Biodiversity and climate extremes: known interactions and research gaps

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Abstract

Climate extremes are on the rise. Impacts of extreme climate and weather events on ecosystem services and ultimately human well-being can be partially attenuated by the organismic, structural, and functional diversity of the affected land surface. However, the ongoing transformation of terrestrial ecosystems through intensified exploitation and management may put this buffering capacity at risk. Here, we summarise the evidence that reductions in biodiversity can destabilise the functioning of ecosystems facing climate extremes. We then explore if impaired ecosystem functioning could, in turn, exacerbate climate extremes. We argue that only a comprehensive approach, incorporating both ecological and hydrometeorological perspectives, enables to understand and predict the entire feedback system between altered biodiversity and climate extremes. This ambition, however, requires a reformulation of current research priorities to emphasise the bidirectional effects that link ecology and atmospheric processes.

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Key Points:

- Mounting evidence suggests that an ecosystem's capacity to buffer the impacts of climate extremes depends on its biodiversity.
- Numerous mechanisms suggest that a reduction in biodiversity could exacerbate climate extremes.
- Understanding the full feedback loop linking biodiversity change and climate extremes requires an ambitious research agenda.

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Abstract

Climate extremes are on the rise. Impacts of extreme climate and weather events on ecosystem services and ultimately human well-being can be partially attenuated by the organismic, structural, and functional diversity of the affected land surface. However, the ongoing transformation of terrestrial ecosystems through intensified exploitation and management may put this buffering capacity at risk. Here, we summarise the evidence that reductions in biodiversity can destabilise the functioning of ecosystems facing climate extremes. We then explore if impaired ecosystem functioning could, in turn, exacerbate climate extremes. We argue that only a comprehensive approach, incorporating both ecological and hydrometeorological perspectives, enables to understand and predict the entire feedback system between altered biodiversity and climate extremes. This ambition, however, requires a reformulation of current research priorities to emphasise the bidirectional effects that link ecology and atmospheric processes.

Plain Language Summary

Climate extremes are increasing and impacting both nature and people. We hypothesise that intact ecosystems, particularly via their biodiversity, can mitigate the impacts of climate extremes. What happens when biodiversity decreases? Could this loss make the effects of climate extremes even worse or change how these events occur? We explore these two questions and summarise the current state of knowledge. We conclude that targeted research efforts at the interface of ecology and atmospheric sciences are needed to answer these questions conclusively.

1 Introduction

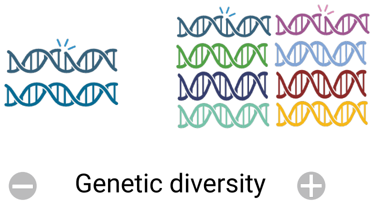
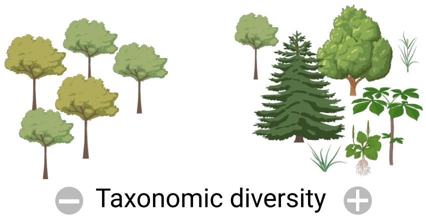
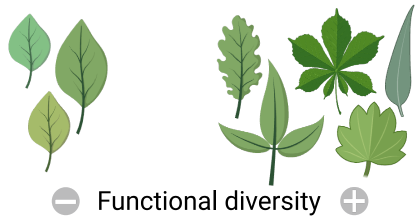
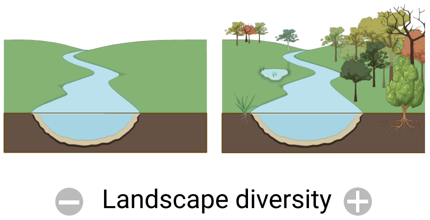
The transformation of terrestrial ecosystems due to land cover change, land management intensification, and environmental pollution, continues to accelerate globally. These interventions lead to a widespread decline in biodiversity and ecosystem functioning (Bellard et al., 2012; Díaz et al., 2019; IPBES, 2019; Jaureguiberry et al., 2022). At the same time, climate change progresses (IPCC, 2021). One effect is that weather and climate-related extremes, such as droughts, heat waves, storms, and heavy rainfall increase in frequency, intensity, and some also in spatial extent (Alexander et al., 2006; Seneviratne et al., 2012; S. Lange et al., 2020; Fowler et al., 2021). Today, such extreme events unprecedented in magnitude and duration occur around the world (Witze et al., 2022), such as the 2018-2020 multi-year drought over Europe (Rakovec et al., 2022). The intensification of extreme weather and climate events, with decreasing return periods and increased intensity, is one of the most critical consequences of anthropogenic climate change (IPCC, 2021; Fischer et al., 2021). But how will these two global mega-trends – biodiversity decline and the intensification of climate and weather extremes – affect each other? This scientifically challenging question has severe societal implications and needs to be addressed urgently in an integrative research approach.

Climate extremes can affect human well-being directly, e.g., via health impacts due to extreme heat (Ebi et al., 2021). However, a wide range of impacts is mediated by land-surface characteristics, in particular vegetation. During heat and drought events, increasing sensible heat fluxes can alter regional land-climate feedbacks and thereby intensify the extreme event (Miralles et al., 2019; Barriopedro et al., 2023). Recently, García-García et al. (in press) revealed that soil hot extremes can intensify faster than air temperature extremes, a phenomenon driven in part by the soil moisture–temperature feedback, which can further dry and warm the soil. Furthermore, heavy precipitation may turn (or not) into catastrophic flooding, erosion, and land-slide events depending on the regional water retention potential, the local storage capacity of soils and flow control of landscapes, and their geomorphological properties and vegetation structure (Brunner et al., 2021; Vári et al., 2022). Both examples demonstrate that terrestrial ecosystems and their vegetation characteristics play a crucial role in controlling the impacts of extreme climate events.

Yet, the modulation of impacts of extreme events not only depends on vegetation structure but also on the functioning of ecosystems (Reichstein et al., 2014; De Boeck et al., 2018; Thonicke et al., 2020a). It is important to note that ecosystem functioning is connected to various dimensions of 'biodiversity', a broad concept embracing (i) genetic diversity, (ii) taxonomic diversity, (iii) functional diversity, (iv) structural diversity within ecosystems, and (v) landscape heterogeneity, to name the most relevant ones for our research context (for an overview and definitions see Tab. 1). These dimensions of biodiversity are not independent from each other, and the role of biodiversity in ecosystems also depends on the available species (identity). Patterns of biodiversity partly reflect biogeographical history, spatial structures in geofactors ('geodiversity'), management, demographic history, or are an effect of internal disturbance dynamics (Bastos et al., 2023). It is widely recognised that losses in biodiversity can threaten the stability of ecosystems and thereby their ability to support human life (Mooney et al., 2009; Pörtner et al., 2021). The reason for this is that changing biodiversity affect characteristic functions of ecosystems (Musavi et al., 2015; Migliavacca et al., 2021), such as their potential to absorb pollutants, store carbon, or provide numerous natural resources. In the context of climate extremes, biodiversity is relevant because it controls how the land surface responds to atmospheric conditions. Modification of the bio(geo)physical and biogeochemical determinants of processes such as fluxes of gases, water, and energy, and the release and absorption of primary emitted particles (Fröhlich-Nowoisky et al., 2016), regulate land-surface climate feedbacks and can thereby affect local to global climate (Bonan, 2008; Santanello et al., 2018; Ukkola et al., 2018; Miralles et al., 2019).

Considering that ecosystems interact with atmospheric conditions, a crucial question arises (Mahecha et al., 2022): Is there a risk that changing biodiversity in ecosystems may not only weaken the resistance of ecosystems to climate extremes and their capacity to provide services, but also exacerbate atmospheric hazards? In other words, may biodiversity changes amplify the risk of weather and climate-related extremes? Pörtner et al. (2023) recently issued a general call for a comprehensive investigation into the intricate relationship between changes in the climate system and biodiversity. Here, we conduct an extensive review of pertinent literature to determine how far we can already give answers to the specific aspect of extremes. We first aim to understand whether higher levels of biodiversity buffer climate extremes (Section 2), and second, explore amplification processes of weather and climate extreme events dynamics in response to declining biodiversity (Section 3). Based on the conclusiveness of the literature on these aspects, we identify key research gaps that should be addressed to understand the full feedback between biodiversity change and climate extremes (Section 4).

Table 1. Biodiversity is 'the variability among living organisms from all sources, [. . .]: this includes diversity within species, between species and of ecosystems' (CBD, 1992). Here, we provide an overview of dimensions of biodiversity relevant to ecosystem responses to and feedback processes with the atmosphere

Dimension	Definition	Illustration
Genetic	Diversity of genetic properties within and across species. Also contains heritable changes in gene function not involving changes in DNA sequence (i.e., epigenetics).	
Taxonomic	Diversity of species, calculated e.g. as species richness or evenness per unit of investigation.	
Functional	Diversity of plant functional traits i.e. the morphological, anatomical, physiological, biochemical properties of plants and their organs.	
Structural	Vertical and horizontal arrangements of physical components of plants and their organs, such as leaf layers and branches.	
Landscape	Diversity and complexity of lateral arrangements of ecosystems within a landscape. Contributes to the overall biodiversity of a region by shaping habitats that support different ecosystems; synonym for 'landscape heterogeneity'.	

2 Biodiversity buffers against weather and climate extremes

Numerous studies investigate how climate extremes impact ecosystems. Two key concepts are frequently used: ecosystem "resistance", which is the capacity to withstand a climate extreme, and ecosystem "resilience", which characterises how fast and complete a system recovers following an extreme event (sensu Hoover et al., 2014; De Keersmaecker et al., 2016). Together, these concepts help to differentiate and quantify the ways in which ecosystems, as a function of their biodiversity, buffer the impact of extreme climatic events (for an illustration see Fig. 1).

Given the various dimensions of biodiversity outlined in Table 1, what specific knowledge do we have about their role in buffering extremes? In terms of taxonomic diversity, it appears that a few particular species often resist climate extremes, keeping up ecosystem functioning, or preventing community collapse under stress (De Laender et al., 2016; Werner et al., 2021). This phenomenon is classically known as "the insurance effect" (Yachi & Loreau, 1999; Loreau et al., 2021) and has been mostly inferred from experimental studies (Kayler et al., 2015; Loreau et al., 2021). For example, Isbell et al. (2015) show that grasslands with higher species diversity when exposed to exceptional dry or wet conditions have higher resistance, an effect attributed to the species-specific responses to particular stressors (Craven et al., 2018). Liu et al. (2022) reported that forest resistances against droughts increase with species richness. However, the insurance effect cannot be attributed to species-specific responses only. Variations in genetic properties of individuals within species can likewise lead to varying resistance to climate extremes. This was shown by Pfenninger et al. (2021), who analysed the susceptibility of individual beech trees to the extreme drought in central Europe in 2018, and illustrated the wide range of drought damages within a single species.

