

Review

Biotic responses to climate extremes in terrestrial ecosystems

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SUMMARY

Anthropogenic climate change is increasing the incidence of climate extremes. Consequences of climate extremes on biodiversity can be highly detrimental, yet few studies also suggest beneficial effects of climate extremes on certain organisms. To obtain a general understanding of ecological responses to climate extremes, we present a review of how 16 major taxonomic/functional groups (including microorganisms, plants, invertebrates, and vertebrates) respond during extreme drought, precipitation, and temperature. Most taxonomic/functional groups respond negatively to extreme events, whereas groups such as mosses, legumes, trees, and vertebrate predators respond most negatively to climate extremes. We further highlight that ecological recovery after climate extremes is challenging to predict purely based on ecological responses during or immediately after climate extremes. By accounting for the characteristics of the recovering species, resource availability, and species interactions with neighboring competitors or facilitators, mutualists, and enemies, we outline a conceptual framework to better predict ecological recovery in terrestrial ecosystems.

INTRODUCTION

Terrestrial ecosystems are composed of aboveground and belowground subsystems (Bardgett and Wardle, 2010; Van der Putten et al., 2001; Wardle et al., 2004), which comprise a large variety of organisms across all major life forms: microorganisms, plants, invertebrates, and vertebrates (De Deyn and Van Der Putten, 2005). Those organisms and their interactions contribute to numerous ecosystem functions, such as carbon sequestration, groundwater recharge, soil erosion control, and disease suppression (Van der Putten et al., 2001; Wardle et al., 2004). Many of these functions result from direct and indirect biotic interactions between aboveground and belowground organisms. For instance, belowground microorganisms and invertebrate decomposers process dead organic matter into inorganic nutrients that are used for plant growth. Plants are then consumed by both aboveground and belowground herbivores, which are then preyed upon by higher trophic organisms. These aboveground-belowground interactions drive biotic feedbacks that influence mass and energy flow between the two subsystems (Wardle et al., 2004; Wolkovich et al., 2014). Climate-change-induced shifts in aboveground-belowground biotic interactions can therefore have far-reaching consequences for terrestrial biodiversity, ecosystem functioning, stability, and restoration (Bardgett and Wardle, 2010; Hooper et al., 2000; Kardol and Wardle, 2010; Wardle et al., 2004). However, currently an in-depth understanding of variation in biotic responses to anthropogenic climate change and ecological consequences for aboveground-belowground interactions is lacking. This lack in insight limits our capacity to manage and restore terrestrial biodiversity under human-induced global changes (Urban et al., 2016; Walther et al., 2002).

Our current understanding of species responses to climate change mainly stems from studies conducted under conditions of gradual change (Post, 2013; Tylisanakis et al., 2008; Urban et al., 2016). For example, these studies focus on phenological shifts and shifts in geographic ranges (Dawson et al., 2011; Van Der Putten et al., 2010; Walther et al., 2002). Increasing frequency of extreme climatic conditions, such as extreme drought, precipitation, or temperatures (Coumou et al., 2013; Coumou and Rahmstorf, 2012; IPCC et al., 2018a), may influence biotic interactions, biodiversity, and ecosystem functioning unprecedentedly (Harris et al., 2018; Prugh et al., 2018; Trisos et al., 2020; Vázquez et al., 2017); this limits current capacity to predict consequences of change, as well as measures for adaptation and mitigation. There are at least two factors that make the outcome of climate extremes on biotic interactions difficult to predict. One is that, in contrast to gradual climate change, extremes push species to their adaptation limits (see glossary

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Box 1. Glossary

Adaptive limits: The maximum capacity of a population to adapt to an environmental change.

Allee effects: An inverse relationship between population density and (per capita) population growth rate. Due to allee effects, a species with very low population size may become locally extinct.

Centrality: Measure of the ability of a particular node in a network to influence its other nodes.

Community: An assemblage of species found together in a specific area or a habitat at a given time, usually interacting with each other.

Competition: The negative interaction between two or more species that depend on the same limiting resources for their survival, growth, and reproduction.

Connectance: The number of actual links in a network divided by the all possible number of links.

Dauer larvae: A developmental stage in some nematode worms to avoid harsh conditions.

Decomposers: Organisms that convert dead organic matter into inorganic nutrients.

Decomposition: The process of conversion of dead organic matter into inorganic matter usually via mass loss.

Dispersal: The movement of an individual of a species from one area to other.

Ecosystem coupling: The overall strength of (correlation-based) associations among species or communities, and with their surrounding abiotic environments.

Embolism: The process of air bubble formation (emboli) in xylem of plants that could obstruct water conduction in xylem.

Equilibrium: The stage at which population of a species remain constant until perturbed.

Facilitation: The positive effect of one species on the other.

Facultative mutualist: Mutualistic interactions that are not critical for the survival of either of the partner species.

Functional traits: Any feature of an organism that indirectly influence their fitness by affecting growth, reproduction, or survival.

Generalist: A species that interacts with many other species.

Geographic ranges: The spatial region that includes all populations of a species.

Herbivores: Organisms that feed on plants.

Hydraulic conductivity: The ease with which a water (or any fluid) can move through pore spaces or fractures in vascular plants.

