Earth's Future

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
- A series of research gaps need to be addressed to understand the full feedback between biodiversity change and climate extremes

Correspondence to:

M. D. Mahecha,
miguel.mahecha@uni-leipzig.de

Biodiversity and Climate Extremes: Known Interactions and Research Gaps

M. D. Mahecha[1,2] , A. Bastos[1,2,3] , F. J. Bohn[4] , N. Eisenhauer[2,5] , H. Feilhauer[1,2] , T. Hickler[6,7] , H. Kalesse-Los[8] , M. Migliavacca[9] , F. E. L. Otto[10] , J. Peng[1,4] , S. Sippel[8] , I. Tegen[8,11] , A. Weigelt[2,5] , M. Wendisch[8] , C. Wirth[2,5] , D. Al-Halbouni[1] , H. Deneke[11] , D. Doktor[2,4] , S. Dunker[2,4] , G. Duveiller[3] , A. Ehrlich[8] , A. Foth[8] , A. García-García[4] , C. A. Guerra[3,5] , C. Guimarães-Steinicke[1] , H. Hartmann[3,12,13] , S. Henning[11] , H. Herrmann[11] , P. Hu[3] , C. Ji[1] , T. Kattenborn[1] , N. Kolleck[14] , M. Kretschmer[8,15] , I. Kühn[2,4,16] , M. L. Luttkus[11] , M. Maahn[8] , M. Mönks[1] , K. Mora[1] , M. Pöhlker[8,11] , M. Reichstein[2,3] , N. Rüger[4,17,18] , B. Sánchez-Parra[2,5] , M. Schäfer[8] , F. Stratmann[11] , M. Tesche[8] , B. Wehner[11] , S. Wieneke[1,2] , A. J. Winkler[3] , S. Wolf[1] , S. Zaehle[2,3] , J. Zscheischler[4,19] , and J. Quaas[2,8]

[1]Institute for Earth System Science and Remote Sensing, Leipzig University, Leipzig, Germany, [2]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany, [3]Max Planck Institute for Biogeochemistry, Jena, Germany, [4]Helmholtz Centre for Environmental Research – UFZ, Leipzig-Halle, Germany, [5]Institute of Biology, Leipzig University, Leipzig, Germany, [6]Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany, [7]Department of Physical Geography, Goethe University Frankfurt, Frankfurt am Main, Germany, [8]Leipzig Institute for Meteorology, Leipzig University, Leipzig, Germany, [9]European Commission, Joint Research Centre, Ispra, Italy, [10]Imperial College London, Grantham Institute for Climate Change and the Environment, London, UK, [11]Leibniz Institute for Tropospheric Research (TROPOS), Leipzig, Germany, [12]Federal Research Centre for Cultivated Plants, Institute for Forest Protection, Julius Kühn-Institute, Quedlinburg, Germany, [13]Faculty of Forest Sciences and Forest Ecology, Georg-August-Universität Göttingen, Göttingen, Germany, [14]Education and Socialization Theory, University of Potsdam, Potsdam, Germany, [15]Department of Meteorology, University of Reading, Reading, UK, [16]Department of Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany, [17]Department of Economics, Leipzig University, Leipzig, Germany, [18]Smithsonian Tropical Research Institute, Balboa, Panama, [19]Technische Universität Dresden, Dresden, Germany

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 summarize the evidence that reductions in biodiversity can destabilize 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 us 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 emphasize the bidirectional effects that link ecology and atmospheric processes.

Plain Language Summary Climate extremes are increasing and impacting both nature and people. We hypothesize 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 summarize 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). Increases in the intensity, frequency and duration of extreme weather and climate events such as droughts, heatwaves, and heavy rainfall, are some of the

S. Sippel, I. Tegen, A. Weigelt,
M. Wendisch, C. Wirth, S. Wolf, J. Quaas
Writing – review & editing:
M. D. Mahecha, A. Bastos, F. J. Bohn,
N. Eisenhauer, H. Feilhauer, T. Hickler,
H. Kalesse-Los, M. Migliavacca,
F. E. L. Otto, J. Peng, S. Sippel, I. Tegen,
A. Weigelt, M. Wendisch, C. Wirth, D. Al-
Halbouni, H. Deneke, D. Doktor,
S. Dunker, G. Duveiller, A. Ehrlich,
A. Foth, A. García-García, C. A. Guerra,
C. Guimarães-Steinicke, H. Hartmann,
S. Henning, H. Herrmann, P. Hu, C. Ji,
T. Kattenborn, N. Kolleck, M. Kretschmer,
I. Kühn, M. L. Luttkus, M. Maahn,
M. Mönks, K. Mora, M. Pöhlker,
M. Reichstein, N. Rüger, B. Sánchez-
Parra, M. Schäfer, F. Stratmann,
M. Tesche, B. Wehner, S. Wieneke,
A. J. Winkler, S. Wolf, S. Zaehle,
J. Zscheischler, J. Quaas

most critical consequences of anthropogenic climate change (Seneviratne et al., 2021). Today, extreme events such as the 2018–2020 multi-year drought in central Europe (Rakovec et al., 2022), the 2022 compound drought-heatwave in most of Europe (van der Woude et al., 2023) and the record shattering 2023 spring heatwave in the western Mediterranean (Lemus-Canovas et al., 2024) are becoming more and more common. Such extreme events impact multiple ecosystem functions and ecological dynamics (Frank et al., 2015; Mahecha et al., 2017; Reichstein et al., 2013), and have the potential to disrupt ecosystem stability (Anderegg et al., 2020; Bastos et al., 2023; Seidl & Turner, 2022). 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 (Mahecha et al., 2022).

