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Funding information

ERA-Net BiodivERsA, Grant/Award Number: 01LC1201; German Federal Ministry of Education and Research (BMBF); BonaRes, Grant/Award Number: 031B0027C; Belgian Federal Science Policy Office (BELSPO); Bulgarian Science Found

Abstract

Higher biodiversity can stabilize the productivity and functioning of grassland communities when subjected to extreme climatic events. The positive biodiversity–stability relationship emerges via increased resistance and/or recovery to these events. However, invader presence might disrupt this diversity–stability relationship by altering biotic interactions. Investigating such disruptions is important given that invasion by non-native species and extreme climatic events are expected to increase in the future due to anthropogenic pressure. Here we present one of the first multisite invader × biodiversity × drought manipulation experiment to examine combined effects of biodiversity and invasion on drought resistance and recovery at three semi-natural grassland sites across Europe. The stability of biomass production to an extreme drought manipulation (100% rainfall reduction; BE: 88 days, BG: 85 days, DE: 76 days) was quantified in field mesocosms with a richness gradient of 1, 3, and 6 species and three invasion treatments (no invader, *Lupinus polyphyllus*, *Senecio inaequidens*). Our results suggest that biodiversity stabilized community productivity by increasing the ability of native species to recover from extreme drought events. However, invader presence turned the positive and stabilizing effects of diversity on native species recovery into a neutral relationship. This effect was independent of the two invader's

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own capacity to recover from an extreme drought event. In summary, we found that invader presence may disrupt how native community interactions lead to stability of ecosystems in response to extreme climatic events. Consequently, the interaction of three global change drivers, climate extremes, diversity decline, and invasive species, may exacerbate their effects on ecosystem functioning.

KEYWORDS

alien invasive species, biological invasion, climate extreme, disturbance, ecosystem functioning, grassland ecosystem, plant–environment interaction, recovery, resilience, resistance

1 | INTRODUCTION

Loss of biodiversity tends to affect ecosystem functioning and stability of grasslands negatively and is likely to affect human society (Cardinale et al., 2012; Hautier et al., 2015, 2018; Tilman, Isbell, & Cowles, 2014). A more diverse plant community leads to an overall more stable community functioning under a wider range of conditions when species react in asynchrony due to compensatory responses (sensu insurance hypothesis: de Mazancourt et al., 2013; Loreau & de Mazancourt, 2013; Tilman et al., 2014; Yachi & Loreau, 1999). Increased stability maintains community productivity while the availability of free resource declines (Gross et al., 2014; Tilman, Reich, & Isbell, 2012). Global change drivers lead to exogenous changes in resource availability and the introduction of non-native species, leading to uncertainty as to whether the diversity–stability relationship persists in the face of extreme climatic events (De Boeck et al., 2018) and invasion (Pinto & Ortega, 2016).

The frequency and magnitude of extreme climatic events, such as drought (Dai, 2013), are predicted to increase in Europe as a result of climate change (Hewitson et al., 2014). Altered drought regimes in semi-natural grasslands might lead to plant mortality, species composition shifts, degradation and desertification, and erosion (Craine et al., 2012; Reichstein et al., 2013; Wang et al., 2011). Strong droughts can cause lasting effects on community composition by selecting for drought tolerant species (e.g. Mediterranean species), resulting in dominance shifts and/or local extinction of drought intolerant species (Alba, NeSmith, Fahey, Angelini, & Flory, 2017; Reichstein et al., 2013; Török, Janišová, Kuzemko, Rusina, & Stevanovic, 2018). Such drought-induced changes in the plant community structure of grasslands might subsequently affect plant productivity as well as ecosystem functioning and the delivery of ecosystem services (Caldeira et al., 2015; Cantarel, Bloor, & Soussana, 2013; Reichstein et al., 2013).

In Europe, species invasions show a stable rate of increase (Butchart et al., 2010; Caldeira et al., 2015; Seebens et al., 2017) which might lead to large scale homogenization and reduced ecosystem (multi-) functioning (Dornelas et al., 2014; Hautier et al., 2018; Vellend et al., 2013). A globally unique feature of Europe is the extensive semi-natural grasslands, whose species-rich communities originate from millennia of low-intensive agricultural use (pastures, hay-meadows) on sites that would naturally support forests (Török

& Dengler, 2018). These semi-natural grasslands are of high importance for dairy and meat production as well as for biodiversity conservation, among other things (Dengler & Tischew, 2018; Török et al., 2018). Generally, European grasslands seem to be rather resistant against plant invasions, being one of the least invaded habitat types in Europe (Chytrý et al., 2008, 2009; Pyšek, Chytrý, & Jarošík, 2010). The exception is invasions by tall forbs, with the reasons not being fully understood (Dengler & Tischew, 2018). Invasives like *Lupinus polyphyllus* and *Senecio inaequidens* increasingly colonize semi-natural grasslands while the former tends to form dominance stands, changing the vegetation structure and species diversity drastically (Hejda, Pyšek, & Jarošík, 2009; Lachmuth, Durka, & Schurr, 2010; Scherber, Crawley, & Porembski, 2003; Thiele, Isermann, Otte, & Kollmann, 2010; Volz & Otte, 2001). Those changes will likely also affect biotic interactions, abiotic processes and consequently ecosystem stability of the invaded habitats (Sousa, Morais, Dias, & Antunes, 2011; Strayer, 2012).

