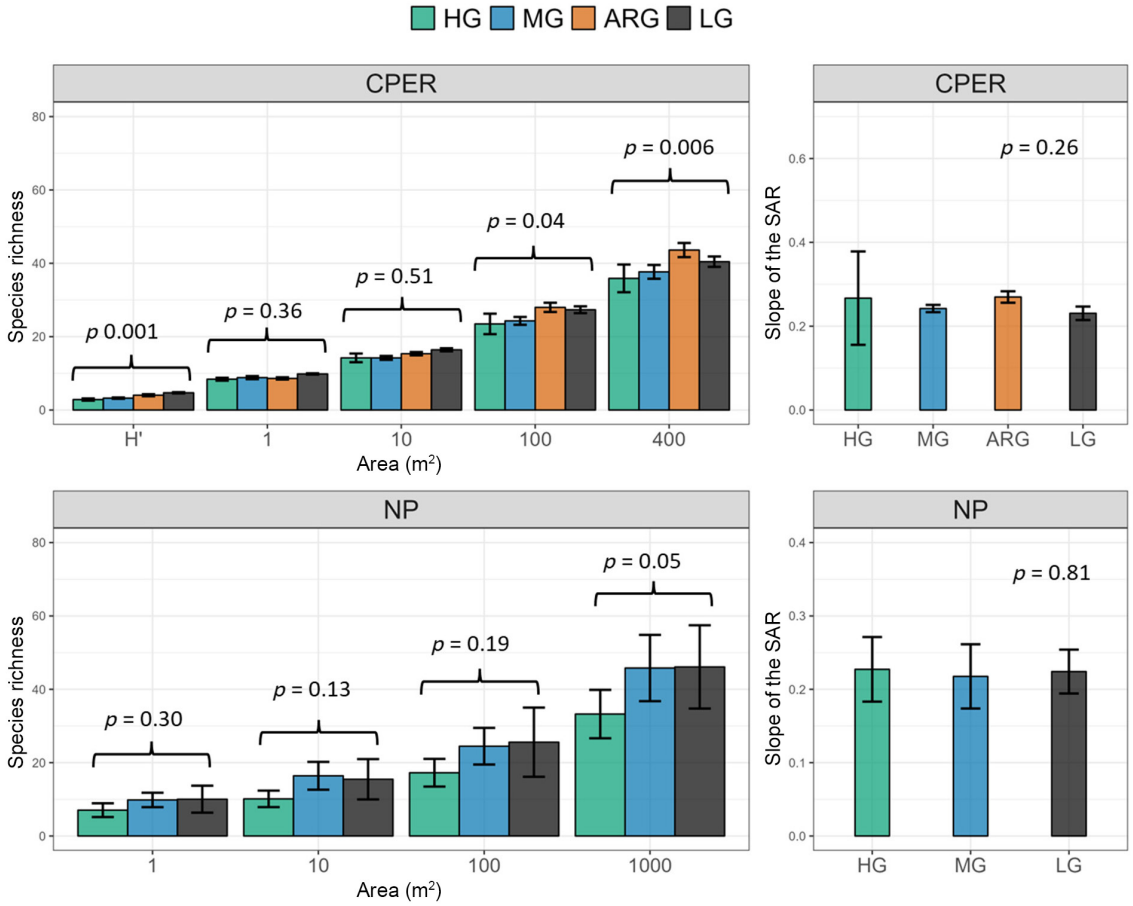

FIGURE 4 Species richness (mean ± SD) across scale at CPER, and NP LTAR sites and in response to the different grazing intensities applied at each site (ARG, adaptive rotational grazing at moderate stocking rate; HG, Heavy Grazing; LG, Light Grazing; MG, Moderate Grazing). *H′* is the exponential of Shannon diversity observed at the 1-m^2 scale calculated based on canopy cover data.

variation in GPP in wetter years at both CPER and NP (Figure 5c,d). We did not observe significant differences in stability between grazing intensities, or significant interactions between grazing intensities and drought severity at both NP and CPER.

