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Patterns and drivers of biodiversity–stability relationships under climate extremes

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Abstract

1. Interactions between biodiversity loss and climate change present significant challenges for research, policy and management of ecosystems. Evidence suggests that high species diversity tends to increase plant community stability under interannual climate fluctuations and mild dry and wet events, but the overall pattern of diversity–stability relationships under climate extremes is unclear.
2. We comprehensively review results from observational and experimental studies to assess the importance of diversity effects for ecosystem function under climate extremes. Both the broad literature review and a meta-analysis focused on the effects of extreme precipitation events on above-ground biomass reveal no significant interaction between species richness and climate extremes.
3. Causes for variation in diversity effects under climate extremes are explored, from stress thresholds to biotic interactions and community assembly, and we consider how these may modulate the outcomes of biodiversity–stability relationships. We also examine how specific characteristics of climate extremes and timing of measurements may interact with mechanisms of diversity–stability relationships.
4. *Synthesis*. Hypotheses tailored to the complexity of diversity effects, the implementation of standardised experiments and the use of trait-based biodiversity measures rather than species richness should lead to better causal understanding of whether and how biodiversity may protect ecosystems from adverse effects of climate extremes.

KEYWORDS
climate change, ecosystem functioning, insurance hypothesis, plant community, plant–climate interactions, resilience, resistance, species richness

1 | INTRODUCTION

Assessing the consequences of human-induced changes to the environment is a key challenge for research, policy and management (Barnard & Thuiller, 2008). Rapid rates of ecosystem degradation and simplification have raised concerns about how biodiversity loss may affect the functioning of ecosystems and their contribution to human well-being via ecosystem services (Cardinale et al., 2012; Hooper et al., 2005). In addition, ecosystems are faced with ongoing climate change and associated alterations in the frequency, intensity, duration and timing of extreme weather events (Fisher & Knutti, 2014; IPCC, 2013). Extreme events such as severe drought and periods of heavy rainfall have the potential to cause dramatic changes in plant physiology, population dynamics and ecosystem structure, with cascading effects on biogeochemical cycling (Frank et al., 2015; Reyer et al., 2013; Smith, 2011). However, the mechanisms determining ecosystem response and recovery to climate extremes remain unclear, making vulnerability assessments uncertain (Kayler et al., 2015).

Over the last decade, an increasing number of studies have investigated the impacts of extreme events, in particular on herbaceous plant communities. Available data indicate high variation in the magnitude of ecosystem responses to climate extremes, ranging from minimal impacts on ecosystem structure and function (Jentsch et al., 2011) to major effects in the short and/or long term (Breda, Huc, Granier, & Dreyer, 2006; De Boeck, Bassin, Verlinden, Zeiter, & Hiltbrunner, 2016; Hoover, Knapp, & Smith, 2014). Such contrasting results among studies have been attributed to differences in the nature of the climate extremes or the ecosystems in question (Frank et al., 2015; Smith, 2011). In particular, levels of biodiversity within ecosystems may play an important role in determining ecosystem responses to climate extremes (Isbell et al., 2015). Considerable evidence from theoretical and experimental studies suggests that high species diversity within ecosystems tends to increase plant community stability, often measured as decreased temporal variability in community biomass (Cardinale et al., 2012; McCann, 2000; Tilman, Wedin, & Knops, 1996). If biodiversity plays a stabilising role for ecosystems subjected to climatic extremes, then not only will diversity loss impair ecosystem function but it may also reduce its capacity to buffer severe environmental fluctuations (Loreau & de Mazancourt, 2013).

Although interest in diversity–stability relationships has a long history (e.g. MacArthur, 1955; McNaughton, 1977), the exact mechanisms underlying diversity–stability relationships remain a subject of debate (Grman, Lau, Schoolmaster, & Gross, 2010; Gross, 2016; Loreau & de Mazancourt, 2013). Positive effects of diversity on community functioning are often linked to differences in sensitivity to fluctuations in environmental factors. More diverse communities are generally considered to have a wider range of sensitivities. Even though species responses vary, community functioning is more stable under a range of conditions due to species asynchrony and compensatory responses (cf. the "Insurance Hypothesis", Gross et al., 2014; Yachi & Loreau, 1999). However, most of the theory on diversity–stability relationships in plant communities focuses on year-to-year stability and/or moderate fluctuations in environmental conditions (Dodd, Silvertown, McConway, Potts, & Crawley, 1994; Gross et al., 2014; Romanuk, Vogt, & Kolasa, 2006; Tilman, Reich, & Knops, 2006; Valone & Hoffman, 2003). It is only relatively recently that studies have also started applying this theory to extreme events (Bloor & Bardgett, 2012; Isbell et al., 2015; Kahmen, Perner, & Buchmann, 2005; Kreyling et al., 2008). Here, we review the literature and synthesise experimental and observational studies which examine the role of biodiversity for ecosystem responses specifically in the context of climate extremes. Next we explore the factors underlying variation in biodiversity–stability relationships under climate extremes. Finally we discuss future research directions that should improve mechanistic understanding of biodiversity–stability effects in a changing environment.

2 | LOOKING FOR EVIDENCE: DOES BIODIVERSITY PROMOTE STABILITY UNDER CLIMATE EXTREMES?

Ecosystem stability is typically considered in terms of resistance ("*the instantaneous impact of exogenous disturbance on system state*") and/or recovery ("*the endogenous processes that pull the disturbed system back towards an equilibrium*") (Hodgson, McDonald, & Hosken, 2015). In the most comprehensive study to date, Isbell et al. (2015) showed that plant species richness increases biomass resistance but not resilience of grasslands under natural precipitation regimes of varying extremity. Moreover, the results from Isbell et al. (2015) suggest that species richness may be more important for stability under moderate rather than extreme events. However, to our knowledge, no review has explicitly addressed diversity–stability relationships under extreme climatic events. Here we consider extreme climatic events in terms of their probability of occurrence, defined statistically as the 10th percentile or less of the distribution from a long-term reference time-period (Knapp et al., 2015).

