



INVITED VIEWS IN BASIC AND APPLIED ECOLOGY



The multiple-mechanisms hypothesis of biodiversity–stability relationships

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ABSTRACT

Long-term research in grassland biodiversity experiments has provided empirical evidence that ecological and evolutionary processes are intertwined in determining both biodiversity–ecosystem functioning (BEF) and biodiversity–stability relationships. Focusing on plant diversity, we hypothesize that multifunctional stability is highest in high-diversity plant communities and that biodiversity–stability relationships increase over time due to a variety of forms of ecological complementarity including the interaction with other biota above and below ground. We introduce the *multiple-mechanisms hypothesis of biodiversity–stability relationships* suggesting that it is not an individual mechanism that drives long-term biodiversity effects on ecosystem functioning and stability but

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that several intertwined processes produce increasingly positive ecosystem effects. The following six mechanisms are important. Low-diversity plant communities accumulate more plant antagonists over time (1), and use resources less efficiently and have more open, leaky nutrient cycles (2). Conversely, high-diversity plant communities support a greater diversity and activity of beneficial interaction partners across trophic levels (3); diversify in their traits over time and space, within and across species, to optimize temporal (intra- and inter-annual) and spatial complementarity (4), create a more stable microclimate (5), and foster higher top-down control of aboveground and belowground herbivores by predators (6). In line with the observation that different species play unique roles in ecosystems that are dynamic and multifaceted, the particular mechanism contributing most to the higher performance and stability of diverse plant communities might differ across ecosystem functions, years, locations, and environmental change scenarios. This indicates “between-context insurance” or “across-context complementarity” of different mechanisms. We introduce examples of experiments that will be conducted to test our hypotheses and which might inspire additional work.

Long-term biodiversity–ecosystem functioning relationships and underlying mechanisms

Ecosystem-level impacts of biodiversity change have been the focus of many experiments since the 1990s. Long-term experiments where biodiversity is manipulated have shown that *the strength of the mostly positive biodiversity effect on ecosystem functioning increases with time*. That is, the initially saturating biodiversity–ecosystem functioning (BEF) relationship typically observed a couple of years after starting the experiment becomes (more) linear in later years (Reich et al., 2012; Meyer et al., 2016; Guerrero-Ramírez et al., 2017; Huang et al., 2018; Bongers et al., 2021; Eisenhauer, 2022; Van Ruijven & Berendse, 2009; Wagg et al., 2022). This has now been shown for primary productivity in both grassland (Reich et al., 2012; Wagg et al., 2022) and forest (Guerrero-Ramírez et al., 2017; Bongers et al., 2021) biodiversity experiments, suggesting that biodiversity effects need time to establish and that old, biodiverse grasslands and forests are highly multifunctional and should be in the focus of nature conservation. The implications of such dissimilar short- versus long-term BEF relationships are important: while short-term studies imply functional redundancy among species, long-term studies support the singular hypothesis of biodiversity (Eisenhauer et al., 2010), meaning that each coexisting species in a community is required for maximizing ecosystem functioning (Allan et al., 2011; Reich et al., 2012; Eisenhauer et al., 2023). Recent studies have investigated the mechanistic basis of the divergence of short-term

from long-term effects by manipulating the temporal evolution of both plant traits (*i.e.*, plant history) and plant–soil interactions (*i.e.*, soil history; see below) (Eisenhauer et al., 2019a; Vogel et al., 2019). Moreover, studies have found evidence that strengthening biodiversity effects are attributable to (i) deteriorating performance of low-diversity communities, (ii) improving performance of high-diversity communities, or (iii) both (Meyer et al., 2016; Guerrero-Ramírez et al., 2017). Since low-diversity plant communities are widely used in landscapes managed for production, such as agricultural systems and tree plantations (Isbell et al., 2017a; b), deteriorating low-diversity communities may compromise the long-term provisioning of vital ecosystem services in managed ecosystems (Eisenhauer et al., 2019b). It is therefore crucial to develop a comprehensive understanding of how *biotic interactions and eco-evolutionary dynamics* are affected by biodiversity and how this influences ecosystem functioning in the short and in the long term.

Recent results show that *both soil and plant history are important determinants of long-term biodiversity effects* (e.g., Vogel et al., 2019; Dietrich et al., 2021; van Moorsel et al., 2021; Fig. 1). In this context, *soil history* refers to the assembly of distinct soil biotic communities and changes in soil nutrient availability over time (Eisenhauer et al., 2019a; Lange et al., 2019) due to differences in plant diversity (Bever et al., 1997; Bever, 2003; Eisenhauer, 2012; Eisenhauer et al., 2012; Wang et al., 2023). Accumulation of specific plant antagonists and imbalanced use of resources can generate ‘negative feedback effects’ on plants at low plant diversity (Maron et al., 2011; Schnitzer et al., 2011; Eisenhauer

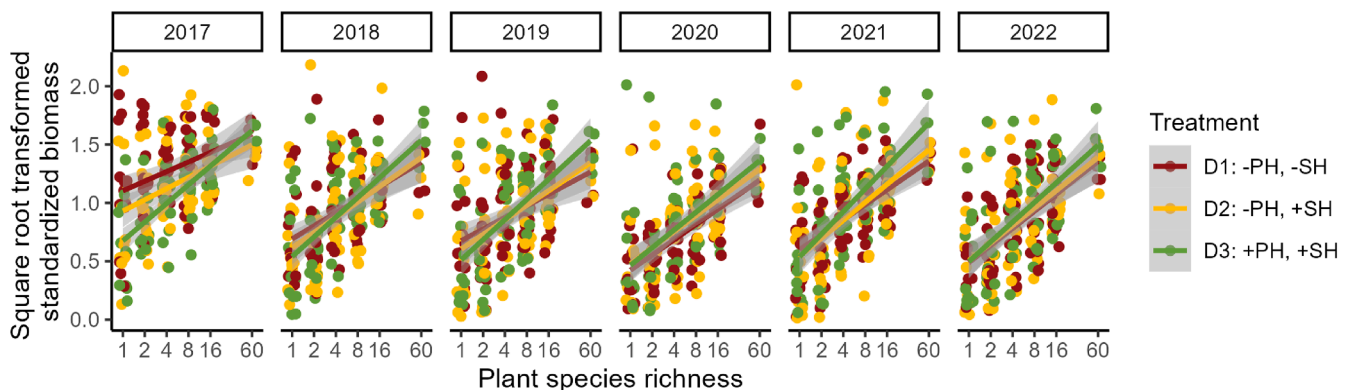


Fig. 1. Effects of plant diversity on plant biomass production as affected by plant history (PH) and soil history (SH). Six years of data from the Δ BEF Experiment (Vogel et al., 2019). We established subplots without soil history and without plant history (treatment D1), by excavating the soil and plant layer to a depth of 30 cm, replacing it with soil of an adjacent arable field of the same soil layer, and sowing the same plot-specific plant species mixtures as in 2002 (new seeds). In subplots with soil history and without plant history (treatment D2), we removed the plant sod by using a digger while keeping the soil of the respective plots, homogenized the upper 30 cm, and sowed the same plot-specific plant species mixtures as in 2002 (new seeds). As the third subplot (treatment D3), we used parts of the existing Main Experiment, which has a grown soil and plant history since 2002. Aboveground biomass was harvested twice per year (~late May/early June and late August/early September) before mowing the entire experimental plots, as typically done in extensively-used meadows in the region. The vegetation was clipped 3 cm above soil surface within two randomly placed frames (20×50 cm) per subplot and sorted by sown species, while non-target weeds, dead, and unidentifiable plant material were removed. After drying at 70 °C for 48 h, samples were weighed and dry mass of target species was summed to community-level values for each subplot. Annual biomass was calculated as the sum of the two individual harvests. These results indicate that the steeper BEF slope was primarily determined by poorly functioning low-diversity plant communities in the initial years of the experiment (see different slopes in 2017) but that these differences among history treatments disappeared over time, as hypothesized (Vogel et al., 2019).