Extreme weather and climate events are rare events that happen at a specific place and time. For a long time, extreme events have mostly been studied from a univariate perspective. More recently, research on compound events (Zscheischler et al., 2018), the spatio-temporal evolution of extremes (Flach et al., 2018; Zscheischler et al., 2013), and record-shattering extremes (Fischer et al., 2021; Fowler et al., 2024) have gained considerable interest in the research community, mostly because of the relevance of these aspects for impacts (see Figure 1 for an overview of these terms). Variations in atmospheric circulation strongly influence 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 (Bastos, Ciais, et al., 2020; Desai et al., 2016; Flach et al., 2018; Kornhuber et al., 2019). Ongoing anthropogenic climate change is expected to increase extreme weather around the globe further, 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 remains a matter of debate (Huguenin et al., 2020).

To understand the necessity of integrating climate extremes and biodiversity, we initially consider two specific examples. The first involves heavy precipitation events, which can lead to catastrophic outcomes such as flooding, erosion, and landslides, dependent on the water retention capacity of catchments and their geomorphological characteristics (Brunner et al., 2021; Saco et al., 2021; Vári et al., 2022). In these scenarios, the importance of biodiversity is evident as the structure of vegetation, both above and below ground, plays a crucial role in controlling water flows and overall hydrological dynamics. However, the extent to which extreme events impact ecosystems is influenced not only by the type and structure of vegetation but also by its functioning. This can be seen when considering the implications of compounded heat and drought events. Here, reduced moisture availability disrupts the land-surface energy balance, enhancing sensible heat fluxes leading to further increases in air temperatures. This process results in a higher evaporative demand, intensifying the heat/drought episode through what is known as the soil moisture–temperature feedback loop. The variety in plants' physiological responses becomes critical in moderating the severity of this feedback, thereby directly impacting human activities, especially agricultural productivity (Barriopedro et al., 2023; Beugnon et al., 2024; Graf et al., 2020; Miralles et al., 2019).

Ecosystem functioning, particularly under extreme conditions, emerges from the complex interplay among various dimensions of "biodiversity" (De Boeck et al., 2018; Reichstein et al., 2014; Thonicke et al., 2020). These dimensions include (a) genetic diversity, (b) taxonomic diversity, (c) functional diversity, (d) structural diversity within ecosystems, and (e) landscape diversity or heterogeneity (see Figure 2 for an overview and definitions). Typically these dimensions of biodiversity are not independent of each other. Additionally, the specific species present ("plant identities') play a critical role in ecosystem processes. As exemplified above, the imprint of biodiversity on ecosystem functioning is generally relevant because it controls how the land surface responds to atmospheric conditions. Biodiversity controls how ecosystems absorb pollutants, store carbon, or provide numerous natural resources. The regulation of water, gas, and energy fluxes, and the release and absorption of primary emitted particles (Fröhlich-Nowoisky et al., 2016; Sanaei et al., 2023) by functional and structural diversity and landscape heterogeneity, contributes to the regulation of land-surface climate feedbacks and can thereby affect local to global climate (Beugnon et al., 2024; Bonan, 2008; Duveiller et al., 2021; Graf et al., 2020; Miralles et al., 2019; Santanello et al., 2018; Ukkola et al., 2018).

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, but also exacerbate atmospheric hazards? In other words, may biodiversity
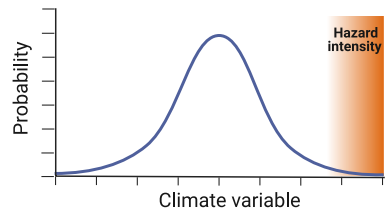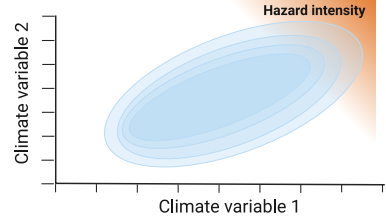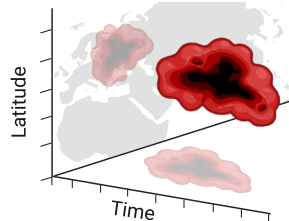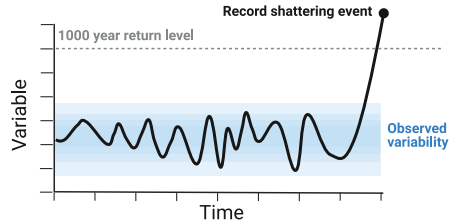
Extreme	Definition	Illustration
Univariate	Rarity of an event relative to a statistical probability distribution, either in terms of intensity, frequency, spatio-temporal extent, duration, in one variable of interest.	
Compound	Multivariate indices of extremes, also referred to as 'compound' extreme 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 magnitude.	
Record-shattering	An event that exceeds previous observed records by a certain margin, typically measured in terms of intensity or the record margin (i.e., exceedance of the previous record), and often improbable without climate change.	

Figure 1. 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). We consider four relevant empirical descriptions of extremes: univariate, multivariate, spatiotemporal, and record-shattering. These categories describe the intensity, frequency, duration, and extent of events, including compound extremes and multiple meteorological drivers.

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 the impact of climate extremes (Section 2), and second, explore amplification processes of weather and climate extreme events dynamics in response to 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).
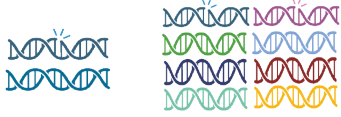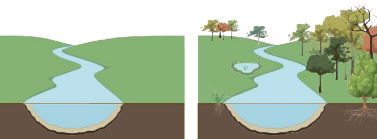
Dimension	Definition	Illustration
Genetic	Diversity of genetic properties within and across species. Also contains heritable changes in gene function not involving changes in DNA sequence (i.e., epigenetics).	Genetic diversity
Taxonomic	Diversity of species, measured typically as species richness per unit of investigation e.g.in manipulative experiments. In field-based surveys as species richness weighed by relative species abundances. Effects of species interactions are likewise considered	Taxonomic diversity
Functional	"The degree to which species vary in their functional traits" (Weiher et al., 2011). These functional traits include, for example, leaf, stem, and root traits in plants that are analysed in the context of studies relating biodiversity to ecosystem processes.	Functional diversity
Structural	The three-dimensional structural complexity of plant communities including, for example, diversity of plant height, diameter, density, or vertical distribution (Staudhammer & LeMay, 2001).	Structural diversity
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.	Landscape diversity

Figure 2. In the seminal definition of the Convention on Biological Diversity (CBD, 1992), biodiversity is "the variability among living organisms from all sources, […]. This includes diversity within species, between species and of ecosystems," pointing to its many facets and scales, which must be distinguished when addressing biophysical and biogeochemical processes (Noss, 1990). The facets in our focus are listed here (Staudhammer & LeMay, 2001; Weiher et al., 2011).