4 | DISCUSSION

4.1 | Relationship between species richness and gross primary productivity magnitude and stability

Our study provides a landscape-scale assessment of the effect of species richness and species turnover on grassland productivity across the continental United States. Our results showed that diverse grasslands are more productive and have more stable productivity in agreement with our hypothesis and earlier studies (Cardinale et al., 2012; Gross et al., 2014; Lefcheck et al., 2015; Wagg et al., 2017; Mahaut et al., 2020). However, these relationships were weak since diversity only explained 16%–22% of the variation in productivity. This is likely due to the observational nature of our study which relies on data collected in natural communities as opposed to experimental studies which control for other covariates. For example, van't Veen et al. (2020) found a negative relationship between species richness and productivity, and that relationship only explained 2.4% of the variation in grassland productivity in Switzerland. Additionally, our results suggest that plots with low species turnover (measured with the slope of the SAR) were more productive, in agreement with previous work (Pastor et al., 1996; Chiarucci et al., 2006). However, this contradicts the hump-shape relationship between spatial turnover and productivity obtained in two grassland ecosystems (Chalcraft et al., 2004). This discrepancy could be due to how spatial turnover was quantified (slope of the SAR vs Jaccard dissimilarity index) and suggests the slope of the SAR presents different properties as a measure of spatial turnover.

In our study, increasing the scale at which species richness was obtained did not affect the direction and strength of the relationship between diversity and productivity. This contrasts with work on forest ecosystems across the continental USA, which highlighted a strong dependency of the spatial grain at which both richness and productivity were measured, with a negative relationship at fine scale and positive relationships at intermediate and coarse scales (Craven et al., 2020). It also contrasts with results from two other grassland ecosystems which highlighted either weak or no relationship at small scales and clear hump-shaped relationships at larger