et al., 2012; Kulmatiski et al., 2012; Mommer et al., 2018). There is ample empirical evidence showing that pathogens and parasites accumulate and spread specifically in low-diversity plant communities, while high-diversity communities dilute target organisms in a diverse matrix of other species and provide more protection via plant mutualists (Latz et al., 2012; Rottstock et al., 2014; Civitello et al., 2015; Wang et al., 2023; Mahon et al., 2024). Increased concentrations of plant antagonists have, in turn, been shown to drive positive biodiversity–ecosystem functioning relationships by decreasing the performance of low-diversity communities (Maron et al., 2011; Schnitzer et al., 2011). In contrast, enhancement of high-diversity communities has been associated with plant diversity-dependent increases in soil fertility through increased storage of carbon and nitrogen (Fornara & Tilman, 2008; Steinbeiss et al., 2008; Reich et al., 2012; Leimer et al., 2016; Dietrich et al., 2023; Lange et al., 2023a). Moreover, there is an accumulation of plant growth-promoting organisms under high plant diversity (*positive feedback effects*) by e.g., mycorrhizal fungi, microbes with the potential for biocontrol of pathogens as well as microbes which catalyze the mobilization of plant available nutrients; Dietrich et al., 2020; Eisenhauer et al., 2012; Latz et al., 2012; Rosenkranz et al., 2012; Eisenhauer et al., 2019a).

Plant history refers to variation in trait expression of plants mediated by micro-evolutionary changes, with an emphasis on traits that are relevant for biotic interactions and feedback effects on ecosystem functioning (Eisenhauer et al., 2019b). The competitive environment, as well as mutualistic and antagonistic multitrophic interaction partners above and below the ground, impose selective pressures on members of the plant community (Lipowsky et al., 2011; Zuppinger-Dingley et al., 2014) and thereby create ‘eco-to-evo’ feedbacks (Hendry, 2016).

Evolutionary changes, such as increased niche differentiation (Zuppinger-Dingley et al., 2014), and increased resource-use complementarity due to community assembly processes (Reich et al., 2012; Roscher et al., 2013b; Wagg et al., 2022), will slowly build up and can thus produce increasing biodiversity effects over time (Eisenhauer et al., 2019b; Thakur et al., 2021; Chen et al., 2022).

BEF research has revealed strong positive effects of biodiversity on various ecosystem functions (e.g., productivity, decomposition, soil carbon storage, herbivory, pollination, and pest regulation; Weisser et al., 2017) and has linked these effects to a range of underlying mechanisms (see Box 1 for definitions). Positive BEF relationships can be observed at different spatial (Cardinale et al., 2012; Hautier et al., 2018; Isbell et al., 2011; Roscher et al., 2005; Thompson et al., 2018; van der Plas et al., 2016) and temporal scales (Guerrero-Ramírez et al., 2017; Reich et al., 2012; Zavaleta et al., 2010), and can be multi-dimensional on both the driver (*i.e.*, multidiversity) and response side (*i.e.*, multifunctionality; Hector & Bagchi, 2007; Lefcheck et al., 2015; Meyer et al., 2018; Schuldt et al., 2018; Soliveres et al., 2016). One of the most important conclusions of BEF research is that the strength of BEF relationships is strongly context-dependent (Eisenhauer et al., 2019b; Isbell et al., 2011; but see Hong et al., 2022). BEF relationships have been shown to depend on climatic conditions (Maestre et al., 2012; Ratcliffe et al., 2017), local site conditions (Allan et al., 2015; Eisenhauer et al., 2019b; Fridley, 2002; Reich et al., 2001), and disturbance and management regimes (Guerrero-Ramírez et al., 2017; Kardol et al., 2018; Weigelt et al., 2009), which interact with biodiversity (Guerrero-Ramírez & Eisenhauer, 2017; but see Craven et al., 2016). Accordingly, mechanisms underlying biodiversity effects have been found to differ from one community to the next.

Box 1. Definitions and main concepts explaining biodiversity-ecosystem functioning and biodiversity-stability relationships (in alphabetical order). For details, see the recent reviews by de Bello et al. (2021), Loreau et al. (2021), Yi and Jackson (2021), and Loreau et al. (2022).

Abiotic facilitation effect: occurs when other species mitigate environmental stress via nutrient enrichment or other changes in the abiotic environment, e.g., microclimate, soil chemical or physical properties (Wright et al., 2017; Barry et al., 2019). Recent work suggests that an accumulation of soil carbon (Lange et al., 2021; Lange et al., 2023a) may increase the buffering capacity of microclimatic conditions in high-diversity plant communities (Huang, Stein et al. 2024).

Biological insurance: general concept used to denote the fact that aggregate ecosystem properties vary less in more diverse communities because of compensatory changes between functionally similar species or phenotypes across time, space, or both (Loreau et al., 2021). Biological insurance theory identified differential responses of species to environmental variations through either time (Yachi & Loreau, 1999) or space (Loreau et al., 2003). The term “**spatial insurance**” is sometimes used in the literature when focusing on spatial dimensions of biological insurance (Weigelt et al., 2008; Loreau et al., 2021; although being less in the focus of the experimental ideas presented below).

Biotic facilitation effect: occurs when biodiversity confers a facilitative effect by diluting the effects of pathogens in high-diversity plant communities (Wright et al., 2017; Eisenhauer et al., 2019b; Huang et al. 2022; Wang et al., 2023) or via enhanced positive soil feedback effects through mutualistic organisms like mycorrhiza (soil nutrient uptake) and rhizobia (N fixation; e.g., in legumes) (Eisenhauer et al., 2012, 2019b).

Buffering/portfolio effect: the increased temporal stability or reduced variability of aggregate ecosystem properties that result from increasing biodiversity (Loreau et al., 2021) because of the statistical averaging of the fluctuations in species properties.

Complementarity: broad concept describing a situation where differences between co-occurring individuals or species may cause enhanced ecosystem functioning in more diverse ecosystems. Barry et al. (2019) separate complementarity into three types: (i) resource-use complementarity or resource partitioning (*i.e.*, different co-occurring species use resources in distinct, complementary ways for growth, defense, and reproduction through resource partitioning), (ii) abiotic facilitation, and (iii) biotic feedbacks (including biotic facilitation). While many of the types of complementarity refer to different species complementing each other in space, temporal complementarity of species might be at least equally important for biodiversity-stability relationships. In this context, a key underlying mechanism of the biodiversity-stability relationship is the **asynchrony** of different species (Loreau & de Mazancourt, 2008; de Bello et al., 2021; Loreau et al., 2021).