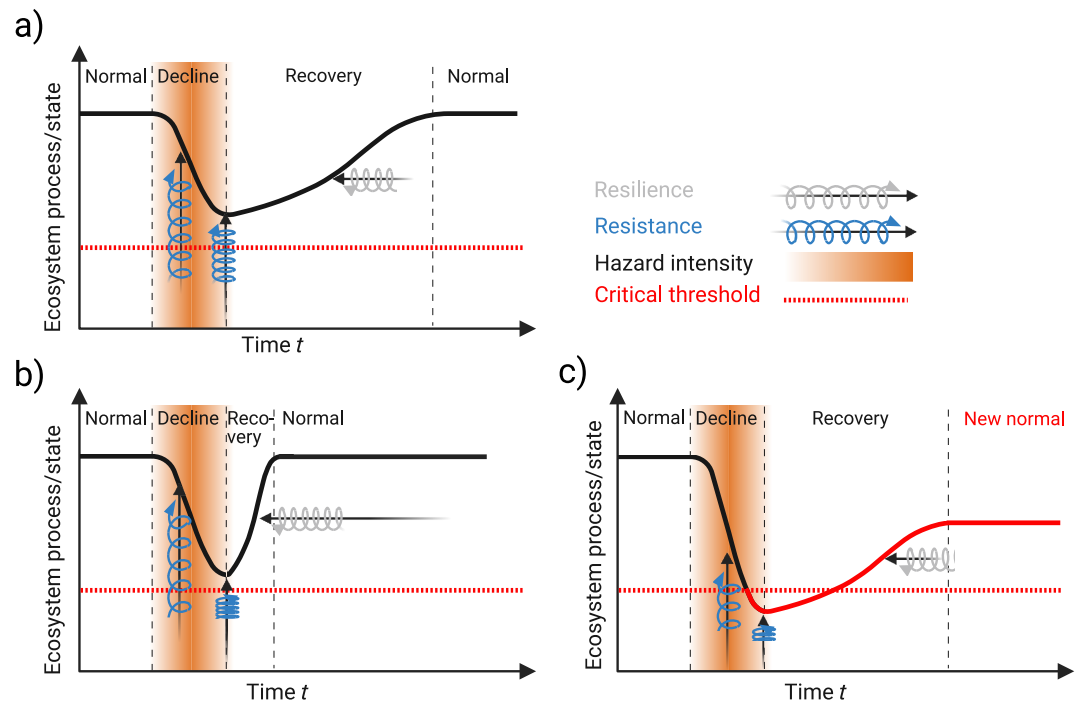**Figure 3.** Buffering capacity. The ability of an ecosystem to resist or absorb changes in its states and functions over time is defined as "resistance." The capacity to recover to pre-event conditions is termed "resilience." Both resistance and resilience act over time, and jointly constitute the "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 resistance such that the critical threshold is reached and no return to pre-event conditions can be achieved.

2. Biodiversity Buffers Against Weather and Climate Extremes

Numerous studies investigate how climate extremes impact ecosystems as a function of their diversity. Two key concepts are frequently used in this context: ecosystem "resistance," which is the capacity to withstand a climate extreme, and ecosystem "resilience," which characterizes 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 how ecosystems buffer the impact of extreme climatic events (for an illustration, see Figure 3). But given the various dimensions of biodiversity outlined in Figure 2, what 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" (Loreau et al., 2021; Yachi & Loreau, 1999). Figure 4 illustrates 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. Such insights have 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 have higher resistance when exposed to exceptional dry or wet conditions, an effect attributed to the species-specific responses to stress (Craven et al., 2018). Recently, Liu et al. (2022) confirmed a positive effect of species richness on resistance to drought using a global satellite-based indicator of drought resistance and tree species composition data from more than half a million forest plots. Variations in the genetic properties of individuals within species can likewise lead to varying resistance to climate extremes. This was shown for example, by Pfenninger et al. (2021), who analyzed 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
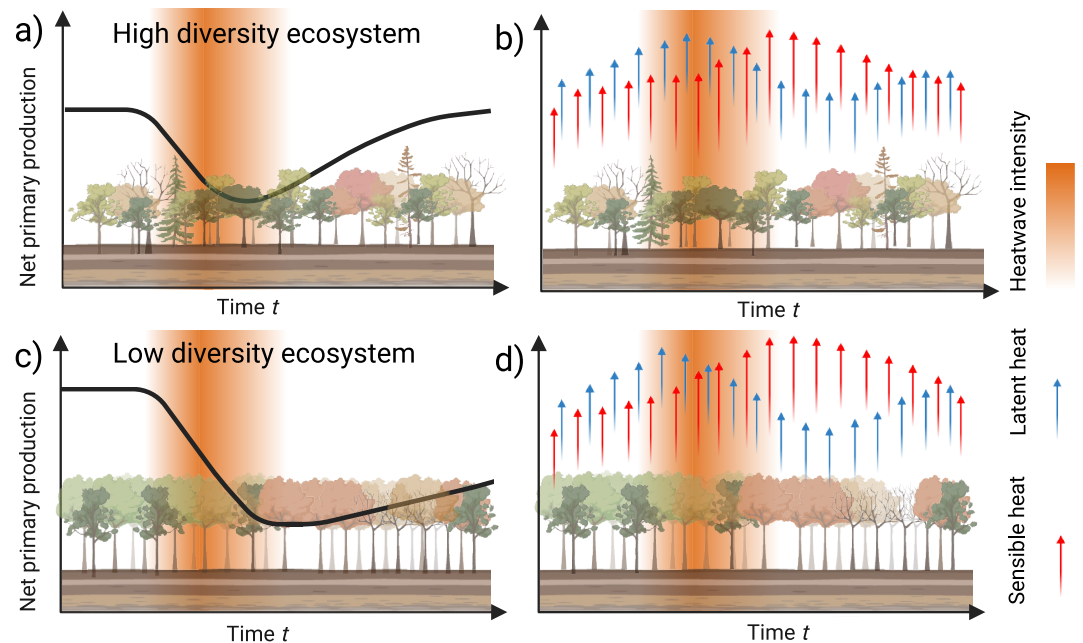
Figure 4. Illustration of the insurance effect: Hypothetical response of net primary production (NPP, net CO_2 uptake rate) to a heatwave (shown in reddish background colors) in (a) a diverse forest, and (c) a mono-culture. Analogous responses for energy fluxes are shown in (b) and (d). While low-diversity forests might initially have higher NPP, their low resistance might imply higher losses and reduced resilience given the lack of species compensation, that is, 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.