Intraspecific genetic diversity is one reason why taxonomic diversity alone is insufficient to explain ecosystem responses to extremes. Another reason is that, at the ecosystem level, responses to extremes are also largely regulated by a system's "functional diversity", defined by the variability of functional traits, such as leaf, stem, or root chemical properties and "structural diversity" (see Table 1). This explains why taxonomic diversity alone plays only a subordinate role in stabilising ecosystem functioning in many cases (Musavi et al., 2017). Mursinna et al. (2018) show that information on root trait diversity is needed to explain an ecosystem's drought sensitivity. Forest responses to droughts

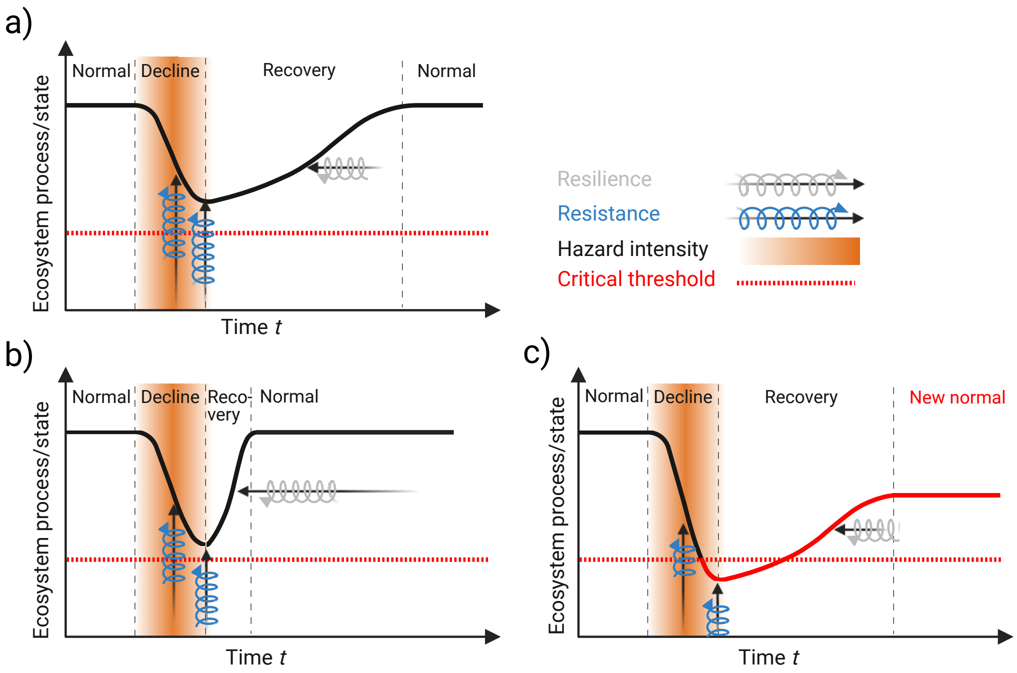


Figure 1. The ability of an ecosystem to resist or absorb changes in its states and functions over time is defined as 'resistance'. The capacity to recover to pre-event conditions is termed 'resilience'. Both resistance and resilience act over time, and jointly constitute the 'buffering capacity'. In this figure we exemplify systems with a) high resistance and low resilience, b) low resistance, and high resilience, and c) very low resilience such that the critical threshold is reached and no return to pre-event conditions can be achieved.

largely depend on the traits associated with isohydric versus anisohydric behaviour of trees (Hartmann et al., 2021; Lübbe et al., 2022). In general, the diversity of functional traits of organisms regulate how fluxes of energy, water, and nutrients are absorbed, stored and released given certain environmental conditions (Violle et al., 2007; Berendse et al., 2015; Anderegg et al., 2019). Even organisms coexisting in the same ecosystem (i.e. species that have passed an identical "environmental filter") exhibit a considerable degree of variation in their functional role, and therefore in their contribution to the resistance of ecosystem with respect to weather and climate-related extreme events (resistance Reyer et al., 2013; Felton & Smith, 2017), and their ability to recover from such events. Figure 2 illustrates conceptually how the insurance effect, mediated via functional diversity, could dampen the reduction of net primary production (NPP) and the increase in sensible heat flux during a heat wave in a more diverse forest, compared to a low-diversity forest.

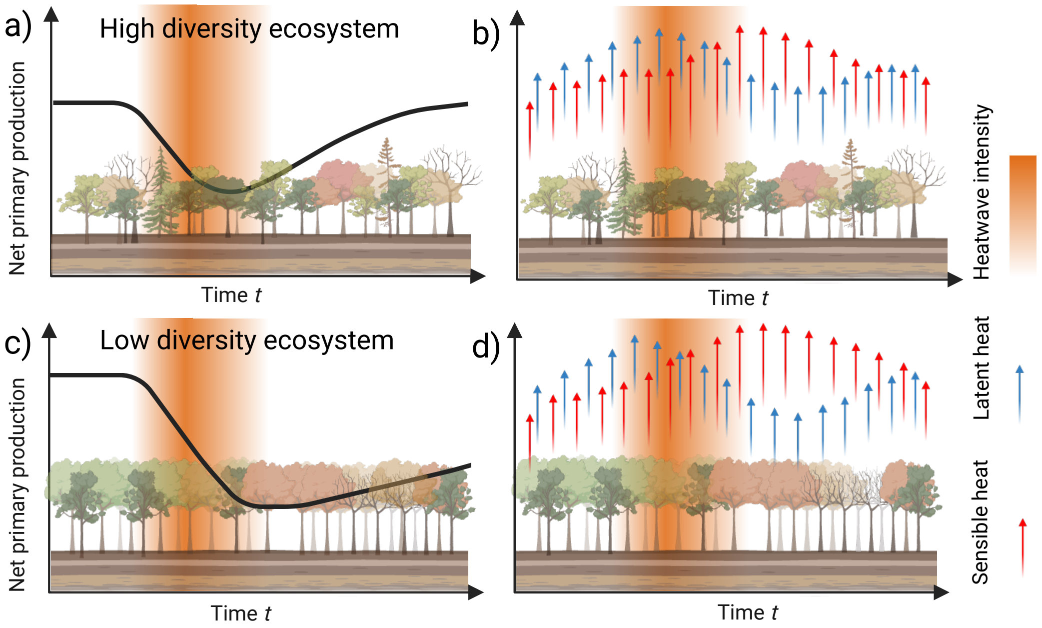
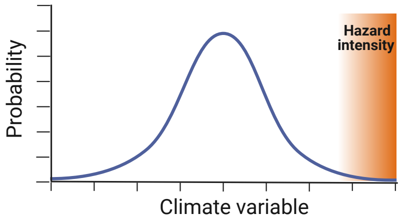
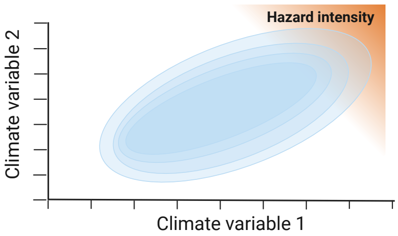
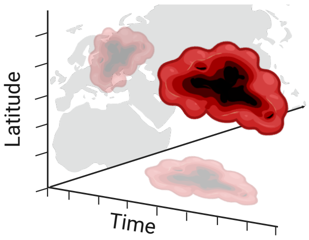
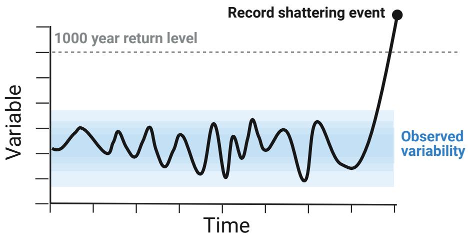


Figure 2. Illustration of the insurance effect: Hypothetical response of net primary production (NPP, net CO_2 uptake rate) to a heatwave (shown in reddish background colours) in a) a diverse forest, and c) a mono-culture. Analogous responses for energy fluxes are shown in b) and d). While low-diversity forests might initially have higher NPP, their low resistance might imply higher losses and reduced resilience given the lack of species compensation, i.e. a low insurance effect. The same effect can be observed for energy fluxes, where the ratios between latent and sensible heat fluxes change more drastically in low-diversity forests, with consequences for both ecosystems and atmospheric energy budgets.

Functional diversity is linked to structural heterogeneity at the stand level: mixtures of growth forms, plant sizes, and demographic stages appear to play an equally important role in the stabilisation of ecosystems. Guimarães-Steinicke et al. (2021) show the dominant effect of varying mixtures of herbs and grasses on the variability of vegetation surface temperatures. The meta-analysis by Craven et al. (2018) emphasises that functional biodiversity dimensions are determined by the asynchrony of abundances and thus affect the stability of ecosystem functioning. Taken together, in a changing climate with increasing occurrence of extreme weather and climate-related events, all dimensions of diversity may cause some degree of insurance against the shocks induced by climate extremes.

The buffering role of biodiversity is, however, a scale-dependent process. In general, translating insights from experiments and theory to large-scale and real-world settings proves difficult (Kreyling et al., 2008; Grossiord et al., 2019; Gonzalez et al., 2020). At the regional to continental scale, predominant and landscape heterogeneity will determine the predominant response mechanisms (Teuling et al., 2010; Flach et al., 2021; Bastos, Fu, et al., 2020). Remote sensing observations are key to overcoming scaling issues (Cavender-Bares et al., 2022), as it can monitor ecosystem responses, extreme weather and climate events from the ground, as well as from airborne- and space-borne platforms, covering local to global scales (Mahecha et al., 2017; Cavender-Bares et al., 2020; Peng et al., 2021). De Keersmaecker et al. (2016) study the resistance and resilience against drought across grasslands in central Europe using optical remote sensing observations. They conclude that nutrient-poor and species-rich grasslands appear to be more resistant, but less resilient against drought. The reverse seems to be true for fertilised, species-poor grasslands. These results are consistent with local experimental studies. The emerging and constantly growing body of global remote sensing data improves our capabilities of tracing biodiversity dynamics (Skidmore et al., 2021; Cavender-Bares et al., 2022), ecosystem management (M. Lange et al., 2022), and multiple land-surface processes (Mahecha et al., 2020). Combined, these data streams can be also used for quantifying how ecosystems buffer the impacts of climate extreme events, a task that should be prioritised.

Table 2. Extreme weather events are rare occurrences at a specific place and time, while climate extremes are persistent patterns of extreme weather (AR6 WG1 Ch. 11 IPCC, 2021). Four empirical descriptions of extremes are relevant: univariate, multivariate, spatiotemporal, and record-shattering. These categories describe the rarity, intensity, frequency, duration, and extent of events, including compound extremes and multiple meteorological drivers.

Extreme	Definition	Illustration
Univariate	Rarity of an event relative to a statistical probability distribution, either in terms of intensity, frequency, spatio-temporal extent, duration, in one variable of interest.	
Compound	Multivariate indices of extremes, also referred to as 'compound' extreme events, include unusual combinations of climate drivers.	
Spatio-temporal	Considering the spatio-temporal extent of an extreme event leads to additional metrics such as an event's duration, geographical coverage, volume, and integrated magnitde.	
Record shattering	Events that exceed previous observational records by multiple orders of magnitude, typically measured by return times, and improbable without climate change.	

3 Biodiversity imprints on atmospheric processes and extremes

Global circulation patterns determine which regions of the world are exposed to high aridity or high humidity, respectively, and during which seasons. Variations in atmospheric circulation also have a strong influence on extreme event occurrences (Coumou & Rahmstorf, 2012). For example, atmospheric blocking situations or recurrent atmospheric wave patterns lead to extended and persistent high-pressure systems or stationary lows, which may cause heatwaves or flooding that have severe consequences for ecosystem functioning (Desai et al., 2016; Flach et al., 2018; Kornhuber et al., 2019; Bastos, Ciais, et al., 2020). Blocking situations are particularly frequent over Europe, and also cause several other types of weather extremes (Kautz et al., 2022). Ongoing anthropogenic climate change is expected to further increase extreme weather around the globe and even the underlying circulation patterns are expected to change (Faranda et al., 2020). However, the extent to which such projected circulation changes are robust over Central Europe remains a matter of debate (Huguenin et al., 2020).