Keystone species: A species that substantially influences the community structure independent of its population size.

Life history traits: Major features of life cycles of organisms directly related to birth and death rates.

Local extinction: The disappearance of a species from a given habitat or ecosystem (mainly due to mortality), while it still exists elsewhere.

Metacommunities: A set of multiple local communities in an area or region, linked by the dispersal of several interacting species from those local communities.

Mutualist: A species that beneficially interact with another species to benefit itself.

Networks: Representation of a system via its components (nodes, e.g. species within a community) and their relationships (links or vertices, e.g. interactions).

Obligate mutualist: Mutualistic interactions that are critical for the survival of each of the partner species.

Osmotic pressure: The measure of a solution's tendency to take in pure solvent by osmosis.

Parasites: Organisms that live inside or on other organisms and often harm but not necessarily kill these other organisms.

Parasitoids: Organisms that live within a living host which eventually kill the host by consuming their tissues.

Pathogens: Organisms that cause disease in other organisms.

Phenological shifts: Shifts in the timing of recurring of any biological phenomena, such as annual budburst, the senescence of plants, the onset of animal migrations or egg production.

Predators: Organisms that consume other organisms by killing them.

Recovery debts: The loss of biodiversity and ecosystem functions during the recovery of ecosystems

Recruitment: The process by which a species adds new individuals to its population.

Regime shifts: Large, abrupt, and persistent change in any key state variable that describes an ecosystem.

Specialist: A species that interacts with only a limited number of other species and that share a long and strong co-evolutionary history.

Specific leaf area: The ratio between leaf area and leaf dry mass.

Stability: The ability of an ecological entity (e.g., population of a species, community properties) to maintain an equilibrium state.

Tipping points: Situations when accelerating change caused by positive feedbacks drive the system to a new state.

in Box 1 for the definition) within a narrow time frame (Harris et al., 2018; Harvey et al., 2020; Jump and Peñuelas, 2005). However, such limits most likely vary across different life forms and their geographic location, which may explain the variability in the response of organisms to the same extreme event (Buckley and Huey, 2016; Vázquez et al., 2017). Second, because of the sheer abiotic stress of extreme events, various

species interactions, such as competition, facilitation, and predation, are simultaneously perturbed at a short timescale (Parmesan et al., 2000; Prugh et al., 2018); this complicates the prediction of species responses, as well as the capacity to propose mitigation measures.

To understand species responses to climate extremes, we first review how major functional and/or taxonomic groups of plants and associated aboveground and belowground biota respond to 3 climate extremes: extreme drought, extreme precipitation, and extreme heat. We chose these three commonly studied climate extremes, as their frequency is increasing at unprecedented rates and, accordingly, their effects on ecosystems are rapidly growing (IPCC et al., 2018a). We do acknowledge that many other climate-related extreme events are also increasing worldwide, such as more severe snow and windstorms, and fire events, and their effects on terrestrial ecosystems can be highly dramatic (Díaz-Yáñez et al., 2019; Jolly et al., 2022). However, in this review we restrict ourselves to three major events, as many other extreme events can be related to temperature and water extremes. Second, we examine how population characteristics of recovering species show different trajectories of recovery after a climate extreme has stopped (Oliver et al., 2015), in relation to availability of resources (Maron et al., 2015), and effects of neighboring competitors (or facilitators) (Thibault and Brown, 2008), mutualists (Derksen-Hooijberg et al., 2018), and enemies (Walter et al., 2012). Finally, building upon the vast available knowledge of how disturbance ecology is proposed to understand climate change impacts (Burton et al., 2020; Newman, 2019; Pinek et al., 2020; Turner et al., 2020), we provide a conceptual framework to show how different trajectories of species recovery may alter aboveground-belowground biotic interactions and how such alterations may affect the dynamics and functioning of terrestrial ecosystems.

WHAT IS A CLIMATE EXTREME?

There is an increasing consensus that the 21st century will continue to see a rise in climate extremes compared with the previous century (Easterling et al., 2000; Rummukainen, 2012; Swain et al., 2020). For instance, in 2015 the largest global area of extreme drought was recorded between 1951 and 2016 (Spinoni et al., 2019). A recent simulation study showed that the relative frequency of present-day extreme temperature events could rise by a factor of 100–250 in the tropics and mid-latitudes in coming decades (Coffel et al., 2018). Heavy precipitation (maximum 5-day precipitation total and maximum 1-day precipitation total) is predicted to increase across the globe even in the regions where mean precipitation is predicted to decrease (Kitoh and Endo, 2016).

Whether a weather or climate episode is an extreme event depends on how rare that event is and on how dramatic its impact is on a system (e.g., societal or ecological) (Seneviratne et al., 2012; Swain et al., 2020; Zscheischler et al., 2020). The Intergovernmental Panel on Climate Change (IPCC) accordingly defines an extreme climate event as a prolonged period below or above the 10th or 90th percentile of a probability density function of weather observations, e.g., daily temperature or precipitation (IPCC et al., 2018b). For simplicity, the IPCC refers to extreme weather events and extreme climate events collectively as climate extremes (IPCC et al., 2018b; Seneviratne et al., 2012). Although the rarity of such events is becoming rarer, ecologists still consider a climate extreme as an event when it also causes a rare response in species, communities, or even an ecosystem (Van de Pol et al., 2017). Rare responses of species are, for example, often related to how much the species are pushed close to or even beyond their adaptive limits (Jentsch and Beierkuhnlein, 2008; Smith, 2011). In this review, we integrate rarity in both climatic (or weather) events and ecological responses.