regulated by the "functional diversity" of ecosystems (see Figure 2). For example, forest responses to droughts largely depend on the diversity of traits associated with the isohydric versus anisohydric behavior of trees (Hartmann et al., 2021; Lübbe et al., 2022). However, it is not only above ground traits that matter. Mursinna et al. (2018) show that functional diversity of root traits can explain the resistance of ecosystems to drought. In general, the diversity of functional traits of organisms regulates how fluxes of energy, water, and nutrients are absorbed, stored, and released given certain environmental conditions (Anderegg et al., 2019; Berendse et al., 2015; Violle et al., 2007). 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 an ecosystem to weather and climate-related extreme events (Felton & Smith, 2017; Reyer et al., 2013), and their ability to recover from such events. The meta-analysis by Craven et al. (2018) emphasizes that functional biodiversity dimensions are determined by the asynchrony of abundances and thus affect the stability of ecosystem functioning.

Structural heterogeneity at the stand level is another dimension of diversity: mixtures of growth forms, plant sizes, and demographic stages induce for example, vertical variability that appears to play an equally important role in the stabilization of ecosystems. Guimarães-Steinicke et al. (2021) report that differences in canopy surface height minimize spatial variation in canopy temperatures. And there is evidence for variations in canopy height to serve as a buffer for heat extremes (Lin et al., 2020). On a broader scale, the composition and heterogeneity of the landscape dictate the extent of land-atmosphere interaction alterations following climate extremes (Bastos, Fu, et al., 2020; Flach et al., 2021). 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 capacity of biodiversity, as illustrated in Figure 3, is a scale-dependent process. At the landscape scale, diversity encompasses the coexistence and interaction of different ecosystems, for example, through species migration or functional exchanges such as pollination. At regional to continental scales, landscape heterogeneity will determine which response mechanisms jointly dominate how ecosystems react to climate extremes (Bastos, Fu, et al., 2020; Flach et al., 2021; Teuling et al., 2010). Generally, applying insights from

experiments and theoretical frameworks to large-scale and real-world contexts is challenging (Grossiord et al., 2019; Kreyling et al., 2008). In this context remote sensing observations are key to overcoming scaling issues (Cavender-Bares et al., 2022; Gonzalez et al., 2020), as they 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 (Cavender-Bares et al., 2020; Mahecha et al., 2017; Montero et al., 2023; Peng et al., 2021). For example, De Keersmaecker et al. (2016) studied the resistance and resilience against drought across grasslands in central Europe using optical remote sensing observations. They showed that nutrient-poor and species-rich grasslands are more resistant, but less resilient against drought than fertilized, species-poor grasslands. One explanation could be that nutrient-poor grasslands are likely having multiple resource limitations such that species may have developed more strategies to resist fluctuations in environmental conditions. Given its consistency with local experimental studies, the study is one example of how the emerging and constantly growing body of global remote sensing data improves our capabilities of tracing biodiversity dynamics (Cavender-Bares et al., 2022; Skidmore et al., 2021), ecosystem management (Lange et al., 2022), and multiple land-surface processes (Mahecha et al., 2020). Combined data streams can also be used to quantify how ecosystems buffer impacts of climate extreme events, a task that should be prioritized.

Another crucial aspect related to the impact of extremes is occurrence timing (Ma et al., 2015): Both ecosystem responses and their imprints on atmospheric conditions change during the seasonal cycle. Ecosystems comprise individual organisms, each following a characteristic phenological cycle and responding differently to environmental conditions. One could argue that the dominance of, for example, functional traits or structural parameters varies seasonally, making specific dimensions of biodiversity of ecosystems likewise time-dependent (Cinto Mejía & Wetzel, 2023; Ma et al., 2020). This can explain why resistance and resilience at the ecosystem level are determined by an interplay between event-timing and a time-dependent buffering capacity. Carry-over effects are a particular aspect of timing, where resistance and resilience are partly determined from an anomalous preceding period (Cinto Mejía & Wetzel, 2023; Sippel et al., 2018; Wolf et al., 2016). For example, warm spring seasons combined with early water scarcity can result in lower summer resistance to extremes (Flach et al., 2018; Sippel et al., 2018), thus potentially amplifying their impacts in subsequent seasons (see Figure 3). In turn, different land surface characteristics that result from spring weather modulate the evolution of summertime heatwaves (Merrifield et al., 2019). 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; Thonicke et al., 2020). Increased disturbance regimes can further influence such feedback loops (Forzieri et al., 2021; Seidl et al., 2017). Recent studies reveal the importance of memory effects from sequential hot drought years on tree growth and stress responses (Bastos, Ciais, et al., 2020; Schnabel et al., 2021). Such events can be considered a particular type of compound event (Figure 1, Zscheischler et al. (2020)), and Figure 5 illustrates how an ecosystem's buffering capacity is weakened by an extreme event over time, such that consecutive droughts may lead to prolonged impacts on vegetation dynamics and functions in subsequent years. This also means that any feedback mechanisms between biodiversity and climate extremes as illustrated in a simplified scheme in Figure 6 must be understood as time-dependent processes.