Although weather- and climate extreme events are primarily triggered by atmospheric processes, land-atmosphere interactions also contribute to their genesis and occurrence. Management and transformation of ecosystems, and consequently biodiversity, can change surface properties, including albedo and emissivity, roughness, evaporative resistance, and heat fluxes (Laguë et al., 2019). These interventions can substantially alter atmospheric humidity, transport dynamics, and, ultimately, cloud evolution and precipitation at regional and global scales (Avissar & Werth, 2005; Machado et al., 2018). It has also been shown that the surface albedo modulates the intensity of heat/drought extreme events through changes in evapotranspiration and vertical energy fluxes, i.e., sensible, latent heat, and radiative energy fluxes (Miralles et al., 2019; Zhou et al., 2019). Since heat and drought amplification mechanisms depend on the type of ecosystem they affect, it is expected that the ecosystem itself can influence how the land-surface processes propagate (Teuling et al., 2017). Ecosystem imprints of this kind can also have remote effects. For instance, Schumacher et al. (2019) show that heatwaves can propagate in space through lateral heat transfer (see also Miralles et al., 2019). Furthermore, ecosystem imprints on atmospheric conditions change with the seasons. At higher latitudes, for example, snow-covered surfaces, might amplify the blocking conditions in winter high-pressure situations. Arctic warming may cause extreme cold air outbreaks in winter and thus influence the mid-latitudes. Given the biophysical imprint of ecosystems on atmospheric processes, management can be of crucial relevance for buffering extreme events.

However, the question we explore is whether there is evidence for biological function and feedback influencing climate extremes. Furthermore, considering the impact of biodiversity on biological functioning, can patterns of biodiversity be directly associated with climate extremes? Possible interaction paths of biodiversity and climate extremes are illustrated in Fig. 3. A key example is clouds, which are influenced by water in its three thermodynamic phases, energy fluxes, the concentration of biogenic volatile compounds (BVOCs), and aerosol particle fluxes mediated by vegetation characteristics (Duveiller et al., 2021), and, at the same time, exert an important and instantaneous climate-extreme buffering effect. In the presence of clouds, hot days remain cooler and, inversely, cold nights become warmer. Plant biodiversity stabilises ecosystem functioning (Musavi et al., 2017), and thus can be considered a key player in this interaction. A more direct effect of biodiversity on atmospheric processes than the control of latent heat is the emission of BVOCs, which impacts the tropospheric oxidising capacity, including substances such as ozone through chemical degradation processes and leads to biogenic particles of secondary origin (Riipinen et al., 2011; Lehtipalo et al., 2018; Riccobono et al., 2014; Luttkus et al., 2022). Additionally, primary biogenic particles such as pollen are also directly emitted, which can foster the heterogeneous freezing of super-cooled cloud droplets by acting as ice-nucleating particles at warmer temperatures than in their absence (O'Sullivan et al., 2018; Kretzschmar et al., 2023). Vegetation stress caused by heat and drought, which can result in biomass burning in the most severe cases, may lead to extremes both in atmospheric aerosol particle emissions and BVOC emissions (Grote et al., 2019). More biogenic particles of primary or secondary origin, are expected to trigger direct and indirect effects including an enhanced aerosol-radiation interaction, an increase of the fraction of diffuse to direct solar radiation, which in turn has a stimulating effect on vegetation productivity and to enhance the land carbon sink (Rap et al., 2015, 2018). Also, such aerosol particles could set off changes in cloud microphysical (droplet size, droplet concentration, and liquid water content) and optical (cloud albedo and transmissivity) properties and, consequently, local precipitation patterns (Niinemets, 2010; Jiang et al., 2018; Sporre et al., 2019). These examples suggest that vegetation plays an important role in the development of local atmospheric chemistry parameters that may strongly shape the development of extreme events. Considering that biodiversity influences veg-

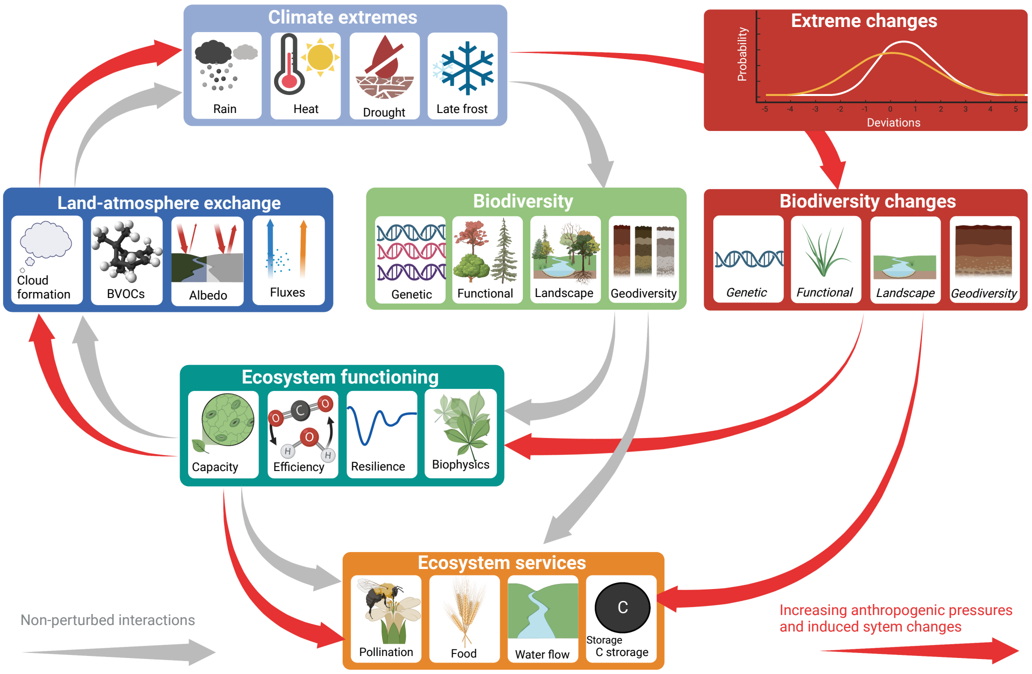


Figure 3. Illustration of the general role of biodiversity as a buffer to climate extremes. “Biodiversity” is understood here as a multifaceted term that embraces everything from genetic, via functional traits, to landscape scale heterogeneity, as it is currently the accepted idea in international frameworks (Pereira et al., 2013), and including “geodiversity” (Gray, 2011). All these dimensions of biodiversity constrain ecosystem functioning (Reichstein et al., 2014), effectively translating climate impulses into fluxes and signals that contribute to multiple feedback mechanisms with the atmosphere (Bonan, 2008). Alterations of biodiversity dimensions must therefore feedback to climate extremes (red arrows), which, considering the future intensification of extremes, have the potential to transform biodiversity itself. Ecosystem services are directly affected by biodiversity and ecosystem functions.

etation dynamics, it stands to reason that biodiversity should have a discernible impact on climate extremes.

A particularly intertwined set of processes links functional diversity and fire regimes (Wirth, 2005). However, in the wake of climate change, fires are also on the rise, which regionally is leading to increased burned area and fire return intervals (Jones et al., 2022). The record breaking 2019/20 fires in Australia were unprecedented in intensity and extent leading to enormous emissions of CO_2 and soot particles (van der Velde et al., 2021). Given that fire dynamics depends on vegetation properties, certain plant traits and the amount of available fuel are important controls of the intensity and development of fires, biodiversity has also an effect on the types of particles emitted. In a recent review, Jones et al. (2022) describe the complexity of the factors to consider when understanding wildfires. From this review and other studies, the important role of fires on particle injection into the atmosphere and the interaction of lightning and pyroconvenction become evident (Altaratz et al., 2010; Dowdy & Pepler, 2018). Processes of this kind are examples of how a biodiversity influences land-surface responses and mechanisms that ultimately affect the atmosphere.

In summary, ecosystem properties and processes can buffer the impacts of weather and climate-related extremes, with their effectiveness often depending on the state of their biodiversity. While it is recognised that biodiversity and land-surface dynamics may influence certain extreme events, the extent of this influence remains inadequately understood. The precise role of biodiversity and the overall magnitude of these effects, from local to global scales, have yet to be clearly quantified. Given the existing evidence of this inter-connectivity, we need to consider whether deliberately increasing functional diversity, through management or rewilding (Svenning et al., 2016) should be re-evaluated in light of its potential to dampen extreme events. Even if shifts in ecosystem characteristics and biodiversity do not significantly alter the frequency of climate extremes, there are multiple processes that have the potential to amplify or dampen a range of weather and climate-related extremes and their impacts. Managing ecosystems for improved drought resistance and resilience (Balch et al., 2020; Pörtner et al., 2021) could be instrumental in influencing land-atmosphere feedbacks. To harness this potential, we need a deeper understanding of these feedback mechanisms. The challenge is not necessarily a shortage of scientific hypotheses, but rather the integration of diverse scientific disciplines, their observational methodologies, and modelling approaches.

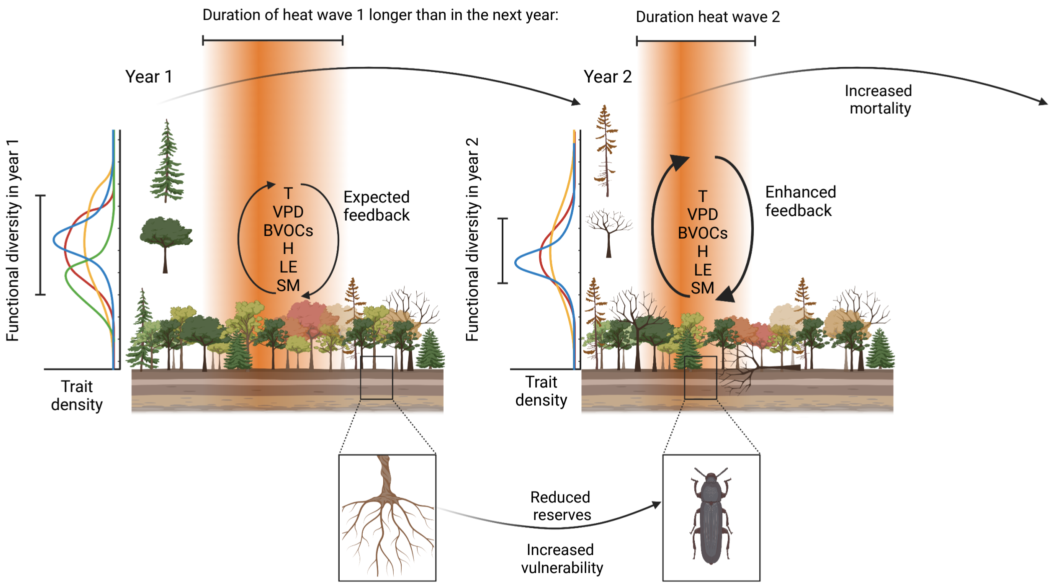


Figure 4. Uncommon temporal sequences and carryover effects. Two consecutive years with combined drought and heatwaves can have particularly strong impacts since species-specific defences can be reduced and lead to higher vulnerabilities to e.g. insects. Reduced chemical defences and generally depleted pools render vegetation more sensitive. The interplay of preconditioning and carryover effects amplifies the impacts of sequential extremes. Abbreviations are: T = temperature, VPD = vapour pressure deficit, BVOCs = biogenic volatile organic compounds, H = sensible heat, LE = latent heat, and SM = soil moisture (Figure created with BioRender.com).