An extensive literature search was conducted for peer-reviewed studies addressing the relationship between biodiversity and ecosystem stability for ecosystems exposed to various climate extremes (droughts, wet spells and heat waves, see Table S1). We used the search engines ISI® Web of Science and Google Scholar as well as cross-referencing to find studies published before August 2016 reporting on the effects of extreme climatic events on plant communities of different diversity. Studies that focused on the performance of single individuals in a neighbourhood varying in diversity (e.g. Metz et al., 2016) were not retained. The following search terms were used: (stability or resistance or resilience), (diversity or species richness), (extreme or severe), (drought or dry or water or wet or precipitation or soil moisture or heat or cold or warm or temperature or climate) and (grass* or plant community). The literature search and subsequent selection returned 43 papers, the majority of which addressed grassland systems (33 articles), with a range of approaches from opportunistic, observational examination of natural extremes in (semi-) natural ecosystems to experimentally imposed events in artificially assembled systems. Based on the authors' own interpretation of results, the support for positive diversity–stability effects was mixed, as neutral and negative effects of diversity on ecosystem stability under extreme events were frequently reported (Table S1).

While the literature search provided a mixed qualitative picture of biodiversity–stability relationships during and after extremes, we also sought a more formal, quantitative conclusion through meta-analysis (see Supporting Information). In brief, we focused our statistical analysis on studies investigating the effects of extremely dry or wet climatic events effects on above-ground biomass as other combinations of climatic driver and/or response variable were represented by too few studies. We retained studies where (1) the climatic event had a return time of one in 10 years or more extreme, (2) climatically extreme years were preceded by a non-extreme year and (3) a true control or normal reference year was available as a baseline. The analysis focused mainly on resistance, and on high and low species richness levels. In studies performed with more than two levels of species richness, the analysis was restricted to the two most extreme species richness levels. In case of natural species richness gradients represented by a single plot at the ends of the gradients, the gradient was restricted to species richness levels with multiple replicates. Biomass data were taken from harvests at the end of the extreme event (resistance), and from the first biomass measure available after the end of the extreme event (recovery). In case of sequential experimental extreme events, we only included biomass responses to the first extreme event in order to exclude carry-over effects of repeated droughts.

The natural logarithm of the response ratio (LRR = ln[treatment mean/control mean]) was used as a metric of treatment effect size (Hedges, Gurevitch, & Curtis, 1999; Koricheva, Gurevitch, & Mengersen, 2013) on above-ground biomass reflecting the relative change in biomass due to treatments. Controls were assigned as low diversity and control plots in manipulation studies (and reference years in observational studies), whereas "treatments" were assigned as high diversity and the extreme event. For all studies, we used the average biomass of high diversity without extreme event, high diversity with extreme event, low diversity without extreme event and low diversity with extreme event treatment combinations to calculate the main effect of species richness, the main effect of the extreme event and the interaction effect size according to Gruner et al. (2008). A significant interaction indicates that the effects of the two factors are not independent: a positive interaction term occurs when the combined effect of treatments is greater than the product of the two main factors (synergistic interaction), whereas a negative interaction term reflects a lower-than-expected effect of treatments in combination (antagonistic interaction). In the present study, a positive diversity–stability relationship is indicated when the deviation in biomass due to the extreme event is lower in high- compared to low-diversity communities. Nonparametric bias-corrected 95% confidence intervals were calculated by bootstrap sampling from effect size pools with 10,000 iterations. The LRR is statistically significant when the boot-strapped 95% confidence interval does not overlap zero. More details on the methodology of the meta-analysis can be found in the Supporting Information.

In total, our analysis comprised data from 28 studies published in 17 articles, the majority of which addressed effects in European grasslands. Nineteen studies considered extremely dry climatic events in grasslands ($n = 17$) or forests ($n = 2$), while nine studies reported on effects of extremely wet climatic events in grasslands. All wet event studies and the majority of the dry event studies were performed with communities of random species composition ($n = 23$), meaning that species are not more likely to be present at a specific diversity level. Irrespective of the type of climatic extreme (dry vs. wet), species richness had a positive effect on biomass production. The extremely dry climatic events had a negative effect on biomass production, while extremely wet climatic events had no net effect on productivity. However, ecosystems containing more plant species did not show greater resistance to climate extremes in terms of above-ground biomass across studies. Moreover, we found no significant interaction between diversity and climate extremes for both the extremely dry and extremely wet events (Figure 1). This result was robust, i.e. the same lack of biodiversity–resistance relationship was found with/without the inclusion of experiments in forests, with/without the inclusion of studies that experimentally manipulated climate extremes and with/without monocultures (see Supporting Information). It should also be noted that the means of the interactions are very close to zero and the confidence intervals are narrow, further reinforcing the robustness of the conclusion of non-significant diversity effects on resistance. For the other component of stability, recovery, fewer studies were available for meta-analysis ($n = 8$). The results reveal a non-significant interaction, but should be treated with caution due to the paucity of data (Figure S1). Taken together, our results suggest a net neutral effect of diversity on stability, reflecting the varied conclusions in literature (Table S1).

Our qualitative and quantitative assessment of studies on biodiversity–stability relationships and extreme events both demonstrate that there are numerous and non-trivial exceptions to the purported general rule that biodiversity increases stability. This raises the question of whether existing concepts of biodiversity–stability derived in the context of mild climate fluctuations are readily transposable to extreme events.