ECOLOGICAL RESPONSES TO CLIMATE EXTREMES

We performed a systematic literature search to find relevant papers on biotic responses to climate extremes. For climate extremes, we included the following search terms: ("extreme events" OR "extreme climate" OR "climate extremes" OR "extreme climatic events" OR "extreme weather events" OR "extreme drought" OR "extreme precipitation" OR "extreme heat" OR "extreme temperature"). These search terms were, in addition, combined separately with three categories of terrestrial organisms: (1) belowground microorganisms and invertebrates, (2) aboveground animals, and (3) plants. The search terms used for belowground microorganisms and belowground invertebrates were as follows: ("soil bacteria" OR "soil fungi" OR "soil protozoa" OR "soil protist" OR "arbuscular mycorrhizal fungi" OR "ectomycorrhizal fungi" OR "decomposers" OR "detritivores" OR "root feeders" OR "symbionts" OR "N fixers" OR "ectoparasites" OR "endoparasites" OR "soil pathogens" OR "earthworms" OR "mites" OR "Collembola" OR "soil micro-arthropods" OR "soil micro-arthropods" OR "soil nematodes" OR "soil predators" OR "soil

herbivores" OR "enchytraeids" OR "soil mesofauna" OR "soil macrofauna" OR "soil tardigrades" OR "soil invertebrates"). For aboveground animals, we used: ("pollinators" OR "herbivores" OR "seed dispersers" OR "seed eaters" OR "predators" OR "parasitoids" OR "leaf pathogens" OR "leaf miners" OR "leaf suckers" OR "leaf chewers" OR "endophytes" OR "hyperparasitoids" OR "granivores" OR "grazers"). And finally, for plants we used: ("plant" OR "plant community" OR "plant interaction" OR "vegetation" OR "grasses" OR "forbs" OR "herbs" OR "trees" OR "crops" OR "grasslands" OR "forest" OR "tropical ecosystems" OR "temperate ecosystems" OR "alpine ecosystems" OR "Antarctic" OR "Savanna" OR "agricult*").

In total, we found 2,496 papers in ISI Web of Science accessed on 10th of April 2018 (cut-off date). We first excluded review papers and those from aquatic ecosystems. Then we removed those papers (1) that only report ecosystem responses, (2) that lacked a functional/taxonomic group or species response that we could assign to a functional/taxonomic group, (3) without a clear definition and context of climate extremes, and (4) from observational studies that did not report pre-extreme event responses. For example, we included a study if author(s) had chosen an experimental manipulation, for example, drought manipulation defined as 45% reduction of mean annual precipitation, based on the rarity of their occurrence from long-term weather data. Rarity of such events can usually range from 2 to 3 decades to several hundreds of years. We also included observational studies when, for instance, a baseline (non-extreme event period) response was provided. We further excluded studies that used predictive models based on observational data and did not provide information on species (or functional/taxonomic group) responses before and during climate extremes. Overall, we were able to collate 325 unique responses for 16 taxonomic and/or functional groups from 194 published studies (Table S1). These 16 groups represent the most studied functional/taxonomic groups of terrestrial ecosystems, namely soil bacteria, soil fungi, soil nematodes, soil Collembola, and larger decomposer organisms belowground and plants, invertebrate herbivores, invertebrate parasitoids, invertebrate predators, vertebrate herbivores, and vertebrate predators aboveground. In addition, we separated plants into grasses, forbs, shrubs, legumes, mosses, and trees.

Our goal was to quantify whether the response to a given climate extreme of a functional/taxonomic group or a species belonging to a functional/taxonomic group was rare. We want to emphasize that our approach is not a conventional meta-analysis but a step to obtain a broad understanding of whether different functional/taxonomic groups show any rare response to three selected climate extremes. For this purpose, we adapted the concept of median lethal dose (LD_{50}) from toxicology, in which the LD_{50} concentration of a chemical causes 50% mortality in a test population (Zbinden and Flury-Roversi, 1981). Accordingly, if a climate extreme caused 50% or more population mortality of a species, we considered this as a "rare response." We included both positive and negative rare responses. We extended this idea to several other fitness responses, e.g., biomass, growth rate, net photosynthesis, seed weight, water use efficiency, survival rate, and feeding rate (detailed list of all response variables are provided in Table S1). We consider that 50% (or more) change in any fitness-related ecological variable is a rare response for any given short- or long-lived organisms (Smith, 2011; Van de Pol et al., 2017). Consequently, if fitness of a species drops to 50% or lower, it should dramatically lower the survival of that species. We are aware that our application of the LD_{50} concept is an arbitrary choice of quantifying a "rare response," as 50% change in one functional group (e.g., bacteria) may not be as rare as 50% change in another functional group (e.g., vertebrates), and therefore, a systematic comparison across functional group responsiveness to climate extremes is often challenging and needs a cautious interpretation whichever approach is used. From more than 300 unique responses that we collated from the literature, we found 126 rare responses. Of these, 116 were negative (Figures 1 and 2, Table S1).