There is a decades-long scientific discussion about the role of biodiversity, in terms of species richness, for ecosystem stability with a large scientific consensus that biodiversity, in terms of (plant) species richness, infers greater temporal stability to ecosystems in case of disturbance or extreme events (e.g. Isbell et al., 2015; Kreyling et al., 2017; Tilman, Reich, & Knops, 2006). However, counterexamples exist (e.g. Hillebrand et al., 2018; Pfisterer & Schmid, 2002) and the question of whether the diversity–stability relationship is linear, hump-, or U-shape is not definite yet (Pennekamp et al., 2018). Ecosystem stability against extreme events—which is often measured as the reciprocal of temporal variability in community biomass (Cardinale et al., 2012)—can be separated into resistance (Pimm, 1984) and recovery (Hodgson, McDonald, & Hosken, 2015). Here we consider resistance as the degree of change of an ecosystem property in response to an extreme climatic event; no change would indicate complete resistance. Recovery is defined as the degree to which an ecosystem property returns to control or predrought levels after the cessation of the extreme event (Bahn & Ingrisch, 2018; Hodgson et al., 2015; Kreyling et al., 2017). Resistance and recovery can be affected differently by biodiversity (De Boeck et al., 2018; Kreyling et al., 2017; Van Ruijven & Berendse, 2010), with the nature and duration of the extreme event potentially playing an important role. Resistance may be more important during ‘press’ events (long-lasting extremes with

brief periods of recovery, e.g. the Californian 2012–2016 drought), as acclimation responses (Zhou, Medlyn, & Prentice, 2016) and species reordering (Evans, Byrne, Lauenroth, & Burke, 2011) have more time to develop. These efficient longer term defences are less likely to manifest during short but intense pulse events (such as in the current study). On the other hand, alleviation of stress following a pulse event is usually more pronounced, promoting fast recovery. In the case of pulse droughts, nutrient flushes upon rewetting can further stimulate recovery (Dreesen, Boeck, Janssens, & Nijs, 2014). Several recent studies on pulse events have indeed found that plant species richness increased the recovery but not the resistance of grasslands (e.g. Kreyling et al., 2017; Van Ruijven & Berendse, 2010). However, counter examples highlighting the importance of biodiversity for the resistance of grasslands against extreme pulse drought events also exist (e.g. Tilman & Downing, 1994).

It is unclear if the diversity–stability-relationship is maintained in the presence of an invader (Pinto & Ortega, 2016). Climate extremes might impact all of the mechanisms conferring ecosystem stability (Cardinale et al., 2012; De Boeck et al., 2018), thus, enabling the establishment of non-native species in the first place (Hautier et al., 2018; Török et al., 2018; Wardle, Bardgett, Callaway, & Putten, 2011). Invasive species might be able to affect the diversity–stability relationship by altering the ability of communities to resist to and/or recover from an extreme event (Wilsey, Daneshgar, Hofmocker, & Polley, 2014). A highly competitive invader or an invader that tolerates abiotic stress more effectively than the native species might be able to outcompete natives before or during an extreme event respectively (Diez et al., 2012). Even with increased resistance of the invader, such indirect competitive effects could diminish the overall resistance of an ecosystem (e.g. to biomass fluctuations) if competitive pressure leads to native species loss (Bernard-Verdier & Hulme, 2019). The same accounts for recovery: if the invader recovers more quickly from harsh climatic conditions then it might impede the partitioning of resources after stress release as the invader instead captures the majority of available resources (De Boeck et al., 2018; Diez et al., 2012).

Here we quantified the effects on community productivity of two invasive species in Europe, the legume *L. polyphyllus* Lindl. and the non-legume forb *S. inaequidens* DC. We further studied their impacts on community resistance and recovery of biomass production to an extreme climatic event (ambient conditions, extreme drought manipulation) in field mesocosms differing in diversity (1, 3, 6 species) at three sites across Europe (Germany, Belgium, Bulgaria). We hypothesized (a) a positive diversity–recovery relationship in native communities exposed to drought, (b) that the presence of invasive species disrupts this relationship, and (c) that extreme drought events facilitate the studied invader species in these semi-natural grasslands.

The work presented here contributes to the global framework of the diversity–stability debate led by long-term, globally distributed grassland experiments such as Drought-Net and Nutrient Network. These investigate the diversity–stability effect across large spatial and temporal scales, taking into account different disturbances yet generally not including issues related to invasive species (Anderson et al., 2018; but see Flores-Moreno et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Experimental design

We tested the effects of invaders on the diversity–stability relationship of grassland communities in a coordinated-distributed mesocosm experiment in the field at three climatically (Table S1) and ecologically different sites across Europe: Belgium (BE), Bulgaria (BG), Germany (DE). Richness levels and species composition, including invader presence, were experimentally established in mesocosms. Then, we exposed them to an artificial severe drought event to study the joint effects of drought, invasion, and species richness on biomass production. The experiment was carried out with three fully crossed factors: (a) invader presence (three factor levels: native species only [no invader]; native species and the invader *L. polyphyllus*; native species and the invader *S. inaequidens*); (b) climatic extremes (two factor levels: severe drought, ambient control); (c) community richness (three factor levels: 1, 3 and 6 species).

The coordinated experiment was implemented using buried field mesocosms. At each site, 132 mesocosms were set up: 72 mesocosm with native communities and 60 mesocosms with invader presence (Figure S1). Each mesocosm had 18 individuals planted, split evenly among the number of species assigned to it. For mesocosms with only native species, 12 locally frequent, native species that naturally occur together on the local soil were selected for each site (Figure S1). From these, 12 different compositions were created which were considered as replicates for the species richness levels (3 sites \times 3 species richness levels \times 12 species compositions \times 2 climate treatments = 216 native species mesocosms in total). Invader monocultures were replicated three times for each invader, while the other two richness levels each had six unique assemblages using the site-specific native species and one invader, yielding a total of 30 compositions \times 2 climate treatments \times 3 sites = 180 mesocosms with invader presence or monocultures of invaders (Figure S1). Each unique species composition was exposed to both a drought treatment and ambient weather conditions (control) at each of three sites. Native study species included three functional groups (forbs, graminoids, legumes) with four species representing each functional group per site (Table S2).