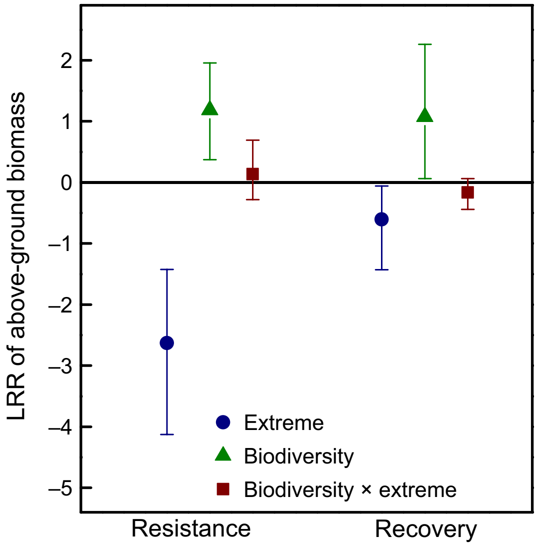

FIGURE 1 Average effect size (natural log response ratio; LRR) of climate extremes, biodiversity and their interaction on above-ground biomass for dry ($n = 19$ studies) and wet ($n = 9$) climate extremes, and for all extremes together ($n = 28$ studies). The effect size of diversity is based on the comparison of high and low species richness levels (mean species richness of 11.7 vs. 1.9 species). Climate extremes have a return time of one in 10 years (or more extreme). Effect sizes are statistically significant when the boot-strapped 95% confidence interval does not overlap the zero line, and a significant interaction indicates that effects of the two factors are not independent

3 | CAUSES FOR VARIATION IN BIODIVERSITY–STABILITY RELATIONSHIPS UNDER CLIMATE EXTREMES

3.1 | Differences between climate extremes

Inconsistent biodiversity effects on stability in the face of climate extremes (Table S1) may in part reflect differences between extremes (types or properties) which generate different impacts for a given probability of occurrence (return time). For example, the most studied type of extreme, drought, can be short term (mostly weeks or months) with (almost) no precipitation (pulse event, e.g. Lanta, Dolezal, Zemkova, & Leps, 2012), or long term (months to years) with prolonged precipitation deficits (press event, e.g. Evans, Byrne, Lauenroth, & Burke, 2011). Recent modelling work has shown that pulse and press droughts of the same magnitude affect primary production and carbon storage differently (Hoover & Rogers, 2016). The chronic nature of press events implies that adverse conditions are long-lasting with only brief periods of recovery, while the "acute" nature of pulse events implies distinct periods of (intense) stress and stress alleviation (Figure 2). The temporal dynamics of extreme events also have significant implications for resistance and recovery. Resistance is likely to be more important during press events, as chronic exposure to stressful conditions gives time to trigger potential acclimation responses (Zhou, Medlyn, & Prentice, 2016) and species reordering (Evans et al., 2011). Pulse droughts are short term, and for a given return time, more likely to exceed extreme soil water stress thresholds (Figure 2) because water saving in such cases often lacks efficiency as drought defence mechanisms are overwhelmed and acclimation is limited (Larcher, 2003). Alleviation of stress following a pulse drought is usually more pronounced than after press droughts, promoting fast recovery via a flush of available nutrients (Dreesen, De Boeck, Janssens, & Nijs, 2014). Potential interactions between properties of climate extremes and the different components of stability, like those described here, are relevant to diversity–stability outcomes as resistance and recovery can be affected differently by biodiversity (Kreyling et al., 2017; Van Ruijven & Berendse, 2010; see Section 3.3).

Apart from the severity and speed of onset of climate extremes, it is also possible that the nature of the extreme itself (e.g. extreme drought vs. extreme precipitation) triggers different or even contrasting diversity-mediated responses. A key aspect here is how plant functional traits and their associated physiological and phenological processes interact with each type of extreme event (Reyer et al., 2013). For example, diversity-induced increases in leaf area (Spehn, Joshi, Schmid, Diemer, & Körner, 2000) or transpiration rates (Kunert, Schwendenmann, Potvin, & Hölscher, 2012) may be a disadvantage under drought (Jucker et al., 2014; Van Peer, Nijs, Reheul, & De Cauwer, 2004; Yang et al., 2016) but could yield beneficial effects under conditions with high temperatures as more of the total leaf surface is at least partially shaded and/or higher transpiration cools leaves, preventing overheating (cf. Moro, Pugnaire, Haase, & Puigdefabregas, 1997). Likewise, a denser canopy generally offers better protection against soil erosion during extreme precipitation events (Hartanto, Prabhu, Widayat, & Asdak, 2003).

Extremes such as drought and hot temperatures are usually associated with reductions of above-ground production, but not every extreme event affects ecosystem functioning negatively. Some can even evoke growth increases, such as very wet weather in a usually dry region (Harpole, Potts, & Suding, 2007). In a recent meta-analysis of grassland experiments, Isbell et al. (2015) reported both higher productivity in wet conditions and higher resistance to wet extremes in high diversity treatments. Unlike positive diversity effects observed in dry extremes, high diversity appears to buffer communities against productivity gains in wet extremes (Isbell et al., 2015). This is a surprising and counter-intuitive result as the mechanisms associated with biodiversity increases, i.e. resource partitioning and the selection effect, are expected to stimulate growth rather than reduce it. Such a lack of divergence in patterns of resistance to dry and wet extremes emphasises that mechanisms of diversity–stability relationships may be confounded by a "one-size-fits-all" approach, and that hypotheses should be tailored to the system and the extreme in question.

