Received: 17 June 2024 | Accepted: 14 November 2024

DOI: 10.1111/1365-2745.14471

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

RESEARCH ARTICLE

Precipitation anomalies may affect productivity resilience by shifting plant community properties

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Funding information
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Handling Editor: Adam Clark

Abstract

1. Climate change is causing marked shifts to historic environmental regimes, including increases in precipitation events (droughts and highly wet periods). Relative to droughts, the impacts of wet events have received less attention, despite heavy rainfall events increasing over the past century. Further, impacts of wet and dry events are often evaluated independently; yet, to persist and maintain their ecosystem functions, plant communities must be resilient to both precipitation events. This is particularly critical because while community properties can modulate the resilience (resistance, recovery, and invariability) of ecosystem functions to precipitation events, community properties can also respond to precipitation events. As a result, community responses to wet and dry years may impact the community's resilience to future events.
2. Using two decades (2000–2020) of annual net primary productivity data from early successional grassland communities, we evaluated the plant community properties regulating primary productivity resistance and recovery to contrasting precipitation events and invariability (i.e. long-term stability). We then explored how resilience-modulating community properties responded to precipitation.
3. We found that community properties—specifically, evenness, dominant species (*Solidago altissima*) relative abundance, and species richness—strongly regulate productivity resistance to drought and predict productivity invariability and tended to promote resistance to wet years. These community properties also responded to both wet and dry precipitation extremes and exhibited lagged responses that lasted into the next growing season. We infer that these connections between precipitation events, community properties, and resilience may lead to feedbacks impacting a plant community's resilience to subsequent precipitation events.
4. *Synthesis*. By exploring the impacts of both drought and wet extremes, our work uncovers how precipitation events, which may not necessarily impact productivity directly, could still cryptically influence resilience via shifts in resilience-promoting properties of the plant community. We conclude that these

precipitation event-driven community shifts may feedback to impact long-term productivity resilience under climate change.

KEYWORDS
above-ground primary productivity, climate extremes, community composition, drought, precipitation, resilience, stability

1 | INTRODUCTION

Climate change is disrupting historic environmental regimes, including increases in the frequency and severity of extreme climatic events, such as droughts and intense rainfall periods (IPCC, 2021; Smith, 2011). The impacts of droughts on plant communities and their associated ecosystem functions are well appreciated. For example, droughts can alter community composition (Gao et al., 2022; Hoover et al., 2014; Xu et al., 2021) and drive significant reductions in primary productivity (Gao et al., 2019; Liu et al., 2023; Su et al., 2022), and these impacts often persist post-drought ('drought legacies'; Müller & Bahn, 2022; Vilonen et al., 2022). The consequences of highly wet periods, by contrast, have thus far received less attention, despite heavy rainfall events increasing over the past century throughout the contiguous United States and in many other regions worldwide (IPCC, 2021; Jay et al., 2018). Further, the impacts of extreme wet and dry events are often evaluated independently (although see Isbell et al., 2015; Sala et al., 2012; Wilcox et al., 2017), despite both types of 'precipitation events' (see Box 1) increasing in many regions. Therefore, to persist and maintain critical ecosystem functions plant communities must be resilient to both of these contrasting precipitation events.

BOX 1 Key terms and definitions

Precipitation event: Periods when water availability is outside 'normal'; a drought (SPEI < −1) or wet event (SPEI > 1)

Standardized precipitation–evapotranspiration index (SPEI): Measure of an ecosystem's water availability resulting from the difference between inputs from precipitation and outputs from potential evapotranspiration

Resilience: A multi-dimensional quality that describes an ecosystem's capacity to absorb perturbations and persist in a reference state

Resistance: The degree to which an ecosystem function (e.g. productivity) changes in response to a perturbation

Recovery: The rate at which an ecosystem function returns to pre-perturbation conditions in the year after a perturbation; sometimes called 'resilience' (e.g. Pimm, 1984)

Invariability: The degree to which an ecosystem function varies through time. Often used synonymously with 'stability'

Resilience is a multi-dimensional quality that describes an ecosystem's capacity to absorb perturbations and persist in a reference state (Box 1; Van Meerbeek et al., 2021). While key assumptions of the resilience concept vary among disciplines (i.e. 'ecological resilience' sensu Holling, 1973 vs. 'engineering resilience' sensu Pimm, 1984), the framework broadly captures both a system's responses to perturbation events and long-term patterns. We can begin to explain variation in resilience across communities and ecosystems by quantifying aspects of resilience—resistance, recovery, and invariability—and linking them to community properties. Resistance is the degree to which an ecosystem function (e.g. productivity) changes in response to a perturbation. Recovery (termed 'resilience' by Pimm, 1984) is the rate at which an ecosystem function returns to pre-perturbation conditions. Invariability (often called 'stability') expresses how an ecosystem function varies through time. While resilience is often assumed to be beneficial, resilience does not necessarily confer increased ecosystem functioning. For example, wet events can increase productivity (Wilcox et al., 2017), and therefore, resilience in this context would diminish productivity benefits.

Plant community properties, including species richness, evenness, and dominance, can influence resilience to environmental perturbations, including precipitation events. However, the properties that promote aspects of resilience to droughts may differ from those promoting resilience to highly wet conditions. Species richness is widely demonstrated to promote resilience through functional diversity and redundancy (i.e. diversity-stability relationship; Ives & Carpenter, 2007; Tilman et al., 1996). Given that a speciose community should exhibit greater response diversity—the range of species' responses to an environmental change (Elmqvist et al., 2003)—diverse communities on average should have a higher probability of maintaining critical functions under stress (i.e. biological insurance theory; Yachi & Loreau, 1999). Prior work leveraging data from 46 grassland diversity manipulation experiments found species richness increased productivity resistance to precipitation events (both wet and dry events), as well as long-term productivity invariability, but not post-event recovery (Isbell et al., 2015). Other aspects of diversity, such as evenness and dominance can further modulate resilience by affecting functional trait distributions (Hillebrand et al., 2008). Although often thought of as being antithetical to one another, evenness and dominance both likely contribute to determining trait distributions in non-monodominant communities. First, evenness within a community can promote resilience by enhancing trait diversity, functional redundancy, and temporal complementarity among species