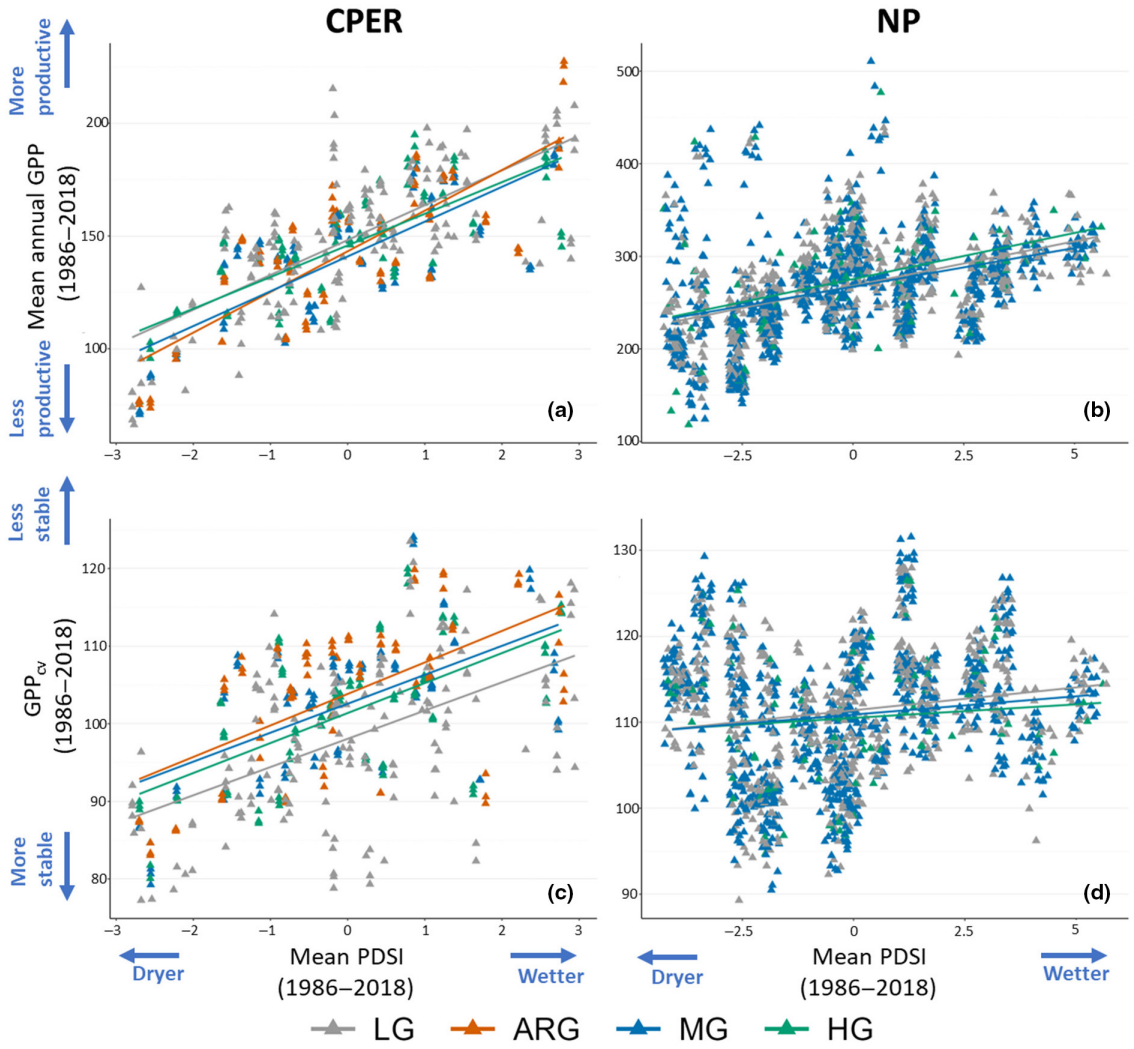

FIGURE 5 Response of mean annual gross primary productivity (GPP) to drought (PDSI) and pasture management at CPER (a) and Northern Plains (b). Coefficient of variation in GPP as a response to drought and pasture management at CPER (c) and Northern Plains (d).

scales (Chalcraft et al., 2004). However, our results are on par with Lisner et al. (2021) who found no effect of spatial resolution on the species richness–productivity relationship. The differing results are likely due to the different spatial scales among studies, with Craven et al. (2020) investigating a much coarser spatial scale (median area = 35,677 km^2) orders of magnitude higher than both ours (400 m^2) and in Lisner et al. (2021) (25 m^2).

4.2 | Effect of intensification on diversity and productivity

In all four case studies, the effect of management intensity on diversity became clearer at larger spatial scales. Overall, species richness decreased as management intensity increased whether the intensification was the result of multifactorial gradients (Arch-UF and SP) or primarily a grazing intensity gradient (CPER and NP). At both Arch-UF and SP, the decrease in species richness with management intensity (from NR to IMP) was due to the seeding of productive non-native grasses (Swain et al., 2013; Boughton et al., 2022; Paudel et al., 2023), and the subsequent fertilization of pastures which has been shown to reduce diversity among grasslands worldwide (Gossner et al., 2016; Koch et al., 2016). In a recent analysis, Seabloom et al. (2021) suggested that species loss due to fertilization increased with spatial scale, which could explain the larger effect of management intensity on diversity at larger scales. Species richness was generally lower in the heavily grazed treatment compared to the LG treatment, but this effect was only clear at the largest scale, especially at NP. The negative effect of HG on species richness agrees with previous studies (Škornik et al., 2010; Porensky et al., 2017) and is likely due to the structural homogeneity created by HG as opposed to LG.

Management intensity infrequently affected diversity at the 1-m^2 scale, emphasizing the importance of exploring the effect of management intensity at higher spatial scales. At the 1-m^2 scale, accounting for species abundance improved our capacity to detect an effect of management intensity. For example, at Arch-UF, IMP harbored many seeded species (e.g., *Desmodium triflorum*, *Desmodium incanum*, *Desmodium heterocarpon*, *Aeschynomene americana*,

Alysicarpus vaginalis), but *Paspalum notatum* was dominant, resulting in a lower exponential of Shannon diversity.