3.2 | Differences in ecosystem sensitivity to stress

Theory stating that diversity stabilises ecosystem functioning in time, is largely derived from observations in systems exposed to mildly

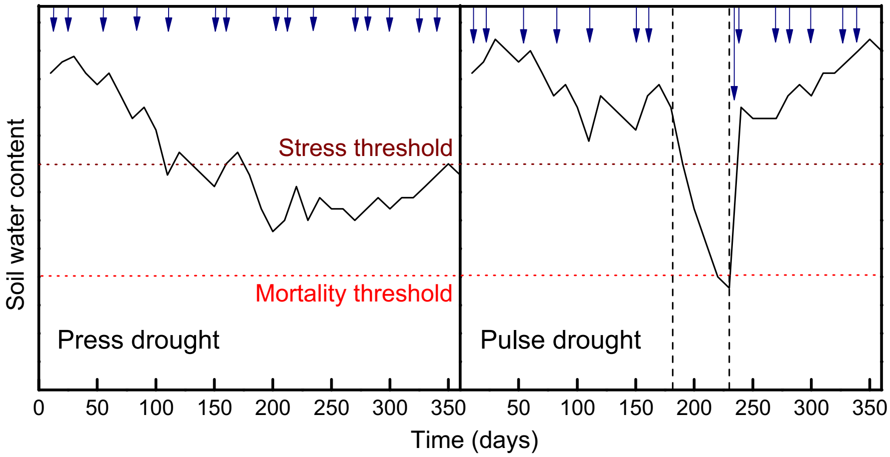

FIGURE 2 Conceptual depiction of a press drought (extended period with sparse precipitation) and a pulse drought (short period with no significant precipitation), identical in return time (extremity). Stress (hypothetical thresholds for species × indicated) reaches less extreme levels during press droughts, but lasts longer and features only short periods when (limited) recovery is possible. Precipitation events are depicted by arrows with a length that scales with precipitation amount

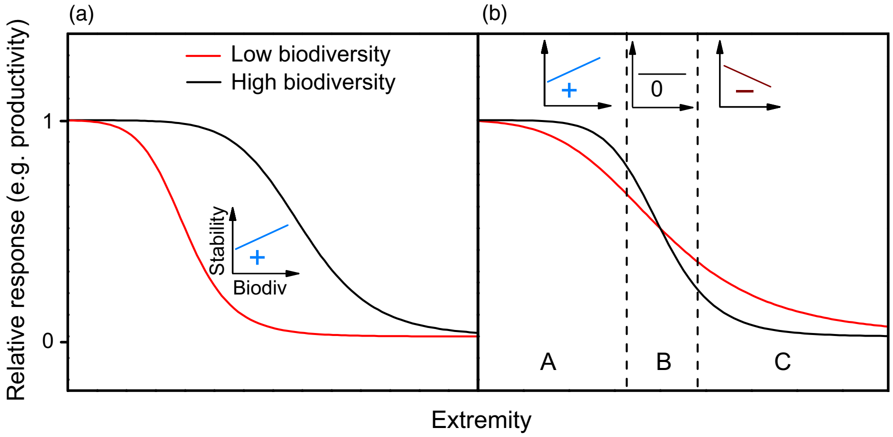

FIGURE 3 Ecosystems can differ in their response (relative to a control, i.e. between 0 and 1) to changes in environmental conditions because of differences in (a) the position of the stress threshold (stress level where responses become substantial) or (b) the steepness of the response curve. Situation (a) would promote positive effects of biodiversity on stability of ecosystem functioning, independent of the extremity of the event (from common to extreme), while situation (b) would give rise to positive (A), neutral (B) or negative (C) outcomes for the biodiversity–stability relationship depending on extremity

fluctuating environmental conditions (Cardinale et al., 2012; McCann, 2000; Tilman et al., 1996). Directly extrapolating this to climate extremes, assumes little or no interaction of biodiversity effects with the return time of the event in question. Such a scenario is depicted in Figure 3a, where the more diverse ecosystem reaches a threshold for reduced functioning further along the extremity axis than the less diverse ecosystem. This results in positive effects of biodiversity on stability across the extremity gradient, as stress-induced decreases in functioning are relatively less at higher diversity (but note that the difference between low- and high-diversity systems decreases again at higher levels of extremity). However, there are reasons to believe this assumption does not hold for many ecosystems. The recent meta-analysis on artificially assembled grassland systems by Isbell et al. (2015) shows that positive diversity effects on resistance to rainfall variation were significantly reduced in extreme (>10-year return time) compared to moderate (4- to 10-year return time) events. It should be noted that the large majority of extremes featured in their analysis had a return time below 50 years and none had a return time above 75 years (calculated via SPEI z-scores, Begueria, Vicente-Serrano, & Angulo-Martínez, 2010), meaning that the analysis explored only part of the extremity gradient. Moreover, what is currently considered rare, is expected to be common in the near future. For example, the 2003 heat and drought in parts of Europe is calculated to have a current return time of *c*. 100 years, but is projected to be a common occurrence by mid-century (Christidis, Jones, & Stott, 2015). In assessing biodiversity–stability relationships under climate extremes, the context of ongoing climate change makes it imperative to also consider events which are currently very rare.