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(Loreau et al., 2021). This is distinct from the effects of richness because even when communities have the same richness, they can differ in evenness. In a low-evenness community, low-abundance species contribute minimally to functional diversity (i.e. low functional evenness). Therefore, not only species counts, but also abundances within the community may be an important determinant of resilience. Second, as dominant species largely determine community-weighted trait values, dominants that are resistant to a given perturbation could confer community-level resilience to that perturbation by sustaining key functions and interactions. Because both species richness and evenness act by increasing trait diversity and temporal complementarity and different species are likely to be more resistant to dry versus wet extremes, these properties might be expected to promote resilience to *both* wet and dry extreme events. In contrast, whether dominance promotes resilience to wet versus dry events likely depends on the specific dominant species and whether it is resistant to drought, inundation, or both.

The characteristics of constituent species and functional groups additionally impact resilience through differences in physiological tolerances, life history and demographic traits, and responses to environmental alterations (Lloret et al., 2012; McGill et al., 2006; Paniw et al., 2021). For instance, a study across eight European grasslands found graminoids are more drought sensitive than forbs (Mackie et al., 2019), although a study comparing drought responses between a single grass and forb species found the opposite (Hoover et al., 2014). Similarly, under stress, non-natives may be less adapted to resource reductions like drought, resulting in reduced growth relative to native species (Liu et al., 2017; Valliere et al., 2019), although the opposite has also been observed (Meisner et al., 2013). Thus, the relative abundances of certain species and functional groups within a community may further regulate productivity resilience although existing data are still too limited to yield general predictions.

While community properties modulate community resilience to precipitation events, they also respond to precipitation events. As a result, community responses to extreme wet and dry years may impact a community's resilience to future events. Such shifts in potentially relevant community properties, including richness, functional diversity, and forb and grass abundances, have been observed in grassland communities in response to drought (Gao et al., 2022; Hoover et al., 2014; Xu et al., 2021) and elevated precipitation (Collins et al., 2012; Yang et al., 2011). Although precipitation legacies—shifts in community properties and processes driven by drought and wet extremes—are increasingly appreciated (Müller & Bahn, 2022; Sala et al., 2012), their impacts on resilience to subsequent events remain poorly characterized. Further, as wet extremes tend to elevate productivity (Sala et al., 2012; Wilcox et al., 2017), we might assume that we can disregard their impacts on a system's resilience. However, wet events may indirectly impact productivity resilience to future extreme events via their effects on community properties, as described above. Consequently, as precipitation is predicted to become increasingly variable under climate change (IPCC, 2021; Smith, 2011), evaluating the interplay between droughts and wet extremes is critical for accurately capturing the current resilience of plant communities and their functions and for predicting resilience to future precipitation events.

Leveraging a two-decadal (2000–2020) record of primary productivity in a temperate grassland community, we evaluated the community-level factors regulating the resistance and recovery of productivity to contrasting precipitation events (Aim 1). We considered how community properties influenced long-term productivity invariability over the two decades (Aim 2). Finally, we explored how the focal community properties associated with resilience responded to precipitation and if precipitation legacies occur within the community (Aim 3). Together, our research investigates feedbacks between precipitation events, community properties, and resilience to explore if the oscillating precipitation events predicted for the future will have consequences for plant community resilience.

2 | METHODS

Above-ground net primary productivity (ANPP) and plant community data were collected at the Kellogg Biological Station Long-Term Ecological Research (KBS LTER) site in Hickory Corners, MI (42°24′ N, −85°22′ W). Prior to European settlement in the 1830s, the local ecosystem was an oak savanna, maintained by periodic burning by the indigenous community (Robertson & Hamilton, 2015). In the mid-1800s, the site was converted to tilled agriculture, primarily for cereal crops (Tomecek & Robertson, 2019). The study plots are six 1 ha (87 × 105 m) grasslands that were released from agriculture in 1989. To prevent tree colonization and maintain communities in an early successional state, the plots have been burned annually since 1997. Additionally, herbicide is applied occasionally (every ~5 years) to manage clonal woody species in the plots. The plots are dominated by *Solidago altissima*, while *Elymus repens*, *Bromus inermis*, *Phleum pratense*, *Aster sagittifolius*, and *Trifolium pratense* are abundant subdominant species. Average richness throughout the study period for each 1 m^2 subplot was 11.6 (SD = 3.4). As the composition of these perennial-dominated communities stabilized a few years after burning began (Gross & Emery, 2012), this study considers community dynamics from 2000 through 2020. During the focal period, the site's mean annual temperature was 9.4°C and mean annual precipitation was 984 mm.

2.1 | Identifying precipitation events

We identified drought and wet events based on the standardized precipitation–evapotranspiration index (SPEI; Box 1; Figure 1). Using meteorological data from KBS LTER (Robertson, 2020), we estimated evapotranspiration (using the Penman-Monteith equation) to calculate SPEI ('SPEI' package; Beguería & Vicente-Serrano, 2023) for a reference period of 1993–2022. We selected