All plants were grown from seed under standardized conditions at each site and planted into field mesocosms in early spring 2014 (more than 3 months before the start of the drought manipulation). Seeds were collected from autochthonous populations close to the study sites (relying on expert knowledge; Table S2). Each mesocosm consisted of a PVC tube of 30 cm diameter and 50 cm height. The base of mesocosms was closed with root matting, permeable for water but impermeable for roots. Consequently, rooting depth was limited to 50 cm in order to standardize the climate treatment effects. This may have interfered with deep-rooting strategies (e.g. Nippert & Knapp, 2007) in turn limiting niche differentiation and the potential diversity effects (Dimitrakopoulos & Schmid, 2004). Mesocosms were buried in the soil to ensure realistic temperature

and drainage patterns, and filled with local soil substrate (homogenized, sieved to 2 cm). Mesocosms were planted with 18 pregrown plant individuals in a systematic arrangement, avoiding conspecific neighbours, and ensuring that edge/centre ratios were similar for each species. Each species had the same number of individuals per mesocosm within each species richness level. Thus, invader mesocosms of species richness level 1 had an invader fraction of 100%; mesocosms of species richness level 3 had an invader fraction of 33.3% (6 out of 18 individuals), and mesocosms with a species richness level of 6 had an invader fraction of 16.7% (3 out of 18 individuals). Upon planting, plants were cut to a height of 6 cm above ground level to standardize the initial conditions. No fertilization was applied. Mortality was checked regularly, and dead individuals were replaced during the first month after planting. Non-target species were weeded out at a monthly interval.

2.2 | Invader species

Two non-native species invasive to Europe, the legume forb *L. polyphyllus* Lindl. and the non-legume forb *S. inaequidens* DC., were selected for this study. Both species exhibit rapid population growth, an ability to alter their local environment, and are habitat generalists, making them interesting study subjects for invasion processes in European semi-natural grasslands (additional information can be found in the supporting information, p. 3; EPPO, 2006; Fremstad, 2010; Global Invasive Species Database [GISD], 2015; Lauterbach & Nehring, 2013; Scherber et al., 2003). *L. polyphyllus* (Fabaceae), the garden lupine, is native to the western parts of North America and Canada (Beuthin, 2012) and was introduced in Europe in the early 1900s (Fremstad, 2010). *S. inaequidens* (Asteraceae), the South African ragwort, is native to South Africa and Lesotho and was introduced in Europe during the late 19th century (Ernst, 1998; Lachmuth et al., 2010). To date, the occurrence and the impact of both invasive species in Europe is more localized (Dengler & Tischew, 2018; Lachmuth et al., 2010), but both invaders are expected to profit from climate change in terms of increasingly favourable conditions and a possible expansion in range (GISD, 2015; Heger & Böhmer, 2006; Lauterbach & Nehring, 2013).

We expect the Mediterranean type invader *S. inaequidens* to cope well with drought (GISD, 2015). Additionally, *S. inaequidens* is highly efficient in capturing free resources (Dassonville et al., 2008; GISD, 2015) and thus, might be able to compromise the resistance as well as the recovery of our native communities. *L. polyphyllus* is a deep-rooting legume which is able to store nutrients in its rhizomes in the event of disturbance and to resprout when conditions are more favourable (Fremstad, 2010; Volz & Otte, 2001). We expect *L. polyphyllus* to recover more quickly from the extreme event, and thus to disrupt the partitioning of resources after stress release. Consequently, we expect *L. polyphyllus* to hamper the recovery of our native species. However, due to its profound root system *L. polyphyllus* might also be able to outcompete native species during the extreme event.

2.3 | Climate treatment

We simulated a pulsed drought event using rainout shelters with 100% rainfall reduction for specific periods during the local growing season. The rainout shelters covered the buried mesocosms and additionally >1.5 m as lateral buffer zones. A randomized block design was applied at each site with either two or three blocks (with each block containing both a rainout shelter and a control). Mesocosms were completely randomized within each drought treatment-block combination. Drought length was standardized across sites with the aim to be extreme compared to past conditions (De Boeck et al., 2019; Schär et al., 2004) and on the basis that such events might become common in the future (Dai, 2013; Seneviratne et al., 2012; Hewitson et al., 2014). Drought length was calculated for each site as 1.5 times the number of consecutive days with <2.5 mm precipitation estimated from the statistical 1,000 year recurrence of such events based on historical data of local precipitation (series length: BE = 111 years, DE = 63 years, BG = 30 years), and constrained within the local growing season (months with mean temperature >5°C and precipitation sum [mm] >2 × mean temperature [°C]; Kreyling et al., 2017). Thus, the extremity of the manipulation is relative to each site, thereby increasing comparability. Ecologically, this is a more meaningful standardization of drought length than simply applying the same drought length to systems under different climatic conditions and, consequentially, different evolutionary adaptation of species and plant traits. The drought treatment started 2/5 of the way into the site-specific growing season (see Table S1 for starting dates). The durations of drought were 76 days in Germany, 85 days in Bulgaria, and 88 days in Belgium. In case of natural drought during the manipulation period, mesocosms growing under ambient weather conditions were irrigated (DE: 4 × 10 mm; BE and BG: never necessary). The drought manipulations were ended by irrigating the droughted mesocosms with 20 mm and the ambient mesocosms with 5 mm, to ensure a temporal synchrony between the postmanipulation rainfall events.

2.4 | Biomass production

Above-ground biomass (B) was harvested at three dates during the experiment: (B0) 2 weeks before the start of the drought treatment ('before drought'), to allow for a standardized quantification of biomass production during the drought period; (B1) directly at the end of drought ('end of drought'); and (B2) at peak biomass the following growing season ('peak following year', used for assessing recovery after drought). Biomass was always harvested at 3 cm above ground, and included all plant material rooted inside the mesocosms. We discarded all biomass of species rooted outside, but growing into, the mesocosm communities (Cancellieri, Mancini, Sperandii, & Filibeck, 2017). We did not sample root biomass. Species-specific biomass harvests were conducted directly after the drought (harvest B1) and at the peak of the following year (harvest B2; BG and DE only). Community biomass harvests were conducted at harvest B0. We

sampled the same mesocosms repeatedly because regular cutting 2–5 times per year is the management regime applied in these semi-natural grasslands across Europe (Blüthgen et al., 2012; Dengler & Tischew, 2018; Ellenberg, 1996).