Our literature search features a broader set of studies, including those on (semi-) natural ecosystems and with imposed extremes, which, though difficult to quantify exactly, often report return times exceeding 50 years (e.g. Bloor & Bardgett, 2012; Jentsch et al., 2011). Across the dataset, we found varied outcomes of the connection between diversity and stability. Given the evidence regarding the variable strength of the diversity–stability relationship presented in both Isbell et al. (2015) and the current study, we suggest that the difference in responses between ecosystems that are richer vs. poorer in species may not be constant with changing extremity. By adapting Figure 3a so that the rate of ecosystem functioning decline is no longer equivalent between more and less diverse systems, positive, neutral or negative diversity–stability relationships are possible depending on the extremity of the event (Figure 3b). This may help explain why studies focusing on interannual variation or mild dry or wet events tend to find positive diversity–stability effects, while studies explicitly focusing on extreme events of variable return time report diverse outcomes (Table S1). In sum, conclusions regarding the effect of diversity on the stability of ecosystem functioning may differ fundamentally along a gradient of extremity.

3.3 | Timing of biomass harvests and interacting effects of recovery

Some authors have suggested that diversity has stabilising effects on ecosystem processes only when time-scales are sufficient to incorporate the average net effects of diversity on both resistance to, and recovery from, climatic stress (Tilman et al., 2006). During both these constituent phases of resilience (as defined by Hodgson et al., 2015), the relationship with diversity may differ significantly. Several studies have reported neutral or even negative biodiversity effects on plant biomass resistance to severe drought but positive diversity effects on recovery and/or resilience (which combines resistance and recovery) (Van Ruijven & Berendse, 2010; Vogel, Scherer-Lorenzen, & Weigelt, 2012). In a recent study that spanned different climate zones, Kreyling et al. (2017) found that only recovery, and not resistance, was stimulated by species richness in grassland mesocosms. Studies that differentially incorporate resistance and recovery may therefore reach different conclusions, contributing to variation in diversity–stability relationships and complicating direct comparisons.

When biomass data are collected immediately after the extreme event, only resistance is taken into account (e.g. Pfisterer & Schmid, 2002; Van Peer et al., 2004), while in long-term biodiversity–stability studies, above-ground productivity is usually collected at fixed points in time, often including end-of-growing season biomass or even biomass produced in the year following the perturbation. This approach yields a measure of stability that very rarely only reflects resistance, and also short- and/or long-term recovery, making direct comparisons across studies less straightforward and contributing to the observed variability in biodiversity–stability relationships. Changes in the influence of biotic interactions on resistance and biodiversity effects could thus help explain why positive diversity effects observed under mild climatic variation may turn neutral or even negative with increasing extremity of environmental conditions.

DeClerck, Barbour, and Sawyer (2006) have proposed that resistance is primarily driven by competition for a single limiting resource (such as water in the case of drought), whereas recovery is driven by the capacity of communities to partition resources in the absence of a single limiting resource after stress relief. This implies that biodiversity is more likely to have a positive effect on recovery, as greater numbers of coexisting species are less likely to be equally limited by the same resource (nutrients, water, light, etc.). In the case of resistance, it is highly probable that the same resource limits the functioning of all species so that resource partitioning is diminished and negative interactions (i.e. competition) become dominant. Such negative interactions would be more likely to develop as the resource in question becomes scarcer, i.e. as the extremity increases (right side of the *X*-axis in Figure 3), in line with findings of Metz and Tielbörger (2016), who demonstrated an increase in competitive effects in a shrubland during dry years. Maestre and Cortina (2004) suggested a shift from facilitation to competition when environmental stress becomes extremely severe. Under milder conditions, competition for the limiting resource would be less intense, and facilitation and other biodiversity-related mechanisms such as the more extensive portfolio of sensitivities at higher diversity would be more prominent (Michalet et al., 2006), increasing the probability of finding neutral or positive effects of biodiversity on stability at the left side of Figure 3b.

Of course, diversity effects on the stability of above-ground productivity may not only simply reflect "plant-only" mechanisms but also plant–soil interactions. Several studies suggest that plant stability to drought may occur at the expense of microbial stability (Bloor & Bardgett, 2012; Orwin & Wardle, 2005), likely driven by shifts in plant–microbial resource partitioning. Confounding effects of plant–soil interactions may arise if microbial communities differ in their sensitivity to extreme events depending on plant diversity (Gordon, Haygarth, & Bardgett, 2008; Schimel, Balser, & Wallenstein, 2007), altering patterns of nutrient release both during and after the climatic extreme. Disentangling the relative role of plant–plant and plant–soil competition for ecosystem responses to environmental change remains a considerable challenge for ecologists. In conclusion, the constituent elements of stability (resistance and recovery) may be differently affected by biodiversity, while interactions with the extremity of the event are likely.

3.4 | Interacting effects of plant community assembly

Diversity–stability relationships may be mediated by mechanisms of community assembly (i.e. the processes that shape community composition) which interact with resistance and recovery, further increasing the range of potential biodiversity–stability outcomes. Mechanisms underlying community assembly, both in natura and in artificial assemblages, play a fundamental role in determining patterns of productivity and trait abundance at different diversity levels. Abiotic and biotic drivers both constrain species establishment (McGill, Enquist, Weiher, & Westoby, 2006) and determine species loss (Vitousek, Mooney, Lubchenco, & Melillo, 1997), with nutrient enrichment in particular reducing species diversity via increases in productivity, competitive exclusion and reduction of species recruitment (Foster & Gross, 1998; Grime, 1973). Species that profit most from nutrient enrichment are often those species with high growth rates, while slow-growing species lose out (cf. Hautier, Niklaus, & Hector, 2009). Consequently, these low-diversity communities are more likely to contain a higher proportion of fast-growing species that are often (but not always, see Grman et al., 2010; Wilsey, Daneshgar, Hofmockel, & Polley, 2014) also more susceptible to drought and other extreme events (Huston, 1997; Ouédraogo, Mortier, Gourlet-Fleury, & Picard, 2013). In contrast, communities with higher species richness are likely to contain a higher proportion of subordinate/slow-growing species, and these may help to buffer the ecosystem function following extreme events (Lepš, Osbornova-Kosinova, & Rejmanek, 1982; Mariotte et al., 2013). Eutrophication-driven diversity losses resulting in highly productive but species-poor plant communities are of global relevance (Sala et al., 2000), especially with regard to potential declining stability of such impoverished ecosystems.