Net biodiversity effects: can be mathematically partitioned into separate but additive **complementarity effects** and **selection effects** when comparing species mixtures to monocultures.

Complementarity effects: are often quantified as the performance of mixtures relative to the performance of the component monocultures according to the additive partitioning method (Loreau & Hector, 2001). They are theoretically attributed to the factors described above for complementarity.

Selection effect: is often quantified using the additive partitioning method and describes a situation where the presence and abundance of species with particular traits affect ecosystem processes (e.g., biomass production; Loreau & Hector, 2001). A selection effect can be detected when species that have the greatest performance in monoculture become dominant in multispecies communities (Loreau et al., 2021).

Disturbances or perturbations: are often classified as pulse (short) or press (longer-term), depending on their duration. What is experienced as a short pulse disturbance by a plant community might be considered a press disturbance for its microbiome and other biota (Shade et al., 2012), due to differences in life history of the different organismic groups.

Extreme climate events: have various definitions in the literature taking a climatological or impact-related perspective (van de Pol et al., 2017), and no universally accepted definition exists (van de Pol et al., 2017). Here, we follow previous work (e.g., Ummenhofer & Meehl, 2017) and apply the climatological definition by the IPCC Special Report on Extreme Events (IPCC, 2012) for a climate extreme as “the occurrence of a value of a weather or climate variable above (or below) a threshold value near the upper (or lower) ends of the range of observed values of the variable (typically 5 % or 10 %)”. Moreover, ‘climate extreme’ is regarded as an aggregate term encompassing both ‘extreme weather’ and ‘extreme climate’ events (Frank et al. 2015). Notably, “the distinction of weather events and climate events is related to the timescale: an extreme climate event occurs on longer timescales than an extreme weather event and can be the accumulation of extreme weather events” (Frank et al., 2015). We note that “climate” is a term used for long-term characteristics, while many extreme events may be more adequately referred to as “weather events”. However, given the dominance of the term “climate extreme events” in the literature (e.g., Pörtner et al., 2021; Mahecha et al., 2022), we use this term for comparability and consistency.

Fast-slow trade-off (with focus on biodiversity-stability relationships): broad hypothesis based on plant functional traits suggesting that “slow” species or communities are more resistant (but recover less quickly) to environmental disturbances, while “fast” species or communities are not resistant to environmental disturbances but recover more quickly (Reich, 2014). For an in-depth review of trait-based mechanisms driving ecosystem stability, see de Bello et al. (2021).

Growth-defense trade-off: it is assumed that plants face a physiological trade-off between either the allocation of resources to defense and away from plant growth and development or reduced investments to root symbionts, like mycorrhiza (Walters & Heil, 2007). As plant pathogens are assumed to accumulate in plant species-poor communities over time, a reduced performance of plant offspring with a history of low diversity compared to high diversity is seen as an adaptation to higher plant investments into defense (Dietrich et al., 2021). Accordingly, the growth-defense trade-off contributes to explain the strengthening of the BEF relationship over time.

Outsourcing-“do-it-yourself” trade-off (with focus on biodiversity-stability relationships): collaboration gradient ranging from “do-it-yourself” soil exploration by roots with high specific length to “outsourcing” by investing carbon into the mycorrhizal partner and hence extraradical hyphae, which requires a large cortex fraction and root diameter (Bergmann et al., 2020). The collaboration gradient likely has consequences for biodiversity-stability relationships. Given the well-established role of mycorrhizal fungi in drought and pathogen resistance, it is likely that species or communities dominated by outsourcing traits might be more resistant to abiotic and biotic stress but recover more slowly. For an in-depth review of trait-based mechanisms driving ecosystem stability, see de Bello et al. (2021).

Performance-enhancing effect: a type of selection effect that applies when environmental conditions vary and the best-performing species are favored under each environmental condition (Loreau et al., 2021).

Recovery: the ability of ecosystem properties to return to their pre-disturbance status after a disturbance (Yi & Jackson, 2021) (Fig. 3).

Resilience: integrated measure of stability, including the resistance and recovery of ecosystem properties in response to a disturbance (Helfgott, 2015; Ingrisch & Bahn, 2018; Yi & Jackson 2021). Many perspectives and definitions exist for resilience (e.g., ecological resilience versus engineering resilience; Holling, 1996), and we mostly refer to resistance and recovery following Isbell et al. (2015) and Fig. 3 below.

Resistance: the ability to resist changes in ecosystem properties (i.e., staying essentially unchanged) in response to a disturbance (Grimm & Calabrese, 2011; van Meerbeek et al., 2021) (Fig. 2).

Stability: a broad concept that we use here to denote a reduced variability of an aggregate ecosystem property, usually through time (i.e., across multiple years; Isbell et al., 2015; Loreau et al., 2021). Stability is often decomposed into the components resistance, recovery, and resilience.

Variability: variation of an ecological property (e.g., plant biomass or production) through either time or space. Classic measures of variability include the variance, standard deviation, or coefficient of variation of the ecological property (Loreau et al., 2021).

Exploring soil- and plant-history effects in more detail, recent work in biodiversity experiments suggests it is not individual mechanisms that drive long-term biodiversity effects on ecosystem functioning, but it is several intertwined processes and organisms across different trophic levels that produce increasingly positive ecosystem effects (“multiple-mechanisms hypothesis”; Box 2). The processes listed below are vital mechanisms in the context of BEF that should be considered together. More specifically, it was demonstrated that (i) specific plant antagonists accumulate and dominate in low-diversity plant communities (Mommer et al. 2018; Thakur et al. 2021; Huang et al. 2022; Amyntas et al. 2023) and correlate especially with “do-it-yourself” root traits (J. Hennecke unpubl. data; Xi et al., 2021) (ii) diverse plant communities support a greater diversity and activity of beneficial interaction partners across trophic levels (Eisenhauer et al. 2017; Dietrich et al. 2020; A. Asato unpubl. data; Amyntas et al., 2023; Li et al., 2023; Zytynska et al., 2016), (iii) use resources more efficiently (Dietrich et al., 2020; Oelmann et al.,

2021), and (iv) diversify in their traits to optimize complementarity (Zuppinger-Dingley et al., 2014). Moreover, energy flux calculations indicate (v) higher top-down control of aboveground herbivores by predators and lower herbivory pressure on plants above (Barnes et al., 2020) and below the ground (Amyntas et al., 2023) in diverse plant communities. Simply put, at low plant diversity, it may be most important for plants to defend themselves against various kinds of antagonists or to have a faster turnover in the populations (shorter life cycle) (Roeder et al., 2019), while at high plant diversity, the resource competition among plant species may make it more important to have beneficial partners in soil to optimize nutrient acquisition and/or to have different or plastic traits in comparison to neighboring plants for use of water, nutrients, and light (Roscher et al., 2015, 2018; Eisenhauer et al., 2019a). Moreover, (vi) high-diversity plant communities provide more stable microclimate conditions than low-diversity plant communities that may be key for the maintenance of multitrophic biodiversity (Lange et al., 2023b; Schnabel et al., 2023) and ecosystem functioning (Huang, Stein et al., 2024). Based on these multiple mechanisms, the