4 Research gaps

Despite substantial progress in understanding the relationship between climate extremes and biodiversity change, there remain substantial scientific gaps that this section will elucidate. While there is a relatively solid understanding of how ecosystems buffer at least specific types of climate extremes, the quantification of biodiversity's impact on related atmospheric processes is less developed. The subsequent points emphasize areas that require further investigation:

- **Quantifying biodiversity buffers across event types:** For other than the well-studied cases of droughts and heatwaves, we have only weak evidence for the dampening or amplifying processes. This concerns mostly the rather small-scale events such as spring frost, heavy precipitation events, solar radiation- or ozone maxima.

These events have been studied less frequently and intensely, even if they are known to have locally important impacts. Radiation extremes, for instance, may evolve locally and regionally in response to specific synoptic situations, due to a lack of evaporation or in reaction to inhomogeneous cloud cover (van Heerwaarden et al., 2021; Fast et al., 2019). Impacts of weather extremes of this kind have been overlooked so far, but may be particularly sensitive to changes in biodiversity.

- **Considering all dimensions of biodiversity:** Genetic, taxonomic, and functional diversity shape buffers and feedback mechanisms in specific ways. How will the changes in these biodiversity dimensions affect the buffering capacity of ecosystems? We assume that the key dimension to consider here is functional diversity. Local features, such as canopy height represent a key buffer against thermal amplification of heat extremes (Lin et al., 2020). Variations in canopy surface height were found to reduce spatial variation in canopy temperatures (Guimarães-Steinicke et al., 2021). Functional diversity similarly controls the amplification/dampening of local climate extremes (Ratcliffe et al., 2016; Pardos et al., 2021), but so does landscape composition (Flach et al., 2021; Bastos, Fu, et al., 2020) and heterogeneity at larger scales (Oehri et al., 2020). What we miss is a global catalogue of how each of the biodiversity dimensions interact with the variety of climate extremes.
- **Embracing multiple spatial and temporal scales:** Just like biodiversity patterns, meteorological drivers are also scale-dependent. Research is needed to include all relevant scales, including micro-meteorological (metres to sub-km), synoptic (up to 1000 km), and hemispheric to global scales, which all appear to be relevant to the occurrence of extremes. Temporally, atmospheric variability ranges from the weather time scales (hours/days) to the interannual and multidecadal patterns of large-scale circulations. Completing our picture of biodiversity buffers and feedback mechanisms at different scales will require addressing feedbacks across spatial and temporal scales. Remote sensing of land surface and atmospheric properties offers the means for studies of this kind, and the first examples show how landscape heterogeneity influences ecosystem functioning across scales (Oehri et al., 2020). Scale-bridging exercises are important since ecosystems not only have characteristic resistances to weather- and climate-related extremes. They are also part of a dynamic pulse-response mechanism Harris et al. (2018) that controls nu-

merous processes at the land-atmosphere interface at different and interacting spatio-temporal scales (see Fig. 2), which need to be understood more deeply.

- **The critical role of time:** Another crucial aspect related to the impact of extremes is their timing. Ecosystems are composed of individual organisms, each following characteristic phenology and responses to environmental conditions. Functional traits vary over time, making the functional diversity of entire ecosystems time-dependent (Ma et al., 2020). In consequence, resistance and resilience at the ecosystem level are determined by an interplay of event-timing and a time-dependent buffering capacity. At longer time scales, an ecosystem's specific succession stage leads to different response trajectories (Johnstone et al., 2016). Besides timing, both duration (von Buttlar et al., 2018) and recurrence (Anderegg et al., 2020; Bastos et al., 2021) of extremes are decisive for an ecosystem's resistance and resilience (Frank et al., 2015; Sippel et al., 2018; Thonicke et al., 2020a). This means that any feedback mechanisms between biodiversity and climate extremes must also be time-dependent.
- **Preconditions are key determinants:** Pre-exposure critically determines how ecosystems' resistance and resilience interact with weather or climate-related extremes. Warm spring seasons combined with early water shortage may result in lower summer resistance to extremes (Flach et al., 2018; Sippel et al., 2018). Lower resistances diminish the buffer capacity of ecosystems, allowing impacts of extremes in subsequent seasons to be more readily amplified (see fig. 1). On longer time scales, increased disturbance regimes can further influence such feedbacks (Seidl et al., 2017; Forzieri et al., 2021). Recent work reveals the importance of memory effects in sequential hot drought years for tree growth and stress responses (Bastos, Ciais, et al., 2020; Schnabel et al., 2021). Figure 4 illustrates how an ecosystem's buffering capacity is weakened by an extreme event, such that consecutive droughts may lead to an even longer-lasting impact on vegetation dynamics and functions in following years. Research on lagged responses, such as the species-specific tree mortality caused by climate extremes, is still in its infancy (Sippel et al., 2018; Cailleret et al., 2019; Zscheischler et al., 2020). Understanding these complex impact chains requires scrutinising their drivers and modulating factors (Zscheischler et al., 2020; Kretschmer et al., 2021).

- **Understanding bidirectional effects:** Land-surface composition plays a crucial role in the development and propagation of certain extreme events. However, predicting how ecosystem's biodiversity shapes land-atmosphere interactions is not yet possible. Even less is known about the imprint of specific biodiversity features and processes that modulate these interactions and regulate extremes. Effects of this type are manifold and range from emission of biogenic aerosol particles acting as ice-nucleating particles required for heterogeneous ice formation in clouds (Jokinen et al., 2015), to carbon cycle effects (Reichstein et al., 2013), and large-scale land-surface-atmosphere interactions (Forzieri et al., 2020). In this context, it is important to recognise the indirect effects of biodiversity in stabilising plant communities and vegetation structure. If biodiversity helps prevent a biome shift from tropical forests to grasslands (see (Sakschewski et al., 2016)), this has major implications for the land-atmosphere feedback. Overall, we find that many research gaps prevent from accurately predicting how changing dimensions of biodiversity are affected and how they, in turn, modulate different types of atmospheric and climatic extremes.
- **From anticipation to sustainable management:** Climate change and the ongoing transformation of terrestrial ecosystems lead to unprecedented constellations of climate extremes and biodiversity. For instance, little is known about whether extremes that exceed historical records by large margins (Fischer et al., 2021) have disproportionately large effects on ecosystems, thus exceeding the adaptive capacities, or whether ecosystems are able to cushion the impact of such drastic extremes. While such events have been observed recently, the rarity of these events, their expected increase in the future, and the limitations of current models to represent the complex feedback between climate extremes and biodiversity across spatio-temporal scales expose another research gap. Currently, even the conceptual basis to address this gap has not yet been developed. It is unclear what level of process complexity and spatio-temporal scales need to be represented for robust projections and whether this is computationally feasible. As a consequence, the strength and even the sign of the feedback between biodiversity change and diverse types of climate extremes at different scales remain unknown. Management for climate adaptation and mitigation would require reliable predictive models that have only

started to represent certain aspects of functional diversity, which needs to be developed much further.

- **Socio-ecological dimensions and systemic risk:** Thinking ahead, we would argue that ultimately empirical and modelling research needs to develop more integrated approaches that consider biodiversity, multiple ecosystem services, and social-ecological dynamics together (Thonicke et al., 2020b) to fully address feedbacks leading to systemic risks of climate extremes (Reichstein et al., 2021). This approach requires collaboration between different disciplines, such as ecology, atmospheric sciences and climatology, psychology, and social sciences. The understanding of the interactions between climate extremes, biodiversity, ecosystem services, and socio-ecological systems can also inform policy and management strategies for reducing greenhouse gas emissions and mitigating the impacts of climate change without sacrificing other ecosystem services. For example, policies that prioritise the protection of critical ecosystems and biodiversity can enhance the resilience of ecosystems to climate extremes and support carbon sequestration, which can help mitigate the impacts of climate change in a no-regret strategy (Erb et al., 2022).

The overarching and unresolved question we identify here is: When do we expect dampening or amplifications due to interactions between biodiversity dynamics and climate extremes? Only by answering this question can we manage ecosystems to maximise their resistance and resilience to future climate conditions, in particular to more frequent extremes. More research is required to understand and quantify such feedback mechanisms and their spatial and temporal dependencies. Local-scale studies are particularly important to quantify changes in biodiversity-related drivers of the climate system. A pivotal issue that remains unresolved is how to quantify the imprints of local and small-scale biodiversity patterns on large-scale synoptic or global circulation patterns. An additional complication is how to identify the remote influence of biodiversity linked to atmospheric teleconnections.

5 Summary and Conclusions

The scientific gaps identified in this paper require a rethinking of current research priorities and the development of an ambitious interdisciplinary agenda. This strategic plan needs to explore the relationships between biodiversity and ecosystem dynamics in response to climate extremes, and as a mechanism in the evolution of climate extremes at multiple spatial scales and across large environmental gradients.

One cornerstone is observations. There is an urgent need for large-scale observational studies to establish causal relationships and their relevance at different spatial and temporal scales. In-situ and remote sensing observations that can simultaneously quantify multiple dimensions of taxonomic, structural, functional, and landscape diversity and composition need to be aligned with the monitoring of atmospheric thermodynamics and composition. There are fundamental advances in satellite-based Earth observations for both climate and ecosystem monitoring (Mahecha et al., 2020; Skidmore et al., 2021) that are increasingly integrated with in-situ observations of biodiversity (Dornelas et al., 2018), global observatories of ecosystem-atmosphere exchanges such as FLUXNET (Baldocchi, 2020), or specific processes such as tree mortality (Hartmann et al., 2018). Machine learning plays a key role in achieving this much-needed data integration (Bodesheim et al., 2022) and is increasingly empowered by deep learning (Reichstein et al., 2019).

Next to high-quality observations, we need powerful models. We must understand how terrestrial ecosystem dynamics feed back into atmospheric variability and how biodiversity modulates these relationships. For this aim, we need a new generation of predictive models that is capable of capturing the interactions between atmospheric processes, biodiversity patterns, and ecosystems. The models need to be able to adequately test hypotheses about feedback mechanisms. The development of functional digital twins of the climate system is now in reach, soon providing climate simulations at the kilometre scale (Bauer et al., 2021; Slingo et al., 2022), but high-resolution simulations alone are likely not enough to accurately reflect the coupling and feedbacks between climate and biodiversity. The digital twin concept for ecosystems is still in a more conceptual phase (Buonocore et al., 2022), as much research needs to be done for realistically representing biodiversity in land-surface models (Scheiter et al., 2013; Bendix et al., 2021). Today, a series of prototypes of a Digital Twin for biodiversity is currently being developed. Once developed, such models will allow to predict in detail what types of management interventions would increase ecosystem resistance and resilience to changing climate extremes.

Today, there is a growing awareness of the interconnections of biodiversity decline and climate change, as shown in a recent report jointly published by IPCC & IPBES (Pörtner et al., 2021; Pörtner et al., 2023) and in a series of policy tools. For instance, the new European Union (EU) Forest Strategy for 2030 and other high-level policy initiatives by the European Commission have recognised the value of the multi-functionality of forests, including their regulatory role in atmospheric processes. However, the observational and modelling bases are rather weak. Elsewhere, the lack of research on the feedback loop linking biodiversity change and climate extremes is also evident in policy, which sometimes pays too little attention to both aspects. One example is the consideration of climate extremes and biodiversity in the Common Agricultural Policy of the EU. The EU's subsidy policy has caused more than 70 percent of agricultural land to grow feed for livestock. This promotes monocultures, the cheap consumption of meat in the EU and harms not only the climate but also biodiversity. At the same time, there is a lack of scientific studies on the interactions between loss of biodiversity and climate extremes. By addressing these critical research gaps, we will significantly enhance our understanding of biodiversity buffers, thereby aiding efforts to preserve their capacity to mitigate climate extremes and safeguard ecosystem resilience.