Belowground microorganisms

Belowground microorganisms are among the most diverse and abundant organisms of terrestrial ecosystems (Bardgett and Van Der Putten, 2014), of which soil bacteria and soil fungi are the most studied taxonomic groups (Bahram et al., 2018; Fierer, 2017). For both bacteria and fungi, we found that the frequency of rare responses to climate extremes were predominately negative, with bacteria being slightly higher in their responsiveness than fungi (Figure 1; higher frequency of rare responses). Extreme temperature can inhibit the growth of soil bacteria but less often so the growth of soil fungi (Xu et al., 2017a). Similarly, extreme drought reduced the abundance of soil bacteria (Nguyen et al., 2018), whereas soil fungi did not respond substantially (Swaty et al., 2004) or even slightly increased their abundance (Walter et al., 2016). These differences in responses might be related to differences in life history and functional traits between these two major groups of belowground microorganisms. Soil bacteria exhibit faster growth than soil fungi, which makes soil bacteria highly responsive and often more

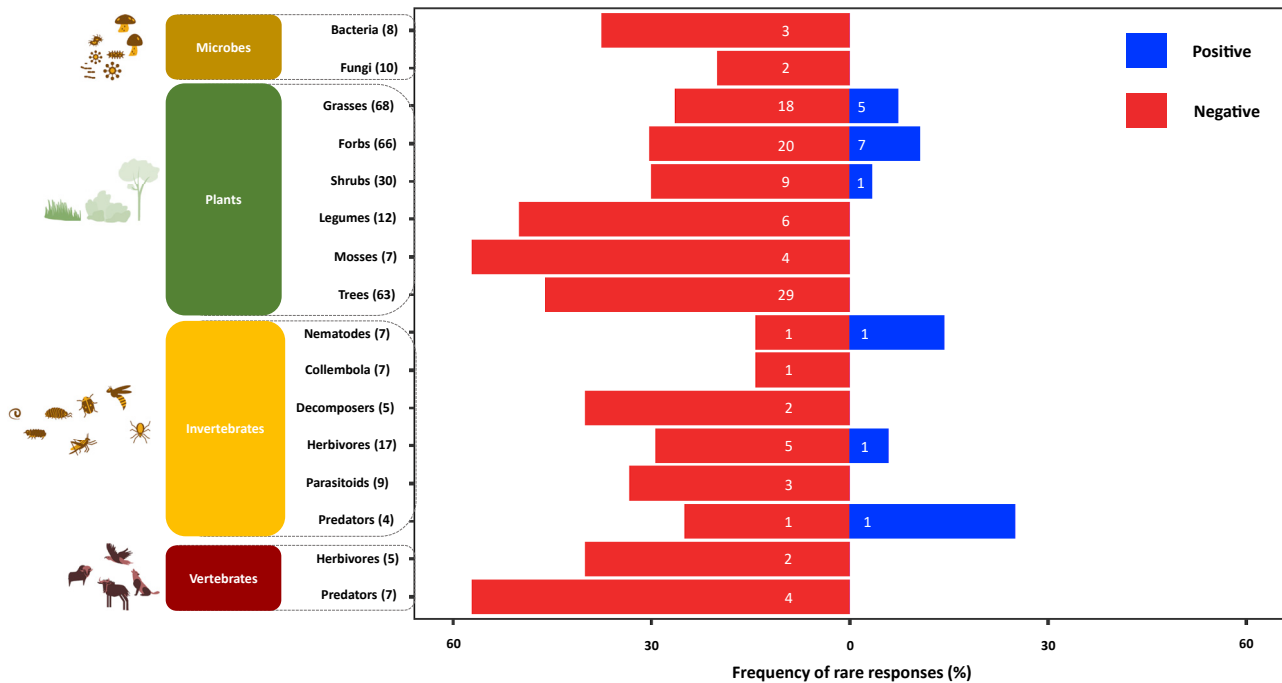


Figure 1. Frequency of rare responses expressed as percentage of rare responses from total number of responses in our systematic literature search

Rare responses are change in $\geq 50\%$ compared with controls or nonclimate extreme reference time of 16 functional and taxonomic groups across three climate extremes (main text for detail). The numbers in parentheses are total number of cases per functional/taxonomic group. The numbers inside the bars stand for the number of rare responses found. The list of studies used to obtain functional group responses are provided in [supplemental information: Table S1](#), and detailed overview of responses across three climate extremes are provided in Figure 2.

sensitive to severe abiotic stress (Holden and Treseder, 2013). Moreover, bacterial communities are characterized by networks that have higher connectance and centrality (de Vries et al., 2018) (see Box 1) due to strong biotic interactions among bacterial species (Zhang et al., 2020). Community stability to perturbations are usually lower when component species interact strongly at a local scale (Gellner and McCann, 2016; McCann, 2000). Although our understanding of the differences between the interaction strengths within bacterial and fungal communities is still limited, such differences could contribute to variation in the vulnerability between bacterial and fungal communities to climate extremes (Montoya et al., 2006).