3. Biodiversity Imprints on Atmospheric Processes and Extremes

While extreme weather and climate events are predominantly initiated by atmospheric processes, land-atmosphere interactions can also significantly contribute to their development and occurrence. Given that land-atmosphere interactions are influenced by ecosystem functions, we anticipate an imprint of biodiversity on atmospheric processes. Here, we discuss four examples of such imprints and their relevance to extreme events: surface energy balance, cloud formation, atmospheric chemistry, and fires.

Terrestrial ecosystems are crucial to the surface energy balance through their regulation of hydrological fluxes over land. Globally, evapotranspiration returns 60% of precipitation over land (Trenberth et al., 2011), where 80%–90% occurs via plant transpiration (Jasechko et al., 2013). Transpiration in turn uses 50%–60% of the mean net radiation over land (Wild et al., 2015). Changes in ecosystem composition and their spatial arrangement in the landscape, which may result from land management practices or changes in land use and cover, can modify surface temperatures via changes in albedo, emissivity, surface roughness, evaporative resistance, and heat fluxes (Duveiller et al., 2018; Laguë et al., 2019). The imprint of biodiversity on the land-atmosphere energy balance is expected to become particularly important during extreme events such as heat/drought extreme events. For
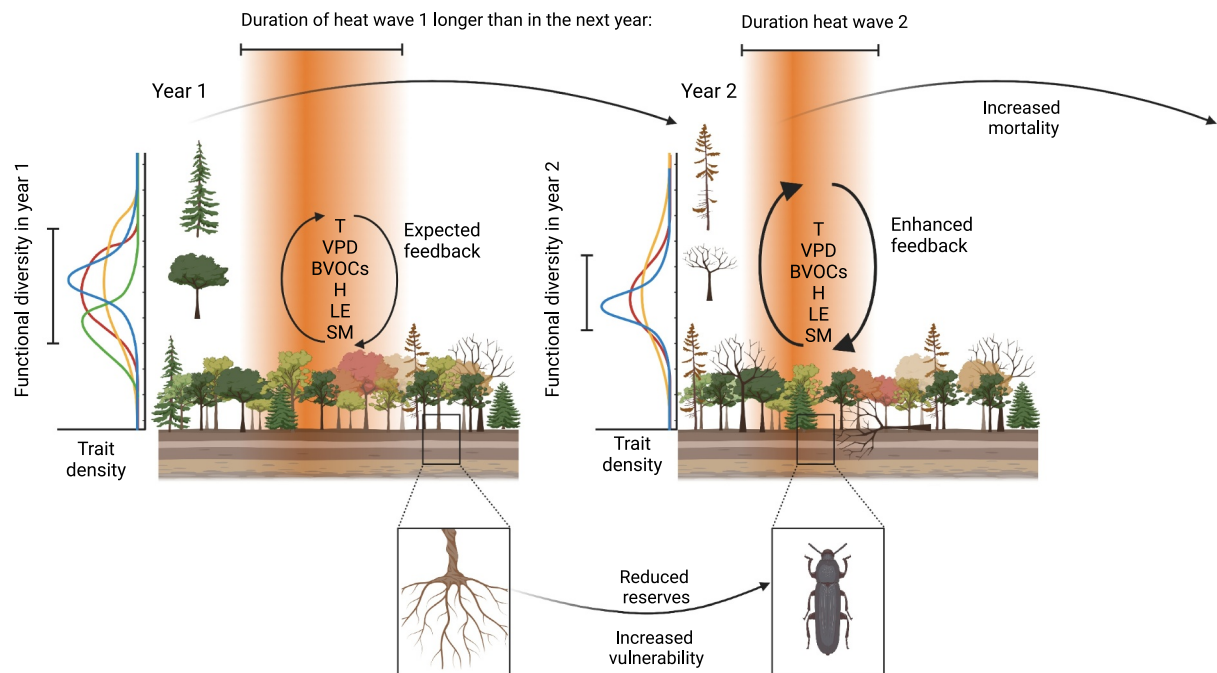
Figure 5. Uncommon temporal sequences and carryover effects. Two consecutive years with combined drought and heatwaves can have particularly strong impacts since species-specific defenses can be reduced and lead to higher vulnerabilities to for example, insects. Reduced chemical defenses and generally depleted pools render vegetation more sensitive. The interplay between preconditioning and carryover effects amplifies the impacts of sequential extremes. Abbreviations are: T = temperature, VPD = vapor pressure deficit, BVOCs = biogenic volatile organic compounds, H = sensible heat, LE = latent heat, and SM = soil moisture.

instance, changing surface albedo is known to modulate the intensity of these events through changes in evapotranspiration and vertical energy fluxes, that is, sensible heat, 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 to the atmosphere.