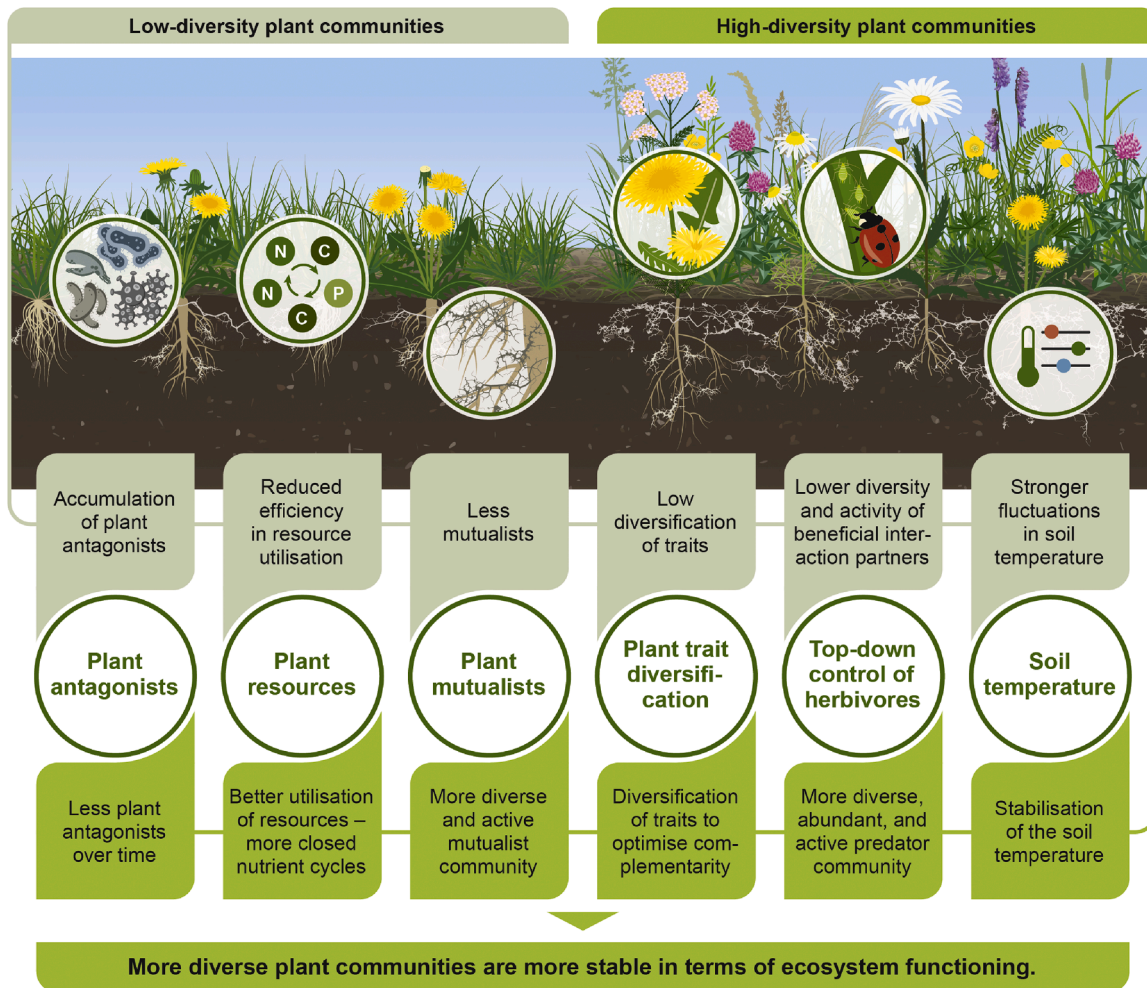


Fig. 2. Visual representation of the multiple-mechanisms hypothesis of biodiversity–stability relationships.

importance of biodiversity for sustaining ecosystem functioning can be attributed to an increasing complementarity among species through time (Reich et al., 2012; Wagg et al., 2022), whereby species are on average able to better maintain, or even increase, their relative productivity over many years in high-diversity communities than in low-diversity communities, e.g., by resource partitioning, facilitation, or biotic interactions (Guerrero-Ramírez et al., 2017; Barry et al., 2019; Eisenhauer et al., 2019a; Wright et al., 2021).

The mechanisms generating stronger biodiversity–ecosystem functioning relationships over time (e.g., enhanced complementarity, abiotic and biotic facilitation, higher resource-use efficiency; Box 1) are also likely to make more diverse plant communities more stable in terms of ecosystem functioning (Isbell et al., 2015; Craven et al., 2018; Wagg et al., 2022). Thus, the temporally increasing biodiversity–ecosystem functioning relationships should lead to increasing biodiversity–stability relationships, but there has been limited empirical evidence collected so far, and the theoretical work is in its infancy (Amyntas et al., 2023). Past research suggests that higher plant species richness can maintain more stable productivity due to a greater likelihood that some species will be able to maintain productivity during times when others cannot, such as during a drought or other disturbances, referred to as the portfolio or insurance effect (Allan et al., 2011; Loreau et al., 2021; Box 1). This

means that ecosystem functioning may be stabilized by species that are temporally asynchronous in their performance as well as by the presence of particularly productive species that exhibit stable population dynamics through time (de Bello et al., 2021; Craven et al., 2018). Recent studies in the Jena Experiment (Roscher et al., 2004) show that the mechanisms stabilizing ecosystem functioning can change with community age (Wagg et al., 2022; Huang, Stein et al., 2024) and that the roles of species’ interannual complementarity (asynchrony) for stabilizing ecosystem functioning may take up to decades to grow in experiments that manipulate plant diversity (Wagg et al., 2022). Moreover, yield decline over time (due to the fact that the Jena Experiment was established on a previously heavily fertilized agricultural field, and the soil continuously lost nutrients through the removal of plant biomass during harvests; Roscher et al., 2004) was lower in high-diversity communities in absolute and relative terms, resulting in temporally strengthening positive effects of richness on productivity, complementarity effects, and stability relationships (Wagg et al., 2022). In the later years of the experiment, asynchrony played a more important role in providing community stability at high plant diversity, and only then were species complementarity effects significantly related to species asynchrony.

Box 2. The multiple-mechanisms hypothesis of biodiversity–stability relationships.

New hypothesis based on an earlier synthesis (Weisser et al., 2017) and recent work in the Jena Experiment (see main text). It suggests that it is not individual mechanisms that drive long-term biodiversity effects on ecosystem functioning and stability, but it is a *multitude of intertwined processes that produce increasingly positive ecosystem effects* (Fig. 2). Important mechanisms include:

- (i) Low-diversity plant communities are dominated by accumulating above- and belowground plant-antagonists (*i.e.*, pests and pathogens) over time;
- (ii) Low-diversity plant communities use resources less efficiently than high-diversity plant communities and have more open, leaky nutrient cycles;
- (iii) High-diversity plant communities support a greater diversity and activity of beneficial interaction partners across trophic levels;
- (iv) High-diversity plant communities diversify in their traits within and across species to optimize temporal (intra- and interannual) and spatial complementarity;
- (v) High-diversity plant communities have greater top-down control of aboveground and belowground herbivores by predators;
- (vi) High-diversity plant communities create more stable environmental conditions than low-diversity plant communities.