2.5 | Response parameters

We used relative measures of resistance and recovery to examine different facets of ecological stability (Donohue et al., 2016; Kreyling et al., 2017; Pimm, 1984). Both metrics are dimensionless, and thus directly comparable between sites and communities with different levels of productivity. We calculated resistance to and recovery from drought for each unique species composition by comparing biomass production between drought treatment and ambient control as:

$$\text{Resistance} = \frac{(B1)_{\text{drought}}}{(B1)_{\text{control}}},$$

$$\text{Recovery} = \frac{(B2)_{\text{drought}}}{(B2)_{\text{control}}},$$

where B1 is the biomass of each community at the end of the drought period and B2 is the biomass of each community at the peak of biomass production in the following year. The resistance index equals 1 for complete resistance and 0 for no resistance (no biomass production during drought). The recovery index equals 1 for complete recovery and is <1 for incomplete recovery. Values >1 indicate overcompensation. Community compositions with <1.5 g dry weight per mesocosm under control conditions (1.5% of all cases) were disregarded because of their high relative uncertainty (e.g. incremental differences in cutting height can have strong relative effects) and their potential to disproportionately inflate errors (grand mean over all measurements is 31.4 ± 1.8 [SE] g per mesocosm).

Survival of invader species as well as native species growing within invader mesocosms were recorded at the end of the drought treatment (B1 harvest). To further quantify the effect of invader presence on native species, we additionally analysed the biomass production of native species growing with and without invader presence. Methods and results of the parameter survival, and the impact of invader presence/absence on native species' biomass production can be found in the supplemental material (Tables S3 and S4).

2.6 | Statistical analysis

All analyses were conducted using the statistical software R 3.4.2 (R Core Team, 2017). We used linear mixed-effects models to test the productivity–richness relationship for native and invader mesocosms under ambient conditions (only for harvest B1). Here we tested the impact of the explanatory variables *species richness* and *invader presence*, as well as their interactions, on above-ground

biomass production (dependent variable). With a second linear mixed-effects model we tested if resistance and recovery to climate treatment depended on the explanatory variables *species richness* and *invader presence* as well as their interactions. A third linear mixed-effects model was used to evaluate the difference in the individual biomass of the two invader species (dependent variable). Here we used the fixed-effects *climate treatment*, *species richness*, and *species* (explanatory variables) as well as their interactions. Model 3 was run four times, once each for the B1 and B2 harvests. Results for the B2 harvest can be found in Figure S2. We additionally used model 3 to test the difference in the invader biomass per community biomass (relative invader biomass) of the two invader species (Figures S3 and S4) using the same fixed-effects as in the analyses of the individual invader biomass.

In case of significant interactions between the fixed-effects *invader presence* (models 1 and 2) or *species* (model 3) with the other explanatory variables (*climate treatment*, *species richness*), we ran additional linear mixed-effects models separately for each level of the categorical variables such as *invader presence* or *species* to determine if there were significant differences in the mean values within this group caused by climate treatment/species richness with Bonferroni correction for multiple testing.

We accounted for possible random effects due to the blocked structure and the multisite character of the experiment by nesting *blocks* within *sites* in all linear mixed-effects models. As we tested for general trends across three countries, we have considered country effects as random factors in our models, not as fixed factors. We only allowed the intercept to vary as a function of the block design, but did not include any other main factors into the random term. *Species richness* was introduced into the models as a linear numeric variable, but note that log-linear and factorial response produced qualitatively the same results.

Models were fit with the *lmer* function in the *lme4* package (version 1.1-12; Bates et al., 2014) and results were extracted with the *ANOVA* function in the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2016) in R. ANOVA tables for the respective models can be found in the supporting information document (part 2, pp. 13–22). We visually checked if the model assumptions of homoscedasticity and normal distribution of residuals were violated. Linear models are robust even towards rather severe violations of the model assumptions (Lo & Andrews, 2015; Wilson, 2007). Consequently, we only transformed our response variables in case of severe violations of the model assumptions. Transformation of the response variables produced qualitatively the same results as non-transformed responses. The response variables *resistance* and *individual biomass* were $\log(x + 1.1)$ -transformed while the response variable *productivity* was $(1 + x)^{0.4}$ -transformed (note that $\log(x + 1.1)$ -transformation produced qualitatively the same results) to meet the model assumptions of homoscedasticity and normal distribution of residuals.

Additionally, we checked for effects of different sample sizes by permuted subsampling of the mesocosms containing only natives and did not see qualitatively different effects.

3 | RESULTS

3.1 | Richness–productivity relationship

Under ambient weather conditions, native species productivity increased with species richness (ANOVA subset natives: $p_{\text{richness}} = .003$; $\text{biomass}_{\text{natives richness level 1}} = 288 \text{ g/m}^2$, $\text{biomass}_{\text{natives richness level 3}} = 395 \text{ g/m}^2$, $\text{biomass}_{\text{natives richness level 6}} = 417 \text{ g/m}^2$; Figure 1, ANOVA-Table S1). But invader presence weakened this diversity effect (ANOVA $p_{\text{richness} \times \text{invader presence}} < .001$; ANOVA-Table S1). Overall, invader communities were more productive than native communities (ANOVA-Table S1). In invaded communities, we observed a trend of increasing productivity at lower richness levels, and thus a higher invader fraction biomass (Figure 1; ANOVA-Table S1).

Native species growing with the invader *S. inaequidens* were 31.3% smaller than natives growing without invader presence (ANOVA $p_{\text{invader presence}} < .001$; ANOVA-Table S2; Table S4). Mean individual biomass of native species growing with *L. polyphyllus* was 7.1% higher compared to native species growing alone (Table S4, ANOVA-Table S2).