In addition to influencing energy and water fluxes, vegetation can serve as a source of atmospheric trace substances such as biogenic volatile organic compounds (BVOCs), pollen, and smoke particles, which may impact cloud formation and the atmospheric radiation budget and processes in complex ways. A prime example of the intricate connections between biodiversity and climate regulation is cloud formation. Clouds are influenced by water in its three thermodynamic phases, energy exchanges (discussed above), as well as BVOCs and aerosol particle fluxes, all of which are affected by vegetation characteristics (Duveiller et al., 2021; Teuling et al., 2017). Furthermore, clouds play a crucial and immediate role in buffering climate extremes: they cool the environment during hot days, buffering heat stress conditions, and keep temperatures warmer during cold nights, buffering against extreme cold. Therefore, biodiversity imprints on cloud formation might contribute to buffer extreme events. For example, BVOCs can initiate the formation of biological secondary organic aerosols (BSOA), altering the cloud condensation nuclei and possibly the ice nucleation properties of particles (Lehtipalo et al., 2018; Riccobono et al., 2014; Riipinen et al., 2011). Primary biogenic particles such as pollen, plant debris, spores and bacteria can additionally foster the heterogeneous freezing of super-cooled cloud droplets by acting as ice-nucleating particles at warmer temperatures than in their absence (Fröhlich-Nowoisky et al., 2016; Kretzschmar et al., 2023; O'Sullivan et al., 2018; Steinke et al., 2020). Since rain is predominantly formed via ice-containing clouds (Mülmenstädt et al., 2015), this implies more frequent rain above pollen-emitting forests (Kretzschmar et al., 2023). 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 (Jiang et al., 2018; Niinemets, 2010; Sporre et al., 2019; Zhang et al., 2024).
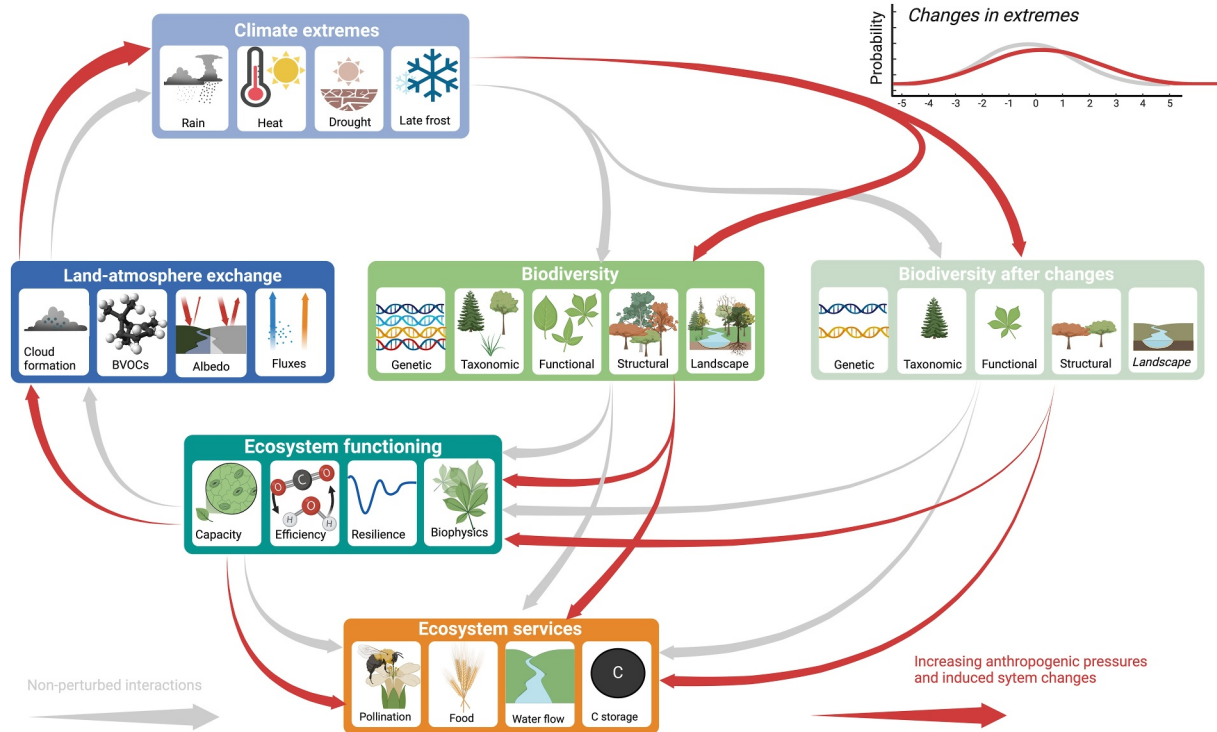
Figure 6. Illustration of the general role of biodiversity as a buffer to climate extremes. "Biodiversity" is understood here as a multifaceted term that embraces everything from genetic, via functional traits, to landscape scale heterogeneity, as it is currently the accepted idea in international frameworks (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.

There are indications that BVOC emissions depend on forests taxonomic and functional diversity, resulting in species-specific impacts on the tropospheric gas and particle phase including oxidant as well as BSOA concentration distributions and diurnal cycles (Luttkus et al., 2022, 2024). Intriguingly, a scoping measurement study by Sanaei et al. (2023) found that increased taxonomic biodiversity might result in lower total BVOC emissions compared to the cumulative emissions of individual species. These findings highlight the need for further research, particularly concerning how BVOC oxidation modifies particles through BSOA and the subsequent effects on clouds, precipitation and climate.

A particularly intertwined set of processes linking functional, structural and landscape diversity and extreme events is related to fires (Rosan et al., 2022; Wirth, 2005). In the wake of climate change, fires are also on the rise in many regions, with increased burned area and reduced 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 depend on vegetation traits and the type and amount of available fuel, biodiversity also has an effect on the types of particles emitted (Miller et al., 2012). In a recent review, Jones et al. (2022) describes 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 between lightning and pyroconvection become evident (Altaratz et al., 2010; Dowdy & Pepler, 2018). However, as detailed in Loudermilk et al. (2022) the full extent of fire-vegetation-atmosphere feedback is currently poorly conceived. In a broader context, there is a need to expand the focus from fire frequency and sometimes severity, to address how a broader range of fire regime attributes affect biodiversity (McLauchlan et al., 2020; Miller et al., 2012).