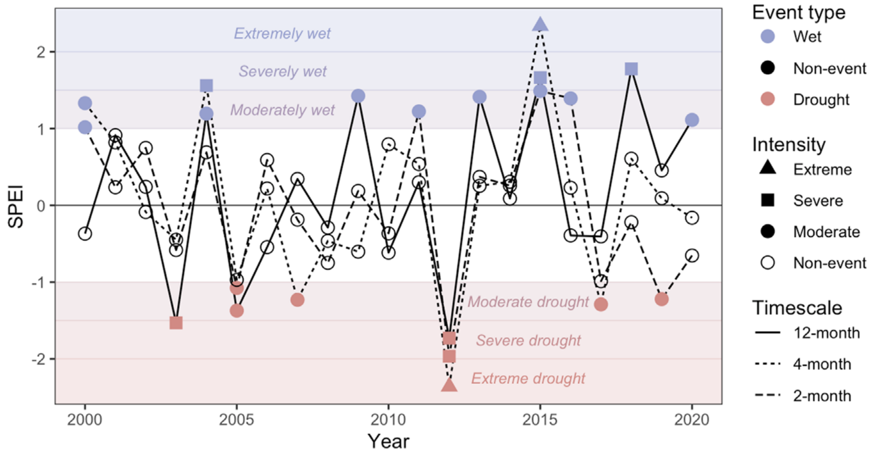

FIGURE 1 August SPEI at KBS LTER between 2000 and 2020 at three timescales (2-, 4-, and 12-month). Colours and shapes denote the precipitation event type and intensity, respectively. Precipitation conditions are considered near normal when SPEI is −0.99–0.99 (Vicente-Serrano et al., 2010). Moderate intensity events occur between |SPEI| 1.00–1.49, severe events between |SPEI| 1.50–1.99, and extreme events when |SPEI| ≥ 2.00. The sign of SPEI denotes whether the event is wetter (+) or drier (−) than normal conditions.

this 30-year period to capture climatic conditions experienced by the local plant community in recent decades. For example, as the community may have become acclimated to the wetter growing seasons observed in recent decades, it may be more sensitive to drought. We used local meteorological data, rather than a gridded product, because KBS LTER is located ~70 km east of Lake Michigan, resulting in precipitation patterns that are locally highly variable due to 'lake effects'.

To capture variation in event duration, which may influence an event's impact on productivity, we calculated SPEI at three timescales: 2-month (equivalent to growing season droughts commonly observed in the region, like the 2012 North American drought), 4-month (equivalent to local growing season length), and 12-month (the timescale for which previous studies have found the strongest responses in temperate grassland productivity; Vicente-Serrano et al., 2013). All SPEI values ended in August (2-month: July–August; 4-month: May–August; 12-month: prior-year September–current-year August). We chose this end point because it corresponds to the timing of peak biomass harvest, from which we approximated community composition (see next section). Precipitation events occurred on more than one timescale in 2000, 2004, 2005, 2012, and 2015. For these years, we only considered the event occurring at the longest timescale because including such years as two or three distinct events (i.e. at each timescale) would lead to pseudoreplication as they are not independent events. To calculate event intensity, we took the absolute value of SPEI. While we detected several 'severe' or 'extreme' 2- and 4-month events in our dataset, they were ultimately excluded from our analyses because those years were also categorized as precipitation events at the longer 12-month timescale. However, for the 2-month timescale, we did not observe 'severe' or 'extreme' wet events (SPEI > 1.50) likely due to regional precipitation seasonality. Intense rainfall typically occurs in the late winter and spring and therefore, did not contribute to the water balance calculations for 2-month (July–August) SPEI values.

2.2 | Above-ground net primary productivity

Peak biomass (late-July or August) was harvested annually in five 1 m^2 (0.5 × 2 m) subplots per 1 ha plot ($N = 5$ subplots × 6 plots = 30 replicates) (Robertson & Snapp, 2020). We used subplot as the level of replication rather than plot for our analyses for several reasons. First, anecdotally the community is highly spatially variable at fine scales. To confirm this statistically, we ran a PERMANOVA ('adonis2' in vegan package) to evaluate the spatial scale at which community variation was predicted, using species' relative abundance data (methods outlined below) for 1999–2020 with 'subplot' nested in 'plot'. Both spatial scales significantly predicted community composition ($p = 0.001$) and explained a comparable amount of variation in composition (plot and subplot $R^2 = 0.14$ and 0.13, respectively). Second, in our models predicting ANPP resistance and recovery (see Aim 1 methods below), we initially included plot as a random effect to account for potential spatial autocorrelation among subplots. The inclusion of this random effect term consistently reduced model fit (evaluated via AIC).

We excluded surface litter, standing dead biomass, and trees and clonal woody species as they are all managed in the plots via annual burning and herbicide application. We sorted all biomass to species (or in rare cases genus); all biomass not identified to the genus-level was reclassified as 'unknown' (on average 2% of total subplot biomass). We then calculated ANPP as the sum across all species of each subplot's biomass. Productivity data from 2007 were excluded from all analyses because plots were not burned that year. Additionally, for all analyses, ANPP observations were excluded if woody species and/or unidentified biomass accounted for >5% total ANPP (55 observations excluded, i.e. 8% of total observations). To estimate the magnitude of precipitation events' impact on ANPP, we calculated the log-response ratio between event year ANPP and long-term average ANPP for each subplot (excluding perturbation years), then ran a linear regression to evaluate the effect of precipitation event type (drought vs. wet), event intensity (|SPEI|), duration, and their interaction on ANPP.

2.3 | Quantifying ANPP resistance, recovery, and long-term invariability

We estimated community resistance to precipitation events as $\frac{\overline{Y_n}}{|Y_e - \overline{Y_n}|}$, where Y_e is perturbation year ANPP and $\overline{Y_n}$ is subplot long-term average ANPP excluding perturbation years (Isbell et al., 2015). As each SPEI timescale identified a different suite of perturbation years, we calculated $\overline{Y_n}$ separately for each timescale. While some event years were not included in the resilience analyses to avoid issues of non-independence (see section 'Identifying precipitation events'), these years were still excluded from $\overline{Y_n}$. Resistance quantifies the system's distance from mean during an event year; if resistance = 2, then productivity is reduced by 50% during an event year relative to mean productivity in non-event years. We calculated recovery as $\left|\frac{Y_e - \overline{Y_n}}{Y_{e+1} - \overline{Y_n}}\right|$, where Y_{e+1} is ANPP in the post-perturbation year (termed 'resilience' by Isbell et al., 2015). Recovery quantifies the system's return rate to mean following an event; if recovery = 2, then in the next growing season, productivity returns to 50% of mean non-event year productivity. When the denominator in the resistance and recovery estimations are very small (i.e. little change in productivity in response to a precipitation anomaly), then resilience measures approach infinity. To address this, for any values exceeding 100, we set both resistance and recovery to a maximum of 100; for resistance, for example, this assumes that the system moves at least 1% away from normal conditions during an event. Several event years were followed by an event in the next year; for these years (2003, 2004, 2011, and 2015–2020), we only calculated resistance, as recovery could not be evaluated because the system did not return to non-perturbation conditions. We estimated long-term invariability as $\frac{\mu}{\sigma}$, or the long-term mean subplot ANPP divided by the long-term standard deviation of subplot ANPP.