3.2 | Native community resistance and recovery from drought

Species richness did not have a significant effect on drought resistance of biomass production (ANOVA $p_{\text{richness}} = .411$; Figure 2a; ANOVA-Table S3), while the ability of native plant communities to recover from a severe drought event did increase with

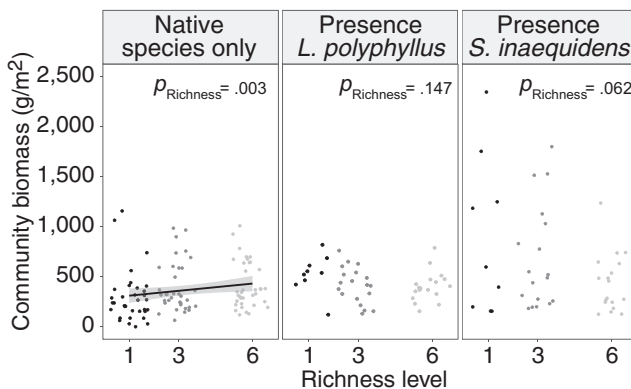


FIGURE 1 Community biomass of the mesocosms growing under ambient weather conditions at the B1 harvest (after drought) shown as a function of richness (black = richness 1, grey = richness 3, light grey = richness 6) considered across all countries, separately for each invasion status. Shown is the community biomass of each mesocosm per invasion status ($n_{\text{natives}} = 213$; $n_{\text{Lupinus polyphyllus}} = 90$; $n_{\text{Senecio inaequidens}} = 90$). Data points were jittered along the x-axis at each richness level to improve visibility of the data distribution. Black solid lines display mixed-effects model fits of the three submodels for every invader presence level (Bonferroni-corrected significance level: $p < .017$; ANOVA-Table S1), and grey shades indicate their respective 95% confidence intervals

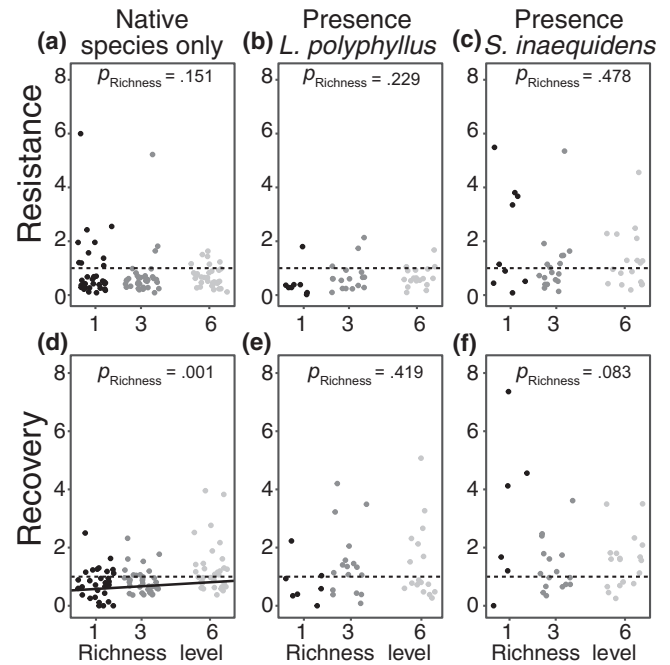


FIGURE 2 Resistance (B1 ANPP harvest; a–c) and recovery (B2 ANPP harvest; d–f) to a severe drought event, shown as a function of richness (black = richness 1, grey = richness 3, light grey = richness 6), separately for each invasion status (resistance: $n_{\text{natives}} = 107$; $n_{\text{Lupinus polyphyllus}} = 45$; $n_{\text{Senecio inaequidens}} = 45$; recovery: $n_{\text{natives}} = 106$; $n_{\text{Lupinus polyphyllus}} = 45$; $n_{\text{Senecio inaequidens}} = 45$). All mesocosms with a ratio above 1 (the dashed line) showed higher biomass production in drought compared to ambient conditions, while all mesocosms with ratios below 1 showed lower biomass production in drought than under ambient conditions. Bonferroni-corrected significance level $p < .017$ for the three submodels of invader presence in recovery to drought. Data points were jittered at each richness level to improve visibility of the data distribution

species richness level (ANOVA subset natives: $p_{\text{richness}} = .001$; $\text{recovery}_{\text{natives richness level 1}} = 0.78 \pm 0.10$, $\text{recovery}_{\text{natives richness level 3}} = 0.86 \pm 0.07$, $\text{recovery}_{\text{natives richness level 6}} = 1.29 \pm 0.15$; Figure 2d, ANOVA-Table S4; Table S5; significant higher level interaction of model 2 across all invader presence levels: see below).

3.3 | Invader impact on resistance and recovery

Invasion status did not alter the richness–resistance relation compared to the (non-significant) relation observed in the native species mesocosms (ANOVA $p_{\text{richness} \times \text{invader presence}} = .379$; Figure 2a–c; ANOVA-Table S3). However, invader presence changed the drought resistance of the affected plant communities (ANOVA $p_{\text{invader presence}} = .011$; ANOVA-Table S3). Depending on the invader species, drought resistance—in terms of sheer biomass production—increased in *S. inaequidens* communities (+83.2%) and decreased in *L. polyphyllus* communities (–18.2%; Figure S7) compared to native species communities.

Invader presence altered the richness–recovery relationship in our experiment (ANOVA $p_{\text{richness} \times \text{invader presence}} = .026$; Figure 2d–f;

ANOVA-Table S4). The presence of both invasive species nullified the positive effect of species richness on the recovery of plant communities (ANOVA subset *L. polyphyllus* $p_{\text{richness}} = .419$; ANOVA subset *S. inaequidens* $p_{\text{richness}} = .083$; ANOVA-Table S4; Figure 2e), possibly due to their high productivity in monocultures (*S. inaequidens*) and intermediate richness levels (*L. polyphyllus*). Both invader species showed increased recovery compared to native species across all species richness levels (ANOVA-Table S4).