Data avaialibility statement

This paper is based on a literature review; no original data have been used. All figures were generated based on conceptual considerations using the biorender.org software.

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Biodiversity and climate extremes: known interactions and research gaps

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Key Points:

- Mounting evidence suggests that an ecosystem's capacity to buffer the impacts of climate extremes depends on its biodiversity.
- Numerous mechanisms suggest that a reduction in biodiversity could exacerbate climate extremes.
- Understanding the full feedback loop linking biodiversity change and climate extremes requires an ambitious research agenda.

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Abstract

Climate extremes are on the rise. Impacts of extreme climate and weather events on ecosystem services and ultimately human well-being can be partially attenuated by the organismic, structural, and functional diversity of the affected land surface. However, the ongoing transformation of terrestrial ecosystems through intensified exploitation and management may put this buffering capacity at risk. Here, we summarise the evidence that reductions in biodiversity can destabilise the functioning of ecosystems facing climate extremes. We then explore if impaired ecosystem functioning could, in turn, exacerbate climate extremes. We argue that only a comprehensive approach, incorporating both ecological and hydrometeorological perspectives, enables to understand and predict the entire feedback system between altered biodiversity and climate extremes. This ambition, however, requires a reformulation of current research priorities to emphasise the bidirectional effects that link ecology and atmospheric processes.

Plain Language Summary

Climate extremes are increasing and impacting both nature and people. We hypothesise that intact ecosystems, particularly via their biodiversity, can mitigate the impacts of climate extremes. What happens when biodiversity decreases? Could this loss make the effects of climate extremes even worse or change how these events occur? We explore these two questions and summarise the current state of knowledge. We conclude that targeted research efforts at the interface of ecology and atmospheric sciences are needed to answer these questions conclusively.

1 Introduction

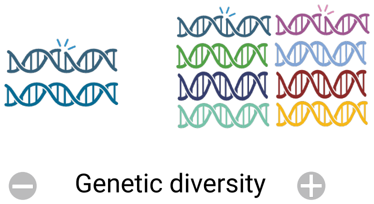
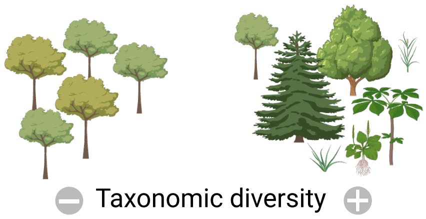
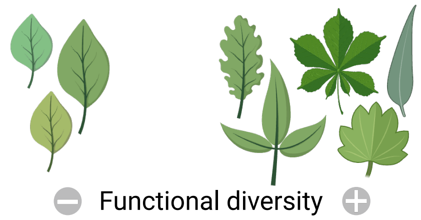
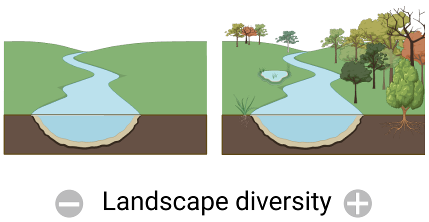
The transformation of terrestrial ecosystems due to land cover change, land management intensification, and environmental pollution, continues to accelerate globally. These interventions lead to a widespread decline in biodiversity and ecosystem functioning (Bellard et al., 2012; Díaz et al., 2019; IPBES, 2019; Jaureguiberry et al., 2022). At the same time, climate change progresses (IPCC, 2021). One effect is that weather and climate-related extremes, such as droughts, heat waves, storms, and heavy rainfall increase in frequency, intensity, and some also in spatial extent (Alexander et al., 2006; Seneviratne et al., 2012; S. Lange et al., 2020; Fowler et al., 2021). Today, such extreme events unprecedented in magnitude and duration occur around the world (Witze et al., 2022), such as the 2018-2020 multi-year drought over Europe (Rakovec et al., 2022). The intensification of extreme weather and climate events, with decreasing return periods and increased intensity, is one of the most critical consequences of anthropogenic climate change (IPCC, 2021; Fischer et al., 2021). But how will these two global mega-trends – biodiversity decline and the intensification of climate and weather extremes – affect each other? This scientifically challenging question has severe societal implications and needs to be addressed urgently in an integrative research approach.

Climate extremes can affect human well-being directly, e.g., via health impacts due to extreme heat (Ebi et al., 2021). However, a wide range of impacts is mediated by land-surface characteristics, in particular vegetation. During heat and drought events, increasing sensible heat fluxes can alter regional land-climate feedbacks and thereby intensify the extreme event (Miralles et al., 2019; Barriopedro et al., 2023). Recently, García-García et al. (in press) revealed that soil hot extremes can intensify faster than air temperature extremes, a phenomenon driven in part by the soil moisture–temperature feedback, which can further dry and warm the soil. Furthermore, heavy precipitation may turn (or not) into catastrophic flooding, erosion, and land-slide events depending on the regional water retention potential, the local storage capacity of soils and flow control of landscapes, and their geomorphological properties and vegetation structure (Brunner et al., 2021; Vári et al., 2022). Both examples demonstrate that terrestrial ecosystems and their vegetation characteristics play a crucial role in controlling the impacts of extreme climate events.

Yet, the modulation of impacts of extreme events not only depends on vegetation structure but also on the functioning of ecosystems (Reichstein et al., 2014; De Boeck et al., 2018; Thonicke et al., 2020a). It is important to note that ecosystem functioning is connected to various dimensions of 'biodiversity', a broad concept embracing (i) genetic diversity, (ii) taxonomic diversity, (iii) functional diversity, (iv) structural diversity within ecosystems, and (v) landscape heterogeneity, to name the most relevant ones for our research context (for an overview and definitions see Tab. 1). These dimensions of biodiversity are not independent from each other, and the role of biodiversity in ecosystems also depends on the available species (identity). Patterns of biodiversity partly reflect biogeographical history, spatial structures in geofactors ('geodiversity'), management, demographic history, or are an effect of internal disturbance dynamics (Bastos et al., 2023). It is widely recognised that losses in biodiversity can threaten the stability of ecosystems and thereby their ability to support human life (Mooney et al., 2009; Pörtner et al., 2021). The reason for this is that changing biodiversity affect characteristic functions of ecosystems (Musavi et al., 2015; Migliavacca et al., 2021), such as their potential to absorb pollutants, store carbon, or provide numerous natural resources. In the context of climate extremes, biodiversity is relevant because it controls how the land surface responds to atmospheric conditions. Modification of the bio(geo)physical and biogeochemical determinants of processes such as fluxes of gases, water, and energy, and the release and absorption of primary emitted particles (Fröhlich-Nowoisky et al., 2016), regulate land-surface climate feedbacks and can thereby affect local to global climate (Bonan, 2008; Santanello et al., 2018; Ukkola et al., 2018; Miralles et al., 2019).

Considering that ecosystems interact with atmospheric conditions, a crucial question arises (Mahecha et al., 2022): Is there a risk that changing biodiversity in ecosystems may not only weaken the resistance of ecosystems to climate extremes and their capacity to provide services, but also exacerbate atmospheric hazards? In other words, may biodiversity changes amplify the risk of weather and climate-related extremes? Pörtner et al. (2023) recently issued a general call for a comprehensive investigation into the intricate relationship between changes in the climate system and biodiversity. Here, we conduct an extensive review of pertinent literature to determine how far we can already give answers to the specific aspect of extremes. We first aim to understand whether higher levels of biodiversity buffer climate extremes (Section 2), and second, explore amplification processes of weather and climate extreme events dynamics in response to declining biodiversity (Section 3). Based on the conclusiveness of the literature on these aspects, we identify key research gaps that should be addressed to understand the full feedback between biodiversity change and climate extremes (Section 4).

Table 1. Biodiversity is 'the variability among living organisms from all sources, [. . .]: this includes diversity within species, between species and of ecosystems' (CBD, 1992). Here, we provide an overview of dimensions of biodiversity relevant to ecosystem responses to and feedback processes with the atmosphere

Dimension	Definition	Illustration
Genetic	Diversity of genetic properties within and across species. Also contains heritable changes in gene function not involving changes in DNA sequence (i.e., epigenetics).	
Taxonomic	Diversity of species, calculated e.g. as species richness or evenness per unit of investigation.	
Functional	Diversity of plant functional traits i.e. the morphological, anatomical, physiological, biochemical properties of plants and their organs.	
Structural	Vertical and horizontal arrangements of physical components of plants and their organs, such as leaf layers and branches.	
Landscape	Diversity and complexity of lateral arrangements of ecosystems within a landscape. Contributes to the overall biodiversity of a region by shaping habitats that support different ecosystems; synonym for 'landscape heterogeneity'.	

2 Biodiversity buffers against weather and climate extremes

Numerous studies investigate how climate extremes impact ecosystems. Two key concepts are frequently used: ecosystem "resistance", which is the capacity to withstand a climate extreme, and ecosystem "resilience", which characterises how fast and complete a system recovers following an extreme event (sensu Hoover et al., 2014; De Keersmaecker et al., 2016). Together, these concepts help to differentiate and quantify the ways in which ecosystems, as a function of their biodiversity, buffer the impact of extreme climatic events (for an illustration see Fig. 1).

Given the various dimensions of biodiversity outlined in Table 1, what specific knowledge do we have about their role in buffering extremes? In terms of taxonomic diversity, it appears that a few particular species often resist climate extremes, keeping up ecosystem functioning, or preventing community collapse under stress (De Laender et al., 2016; Werner et al., 2021). This phenomenon is classically known as "the insurance effect" (Yachi & Loreau, 1999; Loreau et al., 2021) and has been mostly inferred from experimental studies (Kayler et al., 2015; Loreau et al., 2021). For example, Isbell et al. (2015) show that grasslands with higher species diversity when exposed to exceptional dry or wet conditions have higher resistance, an effect attributed to the species-specific responses to particular stressors (Craven et al., 2018). Liu et al. (2022) reported that forest resistances against droughts increase with species richness. However, the insurance effect cannot be attributed to species-specific responses only. Variations in genetic properties of individuals within species can likewise lead to varying resistance to climate extremes. This was shown by Pfenninger et al. (2021), who analysed the susceptibility of individual beech trees to the extreme drought in central Europe in 2018, and illustrated the wide range of drought damages within a single species.