Unlike studies based on natural diversity gradients or communities shaped by deterministic mechanisms, a large number of extreme event studies featuring multiple biodiversity levels use artificial assemblages (28 articles in Table S1) where communities differing in species richness are created in a non-deterministic manner. This means that the low-diversity levels include species also present at all other levels, or feature species that have been picked randomly and not on the basis of their competitive ability. As a result, low-diversity experimental treatments tend to have a greater probability of containing slow-growing species compared with low-diversity plant communities in nature (Lepš, 2004). This in turn implies that artificially assembled, species-poor "experimental communities" may generally be less sensitive to extreme events than "in natura communities" impoverished in a non-random manner (e.g. through eutrophication or invasive species), because the former are less likely to be dominated by fast-growing yet sensitive species.

As a hypothetical example of the possible effects of community assembly on diversity–stability relationships, suppose that plant communities with either artificial or in natura assembly patterns are comprised of two types of species with contrasting productivity (Figure 4). In line with the ideas outlined above, we assume that: (1) relatively more productive species are found in lower diversity communities

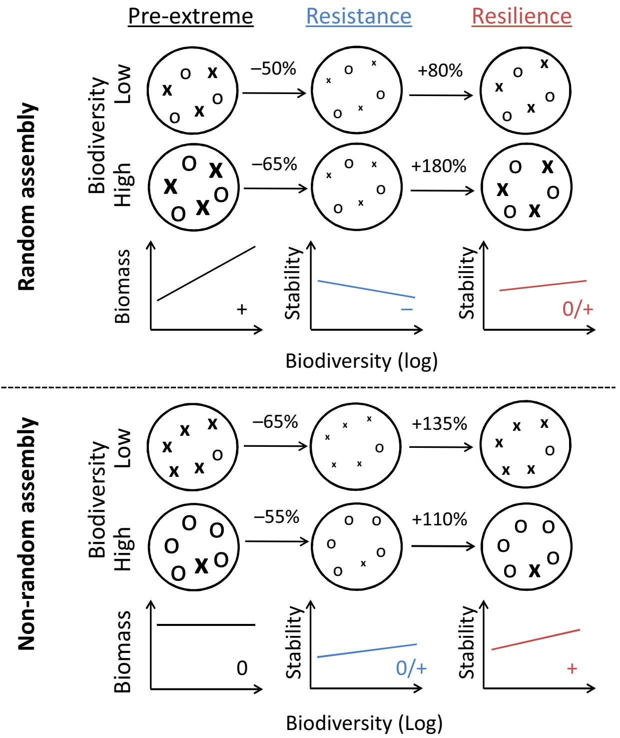

FIGURE 4 A hypothetical example illustrating potential interactions between biodiversity–stability relationships and patterns of community assembly. Two types of species (**X** and O) with contrasting levels of productivity are present: X-type species are twice as productive as O-type species under normal conditions. Biomass production, relative to each species' type inherent production, is represented by font size, and relative changes in community biomass are indicated. Random assembly implies that both species types are equally represented at all diversity levels, while non-random assembly results in a higher proportion of productive species in low-diversity communities (which would be expected under nutrient enrichment, see text). Less productive species are assumed to be more resistant, but to have slow recovery. The effects of biodiversity on stability during and after the extreme events are shown, assuming a limited recovery period. Resilience integrates both resistance and recovery. In this example, positive effects of biodiversity (pre-extreme includes overyielding) are assumed to decrease during the resistance phase, and increase during the recovery phase (cf. DeClerck et al., 2006; Van Ruijven & Berendse, 2010). Details of the calculations can be found in Table S3. Figure S2 depicts results without different diversity effects during resistance and recovery

under non-random vs. random assembly; (2) there is a trade-off between productivity and resistance to extreme events (cf. Ouédraogo et al., 2013); (3) productive species recover faster after the extreme (cf. Lepš et al., 1982); and (4) positive effects of biodiversity are assumed to decrease during the resistance phase, and increase during the recovery phase (cf. DeClerck et al., 2006). Outcomes of diversity vary depending on both the patterns of community assembly and the timing of biomass measurements after the extreme (Figure 4).

While non-random community assembly does not always lead to selection of fast growers in impoverished communities (drivers such as reduced precipitation may even lead to opposite results, cf. Harrison, Gornish, & Copeland, 2015), it is clear that outcomes of diversity–stability studies can vary if plant growth rates or other traits that modulate responses to extreme events are not equally represented at the same biodiversity level between studies. Fundamental diversity-mediated processes may explain further differences between experimental and (semi-) natural communities. Well-established theory states that at higher diversity levels, more of the total available amount of resources (nutrients, light, water) can be used by the community, allowing species-rich communities to "overyield" compared to the monocultures of the composing species (Loreau & Hector, 2001). This overyielding phenomenon (often considered in terms of biomass production) may interact with climate extremes, affecting the outcome of biodiversity–stability relationships. For example, the clear positive relationship between species richness and productivity observed by Van Peer et al. (2004) was reversed during a drought, with increased mortality observed in species-rich communities regardless of species identity. The authors attributed the negative biodiversity–stability relationship to increased water use in the more productive, species-rich communities (cf. Grossiord, Granier, Gessler, Jucker, & Bonal, 2014), which caused them to reach damaging drought levels earlier. Thus, positive diversity effects (increased resource partitioning) under ambient or mildly fluctuating climatic conditions may occur at the expense of ecosystem stability as the event (e.g. drought) gets more extreme. In conclusion, traits of the community that differ between diversity levels, shaped by patterns of community assembly or fundamental diversity-mediated processes, can improve understanding of biodiversity–stability relationships.