Differences between bacterial and fungal responses to climate extremes could also be related to their strategies to overcome abiotic stress. For instance, fungi can redistribute water via mycelial networks, which is an advantage in drier environments (Guhr et al., 2015), but their advantage also depends on how their host plants respond to a given climate extreme. For example, the colonization by mycorrhizal fungi increased with increased root growth of its host plant during extreme precipitation (Walter et al., 2016). In contrast, in the same study, extreme drought negligibly affected mycorrhizal communities, as root biomass of its host plants did not change during an extreme drought (Walter et al., 2016). Soil bacteria do not form redistribution networks but are able to recover fast once the environment becomes favorable (Nguyen et al., 2018). Yet, long-term exposure to extreme abiotic stress can constrain their immediate recovery (de Vries et al., 2018; Jurburg et al., 2017; Thakur et al., 2021), but some bacteria can indeed survive by finding refuge in fungal mycelium, e.g., during drought periods (Jansson and Hofmöckel, 2020). The different responses of soil bacteria and fungi to climate extremes potentially lead to compositional shifts in soil microbial communities, which may influence microbial-mediated soil processes (de Vries et al., 2018; Jassey et al., 2018), such as soil organic matter conversion or carbon sequestration (Jansson and Hofmöckel, 2020; Reichstein et al., 2013).

Belowground invertebrates

Belowground invertebrate organisms are the most diverse group of metazoans in terrestrial ecosystems, and they are generally considered vulnerable to drier soil conditions, as sufficient moisture is crucial for

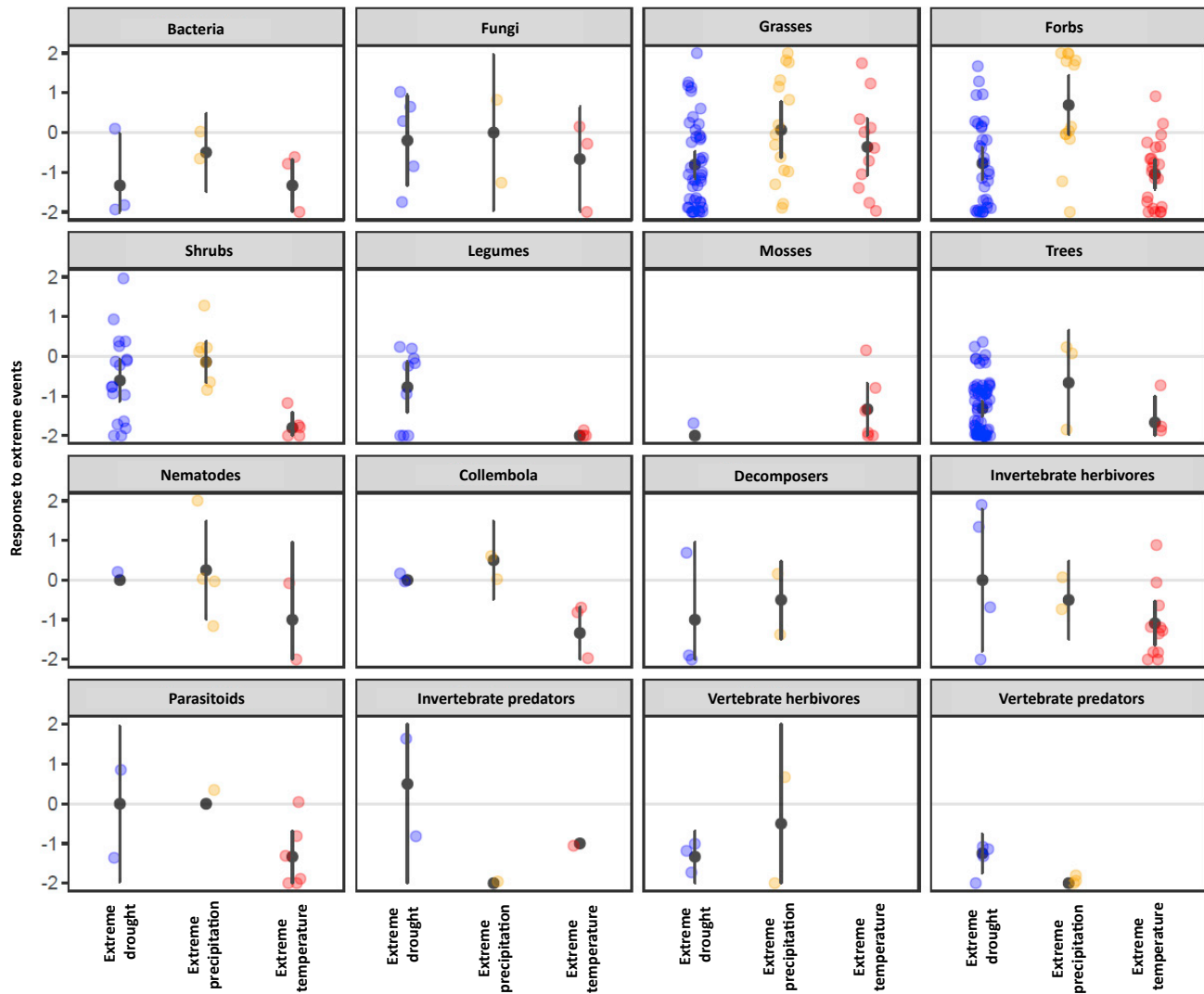


Figure 2. Detailed overview of responses of 16 functional groups to three climate extremes