In line with the observation that different species fulfill unique roles in ecosystems when considering multiple ecosystem functions, years, locations, and environmental change scenarios (Isbell et al., 2011), the prevalence of specific mechanisms contributing to the enhanced performance and stability of diverse plant communities could vary in different contexts. This suggests the existence of "between-context insurance" or "across-context complementarity," indicating that different mechanisms may play a more prominent role in different scenarios or environments. Taken together, these mechanisms might represent a prerequisite for coexistence without competitive exclusion, as interspecific competition for resources is weaker than intraspecific competition (coexistence principles; Turnbull et al., 2016; Eisenhauer et al., 2019a, 2023; Yu et al., 2024).

Given the significant role of plant and soil history in driving biodiversity–productivity relationships (Fig. 1) and the stabilizing mechanisms of biodiversity (Boxes 1 and 2), plant and soil history may be critical components driving long-term biodiversity–stability relationships. Recent work shows that plant-community responses to disturbances like drought and the stability of ecosystem functioning are determined by the history of plant–environment interactions. Under drought, soil history and plant history had species-specific effects on trait expression (shoot, leaf, and root traits) and community functioning (*i.e.*, plant biomass production) (Dietrich et al., 2022). Moreover, drought-selected plants showed greater among-species complementarity (as indicated by a significant positive complementarity effect; Loreau & Hector, 2001) than ambient climate-selected plants when recovering from a subsequent drought, causing stronger biodiversity effects on productivity and better recovery of drought-selected mixtures after the drought (Chen et al., 2022). Moreover, drought was shown to decrease bacterial and fungal richness and modify relationships between plant species richness and microbial groups in experimental microcosms, as well as increase net biodiversity effects via drought-related soil-legacy effects (Xi et al., 2022; note that it may be important to differentiate short-term *versus* long-term drought effects, Albracht et al., 2023). Taken together, these findings suggest that "old" high-diversity plant communities with exposure to recurrent extreme climatic events can improve ecosystem responses to future events through transgenerational reinforcement of species complementarity. However, these prior studies of biodiversity–stability relationships primarily quantified the "complementarity effect" following Loreau and Hector (2001) (Wagg et al., 2022), which is "blind" to the mechanisms, and implies that there must be complementarity of one or more functional traits of the species in more diverse communities (de Bello et al., 2021). This complementarity can be achieved by multiple combinations of different

mechanisms, such as by mechanisms associated with plant traits conferring *e.g.* drought tolerance or by stronger interactions between plants and their microbiome, which can complement or facilitate plant drought resistance traits (de Vries et al., 2020). An important frontier of future work is to go beyond quantifying the "complementarity effect", to identifying and quantifying its underlying mechanisms. In this paper, we focus on biodiversity–stability relationships based on long-term temporal stability, stability of seasonal dynamics, as well as the stability facets resistance and recovery (Box 1). Moreover, we put particular emphasis on the stabilizing role of biodiversity under extreme climate events. We note that "climate" is a term used for long-term characteristics, while many extreme events may be more adequately referred to as "weather events". However, given the dominance of the term "climate extreme events" in the literature (*e.g.*, Pörtner et al., 2021; Mahecha et al., 2022), we use this term for comparability and consistency (Box 1).

Ecosystem stability

Ecosystem stability has a long history of ecological research as well as scientific debate, and it is now of exceptionally high scientific interest given the unprecedented global changes (Hautier et al., 2015; Oliver et al., 2015; de Bello et al., 2021; Loreau et al., 2021). First, with the human population having just reached eight billion people, the stable provisioning of multiple ecosystem services is critical for food security and human health. Second, propelled by increasing climate change, environmental fluctuation and the frequency and intensity of extreme climate events are threatening ecosystems and their services around the world (Pörtner et al., 2021; Mahecha et al., 2022). This gives the quest for stabilizing ecosystem properties particular importance and has sparked the idea of nature-based solutions to address the climate and biodiversity crises in concert (Pörtner et al., 2021; Mahecha et al., 2022). After some initial debate on biodiversity's role in different stability facets (May 1974; Pimm, 1984; McCann, 2000; Ives & Carpenter, 2007; Loreau et al., 2021), maximizing biodiversity is now thought to be key for the development of sustainable management strategies and the stable supply of multiple ecosystem services (Isbell et al., 2017a; Meyer et al., 2018) due to a multitude of mechanisms (Box 1; de Bello et al., 2021; Loreau et al., 2021). However, biodiversity may be particularly important in providing ecosystem resistance, while the effect of biodiversity on recovery might be a less consistent predictor for long-term stability (Isbell et al., 2015). Exploring biodiversity effects on different stability facets and formalizing relationships among stability components may help synthesize previous theoretical and empirical results while also providing new strategies for predicting and enhancing stability and forecasting responses to environmental disturbances. For

example, statistical and experimental attempts to quantify *which* parts of the multiple-mechanisms hypothesis have the greatest impacts on ecosystem stability from one context to another could help identify both: i) which aspects of biodiversity are most important to monitor and manage for optimal stability of ecosystem services, and ii) other management strategies that may be important to consider, coincident with biodiversity, because they could affect stability in ways that are not mediated by biodiversity alone (e.g., strategies for fertilization, livestock grazing, and biomass harvesting). Given the novel results summarized above and the methodological value of direct and persistent manipulations of biodiversity, long-term biodiversity experiments may be particularly valuable in testing the stabilizing effects of biodiversity due to changing stabilizing mechanisms over time (Wagg et al., 2022), including eco-evolutionary feedbacks (Eisenhauer et al., 2019a; van Moorsel et al., 2021; Chen et al., 2022).

To study long-term biodiversity–stability relationships, we suggest that future analyses should follow the theoretical assumptions and definitions of stability components by Isbell et al. (2015) and apply this approach to multiple ecosystem functions and ecosystem multistability (Sasaki et al., 2019; Eisenhauer et al., 2024). These stability measures have the advantage of being dimensionless which facilitates synthesis across scales of space, time, and biological organization and between system levels. The three measures are resistance, recovery, and invariability. These stability measures are also symmetric and can be directly compared between positive and negative disturbances, such as the case

of drought (mostly negative; Isbell et al., 2015) and moderate flooding (Wright et al., 2015) (Fig. 3). To do so, consider a discrete time series representing system levels, such as net primary productivity (e.g., in grassland plant communities) or community density (e.g., in plankton communities). These levels experience periodic disturbances, such as wet and dry climate events, followed by recovery either towards an attractor or away from a repeller after each disturbance. As in previous studies (Isbell et al., 2015), resistance (Ω) is defined as $\Omega \equiv \frac{Y_n}{|Y_e - Y_n|}$, and recovery (Δ) is defined as $\Delta \equiv \left| \frac{Y_e - Y_n}{Y_{e+1} - Y_n} \right|$, where Y_n , Y_e , and Y_{e+1} are values during “normal” times (averaged across all non-perturbed times, such as normal climate years), during a disturbance (such as during a drought), and during one-time unit after a disturbance, respectively. Resistance indicates proximity of the system to normal levels during a disturbance, quantified as the inverse of a proportional displacement from normal levels during a disturbance. For example, if the system is reduced by $\frac{1}{4}$ of its normal level during a disturbance, then $\Omega = 4$ (the inverse of $\frac{1}{4}$). Recovery indicates the rate of change toward ($\Delta > 1$) or away from ($0 < \Delta < 1$) normal levels after a disturbance, quantified as the inverse of proportional lack of recovery after a disturbance. For example, if the system recovers all but $\frac{1}{4}$ of the way from perturbed to normal levels during the time step following a disturbance, then $\Delta = 4$ (the inverse of the $\frac{1}{4}$ proportion remaining). Stability (ζ^2) is the inverse of the coefficient of variation of the time series, where μ and σ are the