4. Biodiversity-Extreme Event Interactions

The examples discussed above suggest that terrestrial vegetation plays an important role in changing, for instance, local atmospheric chemistry or land-atmosphere coupling parameters that may shape the development of extreme events. Considering that biodiversity influences vegetation dynamics, it stands to reason that biodiversity should have a discernible impact on climate extremes, thus potentially influencing their impacts on ecosystems and ecosystem resistance and resilience against extreme weather conditions. For example, some plants respond to drought conditions by reducing stomatal conductance to prevent water loss, which in turn can exacerbate heat anomalies (Sungmin et al., 2022). Severe abiotic (e.g., ozone, heat, drought) and biotic stressors (e.g., herbivore attack and infestation, see also Figure 5), can also induce BVOC emission regulating stress response mechanisms which may lead to extremes both in BVOC and atmospheric aerosol particle emissions (Blande et al., 2014; Grote et al., 2019). More biogenic particles of primary or secondary origin under extreme events are then 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 (Rap et al., 2015, 2018). BVOC emissions further impact the tropospheric oxidizing capacity, including oxidizing substances such as ozone being consumed or formed through BVOC chemical degradation processes thereby impacting BSOA formation. In turn, ozone is also an abiotic plant stressor, resulting in complex interactions under extreme events.

Furthermore, all the mentioned processes 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). Thus, 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), although the specific role of biodiversity in such lateral processes has not been specifically evaluated. Given the examples above, we expect that by altering the characteristics of a weather or climate extreme itself, ecosystems impacted by an extreme event can impact another ecosystem downstream, leading to the possibility of cascading effects. Considering the significant influence of ecosystems on atmospheric processes, land management practices and land cover change must play a crucial role in affecting atmospheric feedback mechanisms (Duveiller et al., 2018; Lugato et al., 2020). Thus, we hypothesize that management should have an effect on extreme events.

A conceptual diagram of how biodiversity and climate extremes are connected is shown in Figure 6. The figure illustrates how climate extremes of various types influence ecosystem functionality. By ecosystem function, we mean, for instance, the biophysical controls of exchange processes, the capacity of ecosystems to utilize nutrients, efficiencies in assimilating CO_2, or their inherent resilience to certain stress (Migliavacca et al., 2021; Musavi et al., 2015; Reichstein et al., 2014). These functional properties are influenced by the different dimensions of biodiversity (as outlined in Figure 2). For example, plant traits affect albedo, thereby providing resistance against extreme events by cooling the local microclimate, that is, by lowering soil temperature and reducing water stress (Iler et al., 2021). An intensification of a specific type of extreme event, such as unprecedented droughts or the compounding of several types of extremes, can modify these intrinsic ecosystem properties. Thus, any change in biodiversity can further alter these pathways. Since ecosystem functioning determines the flow of energy, matter, or particles into the atmosphere, the distribution of subsequent climate extremes may also be affected, closing the feedback loop.

In summary, we presented evidence that 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. Conversely, while it is recognized that biodiversity and land-surface dynamics may influence certain extreme events, the extent of this influence remains inadequately understood. Despite the apparent logical relationship between biodiversity, vegetation attributes, fire-atmosphere dynamics, and their impact on subsequent extreme events, scientific evidence that quantifies these links and their effects on ecosystem resistance and resilience remains sparse. The specific role of biodiversity and the overall magnitude of these effects, from local to global scales, have yet to be quantified. In light of the evidence of this interconnectedness, we need to consider whether deliberately increasing functional diversity, through management or rewilding initiatives (Svenning et al., 2016) should be re-evaluated for its potential to mitigate extreme events, resulting in a win-win situation. Even if shifts in ecosystem characteristics and biodiversity do not substantially 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 to improve their drought resistance and resilience (Balch et al., 2020; Pörtner et al., 2021) could be instrumental in influencing land-atmosphere feedback mechanisms. To leverage 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 modeling approaches.

5. Research Gaps

Understanding the connection between climate extremes and biodiversity change is still in its early stage. Despite the array of evidence delineated herein, significant scientific gaps persist. The subsequent points highlight areas that require further scientific study:

- *Considering all dimensions of biodiversity*: Genetic, taxonomic, functional, and landscape diversity all shape buffers and feedback mechanisms between ecosystems and climate extremes in very specific ways. What we miss is a global catalog and understanding of how each of the biodiversity dimensions interacts with the variety of climate extremes. We need to understand the exact role of different dimensions of biodiversity in these interactions. Only by doing so can we clearly formulate ecosystem management priorities and efficient (e.g., remote sensing based) monitoring strategies.

- *Quantifying biodiversity buffers across event types*: For extreme event types other than the well-studied cases of droughts and heatwaves, evidence for the dampening or amplifying processes remains weak. This concerns particularly the rather small-scale events such as spring frost, heavy precipitation events, solar radiation or ozone maxima, and wind storms. Despite their locally important impacts, these events have received less frequent and intense scrutiny in research. Impacts of weather extremes of this kind have been overlooked so far, but may be particularly sensitive to changes in biodiversity.

- *Embracing multiple spatial and temporal scales*: Similar to biodiversity patterns, meteorological drivers are scale-dependent. The occurrence of extremes is linked to micro-meteorological (meters to sub-km), synoptic (up to 1,000 km), and global scales in space. Temporally, atmospheric variability ranges from the weather time scales (hours/days) to the interannual and multidecadal patterns of large-scale circulations. Achieving a comprehensive understanding biodiversity buffers and feedback mechanisms needs to embrace all these different scales which may be achievable by combining remote sensing and modeling approaches. Scale-bridging endeavors are important since ecosystems exhibit characteristic resistances to weather- and climate-related extremes and are part of a dynamic pulse-response mechanism (Harris et al., 2018) that control numerous processes at the land-atmosphere interface across different and interacting spatio-temporal scales.