For some functional groups, lack of cases per climate extreme prevented the standard errors around the overall mean. This figure is intended only to provide a general overview of how various functional groups of terrestrial ecosystems may respond to a given climate extreme. Each dot represents a unique response.

their foraging success and dispersal (Schimel, 2018; Thakur et al., 2018, 2020b). However, they can utilize soil habitats to buffer higher temperature and move through the soil profile via water films (Barnett and Johnson, 2013; Thakur et al., 2020b). Given the highly compact three-dimensional structure of soils (Thakur et al., 2020b), we suspect that invertebrates living in soils could find cold and moist spots during extreme drought and temperature events although this may eventually depend on the availability of microhabitats.

The most abundant metazoans with nearly 4.5×10^{20} individuals or approximately 0.3 gigatons (van den Hoogen et al., 2019) are free-living soil nematodes that regulate soil functions, such as mineralization of nutrients and plant productivity (Neher, 2010). Nematodes together with Collembola, known for their roles in soil organic matter decomposition and as an important consumer of soil fungi (Rusek, 1998; Thakur and Geisen, 2019), were the most commonly studied taxonomic groups of belowground invertebrates in our literature review. Rare responses of nematodes were both positive and negative; for Collembola we only detected a single negative rare response to an extreme event (extreme heat, Figure 2) (Holmstrup and Bayley, 2013; Torode et al., 2016). Nematode responses to temperature extremes vary among genera (Ilieva-Makulec and De Boeck, 2013) and can depend on their association to plants, which may provide soil

microhabitats with enough moisture, such as inside plant roots, which negate the effects of extreme droughts (Thakur et al., 2017a). Alternatively, several nematode species can produce “dauer larvae” that can survive unfavorable conditions for at least several months (Yeates, 1987). Some Collembola species can prevent water loss by upregulating their osmotic pressure even when the soil water potential reaches the level at which plants may permanently wilt (Holmstrup and Bayley, 2013). In contrast, some Collembola species can be vulnerable during extreme warm winters: the abundance of soil dwelling Collembola species decreased when winter temperatures were experimentally increased to about 5°C in a northern Sweden site (Bokhorst et al., 2012). However, litter dwelling Collembola were less affected, indicating that Collembola could have different adaptations to temperature changes that also could lead to shifts in community composition during temperature extremes. These results indicate that although soil invertebrate communities may not be changing much due to climate extremes, there may still be some winners and loser species, most likely depending on their habitat preferences. Moreover, despite the vast diversity of invertebrate taxonomic groups in soils, our review also highlights that climate extreme studies are limited to a few taxonomic groups of belowground invertebrates, which undermine our ability to understand soil invertebrate responses to anthropogenic climate change.

Plants

Plants were the most studied life forms across climate extreme studies in terrestrial ecosystems (Figure 1). Trees, mosses, and legumes showed the highest frequency of rare responses to climate extremes among the six plant functional groups studied in our review, and majority of these responses were negative (Figure 1). Although grasses, forbs, and shrubs showed rare responses less frequently than the other functional groups of plants, their rare responses were also mostly negative, with only few positive responses mainly to extreme precipitation events (Figures 1 and 2, Table S1).

The overwhelmingly negative response of trees to extreme droughts (Figures 1 and 2) is likely related to higher water tension at low soil water levels, which may prevent the uptake of water by tree roots (Choat et al., 2018). However, this also varies among tree species occurring in the same region (Choat et al., 2018). For example, (stem) hydraulic conductivity (Box 1 for the definition) of an oak species (*Quercus fusiformis*) was reduced by 75% during an extreme drought compared to a 90% reduction in an elm species (*Ulmus crassifolia*) (Kukowski et al., 2013). Despite the lower reduction of hydraulic conductivity, the oak showed higher mortality (34%) than the elm (14%) (Kukowski et al., 2013), which could relate to several other hydraulic traits that determine tree mortality during extreme droughts, for example, root morphology (e.g. rooting depth) (Choat et al., 2018) and sap flow (Kukowski et al., 2013).

Mosses were highly and consistently vulnerable to extreme temperature and dry conditions (Figures 1 and 2). For example, the productivity of a common peat moss (*Sphagnum fallax*) decreased by more than 50% when exposed to extreme dry and warm conditions (Bragazza et al., 2016). Some studies also indicate that extremely dry conditions combined with increased temperatures harm mosses and lichens more compared to vascular plants, particularly in alpine or arctic areas (Bjerke et al., 2011; Brancaleoni and Gerdol, 2014). Mosses are, in addition, more vulnerable to climate extremes than lichens owing to their sensitive phenological stages of organ development (Bjerke et al., 2011). Winter warming in sub-Arctic heathland for instance reduced net photosynthetic rate in mosses (up to 48%) but not in co-occurring lichens (Bjerke et al., 2011).