3.4 | Invader performance

Performance per individual of the two invaders in response to the drought treatment differed marginally (ANOVA $p_{\text{species} \times \text{climate treatment}} = .081$; ANOVA-Table S5a; Figure 3). Under drought, *L. polyphyllus* on average produced less biomass than under ambient conditions (−67.9%), while the drought treatment showed no significant impact upon *S. inaequidens* (on average +12.9% more biomass compared to control mesocosms, but this effect was not significant; ANOVA-Table S5a subset *S. inaequidens*; Figure 3). During the treatment phase of the first year (B1 harvest, resistance), native species showed marginally different effects on the invaders (ANOVA $p_{\text{species} \times \text{richness}} = .058$; ANOVA-Table S5a; Figure 3): under ambient conditions, *L. polyphyllus*' biomass production showed a tendency to be negatively affected by interspecific competition, although this effect was superimposed by the strong negative effect of drought upon the individual biomass of *L. polyphyllus* (ANOVA subset *L. polyphyllus*: $p_{\text{richness}} = .056$; $p_{\text{climate treatment}} = .007$; ANOVA-Table S5a; Figure 3). We did not observe a significant effect of species richness on the drought resistance of *S. inaequidens*.

One year after the extreme event (harvest B2, recovery), performance of the invader species was affected by both, climate treatment and species richness (ANOVA $p_{\text{species} \times \text{climate treatment} \times \text{richness}} = .027$;

ANOVA-Table S5b). Formerly drought-treated *S. inaequidens* individuals growing in interspecific competition with native species were able to regrow significantly more biomass than individuals growing in intraspecific competition (monocultures) or under ambient weather conditions (ANOVA subset *S. inaequidens* $p_{\text{climate treatment} \times \text{richness}} = .0098$; Figure S2; ANOVA-Table S5b). While drought recovery of *L. polyphyllus* seemed not to be dependent on climate treatment or species richness (Figures S2 and S4; ANOVA-Table S5b).

Invader fraction per community biomass at the end of the drought treatment (B1 harvest), as expected, decreased with increasing species richness level in both invader species (ANOVA $p_{\text{species} \times \text{richness}} = .055$; ANOVA-Table S6a). However, the steepness of the decline varied between the two invader species. *S. inaequidens*, contributed 47.2% to the total biomass even in the six species high-diversity mesocosms (ANOVA subset *S. inaequidens* $p_{\text{richness}} < .001$; ANOVA-Table S6a; Figure S3), while the percentage share of *L. polyphyllus* was <20%, outside monocultures (ANOVA subset *L. polyphyllus* $p_{\text{richness}} < .001$; ANOVA-Table S6a; Figure S3). One year after the extreme event (B2 harvest, recovery), the relative share of invader species to the total community biomass was still determined by species richness, but had decreased in total and was more similar between the invader species (ANOVA $p_{\text{richness}} < .001$; ANOVA-Table S6b; Figure S4).

3.5 | Survival

Invader presence during drought (B1 harvest) changed the viability of plant communities depending on invader species and species richness level (ANOVA $p_{\text{richness} \times \text{invader presence}} = .002$; Table S3a, ANOVA-Table S7): Survival of *S. inaequidens* communities showed a tendency to decrease with species richness level (ANOVA subset *S. inaequidens* $p_{\text{richness}} = .042$; ANOVA-Table S7), while those of

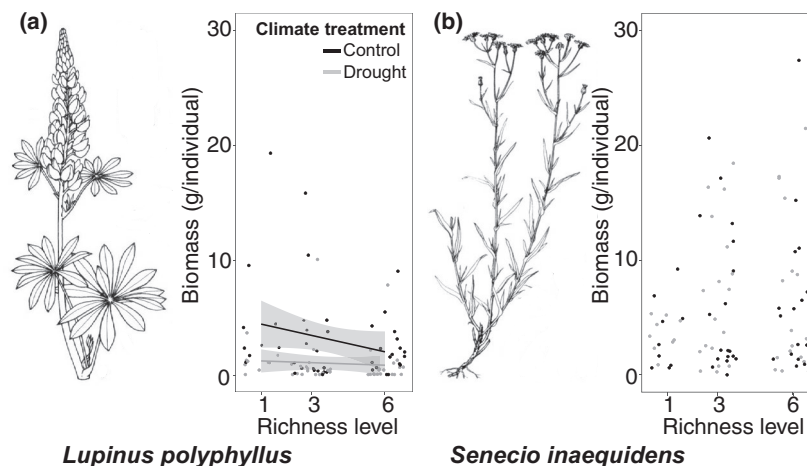


FIGURE 3 Individual invader biomass at the end of the drought treatment (B1 harvest) presented as a function of richness separately for every climate treatment. The mean biomass of an individual calculated for every mesocosm is shown, separately for (a) *Lupinus polyphyllus* ($n_{\text{control}} = 45$; $n_{\text{drought}} = 45$) and (b) *Senecio inaequidens* ($n_{\text{control}} = 45$; $n_{\text{drought}} = 45$). Data points were jittered at each richness level to improve visibility of the data distribution. Solid lines display mixed-effects model fits of the invader specific submodels (Bonferroni-corrected significance level $p < .025$; ANOVA-Table S5a), and grey shades indicate their respective 95% confidence intervals

L. polyphyllus communities increased with decreasing invader fraction (ANOVA subset *L. polyphyllus* $p_{\text{richness}} = .015$; ANOVA-Table S7). We observed a decrease in the survival differences of native plant communities versus invader plant communities with decreasing invader fraction (ANOVA $p_{\text{richness} \times \text{invader presence}} = .002$; ANOVA-Table S7). Survival of *L. polyphyllus* individuals after drought was lower, while the survival of *S. inaequidens* individuals was higher (Table S3b) compared to native species (Table S3a). Presence of invader species decreased the viability of natives (natives within *L. polyphyllus*/*S. inaequidens*; Table S3b) compared to native plant species communities (Table S3a).

The drought treatment decreased the viability of native communities by 11.1%, of *L. polyphyllus* communities by 11.9% and those of *S. inaequidens* by 5.6% (ANOVA $p_{\text{climate treatment}} = .072$; ANOVA-Table S7).

4 | DISCUSSION

4.1 | Presence of the two studied invader species disrupts the positive richness–recovery relationship of semi-natural grasslands in the face of drought

We found a positive diversity–stability relationship of our native species communities for recovery after drought across three European sites. Invader presence disrupted this positive relationship irrespective of the overall invader performance under drought conditions.