Intraspecific genetic diversity is one reason why taxonomic diversity alone is insufficient to explain ecosystem responses to extremes. Another reason is that, at the ecosystem level, responses to extremes are also largely regulated by a system's "functional diversity", defined by the variability of functional traits, such as leaf, stem, or root chemical properties and "structural diversity" (see Table 1). This explains why taxonomic diversity alone plays only a subordinate role in stabilising ecosystem functioning in many cases (Musavi et al., 2017). Mursinna et al. (2018) show that information on root trait diversity is needed to explain an ecosystem's drought sensitivity. Forest responses to droughts

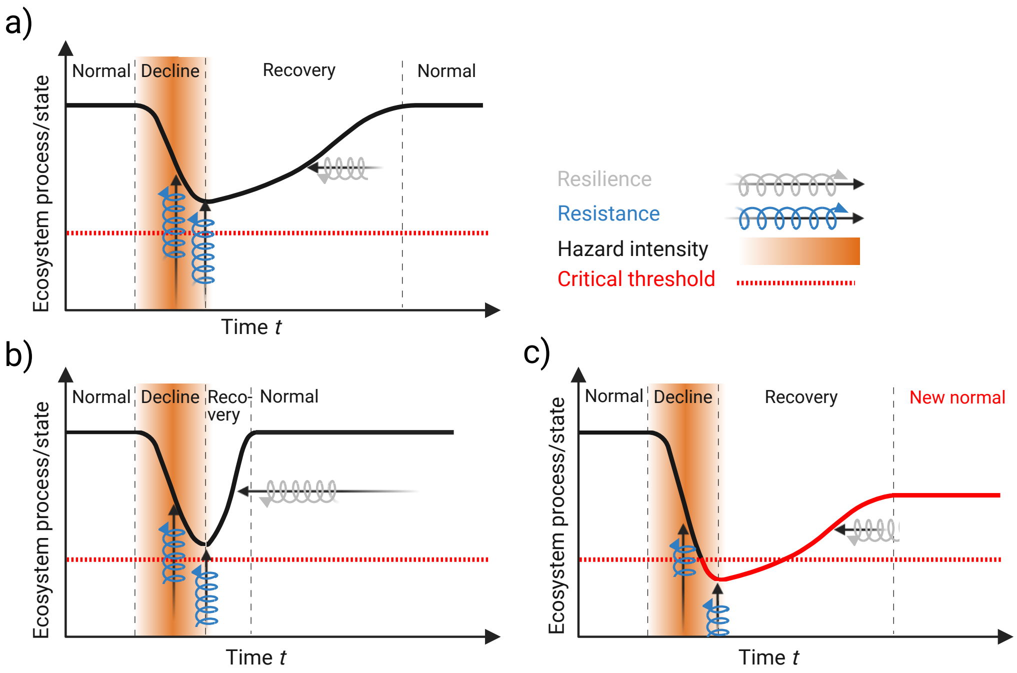


Figure 1. The ability of an ecosystem to resist or absorb changes in its states and functions over time is defined as 'resistance'. The capacity to recover to pre-event conditions is termed 'resilience'. Both resistance and resilience act over time, and jointly constitute the 'buffering capacity'. In this figure we exemplify systems with a) high resistance and low resilience, b) low resistance, and high resilience, and c) very low resilience such that the critical threshold is reached and no return to pre-event conditions can be achieved.

largely depend on the traits associated with isohydric versus anisohydric behaviour of trees (Hartmann et al., 2021; Lübbe et al., 2022). In general, the diversity of functional traits of organisms regulate how fluxes of energy, water, and nutrients are absorbed, stored and released given certain environmental conditions (Violle et al., 2007; Berendse et al., 2015; Anderegg et al., 2019). Even organisms coexisting in the same ecosystem (i.e. species that have passed an identical "environmental filter") exhibit a considerable degree of variation in their functional role, and therefore in their contribution to the resistance of ecosystem with respect to weather and climate-related extreme events (resistance Reyer et al., 2013; Felton & Smith, 2017), and their ability to recover from such events. Figure 2 illustrates conceptually how the insurance effect, mediated via functional diversity, could dampen the reduction of net primary production (NPP) and the increase in sensible heat flux during a heat wave in a more diverse forest, compared to a low-diversity forest.

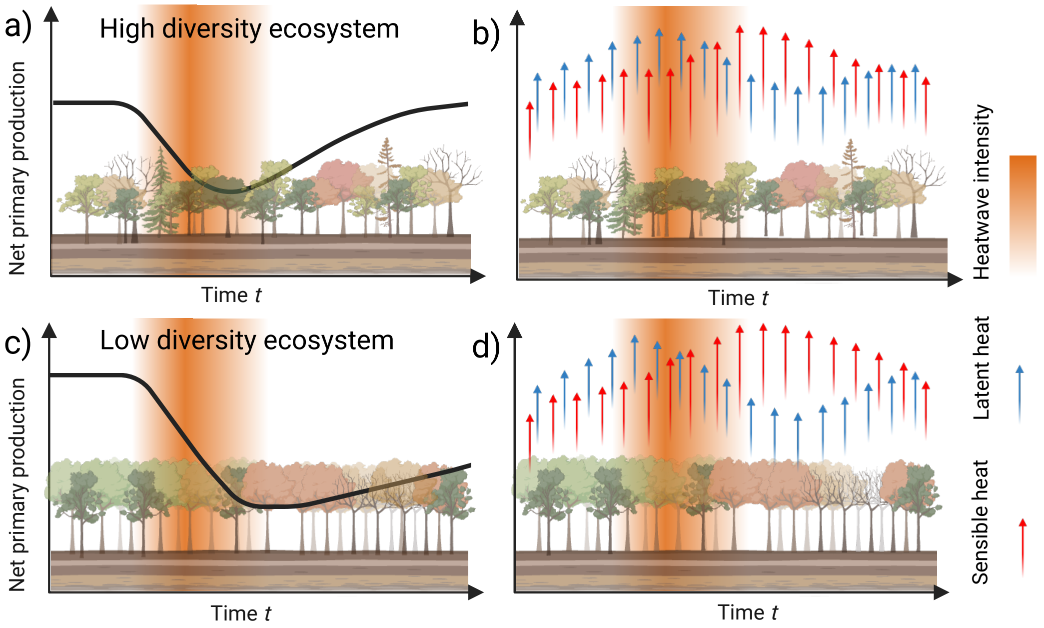
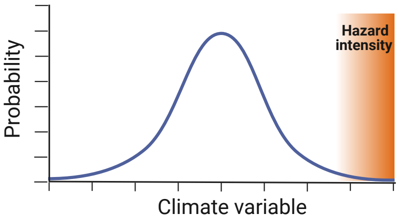
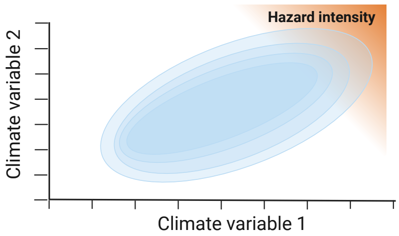
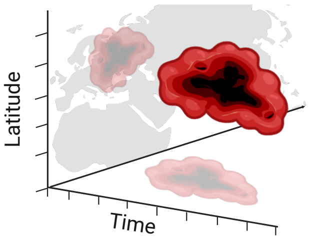
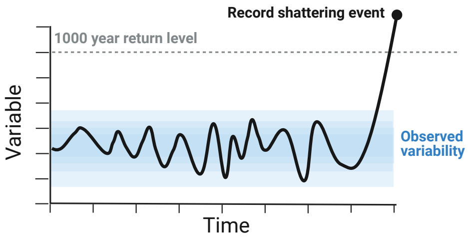


Figure 2. Illustration of the insurance effect: Hypothetical response of net primary production (NPP, net CO_2 uptake rate) to a heatwave (shown in reddish background colours) in a) a diverse forest, and c) a mono-culture. Analogous responses for energy fluxes are shown in b) and d). While low-diversity forests might initially have higher NPP, their low resistance might imply higher losses and reduced resilience given the lack of species compensation, i.e. a low insurance effect. The same effect can be observed for energy fluxes, where the ratios between latent and sensible heat fluxes change more drastically in low-diversity forests, with consequences for both ecosystems and atmospheric energy budgets.

Functional diversity is linked to structural heterogeneity at the stand level: mixtures of growth forms, plant sizes, and demographic stages appear to play an equally important role in the stabilisation of ecosystems. Guimarães-Steinicke et al. (2021) show the dominant effect of varying mixtures of herbs and grasses on the variability of vegetation surface temperatures. The meta-analysis by Craven et al. (2018) emphasises that functional biodiversity dimensions are determined by the asynchrony of abundances and thus affect the stability of ecosystem functioning. Taken together, in a changing climate with increasing occurrence of extreme weather and climate-related events, all dimensions of diversity may cause some degree of insurance against the shocks induced by climate extremes.

The buffering role of biodiversity is, however, a scale-dependent process. In general, translating insights from experiments and theory to large-scale and real-world settings proves difficult (Kreyling et al., 2008; Grossiord et al., 2019; Gonzalez et al., 2020). At the regional to continental scale, predominant and landscape heterogeneity will determine the predominant response mechanisms (Teuling et al., 2010; Flach et al., 2021; Bastos, Fu, et al., 2020). Remote sensing observations are key to overcoming scaling issues (Cavender-Bares et al., 2022), as it can monitor ecosystem responses, extreme weather and climate events from the ground, as well as from airborne- and space-borne platforms, covering local to global scales (Mahecha et al., 2017; Cavender-Bares et al., 2020; Peng et al., 2021). De Keersmaecker et al. (2016) study the resistance and resilience against drought across grasslands in central Europe using optical remote sensing observations. They conclude that nutrient-poor and species-rich grasslands appear to be more resistant, but less resilient against drought. The reverse seems to be true for fertilised, species-poor grasslands. These results are consistent with local experimental studies. The emerging and constantly growing body of global remote sensing data improves our capabilities of tracing biodiversity dynamics (Skidmore et al., 2021; Cavender-Bares et al., 2022), ecosystem management (M. Lange et al., 2022), and multiple land-surface processes (Mahecha et al., 2020). Combined, these data streams can be also used for quantifying how ecosystems buffer the impacts of climate extreme events, a task that should be prioritised.

Table 2. Extreme weather events are rare occurrences at a specific place and time, while climate extremes are persistent patterns of extreme weather (AR6 WG1 Ch. 11 IPCC, 2021). Four empirical descriptions of extremes are relevant: univariate, multivariate, spatiotemporal, and record-shattering. These categories describe the rarity, intensity, frequency, duration, and extent of events, including compound extremes and multiple meteorological drivers.

Extreme	Definition	Illustration
Univariate	Rarity of an event relative to a statistical probability distribution, either in terms of intensity, frequency, spatio-temporal extent, duration, in one variable of interest.	
Compound	Multivariate indices of extremes, also referred to as 'compound' extreme events, include unusual combinations of climate drivers.	
Spatio-temporal	Considering the spatio-temporal extent of an extreme event leads to additional metrics such as an event's duration, geographical coverage, volume, and integrated magnitde.	
Record shattering	Events that exceed previous observational records by multiple orders of magnitude, typically measured by return times, and improbable without climate change.	

3 Biodiversity imprints on atmospheric processes and extremes

Global circulation patterns determine which regions of the world are exposed to high aridity or high humidity, respectively, and during which seasons. Variations in atmospheric circulation also have a strong influence on extreme event occurrences (Coumou & Rahmstorf, 2012). For example, atmospheric blocking situations or recurrent atmospheric wave patterns lead to extended and persistent high-pressure systems or stationary lows, which may cause heatwaves or flooding that have severe consequences for ecosystem functioning (Desai et al., 2016; Flach et al., 2018; Kornhuber et al., 2019; Bastos, Ciais, et al., 2020). Blocking situations are particularly frequent over Europe, and also cause several other types of weather extremes (Kautz et al., 2022). Ongoing anthropogenic climate change is expected to further increase extreme weather around the globe and even the underlying circulation patterns are expected to change (Faranda et al., 2020). However, the extent to which such projected circulation changes are robust over Central Europe remains a matter of debate (Huguenin et al., 2020).