Grasses and forbs generally showed similar frequency of negative rare response to extreme droughts but slightly differently to extreme temperature and precipitation (Figure 2). Although, some grasses may suffer more from extreme droughts than forbs, which could be related to the deeper roots that forbs can grow compared with the shallower roots of grasses (Zeiter et al., 2016). Forbs with lignified stems (woodier) could also withstand severe water stress due to lower risk of embolism (Box 1) during extreme droughts (Lens et al., 2016). A greater vulnerability of grasses to drought could further relate to lower root porosity and nutrient storage compared with forbs. These two traits enable plants to resist drought (Van Der Knaap et al., 2014). However, some grasses, e.g., the common native European grass *Holcus lanatus*, can benefit when higher temperatures enhance soil nutrient mineralization (Kreyling et al., 2015). Common or dominant plant species may also be the ones to respond the most to climate extremes (Gitlin et al., 2006). The dominant legume in several temperate grasslands, *Trifolium repens*, for instance suffered the most when exposed to extreme drought and heat compared to forbs and grasses from the same plant community (Dreesen et al., 2015). Nutrient depletion and/or the inability to acquire limiting nutrients, such as

phosphorus, during climate extremes have been suggested as a key determinant of the poor performance of dominant plants (Dreesen et al., 2015; Gutschick and BassiriRad, 2003). Moreover, common legumes such as *T. repens* are additionally vulnerable to extreme droughts due to their shallow root systems and inability to regulate water losses from their leaves (Skinner et al., 2004; Zwicke et al., 2013).

There are also within-plant species variation in their responses to climate extremes that could potentially be explained by intra-specific trait variability. For instance, intra-specific variability in a number of plants explained the shifts in plant functional composition of sub-alpine grasslands by nearly 50% more than what species turnover (i.e., changes in species composition) could explain during an extreme drought (Jung et al., 2014). A meta-analysis further revealed the importance of phenotypic adjustments in specific leaf area (SLA) of grass species as a key requisite for drought resistance (Wellstein et al., 2017). In general, higher intra-specific trait variability could enhance the chance of species survival during climate extremes (Jump and Peñuelas, 2005). For instance, greater intra-specific variation in hydraulic traits of trees alleviates tree tolerance to extreme droughts (Anderegg, 2015).

Aboveground invertebrates

Rare responses of aboveground invertebrates to climate extremes were mainly reported in insects that were either herbivores or their enemies, i.e., predators and parasitoids (Figures 1 and 2, Table S1). Among these groups, there were greater cases of rare negative responses in herbivores and parasitoids, whereas predators showed a mix of positive and negative rare responses (Figure 1). However, given the extremely lower number of studies on invertebrate predators, our results on their rare response frequency should be interpreted with caution (Figure 1). In addition, most of these responses were negative rare responses to extreme temperature (Figure 2). Some studies showed an increase in insect herbivory after extreme temperature, possibly due to reduced plant defenses (Rouault et al., 2006; Walter et al., 2012), which in turn enhanced insect herbivore densities. There were also several cases of decline in insect herbivore abundance mainly as a result of extreme temperature (Table S1), which may relate to failure of insects in meeting their metabolic demands at high temperatures (Sentis et al., 2014). Extreme temperatures in combination with changes in the abundance of their enemy can further influence insect herbivores (i.e., via predation and/or parasitism). For instance, aphid abundances severely declined at extreme high temperatures only in the presence of their predators (Sentis et al., 2017). The same experiment also reported the absence of trait plasticity (e.g., change in body size to lower metabolic rates) with increasing temperatures in aphids, which further contributed to their population decline (Sentis et al., 2017). In fact, similar results were found for belowground invertebrates such as Collembola that had greater vulnerability to predation and an absence of phenotypic plasticity at high temperatures (Thakur et al., 2017b). The response of invertebrates to climate extremes may therefore depend on their metabolic adjustments along with how they are affected by other trophic groups (Harvey et al., 2020).

Negative rare responses in parasitoids to extreme temperatures could be due to their high dependency on the life cycle of their hosts. It has been suggested that changes in host responses during climate extremes are likely to phenologically isolate parasitoids from their hosts (Harvey, 2015; Jeffs and Lewis, 2013). For instance, when the rate of parasitoid evolution cannot match with the rate of phenological shifts of their hosts during climate extremes, it is more likely that parasitoid populations will suffer (Jeffs and Lewis, 2013). Indeed, negative responses of parasitoids to extreme temperature were mainly driven by such phenological isolations (Duan et al., 2014; Wetherington et al., 2017).

Aboveground vertebrates

Vertebrate herbivores and predators only showed negative rare responses (Figure 1), and these responses stem from studies investigating either extreme drought or to a lower extent extreme precipitation events. We found no study on extreme temperatures in our review. Overall, the aboveground vertebrates were the least studied group in our review despite their important roles in aboveground-belowground interactions in terrestrial ecosystems (Figures 1 and 2). Vertebrate herbivores influence aboveground-belowground interactions mainly through their foraging (plant feeding, dung production) and movement (e.g. trampling), which can directly alter belowground processes and indirectly affect belowground organisms (Bardgett and Wardle, 2003, 2010; Sitters and Olde Venterink, 2015). Loss of aboveground vertebrates can therefore alter the coupling between a wide range of aboveground and belowground organisms and could lead to a net loss of ecosystem functioning (Risch et al., 2018).