- *Preconditions are key determinants*: Pre-existing conditions may be induced by ecosystem recovery from earlier disturbances, or from preceding unusual weather and climatic trajectories. For example, winter and spring seasons are warming quickly, which leads to phenological shifts and to potentially enhanced water depletion with associated lower resistance to extremes in summer or in following seasons (see Figure 3).
  On longer time scales, changes in disturbance regimes and memory effects from hot-dry years can further induce lagged memory effects and reduced resistance. Despite this conceptual basis, however, a key research gap remains in how and which pre-existing conditions mechanistically determine ecosystems' resistance and resilience to weather or climate-related extremes (Figure 5), and how these effects depend on different dimensions of biodiversity.

- *Understanding feedback loops*: Predicting how exactly biodiversity shapes land-atmosphere interactions is not yet possible today. Even less understood are the specific biodiversity features and processes that modulate these interactions and regulate extremes. The involved processes are manifold and range from the emission of biogenic aerosol particles acting as ice-nucleating particles required for heterogeneous ice formation in clouds, and large-scale land-surface-atmosphere interactions. In this broad context, it might be essential to also consider the indirect effects of biodiversity in stabilizing plant communities and vegetation structure. For instance, if biodiversity can prevent a biome shift from tropical forests to grasslands (see e.g. (Sakschewski et al., 2016)), it must have major implications for feedbacks between land and atmosphere. 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 exceed historical records by large margins (Fischer et al. (2021), Figure 1). These events are likely to impose disproportionately large effects on ecosystems, potentially exceeding the adaptive capacities. Ecosystems are typically adapted to historical weather and climate conditions, raising questions about their ability to mitigate the impact of such drastic extremes. While such events have been observed recently, their rarity, projected increase in frequency, and the inherent limitations of current models to represent the complex feedback between climate extremes and biodiversity across spatio-temporal scales expose another research gap. Currently, there is no conceptual framework to address this gap. It is unclear what level of process complexity and spatio-temporal scales need to be incorporated into models to generate robust projections, and whether this is computationally feasible. Consequently, the strength and even the direction of the feedback between biodiversity change and various types of climate extremes remain elusive. Effective management strategies for climate adaptation and mitigation require the development of reliable predictive models that adequately represent the nuances of functional diversity, an area that needs further advancement.

- *Societal dimensions and systemic risk*: Looking forward, we argue that empirical and modeling research need to adopt more integrated approaches that encompass biodiversity, multiple ecosystem services, and socio-ecological dynamics (Thonicke et al., 2020). Such an approach is essential to comprehensively address feedback loops leading to systemic risks associated with climate extremes (Reichstein et al., 2021). Achieving this necessitates collaboration across different disciplines, such as ecology, atmospheric sciences and climatology, psychology, and social sciences. Understanding the interactions between climate extremes, biodiversity, ecosystem services, and long-term societal demands can also inform policy-making and management strategies to reduce greenhouse gas emissions and mitigate the impacts of climate change without sacrificing other ecosystem services. For example, policies that prioritize 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 through a no-regret strategy (Erb et al., 2022).

The overarching and unresolved question we identify here is: Under which conditions do we expect dampening or amplifications due to interactions between biodiversity and climate extremes? Only by answering this question, taking into account all the different dimensions of biodiversity and types and dynamics of extremes, can we effectively manage ecosystems to maximize their resistance and resilience against future climate conditions, particularly amidst 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.

6. Conclusions

The scientific gaps identified in this paper call for the formulation of an ambitious interdisciplinary research agenda. We need to explore the multiple relationships between biodiversity and climate extremes across spatial scales and extensive environmental gradients. One cornerstone is observations. In situ and remote sensing observations that can simultaneously quantify multiple dimensions of taxonomic, structural, functional, and landscape diversity and composition need to be harmonized with the monitoring of atmospheric thermodynamics and composition. There are fundamental advances in satellite-based Earth observations for both climate and ecosystem monitoring (Montero et al., 2023; 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).

In addition 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, we need a new generation of predictive models, which are capable of capturing the complex interactions between atmospheric processes, biodiversity patterns, and ecosystems. Crucially, these models should facilitate adequate testing of hypotheses concerning feedback mechanisms. Although functional digital twins of the climate system are now in reach, soon providing climate simulations at the kilometer-scale resolutions (Bauer et al., 2021;

Slingo et al., 2022), it is unlikely that high-resolution simulations alone can fully encapsulate the coupling and feedback loops between climate and biodiversity. The digital twin concept for ecosystems is still in a conceptual phase (Buonocore et al., 2022), substantial research is imperative to realistically represent biodiversity in land-surface models (Bendix et al., 2021; Scheiter et al., 2013). Today, several prototypes of a Digital Twin for biodiversity are currently being developed (de Koning et al., 2023), but these will not be able to fully predict the feedback loops described here and thus must be used in concert with fully dynamic modeling schemes.

Today, there is a growing awareness of the intricate interplay between biodiversity decline and climate change, as shown in a recent collaborative report jointly published by IPCC and IPBES (Pörtner et al., 2021, 2023) and in a series of policy directives. For instance, the new European Union (EU) Forest Strategy for 2030 and policy initiatives by the European Commission have recognized the value of the multi-functionality of forests, including their regulatory role in atmospheric processes. However, the observational and modeling frameworks are still rather weak to support policy decisions. Elsewhere, the lack of research on the feedback loop linking biodiversity changes and climate extremes is also evident in policy, which sometimes pays insufficient attention to both aspects. New policy tools (e.g., the Carbon Removal Certification Proposal by the European Union) and nature-based climate solutions, including climate-smart forestry, aim to address this issue by implementing management actions that improve biodiversity. Simultaneously, there is a shortage of scientific studies on the interactions between changes in biodiversity, climate extremes, and biophysical feedbacks. By addressing these critical research gaps, we can significantly enhance our understanding of biodiversity's buffering capacities and better support policy decisions. In doing so, we strengthen the ability to mitigate the impacts of climate extremes and enhance ecosystem resilience, thereby safeguarding our planet's ecological integrity.

Data Availability 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.com software.

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