Although weather- and climate extreme events are primarily triggered by atmospheric processes, land-atmosphere interactions also contribute to their genesis and occurrence. Management and transformation of ecosystems, and consequently biodiversity, can change surface properties, including albedo and emissivity, roughness, evaporative resistance, and heat fluxes (Laguë et al., 2019). These interventions can substantially alter atmospheric humidity, transport dynamics, and, ultimately, cloud evolution and precipitation at regional and global scales (Avissar & Werth, 2005; Machado et al., 2018). It has also been shown that the surface albedo modulates the intensity of heat/drought extreme events through changes in evapotranspiration and vertical energy fluxes, i.e., sensible, latent heat, and radiative energy fluxes (Miralles et al., 2019; Zhou et al., 2019). Since heat and drought amplification mechanisms depend on the type of ecosystem they affect, it is expected that the ecosystem itself can influence how the land-surface processes propagate (Teuling et al., 2017). Ecosystem imprints of this kind can also have remote effects. For instance, Schumacher et al. (2019) show that heatwaves can propagate in space through lateral heat transfer (see also Miralles et al., 2019). Furthermore, ecosystem imprints on atmospheric conditions change with the seasons. At higher latitudes, for example, snow-covered surfaces, might amplify the blocking conditions in winter high-pressure situations. Arctic warming may cause extreme cold air outbreaks in winter and thus influence the mid-latitudes. Given the biophysical imprint of ecosystems on atmospheric processes, management can be of crucial relevance for buffering extreme events.

However, the question we explore is whether there is evidence for biological function and feedback influencing climate extremes. Furthermore, considering the impact of biodiversity on biological functioning, can patterns of biodiversity be directly associated with climate extremes? Possible interaction paths of biodiversity and climate extremes are illustrated in Fig. 3. A key example is clouds, which are influenced by water in its three thermodynamic phases, energy fluxes, the concentration of biogenic volatile compounds (BVOCs), and aerosol particle fluxes mediated by vegetation characteristics (Duveiller et al., 2021), and, at the same time, exert an important and instantaneous climate-extreme buffering effect. In the presence of clouds, hot days remain cooler and, inversely, cold nights become warmer. Plant biodiversity stabilises ecosystem functioning (Musavi et al., 2017), and thus can be considered a key player in this interaction. A more direct effect of biodiversity on atmospheric processes than the control of latent heat is the emission of BVOCs, which impacts the tropospheric oxidising capacity, including substances such as ozone through chemical degradation processes and leads to biogenic particles of secondary origin (Riipinen et al., 2011; Lehtipalo et al., 2018; Riccobono et al., 2014; Luttkus et al., 2022). Additionally, primary biogenic particles such as pollen are also directly emitted, which can foster the heterogeneous freezing of super-cooled cloud droplets by acting as ice-nucleating particles at warmer temperatures than in their absence (O'Sullivan et al., 2018; Kretzschmar et al., 2023). Vegetation stress caused by heat and drought, which can result in biomass burning in the most severe cases, may lead to extremes both in atmospheric aerosol particle emissions and BVOC emissions (Grote et al., 2019). More biogenic particles of primary or secondary origin, are expected to trigger direct and indirect effects including an enhanced aerosol-radiation interaction, an increase of the fraction of diffuse to direct solar radiation, which in turn has a stimulating effect on vegetation productivity and to enhance the land carbon sink (Rap et al., 2015, 2018). Also, such aerosol particles could set off changes in cloud microphysical (droplet size, droplet concentration, and liquid water content) and optical (cloud albedo and transmissivity) properties and, consequently, local precipitation patterns (Niinemets, 2010; Jiang et al., 2018; Sporre et al., 2019). These examples suggest that vegetation plays an important role in the development of local atmospheric chemistry parameters that may strongly shape the development of extreme events. Considering that biodiversity influences veg-

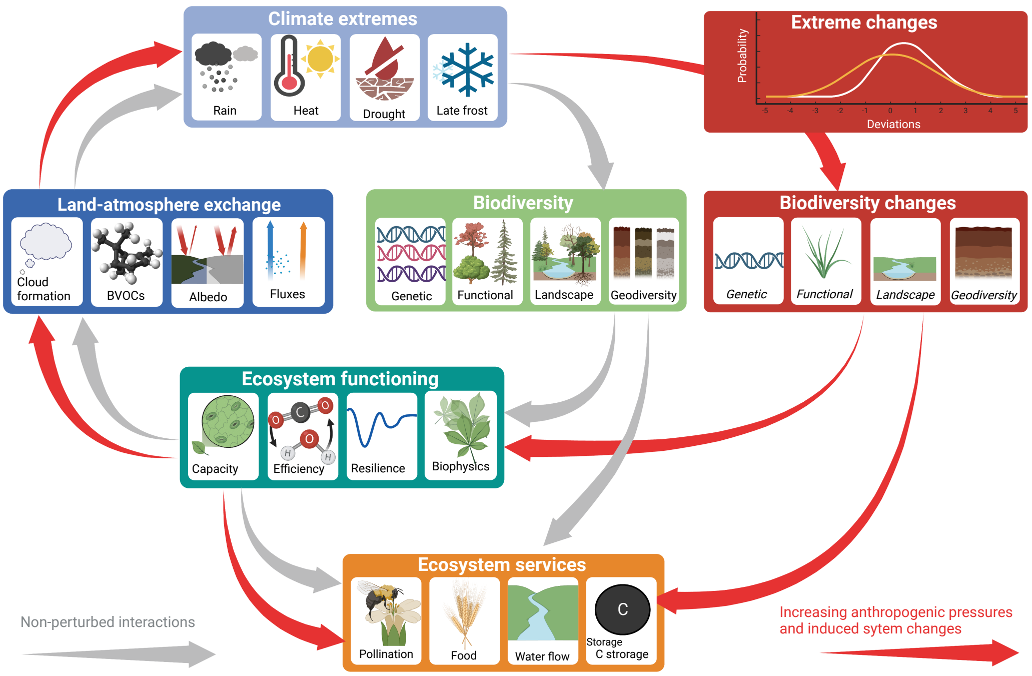


Figure 3. Illustration of the general role of biodiversity as a buffer to climate extremes. "Biodiversity" is understood here as a multifaceted term that embraces everything from genetic, via functional traits, to landscape scale heterogeneity, as it is currently the accepted idea in international frameworks (Pereira et al., 2013), and including "geodiversity" (Gray, 2011). All these dimensions of biodiversity constrain ecosystem functioning (Reichstein et al., 2014), effectively translating climate impulses into fluxes and signals that contribute to multiple feedback mechanisms with the atmosphere (Bonan, 2008). Alterations of biodiversity dimensions must therefore feedback to climate extremes (red arrows), which, considering the future intensification of extremes, have the potential to transform biodiversity itself. Ecosystem services are directly affected by biodiversity and ecosystem functions.

etation dynamics, it stands to reason that biodiversity should have a discernible impact on climate extremes.

A particularly intertwined set of processes links functional diversity and fire regimes (Wirth, 2005). However, in the wake of climate change, fires are also on the rise, which regionally is leading to increased burned area and fire return intervals (Jones et al., 2022). The record breaking 2019/20 fires in Australia were unprecedented in intensity and extent leading to enormous emissions of CO_2 and soot particles (van der Velde et al., 2021). Given that fire dynamics depends on vegetation properties, certain plant traits and the amount of available fuel are important controls of the intensity and development of fires, biodiversity has also an effect on the types of particles emitted. In a recent review, Jones et al. (2022) describe the complexity of the factors to consider when understanding wildfires. From this review and other studies, the important role of fires on particle injection into the atmosphere and the interaction of lightning and pyroconvenction become evident (Altaratz et al., 2010; Dowdy & Pepler, 2018). Processes of this kind are examples of how a biodiversity influences land-surface responses and mechanisms that ultimately affect the atmosphere.

In summary, ecosystem properties and processes can buffer the impacts of weather and climate-related extremes, with their effectiveness often depending on the state of their biodiversity. While it is recognised that biodiversity and land-surface dynamics may influence certain extreme events, the extent of this influence remains inadequately understood. The precise role of biodiversity and the overall magnitude of these effects, from local to global scales, have yet to be clearly quantified. Given the existing evidence of this inter-connectivity, we need to consider whether deliberately increasing functional diversity, through management or rewilding (Svenning et al., 2016) should be re-evaluated in light of its potential to dampen extreme events. Even if shifts in ecosystem characteristics and biodiversity do not significantly alter the frequency of climate extremes, there are multiple processes that have the potential to amplify or dampen a range of weather and climate-related extremes and their impacts. Managing ecosystems for improved drought resistance and resilience (Balch et al., 2020; Pörtner et al., 2021) could be instrumental in influencing land-atmosphere feedbacks. To harness this potential, we need a deeper understanding of these feedback mechanisms. The challenge is not necessarily a shortage of scientific hypotheses, but rather the integration of diverse scientific disciplines, their observational methodologies, and modelling approaches.

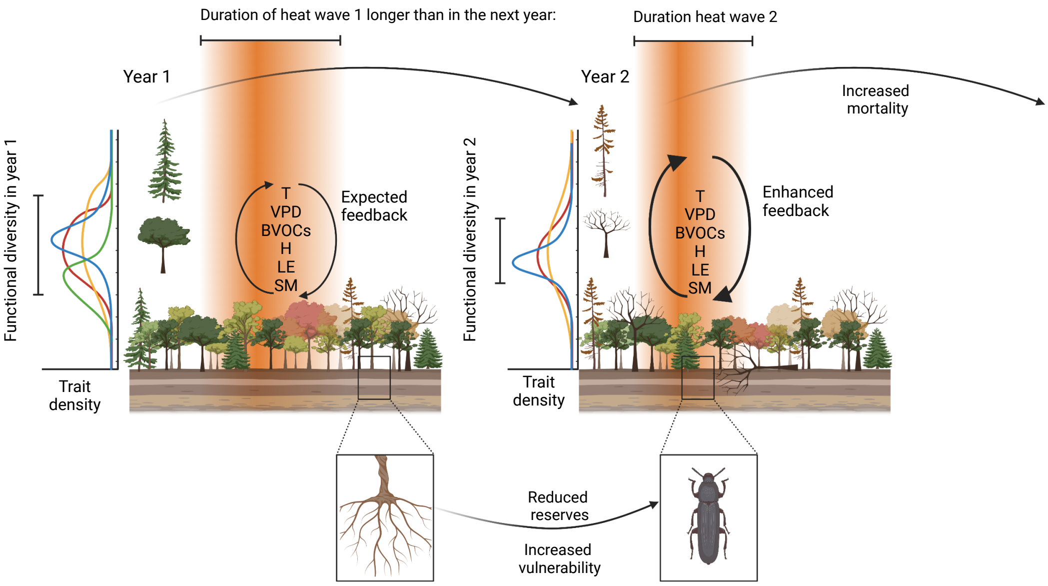


Figure 4. Uncommon temporal sequences and carryover effects. Two consecutive years with combined drought and heatwaves can have particularly strong impacts since species-specific defences can be reduced and lead to higher vulnerabilities to e.g. insects. Reduced chemical defences and generally depleted pools render vegetation more sensitive. The interplay of preconditioning and carryover effects amplifies the impacts of sequential extremes. Abbreviations are: T = temperature, VPD = vapour pressure deficit, BVOCs = biogenic volatile organic compounds, H = sensible heat, LE = latent heat, and SM = soil moisture (Figure created with BioRender.com).

4 Research gaps

Despite substantial progress in understanding the relationship between climate extremes and biodiversity change, there remain substantial scientific gaps that this section will elucidate. While there is a relatively solid understanding of how ecosystems buffer at least specific types of climate extremes, the quantification of biodiversity's impact on related atmospheric processes is less developed. The subsequent points emphasize areas that require further investigation:

- **Quantifying biodiversity buffers across event types:** For other than the well-studied cases of droughts and heatwaves, we have only weak evidence for the dampening or amplifying processes. This concerns mostly the rather small-scale events such as spring frost, heavy precipitation events, solar radiation- or ozone maxima.