4 | EXPERIMENTAL APPROACHES TO IMPROVE DIVERSITY–STABILITY UNDERSTANDING

Throughout this review, we have discussed how biotic (community assembly, biodiversity effects on community traits prior to the event) and abiotic factors (the nature and return time of climate events, underlying resource availability) can modulate possible stabilising effects of biodiversity under climate extremes. Variation in the drivers of diversity effects and the components of stability considered can combine to give rise to a plethora of possible outcomes of biodiversity–stability relationships. We argue that assessments of the role of biodiversity in stabilising ecosystem functioning would benefit from clear comparisons between studies which account for confounding factors and provide explicit details on the return time of the event (see also Smith, 2011). Some standardisation is possible, for example by systematically using return times of one in 10 years or more (Knapp et al., 2015), and by using indices which are clearly coupled to return times such as SPEI in the case of dry or wet extremes (Begueria et al., 2010). Valuable insights can also be gained by collecting data along an extremity gradient (i.e. multiple levels of return time). Changes in biodiversity–stability relations along gradients of stress intensity as suggested in Figure 3b could be revealed by gradient approaches

TABLE 1 Overview of studies included in the meta-analyses (multiple datasets derived from single studies are indicated where applicable). Timing, duration and nature of extreme events (natural or experimentally imposed) are indicated. The time window used (e.g. SPEI-1 = 1-month window) was based on the event length indicated in the study. If only a dry or wet year was mentioned (without further specification), the window was set to SPEI-12. In the case of experimental drought, no *z*-values from the SPEI database could be derived and event duration and precipitation amounts were used to assess whether the event qualified as extreme. Communities were either artificially assembled (a) or selected in natura (n). Studies predominantly focused on grasslands (asterisk indicates when this was not the case)

Reference	Location	Datasets	Extreme	Period	Duration	SPEI	*z*-value	Setting	Composition	Species richness
DeClerck et al. (2006)*	USA (CA)	1	Dry, natural	1940–2004	Dry summers	SPEI-9	<−1.54	Field*	n	1–4
Jucker et al. (2014)*	Spain (Alto Tajo)	1	Dry, natural	2005	Dry year	SPEI-12	−1.71	Field*	n	1, 2, 3, 4
Kennedy et al. (2003)	South Africa (Kruger NP)	1	Dry, natural	01/’91–12/’93	36 months	SPEI-36	−1.68	Field	n	3–13
Lanta et al. (2012)	Czech Republic (Benešov)	1	Dry, experiment	05/’03–09/’03	4 months	n/a	n/a	Field	a	1, 3, 6, 12
Lanta et al. (2012)	Czech Republic (Benešov)	1	Dry, experiment	n/a	30 days	n/a	n/a	Mesocosm	a	1, 3, 6
Lepš et al. (1982)	Czech Republic (Srbsko)	1	Dry, natural	04/’76–06/’76	3 months	SPEI-3	−1.28	Field	n	13, 18
Mariotte et al. (2013)	Switzerland (La Frétaz)	1	Dry, experiment	07/’10–09/’10	8 weeks	n/a	n/a	Field	n	8, 13
Pfisterer and Schmid (2002)	Switzerland (Lupsingen)	1	Dry, experiment	07/’98–09/’98	8 weeks	n/a	n/a	Field	a	1, 2, 4, 8, 22
Spehn et al. (2005)	Germany (Bayreuth)	1	Dry, natural	09/’97–08/’98	Dry year	SPEI-12	−1.80	Field	a	1, 2, 4, 8, 16
St. Clair, Sudderth, Castanha, Torn, and Ackerly (2009)	USA (Richmond)	2	Dry, experiment	11/’05–05/’07	6 months	n/a	n/a	Mesocosm	a	1, 7
Van Ruijven and Berendse (2010)	Netherlands (Wageningen)	1	Dry, natural	06/’06–07/’06	2 months	SPEI-2	−2.41	Field	a	1, 2, 4, 8
Vogel et al. (2012)	Germany (Jena)	4	Dry, experiment	07/’08–09/’08	6 weeks	n/a	n/a	Field	a	1, 2, 4, 8, 16, 60
Wang, Yu, and Wang (2007)	China (Heishiding)	1	Dry, experiment	06/’05–10/’05	4 months	n/a	n/a	Field	a	1–40
Wilsey et al. (2014)	USA (TX)	2	Dry, natural	10/’10–09/’11	Dry year	SPEI-12	−2.05	Field	a	1, 9
Caldeira, Hector, Loreau, Pereira, and Eriksson (2005)	Portugal (Lezirias)	1	Wet, natural	10/’97–06/’98	Wet gr. season	SPEI-9	1.45	Field	a	1, 2, 4, 8, 14
Guo, Schaffer, and Buhl (2006)	USA (Devils Lake)	1	Wet, natural	09/’04–08/’05	Wet year	SPEI-12	1.35	Field	a	1, 8, 16
Kirwan et al. (2014)	Canada (Lévis)	1	Wet, natural	08/’05–07/’06	Wet year	SPEI-12	2.15	Field	a	1, 4
Kirwan et al. (2014)	Norway (Holt)	1	Wet, natural	09/’04–08/’05	Wet year	SPEI-12	1.84	Field	a	1, 4
Spehn et al. (2005)	Greece (Mytilini)	1	Wet, natural	06/’98–05/’99	Wet year	SPEI-12	1.73	Field	a	1, 2, 4, 8, 18
Spehn et al. (2005)	Sweden (Umeå)	1	Wet, natural	09/’97–08/’98	Wet year	SPEI-12	1.92	Field	a	1, 2, 3, 4, 8, 12
St Clair et al. (2009)	USA (Richmond)	2	Wet, experiment	11/’05–05/’07	6 months	n/a	n/a	Mesocosm	a	1, 7
Wright et al. (2015)	Germany (Jena)	1	Wet, natural	05/’13–06/’13	2 months	SPEI-2	2.25	Field	a	1, 4, 8, 12, 16