2.4 | Predictors of ANPP resistance and recovery (Aim 1)

We approximated annual subplot species richness and Simpson's evenness from biomass data. We estimated species' relative abundance in each subplot by dividing species' subplot ANPP by total subplot ANPP. From these species relative abundances, we calculated the annual relative abundance of all non-native species and of all forb species in each subplot based on qualitative trait data (University of Michigan Herbarium, 2022; USDA & NRCS, 2022). Grass species relative abundance was not included as a predictor because most non-forb species in the community are graminoids, and therefore, grass abundance was highly correlated with forb relative abundance (Pearson's correlation coefficient = −0.93). We also calculated the relative abundance of *Solidago altissima* (tall goldenrod; previously identified on the KBS LTER as *S. canadensis*, Canada goldenrod, prior to nomenclature updates to the *Solidago* genus) in each subplot. *Solidago altissima* is the long-term average dominant species in 87% of subplots, accounting on average for 40% of subplot biomass.

We selected an a priori set of community and precipitation event properties that we predicted may influence resilience in this system: richness, evenness, dominant species relative abundance, non-native species relative abundance, forb relative abundance, event intensity, event duration, event type, richness × intensity, richness × duration, event type × each community predictor. We included interactions between richness and event duration/intensity because diversity's stabilizing effects may depend on a perturbation's duration and intensity (Isbell et al., 2015). We additionally included interactions between event 'type' (i.e. drought vs. wet) and all community predictors to evaluate if predictors of resistance and recovery differed between these precipitation events. Refer to Table S1 for additional rationale on the included community and event properties. From this global model, we used stepwise AIC analysis ('stepAIC' in 'MASS' package) to select best-fit general linear models that predicted ANPP resistance and recovery to all perturbation years. We used prior-year community properties to predict resistance and recovery to current-year precipitation events (e.g. 1999 community properties for predicting responses in 2000). This is because end-of-growing season biomass was used to estimate community properties and is likely influenced by precipitation anomalies occurring in that year. Although the plots are burned annually, there are essentially no annual species and each growing season, the community returns from below-ground stock; therefore, end-of-growing-season community properties are informative of the community's 'starting point' for the subsequent growing season. As mentioned above, to address potential spatial autocorrelation among subplots within plots, we evaluated how the inclusion of random effects ('plot', and 'subplot' nested in 'plot') affected model performance. We found that model performance was reduced when random effects were included (evaluated by AIC), and therefore, dropped them from our analysis.

Because we detected significant event type × community predictor interactions, we applied the same best-fit models (excluding the 'event type' term and its interactions) to drought and wet events separately to further evaluate the extent to which predictors differed between precipitation events. For all models, we log-transformed resistance and recovery to meet the assumptions of normality and homoscedasticity and confirmed that there was no multicollinearity among predictor variables by assessing variance inflation factors ('vif' in 'car' package).

2.5 | Predictors of long-term ANPP invariability (Aim 2)

To identify the community properties that promote long-term ANPP invariability, for each subplot, we calculated long-term average richness, evenness, dominant species relative abundance, non-native relative abundance, and forb relative abundance. As temporal variability in these properties may also impact invariability, we also calculated long-term variation of each factor. We then evaluated the factors (long-term averages and variation) that predict long-term ANPP invariability, again using stepwise AIC to select the best-fit general linear model.

2.6 | Community responses to precipitation events (Aim 3)

We assessed the effect of precipitation and evapotranspiration (quantified via the standardized precipitation–evapotranspiration index, SPEI) on our five focal community properties (richness, evenness, *S. altissima* relative abundance, forb relative abundance, and non-native species relative abundance). We thereby evaluated how precipitation impacts the community properties that may modulate ANPP resistance, recovery, and long-term invariability. We constructed separate models for each of the three SPEI timescales (2-, 4-, and 12-month) and for each community property. As community properties may respond nonlinearly to environmental conditions, in each model, we included a quadratic term (i.e. $SPEI^2$), which was dropped from the model if it did not improve model fit when assessed by AIC. Finally, to determine if legacies of precipitation availability persisted within the community, we performed the same analysis, but instead regressed SPEI on next-growing-season community properties (e.g. $\text{richness}_{T+1} \sim \text{SPEI}_T$). All statistical analyses were performed in R (version 4.3.2; R Core Team, 2023).

3 | RESULTS

3.1 | Impact of precipitation events on ANPP

Droughts and wet events differed in their impacts on above-ground primary productivity, and the magnitude of dry or wet event effects on ANPP differed across event durations and intensities ($p \le 0.01$ for all predictors and interactions; Table S2). Unsurprisingly, stronger drought events yielded greater reductions in ANPP, as moderate droughts ($-1.49 < \text{SPEI} < -1.00$) had no effect on ANPP (mean ± 95 CI = −3% ± 4%), but severe ($-1.99 < \text{SPEI} < -1.50$) and extreme ($\text{SPEI} < -2.00$) droughts reduced ANPP on average by 35% (±8%) and 43% (±7%), respectively (Figure 2a–c). In contrast, moderate wet events ($1.49 > \text{SPEI} > 1.00$) reduced ANPP by 6% (±4%), while severe wet events ($1.99 > \text{SPEI} > 1.50$) increased ANPP by 8% (±5%), particularly for the shorter-term 2- and 4-month events, and extreme wet events ($\text{SPEI} > 2.00$) did not significantly affect ANPP (8% ± 10%). When averaged across all event intensities and durations, droughts reduced ANPP by 22%, while wet events on average did not significantly alter productivity (Figure 2d).