These events have been studied less frequently and intensely, even if they are known to have locally important impacts. Radiation extremes, for instance, may evolve locally and regionally in response to specific synoptic situations, due to a lack of evaporation or in reaction to inhomogeneous cloud cover (van Heerwaarden et al., 2021; Fast et al., 2019). Impacts of weather extremes of this kind have been overlooked so far, but may be particularly sensitive to changes in biodiversity.

- **Considering all dimensions of biodiversity:** Genetic, taxonomic, and functional diversity shape buffers and feedback mechanisms in specific ways. How will the changes in these biodiversity dimensions affect the buffering capacity of ecosystems? We assume that the key dimension to consider here is functional diversity. Local features, such as canopy height represent a key buffer against thermal amplification of heat extremes (Lin et al., 2020). Variations in canopy surface height were found to reduce spatial variation in canopy temperatures (Guimarães-Steinicke et al., 2021). Functional diversity similarly controls the amplification/dampening of local climate extremes (Ratcliffe et al., 2016; Pardos et al., 2021), but so does landscape composition (Flach et al., 2021; Bastos, Fu, et al., 2020) and heterogeneity at larger scales (Oehri et al., 2020). What we miss is a global catalogue of how each of the biodiversity dimensions interact with the variety of climate extremes.
- **Embracing multiple spatial and temporal scales:** Just like biodiversity patterns, meteorological drivers are also scale-dependent. Research is needed to include all relevant scales, including micro-meteorological (metres to sub-km), synoptic (up to 1000 km), and hemispheric to global scales, which all appear to be relevant to the occurrence of extremes. Temporally, atmospheric variability ranges from the weather time scales (hours/days) to the interannual and multidecadal patterns of large-scale circulations. Completing our picture of biodiversity buffers and feedback mechanisms at different scales will require addressing feedbacks across spatial and temporal scales. Remote sensing of land surface and atmospheric properties offers the means for studies of this kind, and the first examples show how landscape heterogeneity influences ecosystem functioning across scales (Oehri et al., 2020). Scale-bridging exercises are important since ecosystems not only have characteristic resistances to weather- and climate-related extremes. They are also part of a dynamic pulse-response mechanism Harris et al. (2018) that controls nu-

merous processes at the land-atmosphere interface at different and interacting spatio-temporal scales (see Fig. 2), which need to be understood more deeply.

- **The critical role of time:** Another crucial aspect related to the impact of extremes is their timing. Ecosystems are composed of individual organisms, each following characteristic phenology and responses to environmental conditions. Functional traits vary over time, making the functional diversity of entire ecosystems time-dependent (Ma et al., 2020). In consequence, resistance and resilience at the ecosystem level are determined by an interplay of event-timing and a time-dependent buffering capacity. At longer time scales, an ecosystem's specific succession stage leads to different response trajectories (Johnstone et al., 2016). Besides timing, both duration (von Buttlar et al., 2018) and recurrence (Anderegg et al., 2020; Bastos et al., 2021) of extremes are decisive for an ecosystem's resistance and resilience (Frank et al., 2015; Sippel et al., 2018; Thonicke et al., 2020a). This means that any feedback mechanisms between biodiversity and climate extremes must also be time-dependent.
- **Preconditions are key determinants:** Pre-exposure critically determines how ecosystems' resistance and resilience interact with weather or climate-related extremes. Warm spring seasons combined with early water shortage may result in lower summer resistance to extremes (Flach et al., 2018; Sippel et al., 2018). Lower resistances diminish the buffer capacity of ecosystems, allowing impacts of extremes in subsequent seasons to be more readily amplified (see fig. 1). On longer time scales, increased disturbance regimes can further influence such feedbacks (Seidl et al., 2017; Forzieri et al., 2021). Recent work reveals the importance of memory effects in sequential hot drought years for tree growth and stress responses (Bastos, Ciais, et al., 2020; Schnabel et al., 2021). Figure 4 illustrates how an ecosystem's buffering capacity is weakened by an extreme event, such that consecutive droughts may lead to an even longer-lasting impact on vegetation dynamics and functions in following years. Research on lagged responses, such as the species-specific tree mortality caused by climate extremes, is still in its infancy (Sippel et al., 2018; Cailleret et al., 2019; Zscheischler et al., 2020). Understanding these complex impact chains requires scrutinising their drivers and modulating factors (Zscheischler et al., 2020; Kretschmer et al., 2021).

- **Understanding bidirectional effects:** Land-surface composition plays a crucial role in the development and propagation of certain extreme events. However, predicting how ecosystem's biodiversity shapes land-atmosphere interactions is not yet possible. Even less is known about the imprint of specific biodiversity features and processes that modulate these interactions and regulate extremes. Effects of this type are manifold and range from emission of biogenic aerosol particles acting as ice-nucleating particles required for heterogeneous ice formation in clouds (Jokinen et al., 2015), to carbon cycle effects (Reichstein et al., 2013), and large-scale land-surface-atmosphere interactions (Forzieri et al., 2020). In this context, it is important to recognise the indirect effects of biodiversity in stabilising plant communities and vegetation structure. If biodiversity helps prevent a biome shift from tropical forests to grasslands (see (Sakschewski et al., 2016)), this has major implications for the land-atmosphere feedback. Overall, we find that many research gaps prevent from accurately predicting how changing dimensions of biodiversity are affected and how they, in turn, modulate different types of atmospheric and climatic extremes.
- **From anticipation to sustainable management:** Climate change and the ongoing transformation of terrestrial ecosystems lead to unprecedented constellations of climate extremes and biodiversity. For instance, little is known about whether extremes that exceed historical records by large margins (Fischer et al., 2021) have disproportionately large effects on ecosystems, thus exceeding the adaptive capacities, or whether ecosystems are able to cushion the impact of such drastic extremes. While such events have been observed recently, the rarity of these events, their expected increase in the future, and the limitations of current models to represent the complex feedback between climate extremes and biodiversity across spatio-temporal scales expose another research gap. Currently, even the conceptual basis to address this gap has not yet been developed. It is unclear what level of process complexity and spatio-temporal scales need to be represented for robust projections and whether this is computationally feasible. As a consequence, the strength and even the sign of the feedback between biodiversity change and diverse types of climate extremes at different scales remain unknown. Management for climate adaptation and mitigation would require reliable predictive models that have only

started to represent certain aspects of functional diversity, which needs to be developed much further.

- **Socio-ecological dimensions and systemic risk:** Thinking ahead, we would argue that ultimately empirical and modelling research needs to develop more integrated approaches that consider biodiversity, multiple ecosystem services, and social-ecological dynamics together (Thonicke et al., 2020b) to fully address feedbacks leading to systemic risks of climate extremes (Reichstein et al., 2021). This approach requires collaboration between different disciplines, such as ecology, atmospheric sciences and climatology, psychology, and social sciences. The understanding of the interactions between climate extremes, biodiversity, ecosystem services, and socio-ecological systems can also inform policy and management strategies for reducing greenhouse gas emissions and mitigating the impacts of climate change without sacrificing other ecosystem services. For example, policies that prioritise the protection of critical ecosystems and biodiversity can enhance the resilience of ecosystems to climate extremes and support carbon sequestration, which can help mitigate the impacts of climate change in a no-regret strategy (Erb et al., 2022).

The overarching and unresolved question we identify here is: When do we expect dampening or amplifications due to interactions between biodiversity dynamics and climate extremes? Only by answering this question can we manage ecosystems to maximise their resistance and resilience to future climate conditions, in particular to more frequent extremes. More research is required to understand and quantify such feedback mechanisms and their spatial and temporal dependencies. Local-scale studies are particularly important to quantify changes in biodiversity-related drivers of the climate system. A pivotal issue that remains unresolved is how to quantify the imprints of local and small-scale biodiversity patterns on large-scale synoptic or global circulation patterns. An additional complication is how to identify the remote influence of biodiversity linked to atmospheric teleconnections.

5 Summary and Conclusions

The scientific gaps identified in this paper require a rethinking of current research priorities and the development of an ambitious interdisciplinary agenda. This strategic plan needs to explore the relationships between biodiversity and ecosystem dynamics in response to climate extremes, and as a mechanism in the evolution of climate extremes at multiple spatial scales and across large environmental gradients.

One cornerstone is observations. There is an urgent need for large-scale observational studies to establish causal relationships and their relevance at different spatial and temporal scales. In-situ and remote sensing observations that can simultaneously quantify multiple dimensions of taxonomic, structural, functional, and landscape diversity and composition need to be aligned with the monitoring of atmospheric thermodynamics and composition. There are fundamental advances in satellite-based Earth observations for both climate and ecosystem monitoring (Mahecha et al., 2020; Skidmore et al., 2021) that are increasingly integrated with in-situ observations of biodiversity (Dornelas et al., 2018), global observatories of ecosystem-atmosphere exchanges such as FLUXNET (Baldocchi, 2020), or specific processes such as tree mortality (Hartmann et al., 2018). Machine learning plays a key role in achieving this much-needed data integration (Bodesheim et al., 2022) and is increasingly empowered by deep learning (Reichstein et al., 2019).

Next to high-quality observations, we need powerful models. We must understand how terrestrial ecosystem dynamics feed back into atmospheric variability and how biodiversity modulates these relationships. For this aim, we need a new generation of predictive models that is capable of capturing the interactions between atmospheric processes, biodiversity patterns, and ecosystems. The models need to be able to adequately test hypotheses about feedback mechanisms. The development of functional digital twins of the climate system is now in reach, soon providing climate simulations at the kilometre scale (Bauer et al., 2021; Slingo et al., 2022), but high-resolution simulations alone are likely not enough to accurately reflect the coupling and feedbacks between climate and biodiversity. The digital twin concept for ecosystems is still in a more conceptual phase (Buonocore et al., 2022), as much research needs to be done for realistically representing biodiversity in land-surface models (Scheiter et al., 2013; Bendix et al., 2021). Today, a series of prototypes of a Digital Twin for biodiversity is currently being developed. Once developed, such models will allow to predict in detail what types of management interventions would increase ecosystem resistance and resilience to changing climate extremes.

Today, there is a growing awareness of the interconnections of biodiversity decline and climate change, as shown in a recent report jointly published by IPCC & IPBES (Pörtner et al., 2021; Pörtner et al., 2023) and in a series of policy tools. For instance, the new European Union (EU) Forest Strategy for 2030 and other high-level policy initiatives by the European Commission have recognised the value of the multi-functionality of forests, including their regulatory role in atmospheric processes. However, the observational and modelling bases are rather weak. Elsewhere, the lack of research on the feedback loop linking biodiversity change and climate extremes is also evident in policy, which sometimes pays too little attention to both aspects. One example is the consideration of climate extremes and biodiversity in the Common Agricultural Policy of the EU. The EU's subsidy policy has caused more than 70 percent of agricultural land to grow feed for livestock. This promotes monocultures, the cheap consumption of meat in the EU and harms not only the climate but also biodiversity. At the same time, there is a lack of scientific studies on the interactions between loss of biodiversity and climate extremes. By addressing these critical research gaps, we will significantly enhance our understanding of biodiversity buffers, thereby aiding efforts to preserve their capacity to mitigate climate extremes and safeguard ecosystem resilience.

Data avaialibility statement

This paper is based on a literature review; no original data have been used. All figures were generated based on conceptual considerations using the biorender.org software.

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