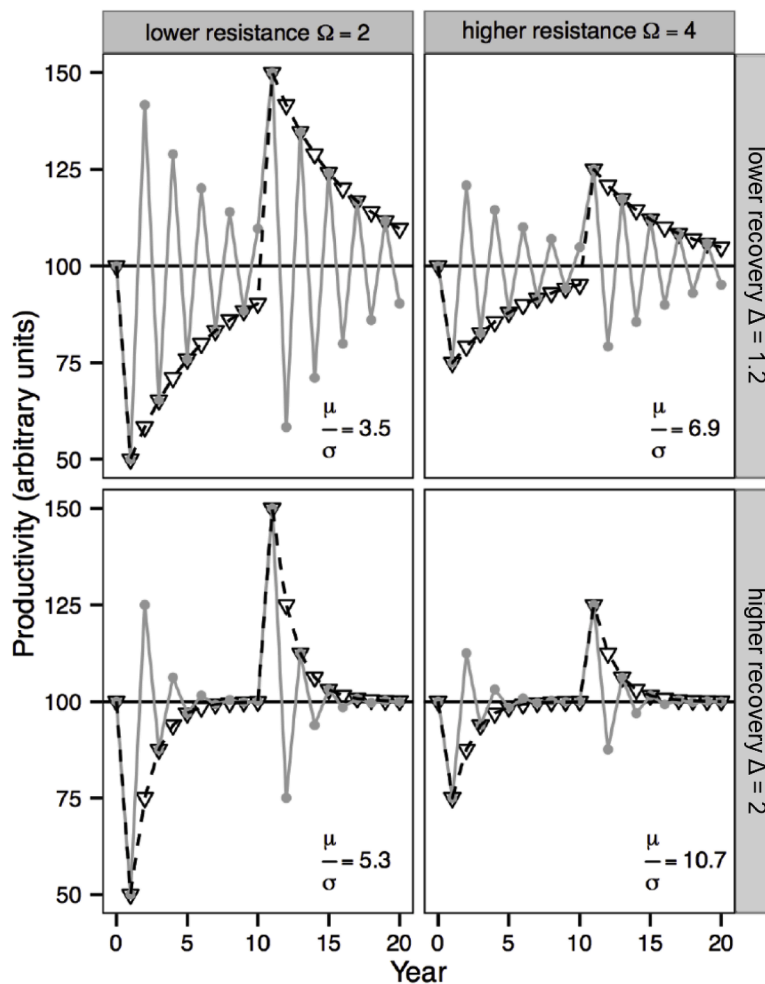


Fig. 3. Illustration of how stability can depend on both resistance and recovery. These hypothetical time series show contrasting cases of resistance to and recovery after an extreme drought in year one and an extreme wet event in year 11, with recovery following each event. Stability (ζ^2) can be increased by increasing resistance (Ω), recovery (Δ), or both. Dashed black lines and triangles show monotonic recovery. Gray lines and points show recovery via damped oscillations. Figure modified from Isbell et al. (2015).

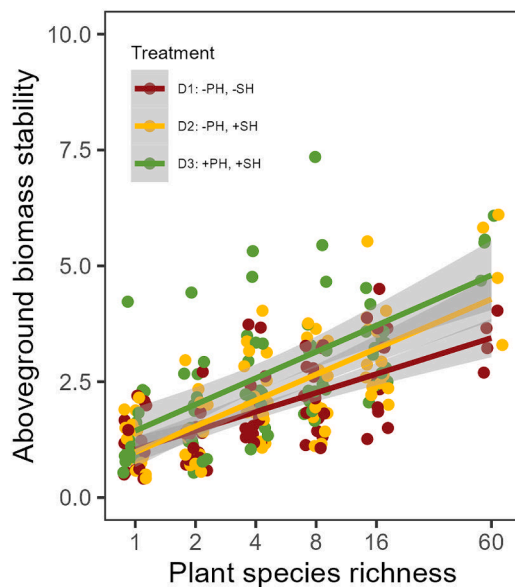


Fig. 4. Long-term plant diversity effects on ecosystem stability. Effects of plant diversity on the stability of plant biomass production as affected by plant (PH) and soil history (SH). D1: without PH, without SH (red line); D2: without PH, with SH (yellow line); D3: with PH, with SH (green line) (see legend of Fig. 1 for details). Data from the Δ BEF Experiment (Vogel et al., 2019).

temporal mean and standard deviation, respectively. There have been multiple absolute and relative stability indices in the ecological literature (e.g., McCann, 2000; van Ruijven & Berendse, 2010; Donohue et al., 2013; Kéfi et al., 2019), and discussing their pros and cons would go beyond the scope of our paper. Note that we refer to proportional changes (Isbell et al., 2015), and in time-series analyses, we intend to propose data to account for potential directional changes over time.

Indeed, recent studies provide empirical evidence that the stabilizing effects of biodiversity increase over time for several ecosystem functions, and that plant- and soil-history effects contribute to this development. First, even though soil temperature is essential for many soil processes that include cycling of water and elements as well as metabolic activities of plants and microbes, which are important for ecosystem responses to climate change and extremes, few studies have investigated whether plant diversity can buffer fluctuations in soil temperature.

Using a unique dataset to investigate the effects of plant diversity on soil temperature stability at 5 and 15 cm depth across 18 years, Huang, Stein et al. (2024) showed that more diverse plant communities had warmer temperatures in winter and cooler temperatures in summer, such that diversity buffered the seasonal shift in soil temperature over time. Using structural equation models, it was observed that plant diversity increased soil temperature stability ($\frac{\sigma}{\mu}$), both within and across seasons, by increasing both plant cover and soil organic carbon concentrations (Huang, Stein et al., 2024). Moreover, plant diversity effects on buffering soil temperature increased significantly over time, intensifying especially on hot days and in dry years; thus, the absence of this buffering effect, such as in low-diversity grasslands, would likely exacerbate the negative effects of heat and drought, which often co-occur, on the function of this grassland (Huang, Stein et al., 2024).

Second, we used plant biomass data from the Δ BEF Experiment (Vogel et al., 2019), a sub-experiment within the Jena Experiment testing effects of plant and soil history, sampled in the years 2017–2022, which include two exceptionally strong summer droughts in 2018 and 2019 (see legend of Fig. 1 and Box 3 for details on the experiment). We calculated the temporal stability ($\frac{\sigma}{\mu}$) of plant biomass production and tested for potential stabilizing effects of plant diversity as well as plant and soil history (Fig. 4). In all treatments, plant diversity had significant positive effects on productivity stability. However, stability of plant biomass production, including resistance to the summer droughts, tended to be lower for plant communities grown on soils that had not co-evolved with the plants over time (i.e., without soil history, $F_{(1, 78)} = 6.06$, $P = 0.016$) and for plant communities for which the plant genotypic diversity was not allowed to evolve over time (i.e., without plant history, $F_{(1, 78)} = 3.92$, $P = 0.051$) (Fig. 4). The effects of plant diversity in plant communities without soil history were weaker than in plant communities with soil history (Fig. 4; $F_{(1, 78)} = 3.61$, $P = 0.061$). Overall, these results highlight the importance of old and biodiverse plant communities for ecosystem functioning and its stability. Future work should test the theoretical predictions outlined above for multiple ecosystem functions and ecosystem multistability by considering the multiple mechanisms hypothesis of long-term biodiversity effects. Although we test our hypotheses in BEF experiments, we note that direct comparisons between experimental and observational data have to be done with care (e.g., Jochum et al., 2020; Oelmann et al., 2021), and BEF experiments are particularly useful to test biodiversity theory and mechanisms by simulating local biodiversity loss (Eisenhauer et al., 2016).