At Arch-UF and SP sites, we expected management intensification to increase productivity, since intensification consisted of seeding productive grasses and subsequent fertilization. However, this response was only observed at Arch-UF where IMP were more productive than the NR. At Arch-UF, the productivity of IMP was also less stable through time and more sensitive to droughts than that of NR. This latter result is in agreement with a European grassland study, showing that semi-natural grasslands exhibited higher resistance to drought and temperature anomalies compared to intensively managed grasslands (De Keersmaecker et al., 2016). The lack of an effect of management intensity on GPP at SP was in line with CO_2 sink strength, but in contrast to ground biomass measurements, which showed a positive effect of intensification on biomass (Paudel et al., 2023). Management history could explain why Arch-UF and SP sites responded differently to management intensification. At Arch-UF, management intensification started almost 70 years ago, whereas at SP management intensification is more recent. Additionally, IMP at Arch-UF were periodically fertilized, limed, and heavily ditched to maximize productivity, while in SP these pastures were only annually fertilized with N and treated with herbicide to suppress broad-leaved forbs (Paudel et al., 2023). At both CPER and NP, we did not observe a significant effect of grazing management on productivity and its variation over time. The vegetation at these sites responded similarly to the drought with higher productivity in wet conditions vs dry conditions. The lack of an effect of grazing intensity on productivity could be explained by the long evolutionary history of grazing at these sites where large herbivores have been present long before ranching occurred. While intense grazing may filter out some plant species, species adapted to high grazing intensity are able to compensate for increased biomass removal. It is important to note that the high grazing intensity implemented was not outside the normal range that plants may have been exposed to through evolutionary time. At NP, *Poa pratensis* was abundant in all treatments due to its tolerance to varying grazing levels, hence hindering potential grazing intensity effects on productivity (Toledo et al., 2023).

4.3 | Standardizing quantification of intensification across multiple ecosystems

In this study, we investigated management intensification using four case studies analyzed separately. At CPER and NP, grazing intensity was the main driver of intensification, whereas at SP and Arch-UF management intensification was a complex interplay of seeding, fertilization, drainage, and livestock stocking rate. Future research should identify indicators of intensification general enough to be applicable across sites and landscapes (Firbank et al., 2007; Ruiz-Martinez et al., 2015). They should combine information on different management activities and account for site-specific factors/conditions. For example, although livestock stocking rates can easily be obtained from multiple sites, what constitutes a light stocking rate at one site may represent a moderate stocking rate at another site due to different carrying capacities. Thus, the absolute stocking rate would not be an appropriate indicator of intensification across sites. Standardized indicators would enable general assessment of the effect of management intensification across agroecosystems, and potentially facilitate the development of sustainable practices. Unfortunately, information on management is often very limited in public databases, rendering quantitative assessment of management intensity difficult. For example, the NEON database did not include any detailed information on management intensity surrounding Whittaker plots.

5 | CONCLUSIONS

Our study highlights the general but weak importance of plant diversity for productivity across grasslands in North America. Interestingly, there was evidence for a negative relationship between spatial species turnover and productivity, which may have been due to the limited number of plant communities included in the analysis. Management intensification was a strong driver of diversity, but this effect was often only detected at larger spatial scales. Surprisingly, management intensification did not always result in greater plant productivity, although it may have resulted in greater livestock production, a provisioning service not explored here. In grasslands where intensification contributes to higher ecosystem productivity, it is not necessarily associated with higher stability in productivity, emphasizing the need to develop alternative management promoting both high productivity and high stability, such as maintaining a combination of low-intensity pastures (e.g., NR and SNP) along with high-intensity-managed pastures. Future work should also explore how plant diversity and management intensification affect other ecosystem services such as nutrient cycling and secondary production across different spatial and temporal scales.