*Forest.

using increasingly severe climatic disturbances (i.e. longer return times), where possible thresholds or tipping points may be identified (Kreyling, Jentsch, & Beier, 2014). Furthermore, studies should make the distinction between resistance and recovery by collecting data at adequate time intervals, as focusing on the constituent elements of stability offers added value for the interpretation of responses and mechanisms involved (see Van Ruijven & Berendse, 2010). Finally, results obtained in artificially assembled communities should be tested in natura to take differences propagated by community assembly into account and to verify whether the results can be directly translated to real-world systems (Wardle, 2016). Here, it is especially important to consider environmental drivers that can affect both diversity and stability (Ives & Carpenter, 2007). We earlier discussed the importance of nutrient enrichment and implications for diversity–stability relationships, and also adaptations to local climate can be relevant. For example, in the study of Lloret et al. (2007), the nature of relationships between species richness and drought resistance depended on the type of forest (Table S1), which in turn depended on climate and historical selective pressures. To be able to fully explain relationships between diversity and stability, hypotheses need to be adjusted to include the multitude of contributing factors (Ives & Carpenter, 2007).

Another issue that hinders comparisons and extrapolation in diversity–stability research involves the different definitions of diversity across studies. Although most studies in our literature search quantified biodiversity through species richness, diversity constitutes more than merely species numbers. Indeed, the use of plant trait variation and functional diversity metrics may be more appropriate for investigating diversity–stability relationships. Increasing evidence suggests that the values and/or variance of plant traits in a given community (functional diversity sensu Diaz et al., 2007) play a key role in modulating ecosystem responses to environmental change (Jung et al., 2014; Polley, Isbell, & Wilsey, 2013; Suding et al., 2008). Some studies that reported an absence of positive diversity effects based on species richness have hypothesised that this reflected a lack of functional or trait diversity within the community (e.g. Carter & Blair, 2012; Kennedy, Biggs, & Zambatis, 2003; Lübbe, Schuldt, Coners, & Leuschner, 2016), leading to species responding similarly to an extreme event. Limited trait diversity may constrain possible stabilising effects of asynchrony (DeClerck et al., 2006), or lead to accessing resources on similar spatial and temporal scales, minimising potential complementary effects. Evenness effects can add further complexity: species asynchrony is expected to be more important in communities with a relatively even distribution of biomass among the constituent species, whereas the traits of the dominant species are likely to be critical for stability in communities with an uneven biomass distribution (Hillebrand, Bennett, & Cadotte, 2008; Wilsey et al., 2014). Explicitly considering evenness and trait variation in biodiversity or not may therefore lead to different conclusions regarding the role of diversity in the stability of ecosystem functioning.

We suggest that trait-based approaches may pave the way towards a more fundamental understanding of the role of "diversity" on the stability of ecosystem functioning. Trait-based approaches are expected to be particularly useful when plant communities are dominated by a few species of the same functional group (Polley et al., 2013), or for responses to short-term events such as extreme droughts, which induce rapid functional responses via shifts in species abundance (Jung et al., 2014) or plant plasticity. Within a single species, functional diversity expressed by genotypes has been shown to improve recovery after climatic extremes (Reusch, Ehlers, Hämmerli, & Worm, 2005), and intraspecific variation in stress response can actually reach similar levels to interspecific variation (Beierkuhnlein, Thiel, Jentsch, Willner, & Kreyling, 2011; Malyshev et al., 2016; but see Prieto et al., 2015). Varying patterns of functional diversity could thus help explain discrepancies between results of biodiversity–stability studies to date.

5 | CONCLUSIONS

Our review indicates that more diverse ecosystems do not systematically buffer the impacts of climate extremes on ecosystem functioning better than less diverse ecosystems. We highlight several factors that can modulate or confound diversity–stability relationships under extreme events, and may explain mixed results across studies to date. In order to better assess if and when higher biodiversity can buffer climate extreme impacts, which is highly relevant both for the functioning of (semi-) natural ecosystems and the enhancement of food security in a climate change context (Altieri, Funes-Monzote, & Petersen, 2012), the broad paradigms in traditional diversity–stability literature need to be re-evaluated. We encourage further research in this area, and the implementation of studies that: (1) apply climatic extremes in a standardised manner, (2) compare responses in artificially assembled and (semi-) natural ecosystems, explicitly considering community assembly, (3) quantify differences in biodiversity using trait-based metrics and (4) explicitly separate resistance and recovery. Robust experiments and clear hypotheses adjusted to the specific system and extreme in question will enhance our mechanistic understanding of biodiversity–stability effects.

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AUTHORS' CONTRIBUTIONS

H.J.D.B., J.M.G.B. and M.Z. designed the study and performed the literature search; M.Z. analysed the data; H.J.D.B., J.M.G.B. and M.Z. wrote the first draft; all authors contributed substantially to revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6g8n1 (De Boeck, 2017). Data for the meta-analyses were retrieved from published studies (see Table 1).

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