3.2 | Predictors of ANPP resistance and recovery (Aim 1)

The community and event properties that best predicted resilience to extreme precipitation events differed between resistance and recovery and between drought and wet events (Table 1; Figure 3). For example, in the full resistance model, we detected interactions between forb relative abundance (a community property) and event

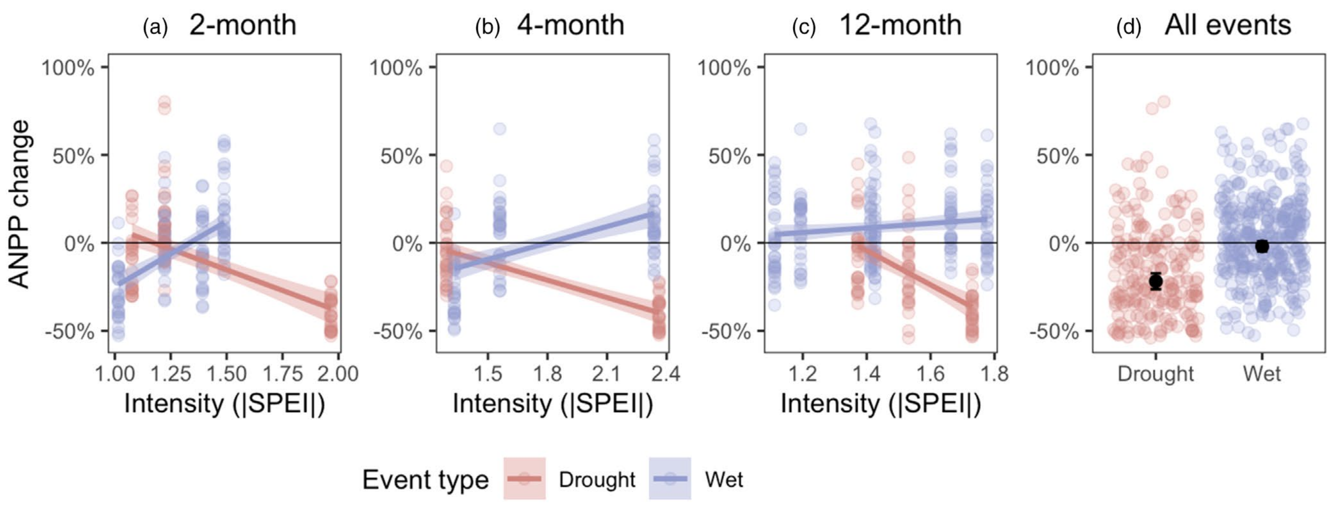

FIGURE 2 The effect of precipitation events (i.e. drought or wet event) on above-ground net primary productivity (ANPP) depends on event intensity (a–c). For droughts, event intensity reduced ANPP, while wet event intensity tended to increase ANPP. On average, droughts significantly reduced ANPP, while wet events did not alter productivity (d). In (a–c), points indicate observed subplot ANPP change from long-term non-event mean, and error bars indicate 95% confidence intervals around estimated ANPP change given event intensity. Sample sizes vary because each timescale had a different number of precipitation events (refer to Figure 1). In (d), coloured points indicate observed subplot ANPP change, and black points indicate event type-mean ANPP effect with 95% confidence intervals.

TABLE 1 Predictors of resistance and recovery to all precipitation events, and drought and wet events separately. Bolded model results indicate a significant predictor of resistance and recovery (***p=0–0.001; **p=0.001–0.01; *p=0.01–0.05); non-significant predictors selected in the best-fit all-events models are also reported. The sign of the regression coefficient (β) indicates the direction of the relationship.

Predictors	All events: Resistance, adj. R^2=0.11	All events: Recovery, adj. R^2=0.03	Drought: Resistance, adj. R^2=0.23	Wet: Resistance, adj. R^2=0.03	Wet: Recovery, mult. R^2=0.04
Richness	p=0.15, β=+		*, β=+	p=0.73, β=+	
Non-native %					
Dominant %	**, β=+		*, β=+	p=0.14, β=+	
Evenness	***, β=+		*, β=+	**, β=+	
Forb %	p=0.22, β=+		p=0.49, β=+	p=0.12, β=−	
Intensity	***, β=−	p=0.09, β=−	***, β=−	p=0.93, β=+	p=0.08, β=−
Duration	p=0.06, β=+		p=0.07, β=+	p=0.78, β=+	
Event type (wet=+)	p=0.63, β=+	p=0.12, β=+	N/A	N/A	N/A
Richness × Intensity					
Richness × Duration					
Richness × Type					
Non-native %×Type					
Dominant %×Type					
Evenness × Type					
Forb %×Type	*, β=−		N/A	N/A	
Intensity × Type	***, β=+		N/A	N/A	
Duration × Type	p=0.10, β=−		N/A	N/A	

Note: All considered community and event properties and interactions are presented, and greyed-out cells indicate predictors that were not selected in the best-fit all-events models.