One year after the extreme drought event, community productivity had fully recovered and in some cases even overcompensated, particularly in the high-diversity mesocosms of native communities. Native species richness improved the drought recovery of biomass production in our multisite experiment and, thus, provided ecosystem stability in the face of extreme climatic events in uninvaded assemblages. These findings are consistent with previous studies showing positive relationships between diversity and recovery after extreme climatic events independent from the overall productivity of the communities (Allison, 2004; DeClerck, Barbour, & Sawyer, 2006; Kreyling et al., 2017; Van Ruijven & Berendse, 2010; Vogel, Scherer-Lorenzen, & Weigelt, 2012).

The presence of *L. polyphyllus* and *S. inaequidens* nullified the positive richness–recovery effect found in our native communities. The disruption of the positive richness–recovery relationship in the presence of invasive species is most likely due to their high productivity and the decreasing relative invader fraction with increasing richness. *S. inaequidens* communities showed a stronger resistance and recovery than *L. polyphyllus* communities and the native species communities. This resulted in the neutralization of the positive diversity–stability relationship of native communities wherever *S. inaequidens* contributed more to the community biomass. *S. inaequidens*' ability for enhanced nutrient uptake modifies ecosystem functions by depleting the topsoil nutrient pools and thus reduces the above-ground biomass of the invaded sites (Dassonville et al., 2008; GISD, 2015). Consequently, *S. inaequidens* might have been able to

capture free resources more efficiently than natives both during and after the drought event, likely leading to competitive advantages due to greater growth and development. The highly competitive invader *S. inaequidens* might be able to dominate native communities through increased stress tolerance (Daehler, 2003; Davis, Grime, & Thompson, 2000; Diez et al., 2012), more efficient uptake of limiting resources during the extreme drought (Funk & Vitousek, 2007; Huston, 2004; Vilà & Weiner, 2004), and by more rapid uptake of available resources after stress relief compared to slower growing native species. Thus, *S. inaequidens* seems to increase the competitive pressure on the native species during the drought event and likely disturbs the partitioning of resources after stress release.

L. polyphyllus communities also showed a higher and overcompensating recovery compared to native species, despite an average drought resistance in terms of above-ground biomass production. This high ability to recover from a severe drought event in *L. polyphyllus* suggests increased resource allocation to the roots. *L. polyphyllus* is resistant to above-ground biomass removal due to its rhizomes, which enable the invader to resprout multiple times as well as to spread vegetatively by polycormons up to 0.2 m/year (Volz, 2003; Volz & Otte, 2001). Consequently, *L. polyphyllus* might be able to dominate native communities due to its ability to recover quickly after an extreme event (Daehler, 2003; Davis et al., 2000; Diez et al., 2012), and is likely to benefit from the reduced competitive strength of drought-affected native species. However, *L. polyphyllus* does not seem to disturb the partitioning of resources after stress release as natives growing with the non-native legume produced more biomass in both control and drought conditions compared to native species without invader presence.

Many invasive species show such opportunistic traits (Burns & Winn, 2006; Daehler, 2003; Funk, 2008; Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006). Consequently, the presence of competitive and stress tolerant invaders might be able to overturn the positive diversity–stability relationship of native grassland communities (Wilsey et al., 2014). While stability, in terms of biomass production, of native species communities seems to have profited from species richness, that is native species growing in a mixture of potentially asynchronous species, stability of the invader mesocosms seems to be inferred largely by highly productive invasives and their respective share in the entire community (Wilsey et al., 2014). Consequently, the overall stability of the native versus the invader communities may be inferred by two different mechanisms but might ultimately lead to stable—in terms of sheer biomass production—grassland communities (Wilsey et al., 2014). However, both invasive species tested in this study are pasture weeds and their presence might lead to a reduction in fodder value and thus, to economic losses (since the quality of hay production is reduced due to the presence of those species) especially if they occupy large parts of the affected grasslands (Bossdorf, Lipowsky, & Prati, 2008; Hensgen & Wachendorf, 2016). Additionally, invader presence in semi-natural grasslands will certainly lead to significant change with respect to species richness, habitat provision, nutrient cycling, and water regulations (Klinger et al., 2019; Ramula & Sorvari, 2017; Thiele et al., 2010).

Resistance to the applied pulsed drought event was unrelated to species richness in our study. Current state of the art

knowledge reports contrasting effects of sudden pulse events (De Boeck et al., 2018; Dreesen et al., 2014; Kreyling et al., 2017; our study) versus prolonged chronic drought events in grassland communities (De Boeck et al., 2018; Zhou et al., 2016). Prolonged chronic drought events give time to trigger acclimation processes and therefore ecosystems have time to build up resistance in the case of press events (De Boeck et al., 2018; Zhou et al., 2016); while in pulse drought events stability is usually inferred via recovery due to a sudden increase of available resources at the end of the climatic event (De Boeck et al., 2018; Dreesen et al., 2014). However, interpretation of results is not always straight forward as the diversity–stability effect, in terms of insurance due to species asynchronous reactions to stress, might heavily depend upon the characteristics of the stressor (e.g. intensity), the affected community, and the response variable under consideration (Allison, 2004; Blake & Duffy, 2010).