AUTHOR CONTRIBUTIONS

Grégory Sonnier and Elizabeth H. Boughton conceived the study with early contributions from David J. Augustine, Shishir Paudel, Lauren M. Porensky, David Toledo, Raoul K. Boughton, and Philip A. Fay. Grégory Sonnier, Elizabeth H. Boughton, David J. Augustine, Shishir Paudel, Lauren M. Porensky, David Toledo, Philip A. Fay led data collection in each of the LTAR sites used in this study. Shefali Azad and Nicole Kaplan contributed to data management of LTAR network sites. Kate M. Thibault is the NEON science lead who provided insight into the NEON data set and data organization. Grégory Sonnier performed the analysis and prepared the figures. Grégory Sonnier and Elizabeth H. Boughton wrote the manuscript with early input from all other authors. All authors have contributed to the final manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGEMENTS

This work would not have been possible without the help of many research assistants, field technicians, and research interns that helped collect plant diversity data in LTAR and NEON sites. This research is a contribution from the Long-term Agroecosystem Research (LTAR)

network. LTAR is supported by the United States Department of Agriculture. The National Ecological Observatory Network is a program sponsored by the National Science Foundation and operated under cooperative agreement by Battelle. This material is based in part upon work supported by the National Science Foundation through the NEON Program.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare. All co-authors have seen and agree with the contents of the manuscript and there is no financial interest to report.

DATA AVAILABILITY STATEMENT

The raw data set used in this work are publicly available from the NEON data portal (plant presence and percent cover (DP1.10058.001), RELEASE-2021. https://doi.org/10.48443/abge-r811. Dataset accessed from https://data.neonscience.org) and Google Earth Engine. The data sets generated during the current study are available from the corresponding author and will be made available on the Environmental Data Initiative portal upon acceptance (https://edirepository.org/).

ORCID

Grégory Sonnier https://orcid.org/0000-0002-0614-7033
David J. Augustine https://orcid.org/0000-0003-3144-0466
Shishir Paudel https://orcid.org/0000-0002-0794-5096
Lauren M. Porensky https://orcid.org/0000-0001-6883-2442
Maria Silveira https://orcid.org/0000-0003-2166-3156
David Toledo https://orcid.org/0000-0001-5162-4428
Raoul K. Boughton https://orcid.org/0000-0002-3501-5697
Dawn M. Browning https://orcid.org/0000-0002-1252-6013
Patrick E. Clark https://orcid.org/0000-0003-4299-1853
Philip A. Fay https://orcid.org/0000-0002-8291-6316
Nicole Kaplan https://orcid.org/0000-0003-1090-9173
Kate M. Thibault https://orcid.org/0000-0003-3477-6424
Kristen S. Veum https://orcid.org/0000-0002-6492-913X
Elizabeth H. Boughton https://orcid.org/0000-0003-0932-280X

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SUPPORTING INFORMATION

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

Appendix S1. List of NEON and LTAR sites used in this study.

Appendix S2. Modified Whittaker plot design used by all sites included in this study.

Appendix S3. Panel showing the relationships between mean annual gross primary productivity (GPP) and species richness observed at 10, 100 and 400 m^2 (top panels), and between coefficient of variation in GPP and species richness observed at 10, 100 and 400 m^2 (bottom panels).

Appendix S4. Top models testing the effect of species richness (*S*) at 1 m^2, slope of the species–area relationship (*z*) and environmental covariates (Palmer drought index [PDSI], latitude [Lat], precipitation [Precip] and vegetation class [VegClass]) on mean annual gross primary productivity (GPP) across our data set.

Appendix S5. Top models testing the effect of species richness (*S*) at 1 m^2, slope of the species–area relationship (*z*) and environmental covariates (Palmer drought index [PDSI], latitude [Lat], precipitation [Precip] and vegetation class [VegClass]) on the coefficient of variation of gross primary productivity (GPPcv) across our data set.

How to cite this article: Sonnier, G., Augustine, D.J., Paudel, S., Porensky, L.M., Silveira, M., Toledo, D. et al. (2024) Impact of plant diversity and management intensity on magnitude and stability of productivity in North American grazing lands. *Applied Vegetation Science*, 27, e12776. Available from: https://doi.org/10.1111/avsc.12776