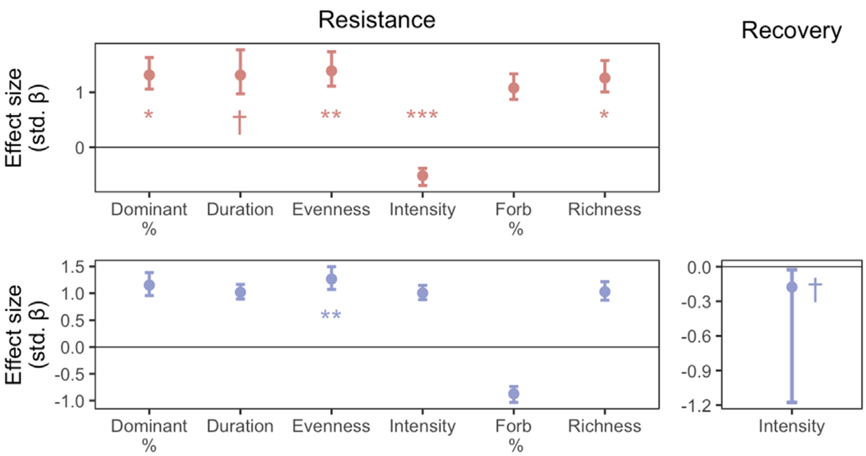

FIGURE 3 The community and event properties that best predicted resilience to precipitation events differed between resistance (left) and recovery (right) and between drought (above in pink) and wet events (below in blue). Error bars on standardized regression coefficients indicate 95% confidence intervals around mean effect size (***p=0–0.001; ** p = 0.001-0.01; *p=0.01–0.05; †p=0.05–0.1).

type, such that increased forb abundance tended to increase resistance to drought but decrease resistance to wet events (Table 1). Overall, community and event properties explained more variance for resistance than recovery (adj. R^2=0.11 and 0.03, respectively), and explained considerably more variation for drought than wet events (resistance adj. R^2=0.23 and 0.03 for drought and wet events, respectively). Unfortunately, because 2005 was the only drought year not followed by another precipitation event, we could not evaluate drought recovery.

For droughts, dominant species relative abundance (p=0.02), evenness (p=0.005), and species richness (p=0.05) were positively related to increased ANPP resistance (Figure 3). By contrast, only evenness significantly predicted ANPP wet event resistance (p=0.006), although effect sizes for most predictors were comparable to those for drought (Figure 3). All other variables, except for event duration and event intensity (see Table 1), were non-significant in the event type specific models. In contrast to resistance, no community properties predicted recovery from

TABLE 2 Rela -year (top) and prior-year (bottom) SPEI and community properties; reported values are regression coefficients and if applicable, level of significance (**p=0–0.001; **p=0.001–0.01; *p=0.01–0.05; †p=0.05–0.1).

	Predictors:	Richness	Non-native species	Dom. Species	Evenness	Forbs
Current year	2-month SPEI	SPEI: 0.09 SPEI²: −0.66***	SPEI: 0.53 SPEI²: −4.83***	SPEI: 1.24 SPEI²: 6.56***	SPEI: −0.004 SPEI²: −0.007†	SPEI: 0.17
	4-month SPEI	SPEI: 0.31* SPEI²: −0.32***	SPEI: 2.51**	SPEI: −2.17* SPEI²: 2.38***	SPEI: −0.001 SPEI²: −0.004†	SPEI: 0.68
	12-month SPEI	SPEI: −0.24* SPEI²: −0.40***	SPEI: 0.77	SPEI: −1.66† SPEI²: 1.98*	SPEI: 0.01***	SPEI: −0.16
Prior year	2-month SPEI	SPEI: −0.06 SPEI²: −0.40**	SPEI: 3.53***	SPEI: −1.52 SPEI²: 3.02**	SPEI: 4.073×10⁻⁵	SPEI: −0.97
	4-month SPEI	SPEI: −0.22†	SPEI: 2.63***	SPEI: −2.10** SPEI²: 1.61**	SPEI: 0.007†	SPEI: 0.13
	12-month SPEI	SPEI: −0.22†	SPEI: −0.31 SPEI²: −2.15*	SPEI: −0.85 SPEI²: 3.39***	SPEI: 0.007† SPEI²: −0.007†	SPEI: −0.50

Note: Plots show the form (linear or quadratic) and direction of the relationship between SPEI and the community property.

precipitation events. The reduced predictive ability for recovery relative to resistance may be due to lower sample sizes (n=96 and 388, respectively) because fewer events could be used to assess recovery as many event years were followed by an event in the next year.

3.3 | Predictors of long-term ANPP invariability (Aim 2)

Communities that maintained greater richness (p<0.001) and evenness (p<0.001) through time (i.e. higher long-term averages) had increased long-term ANPP invariability. Long-term average forb relative abundance tended to reduce invariability (i.e. increased variability), although not significantly (p=0.09). Unexpectedly, long-term variation in evenness (p=0.05) and in dominant species relative abundance (p<0.001) also increased invariability, while long-term variation in non-native species relative abundance was related to reduced invariability (p=0.05). While a long history of theory and empirical work provides rationale for why mean richness and other community properties would affect invariability, associations between variation in community properties and invariability are harder to explain. However, we posit that the importance of temporal variation in community properties may be due to compensatory dynamics among species in the community (see discussion section on temporal variation for elaboration). Cumulatively these factors explained 65% of variation in long-term ANPP invariability.

3.4 | Community responses to precipitation events (Aim 3)

Most focal community properties responded significantly to precipitation, although the form (i.e. linear or quadratic) and direction of these relationships often varied among timescales for a given community property (Table 2). Across SPEI timescales, richness was reduced in wetter and drier years (negative quadratic function); conversely, dominant species relative abundances were lowest in average precipitation years and highest in wetter or drier conditions (positive quadratic function). The responses of evenness and non-native species relative abundance varied across timescales. At the 2- and 4-month timescales, both dry and wet extremes reduced evenness, although not significantly, while at the annual scale, evenness was positivity correlated with wet conditions. For non-native species, at the 2-month scale, precipitation events reduced their relative abundance, while at the 4-month scale, their relative abundances were higher under wet conditions. We did not find correlations between forb species relative abundance and SPEI at any timescale. Finally, we found that similar patterns (i.e. form and direction of relationship) in community properties (except forb relative abundance) occurred with prior-year SPEI as with current-year SPEI (Table 2), suggesting legacies of precipitation events persist within the plant community.