Box 3. Novel experimental approaches to address current knowledge gaps – a case study in the Jena Experiment.

To build on the many recent developments in the field and address current research frontiers, we present some targeted experiments to inspire future work. We propose to use a set of three complementary experimental approaches (field experiment, Ecotron experiment, and microcosm experiments; Fig. 5) as well as extensive synthesis to advance the mechanistic understanding of biodiversity-stability relationships by focusing on long-term effects of plant diversity on ecosystem functioning. Before we outline these case studies in more detail, we provide a short overview of the different sub-experiments within the Jena Experiment. <http://the-jena-experiment.de/index.php/design-2/>

a. Overview of experiments

CoMic Experiments: NEW Complementary Microcosm experiments will build on the Common Research Platform provided by the DrY Experiment and help individual subprojects to study additional abiotic and biotic stressors as well as stabilizing mechanisms (see below for details). CoMic Experiments run by different subprojects have unique names (see below and Supplementary Materials).

Δ BEF Experiment: Plant diversity experiment established in 2016 to explore mechanisms underlying the strengthening relationships between biodiversity and ecosystem functioning over time (Vogel et al., 2019) with a focus on soil and plant history. We therefore reestablished the plant communities of the Main Experiment with new seeds and old or new soil again in 2016. By comparing these treatments with the original communities set up in 2002, we test whether old communities (= with history) have stronger plant diversity effects on plant productivity than young ones (= without history) and if this depends on soil- or plant-related processes. We established subplots without soil history (-SH), without plant history (-PH), and with plant and soil history (+PH+SH) (Fig. 1). For removing the plant and soil history, the soil and plant layer to a depth of 30 cm were replaced by soil of an adjacent arable field of the same soil layer, and sowing the same plot-specific plant species mixtures as in 2002 (new seeds). In subplots without plant history and with soil history and (-PH+SH), we removed the plant sod by using a digger while keeping the soil of the respective plots, homogenized the upper 30 cm, and sowed the same plot-specific plant species mixtures as in 2002 (new seeds). As the third subplot (+PH+SH), we used parts of the existing Main Experiment, which has an established soil and plant history since 2002.

This treatment serves as a long-term control. This experiment has been terminated.

Drought Experiment: The treatments of this experiment were nested in the plots of the *Main Experiment* and ran from 2008 to 2016 (Vogel et al., 2013). We induced a prolonged summer drought period by means of transparent rainout shelters for 6 weeks in summer. Rain shelters were made of a wooden frame and PVC sheets and had a size of 2.6 × 3 m. Each rain shelter covered two subplots (each had a size of 1 × 1 m), of which one received no water when rain shelters were installed ('drought'), while one was watered with collected rainwater to control for shelter effects ('control'). This experiment has been terminated.

DrY Experiment: Proposed NEW experiment to (1) test the response shape of ecosystem resistance and recovery to increasing drought intensity (*DrY Experiment*) and (2) prepare the *ResCUE Experiment* (see below) and subproject-specific microcosm experiments (*CoMic Experiments*; see below). The experiment will help to determine the conditions that cause stress in plant and soil communities in realistic ways (e.g., such as seen under extreme climatic conditions in the field) and develop a *Common Research Platform* with standardized soil (taken from the same location at the Jena Experiment field site) as well as common plant species and communities (e.g., to compare the results of different microcosm studies performed at different locations). This experiment will be conducted in the iDiv Greenhouse in Leipzig in 2024.

JenaTron Experiment: In spring 2022, we excavated two monoliths of each of 22 selected plots of the former *Trait-Based Experiment* covering a gradient from 1 to 3 plant species, and additional four monoliths of a selected 6 species plot (48 monoliths in total; soil with plant community-specific history; +SH). In addition, we excavated 48 monoliths from the bare ground plots of the *Main Experiment* (soil without plant community-specific soil history; -SH). From all four monoliths, the upper soil layer was gently removed, and newly grown plant individuals were transplanted, either gained from seed material from a supplier (without plant history; -PH) or collected from the selected plots of the former *Trait-Based Experiment* (with plant history; +PH). This resulted in four treatments in each EcoUnit of the iDiv Ecotron: (1) 'with plant history, with soil history' (+PH+SH); (2) 'without plant history, with soil history' (-PH+SH); (3) 'with plant history, without soil history' (+PH-SH); and (4) 'without plant history, without soil history' (-PH-SH). The experiment ran for 6 months and was destructively sampled in October 2022. This experiment has been terminated.

Main Experiment: Plant diversity experiment with sown plant species richness levels of 1, 2, 4, 8, 16, and 60 species that was set up in 2002 (Roscher et al., 2004; Weisser et al., 2017) and is still running. All subprojects will work on all or a selection of the 80 plots of this experiment to study long-term biodiversity-stability relationships and mechanisms underlying BEF as well as perform synthesis work.

Monocultures: Monocultures of all 60 plant species were set up in 2002 (plot size today: 1 m²) in parallel to the *Main Experiment* to allow for plant species-specific trait measurements, phenology assessments, and applying the additive partitioning method (Loreau & Hector, 2001). These plots will be maintained.

ResCUE Experiment: Proposed NEW experiment to study plant diversity-mediated resistance and recovery under climate extremes (hot drought) in the iDiv Ecotron in 2026.

Trait-based Experiment: Plant diversity experiment with sown plant species richness levels of 1, 2, 3, 4, and 8 species that was set up in 2010 (Ebeling et al., 2014; Weisser et al., 2017) and was terminated in 2021. Species fall into three different species pools with different trait combinations focused on spatial resource use (e.g., root characteristics), temporal resource use (e.g., plant phenology), or on both together. A selection of plots was used for the *JenaTron Experiment*.

b. Experiments to study plant diversity-stability relationships

While the *Jena Main Experiment* (Roscher et al., 2004; Weisser et al., 2017) allows testing the climate drivers of biodiversity-ecosystem functioning and -stability relationships due to observed climatic variability, the Ecotron experiment and microcosm experiments enable us to experimentally manipulate abiotic and biotic stresses and zoom in on the mechanisms underlying the effects of plant diversity on the stability, resistance, and recovery of multiple ecosystem functions. The overarching hypotheses are that (i) **plant diversity stabilizes multiple ecosystem functions (ecosystem multistability)**, (ii) **these stabilizing effects of plant diversity increase over time** (Huang, Stein et al., 2024; Fig. 5A), and (iii) **can be predicted based on short-term resistance to effects of climate extremes** (Isbell et al., 2015; Fig. 5B). To understand the stabilizing effects of plant diversity, important multitrophic interaction partners above and below the ground need to be considered, including microorganisms and animals. This includes also the use of synthetic communities of microbiota and soil animals and aboveground consumers, with well-defined functional traits to improve our understanding of above- and belowground interactions. The planned research projects will use and synthesize data from the *ΔBEF Experiment* (Vogel et al., 2019) and *JenaTron Experiment* (Eisenhauer et al., 2019b) to evaluate eco-evolutionary dynamics in BEF relationships (Box 2). In all experimental and synthesis approaches, studying the stabilizing features of ecosystems will be key to better understanding why high-diversity plant communities function better than low-diversity plant communities and why this difference increases over time (Reich et al., 2012; Guerrero-Ramírez et al., 2017; Wagg et al., 2022).