The diversity effects observed in this experiment appear to be relatively small. This might be due to the chosen community composition used in the experiment, or due to the relatively short spatial and temporal scales tested. Previous literature has shown that different stability components do not necessarily covary positively along a diversity gradient, but are rather likely to show opposing effects (Pennekamp et al., 2018). That is, species richness may have had no effect on resistance in this study, but might have increased temporal stability in the long run. Extreme drought can induce stochastic effects in community development and therefore impair predictability even under homogeneous abiotic conditions (Kreyling, Jentsch, & Beierkuhnlein, 2011). For example, if immigration and extinction follow different temporal dynamics, a reduction in environmental quality (here, due to drought) could lead to a temporal increase of species richness (Hillebrand et al., 2018). Additionally, recent evidence suggests that non-monotonic effects, that is hump- or U-shaped effects of diversity, on overall ecosystem stability are likely (Pennekamp et al., 2018). Thus, depending on the ecosystem under consideration biodiversity may increase stability when biodiversity is low, and decrease stability in cases of high biodiversity or the other way round in cases of a U-shaped relationship (Pennekamp et al., 2018). Note that the level of abiotic stress tested in this study (drought-induced biomass reduction of 28%) is comparable to those of natural drought events such as the Central European summer heat waves in 2003 and 2018 (Ciais et al., 2005; Toreti et al., 2019) as well as preceding studies on diversity–stability relationships (Isbell et al., 2015; Kreyling et al., 2017; Pfisterer & Schmid, 2002; Van Ruijven & Berendse, 2010).

4.2 | Extreme drought events lead to a facilitation of the two studied invader species in semi-natural grasslands

Our results revealed facilitation of invasive species in semi-natural grasslands due to extreme drought events, though the pathway to this effect varied between the two invaders. *S. inaequidens* showed increased resistance of biomass production during drought as well

as an increased ability to recover from such an extreme event. The increased biomass (relative to plants in ambient conditions) of *S. inaequidens* in the recovery to drought indicates a high potential of the species to acquire free resources, such as those released from soil C and N mineralization that follows re-wetting of the dry soil (sensu Birch effect; Birch, 1958; Borken & Matzner, 2009; Ingrisch et al., 2018) and the decreased survival of natives in the presence of *S. inaequidens*. Such an effect was not visible in the recovery of biomass production of *L. polyphyllus* (relative to plants in ambient conditions), nor was the survival of the non-native legume better compared to the native species in either climate treatment (even to the contrary). Windows of opportunity for establishment and spread of invasive species arise in the time lag between when invasive species are able to recover and when abiotic conditions become suitable again for native communities (Diez et al., 2012). According to our results, *L. polyphyllus* might not be able to use the 'invasion window' (Diez et al., 2012) arising during the drought event, but the slightly improved recovery of the legume invader might be sufficient enough to outcompete native species after the drought event. A recent study indicates that a slight performance advantage of *L. polyphyllus* under combined extreme drought and competition effects might be enough for the legume invader to outcompete native species during phases of increased abiotic stress and thus, to use the arising 'invasion window' (Vetter et al., 2019). But, it is likely that *S. inaequidens* will profit from a future increase of extreme climatic events (Hewitson et al., 2014) by using this key temporal aspect—the arising invasion window during drought—to expand its competitive advantage over native species and thus increasing its cover.

The invader impact upon native species performance—in terms of reduction in biomass production of the native species—was more pronounced in *S. inaequidens* relative to *L. polyphyllus*. The observed asymmetric competition is likely due to *S. inaequidens* being a better interspecific competitor and the combination of both stressors seemed to be beneficial for its biomass production. *L. polyphyllus* seemed to be a weaker interspecific competitor which suffered under the presence of the native species as well as the drought treatment, thus it struggled with both, the single effect of competition as well as the combination of competition and extreme climatic events. Native plants growing with *L. polyphyllus* in communities did not suffer from the presence of the non-native legume—in terms of reduced biomass production—as strongly as native plants growing within *S. inaequidens* communities. *S. inaequidens* seems to be better adapted to a possibly drier future climate (EPPO, 2006) than *L. polyphyllus*. *S. inaequidens* and *L. polyphyllus* have different plant–soil relationships, with the former being adept at depleting topsoil nutrient content (Dassonville et al., 2008; GISD, 2015) and the latter being a legume and potentially increasing the plant available nitrogen in the invaded habitats (Otte & Maul, 2005; Thiele et al., 2010; Volz, 2003). In other words, where *S. inaequidens* directly competes with natives, *L. polyphyllus* may facilitate native species due to (a) direct fertilization or (b) by using the rhizobia's nitrogen instead of the available soil nitrogen content, thus resulting in higher net soil N availability for the native species in both ambient and stressful environmental conditions.

In sum, we showed that the interaction of extreme climatic events and invasive species might not only disrupt the ability of native communities to recover from drought, but that extreme events might also facilitate non-native invaders, at least if they are well adapted to the future climate (Wilsey et al., 2014). Generalizing from our two target invader species, invaders of warm origin may profit from a drier future climate in Central Europe, while invaders from cold regions may struggle with the combined effects of drought and native species competition.

ACKNOWLEDGEMENTS

This work was funded by ERA-Net, BiodivERsA (SIGNAL; <http://www.bayceer.uni-bayreuth.de/signal/index.php?lang=de>; Funding ID 01LC1201), the German Federal Ministry of Education and Research (BMBF), BonaRes (SUSALPS; <https://www.susalps.de/en/>; Funding ID: 031B0027C), the Belgian Federal Science Policy Office (BELSPO), and the Bulgarian Science Found. We thank numerous students and technicians for field assistance, and two anonymous reviewers for their thoughtful recommendations, which helped to further improve our manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTION

A.J. and J.K. conceived the project and the experiment. Organization of the experimental sites and data collection was split per site: H.J.D.B., I.N., and S.B. contributed experimental data for site BE; D.S. and I.A. contributed experimental data for site BG; and A.J., B.J.B., J.D., J.K., M.A.S.A.-K., M.A.S., P.v.G., P.A.W., V.M.S.V., and M.Z. contributed experimental data for site DE. B.J.B., M.A.S. and V.M.S.V. designed the figures; and M.A.S. and B.J.B. produced the graphics. V.M.S.V. assembled and analyzed the data; and V.M.S.V. wrote the manuscript with substantial input from J.K. and P.A.W. All other co-authors contributed substantially in revising the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.11766231.v1>. R scripts are available from the corresponding author upon reasonable request.


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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Vetter VMS, Kreyling J, Dengler J, et al. Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought. *Glob Change Biol.* 2020;26:3539–3551. <https://doi.org/10.1111/gcb.15025>