4 | DISCUSSION

We explored the impacts of precipitation events, which are forecasted to increase in frequency and severity under climate change (IPCC, 2021; Smith, 2011), on productivity in a grassland community. As expected, naturally occurring droughts substantially reduced primary productivity. Productivity resistance to drought increased with relative abundance of the dominant species (*Solidago altissima*), evenness, and species richness, while both drought resistance and recovery decreased with drought intensity (i.e. lower SPEI reduced both aspects of resilience). By contrast, wet periods on average caused no deviation in productivity from long-term averages (although extremely wet years typically increased productivity and minor wet events tended to reduce productivity), differing from the findings of a meta-analysis that ANPP is typically more sensitive to simulated precipitation additions than reductions (Wilcox et al., 2017). Our results may differ because the meta-analysis evaluated responses across sites spanning a wide range of climatic conditions (mean annual precipitation: 161–1632 mm; mean annual temperature: −4.8–22.0°C), and therefore, may be driven by arid systems' high sensitivity to elevated precipitation and/or because most simulated precipitation additions are quite extreme (e.g. in this meta-analysis, on average precipitation addition, plots received 43% more rainfall than control plots). Despite wet events' minimal impact on ANPP, evenness positively predicted productivity resistance to extreme wet events. While resilience is often viewed as a desirable, resistance to extreme wet events means that those communities with higher evenness are unable to take advantage of extremely wet years (although they may also be less harmed by the slightly negative effects of minor wet events). While other community properties did not significantly predict resistance to wet events, the magnitude and direction of effect sizes were comparable to those for drought resistance except for forb abundance, which promoted drought resistance but inhibited resistance to wet events. Thus, many properties promoting resistance to dry events may also limit positive productivity responses to high precipitation events, but forb abundance both reduces productivity declines due to drought and tends to increase a community's ability to take advantage of wet years.

4.1 | Precipitation legacies point to shifting resilience dynamics

At first glance, our results would suggest that wet events are relatively inconsequential for productivity in this system. However, our research points to potential complex shifts in resilience under climate change via precipitation-driven shifts in community properties. For example, we found that wet years (i.e. high SPEI values at the 12-month timescale) promoted evenness (Figure 4a; model-predicted relationships shown

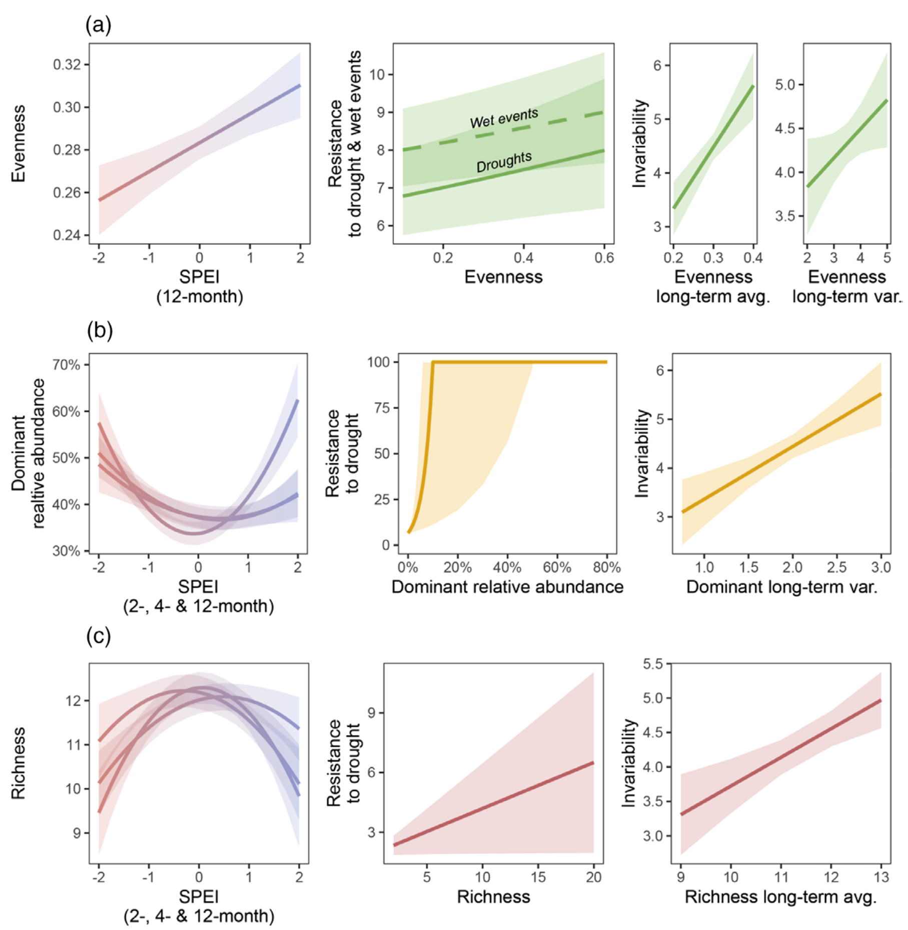

FIGURE 4 Precipitation-driven changes in community properties may lead to complex resilience shifts. Wet periods promoted evenness in the community (a), while both wet and dry extremes were associated with increased dominant species relative abundance (b). (The saturating relationship between dominant species relative abundance and drought resistance (centre panel of (b)) results from setting resistance to have a maximum of 100. Refer to Section 2.3 of the methods for additional details.) As both evenness and dominant species abundance enhanced resistance and invariability, precipitation events may counterintuitively lead to increased resilience to future drought. Conversely, both wet and drought periods reduced richness (c). Because richness is associated with increased resistance and invariability, increased precipitation variability may reduce resilience to future events. Plotted lines show predicted relationships (estimated marginal means) from best-fit models and error bars indicate 95% confidence intervals.

in main text but see Figure S1 for plots of observations). Evenness increased ANPP resistance to both droughts and wet events, and subplots with higher long-term average evenness had increased long-term ANPP invariability. Therefore, wet events, via increasing evenness, may indirectly increase the system's resilience to subsequent precipitation events and stabilize productivity through time. Similarly, at all timescales, we found that both droughts and wet conditions increased *S. altissima* relative abundance, and increased *S. altissima* abundance promoted drought resistance (Figure 4b). Thus, the effects of increased precipitation variability on ANPP may be buffered by community responses to extreme events. By contrast, at all timescales both dry and wet extremes reduced richness within the community. Because richness increased drought resistance and long-term invariability, the effects of extreme events on species richness are likely to exacerbate the direct effects of drought on ANPP and increase temporal variation in ANPP (Figure 4c).