In the *Main Experiment*, which is a grassland biodiversity experiment initiated in a floodplain in 2002 and has been maintained to the present, we will test the hypothesis that plant diversity stabilizes multiple ecosystem functions and that these stabilizing effects of plant diversity increase over time (Fig. 4A). Moreover, the *Main Experiment* has experienced multiple extreme climate events over the past two decades, which allows us to test the hypothesis that the (stabilizing) effects of plant diversity are most pronounced under harsh environmental conditions (Huang, Stein et al., 2024). The *Main Experiment* offers unique long-term time series datasets on multiple ecosystem functions. Data from the *Drought Experiment* (Vogel et al., 2013), a field study using rainout shelters on subplots of the *Main Experiment* (Box 3), will allow us to calculate resistance to summer drought and can be used to test the hypothesis that long-term stability can be well predicted based on short-term resistance. In the Ecotron experiment (*ResCUE*), we will induce a standardized hot drought (that cannot be guaranteed under field conditions) to study the resistance and recovery of multiple ecosystem functions as well as the underlying mechanisms using repeated samplings and ¹³C and ¹⁵N labeling. This setup will allow us to test the hypothesis that plant diversity has a strong positive effect on the resistance of multiple ecosystem functions, while the effect on recovery might be weaker (Fig. 5B; for design details, see Supplementary Materials). In the *DrY Experiment*, we will use microcosms to test the hypothesis that the stabilizing effects of plant diversity increase with increasing drought intensity, until a certain threshold is reached (Baert et al., 2018; Fig. 5C). Moreover, this experiment will serve as the basis for developing a *Common Research Platform* for *CoMic Experiments* (for design, see Supplementary Materials).

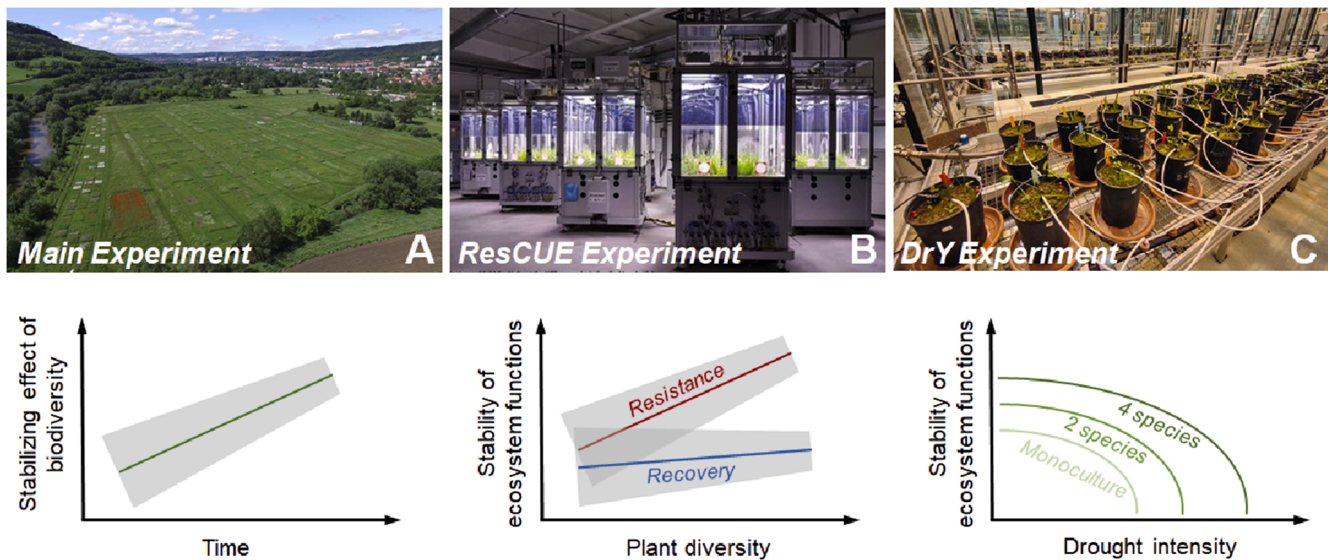


Fig. 5. Main experimental infrastructures and hypotheses. Main Experiment (A), ResCUE Experiment (B), and DrY Experiment (C); for details, see Box 2 and main text.

Conclusions

We here establish the hypotheses that multifunctional stability is highest in high-diversity plant communities and that biodiversity–stability relationships increase over time due to a variety of forms of ecological complementarity. We introduce the multiple-mechanisms hypothesis of biodiversity–stability relationships, suggesting that it is not an individual mechanism that drives long-term biodiversity effects on ecosystem functioning and stability, but that a multitude of intertwined processes produce increasingly positive ecosystem effects including interactions with other biota above- and belowground. This concept implies “between-context insurance” or “across-context complementarity” of different stabilizing mechanisms, indicating that different mechanisms may play a more prominent role in different scenarios or environments. In addition to introducing this novel concept, we provide examples of concrete experiments that will be conducted to test our hypotheses. These experiments may inspire future work on the stabilizing features of ecosystems.

CRedit authorship contribution statement

Nico Eisenhauer: Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Kevin Mueller:** Conceptualization, Writing – review & editing. **Anne Ebeling:** Conceptualization, Investigation, Writing – review & editing. **Gerd Gleixner:** Conceptualization, Investigation, Writing – review & editing. **Yuanyuan Huang:** Conceptualization, Data curation, Formal analysis, Visualization, Writing – review & editing. **Anna-Maria Madaj:** Conceptualization, Writing – review & editing. **Christiane Roscher:** Conceptualization, Investigation, Writing – review & editing. **Alexandra Weigelt:** Conceptualization, Investigation, Writing – review & editing. **Michael Bahn:** Conceptualization, Writing – review & editing. **Michael Bonkowski:** Conceptualization, Writing – review & editing. **Ulrich Brose:** Conceptualization, Writing – review & editing. **Simone Cesarz:** Conceptualization, Writing – review & editing. **Hannes Feilhauer:** Conceptualization, Writing – review & editing. **Claudia Guimaraes-Steinicke:** Conceptualization, Writing – review & editing. **Anna Heintz-Buschart:** Conceptualization, Writing – review & editing. **Jes Hines:** Conceptualization, Writing – review & editing. **Markus**

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Declaration of interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Nico Eisenhauer reports financial support was provided by German Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baee.2024.07.004](https://doi.org/10.1016/j.baee.2024.07.004).

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Further reading

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