Taken together, these linkages between precipitation events, community properties, and resilience may lead to feedbacks that affect long-term productivity resilience. In other words, because of their effects on community properties, precipitation events—even wet extremes with minimal direct effects on ANPP—are likely to influence resilience to future precipitation events. While the potential implications of drought legacies on resilience to subsequent events is gaining appreciation (Müller & Bahn, 2022), our findings suggest that legacies of wet events also can further affect future resilience. As precipitation anomalies in both directions become increasingly frequent and severe into the future (IPCC, 2021; Smith, 2011), consideration of the lasting impacts of both wet and dry events is critical for accurately predicting the future resilience of plant communities and their associated ecosystem functions.

4.2 | Diversity via evenness and richness regulated drought resilience

While the role of richness in promoting resilience to disturbance has been particularly well-studied (Craven et al., 2016; Isbell et al., 2015; Kreyling et al., 2017; Van Ruijven & Berendse, 2010) and was supported by our findings, we found that additional community properties (evenness and dominant species relative abundance) strongly regulated productivity resistance to drought and long-term invariability. Evenness likely contributes to these aspects of resilience via enhancing functional diversity and complementarity among species (Loreau et al., 2021). While functional richness explains the *variety* of niche space occupied by the community, functional evenness explains the *extent* to which niche space is utilized; if all available niches are evenly utilized, we would expect increased productivity invariability (Mason et al., 2005). Thus, studies only considering diversity via species richness may fail to capture an important aspect of diversity, evenness, in contributing to productivity resilience. In our system, dominance likely contributes to resilience because the dominant species was previously found to be more temporally stable than subordinate community members (Grman et al., 2010).

We were able to study these other community properties because of our long-term data from a natural and highly variable community (as opposed to biodiversity experiments that largely manipulate only richness). However, while leveraging long-term datasets is a powerful approach for exploring complex ecological processes, such as the resilience feedbacks we outlined above, there are limitations intrinsic to observational methods. Namely, from our study we cannot conclusively determine if resilience to precipitation events is driven by diversity (richness and evenness) or an unaccounted-for correlated variable(s).

4.3 | Temporal variation in community properties promoted long-term invariability

We found that subplots with higher long-term variation in evenness and *S. altissima* relative abundance had increased long-term ANPP invariability (last panels of Figure 4a,b). While initially counterintuitive that more temporally variable communities would have more stable functioning, these findings point to the potential role of compensatory dynamics in this system, wherein asynchronous responses among species to environmental fluctuations scale to stabilize community productivity through time (Gonzalez & Loreau, 2009). Here, we suggest that fluctuations in *S. altissima* abundance may be offset by asynchronous responses in the subdominant community members (Hector et al., 2010).

5 | CONCLUSIONS

We explored the role of plant community properties in regulating primary productivity resilience to precipitation events in a temperate grassland. We found that drought has much stronger effects on ANPP than wet events, but both wet and dry events alter community properties—in particular, evenness, dominant species relative abundance, and richness. These same community properties strongly regulate productivity resistance to drought and are associated with long-term invariability. As a result, even though extreme wet events had minimal effects on ANPP, they may nonetheless affect resilience to future extreme droughts. More generally, we infer that these connections between precipitation events, community properties, and resilience may lead to feedbacks with implications for long-term productivity resilience. As precipitation events increase in frequency and severity under climate change, future work may explore the generalizability of such feedbacks in plant communities, as well as evaluate these feedbacks in relation to the resilience of other ecosystem functions.

AUTHOR CONTRIBUTIONS

Sierra Perez and Jennifer Lau conceived this study and designed analysis methodology. Mark Hammond provided field methodological background. Sierra Perez analysed the data and led manuscript writing. All authors contributed to the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Stacey VanderWulp and KBS LTER core lab technicians for collecting, processing, and maintaining the long-term ANPP dataset that made this analysis possible. We thank Forest Isbell, Don Schoolmaster, and Mallory Barnes for methodological guidance, and Heather Reynolds and Nameer Baker for manuscript feedback. Sierra Perez was supported by the Indiana University Kindig Fellowship while conducting this research. Support for this research was provided by the NSF Long-term Ecological Research Programme (DEB 2224712) at the Kellogg Biological Station and by Michigan State University AgBioResearch. This is KBS contribution #2395.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14471.

DATA AVAILABILITY STATEMENT

All data are available through the Kellogg Biological Station LTER's data catalogue. Meteorological data can be accessed at https://lter.kbs.msu.edu/datatables/12 (Robertson, 2020). Above-ground biomass data can be accessed at https://lter.kbs.msu.edu/datatables/40 (Robertson & Snapp, 2020).

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SUPPORTING INFORMATION

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

Table S1: Rationale for inclusion of community and event type predictor variables and interaction terms in the resistance and recovery global models.

Table S2: Predictors of the magnitude of precipitation events' impact on aboveground primary productivity.

Figure S1: Observed values of response variables, indicated by points, underlying the predicted relationships from best-fit models shown in Figure 4.

How to cite this article: Perez, S., Hammond, M., & Lau, J. (2024). Precipitation anomalies may affect productivity resilience by shifting plant community properties. *Journal of Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2745.14471