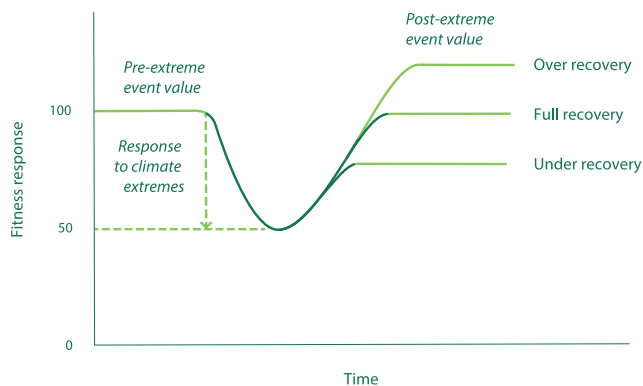


Figure 3. Three types of recovery to climate extremes after a decline in species fitness or demography-related response

For the ease of illustration and to illustrate the rare response, we chose to show a 50% decline in any fitness-related measure during a climate extreme event. After the climate extreme, species begin to recover over time and can attain one of the three types of recovery. The y axis values are hypothetical.

Large vertebrate animals are often considered to be more vulnerable to disturbances than smaller ones due to their slower growth and reproduction rates (Powers and Jetz, 2019; Ripple et al., 2014). A recent synthesis indeed revealed that large-body-sized vertebrates are at a disproportionately higher extinction risk due to anthropogenic climate change than smaller-body-sized vertebrates (Dirzo et al., 2014). Although we obtained too few cases to compare small- and large-body-sized vertebrate responses to any of the climate extremes, all vertebrates, from muskrat to elephant, showed negative responses to climate extremes (Figures 1 and 2, Table S1). For example, an extreme drought in Tanzania in 1993 dramatically increased elephant calf mortality (Foley et al., 2008). Similarly, a global study recently showed that more than 20% of primate species, particularly those living in south east Asia and west Africa, were highly vulnerable to extreme droughts due to their highly fragmented habitats (Zhang et al., 2019). Greater vulnerability of large vertebrate herbivores to climate extremes is generally caused by severe declines in their food resources, which are more probable in fragmented landscapes. Moreover, the survival of large vertebrates during climate extremes depends on behavioral adjustments during resource shortages and physiological stress, which is often obtained from experience (Ducatez et al., 2020; Foley et al., 2008; Sergio et al., 2018). For instance, calf mortality in elephants during Tanzanian extreme drought mentioned earlier was much lower for experienced than young mothers (Foley et al., 2008).

Vertebrate predators showed a higher frequency of rare responses to climate extremes than herbivores (Figures 1 and 2); this was even true for small-body-sized vertebrate predators. For example, an insectivore bird (*Vireo atricapilla*) became highly susceptible to brood parasitism (by *Molothrus ater*) with severe effects on its population size during an extreme drought in North America (Colón et al., 2017). Food scarcity during climate extremes also enhance the vulnerability of vertebrate predators. For example, during and after extreme precipitation in Northern Australia, python populations severely declined (~30 times reduction in populations in about 20 years) mainly due to a dramatic decline in their main prey, dusky rats (Ujvari et al., 2016). Another study showed that site occupancy of the semi-aquatic American mink declined by more than 20% when its preferred prey, the muskrat, declined by more than 50% during an extreme drought (Ahlers et al., 2015).

RECOVERY AFTER CLIMATE EXTREMES

As we found that all 16 taxonomic/functional groups respond negatively (and often showing a rare negative response), it is important to understand if and how they recover after climate extremes have stopped (Figure 3). Moreover, variation in responses of different functional/taxonomic groups during or immediately after climate extremes is important to link how terrestrial biodiversity and ecosystem functioning may change after climate extremes (Smale et al., 2019). Species-specific or functional-group-specific changes in community composition depend on how organisms continue to respond after a given climate extreme (Figure 3). Here, we define such post-climate extreme responses broadly as “recovery,” which could be measured at the species, community, or ecosystem level. Theoretical studies use species recovery, e.g., measuring their population dynamics, to predict community stability, for example, by using the time taken

to reach a certain population level, assuming it to reach its equilibrium (Donohue et al., 2016; Scheffer et al., 2015). Here, we adhere mainly to empirical patterns of species recovery without necessarily relying on the equilibrium assumption. Community recovery is often expressed as an aggregated measure of a community, for example, biomass or species diversity within the community. Community recovery can also be measured in terms of how species interactions recover after climate extremes, such as by studying the network characteristics of ecological communities (Moreno-Mateos et al., 2020; Morriën et al., 2017). Finally, ecosystem recovery is studied either as the recovery of metacommunities (Box 1) and/or by focusing on a given ecosystem process, such as ecosystem productivity or decomposition rates.

In general, at the species level (measured often in terms of their population or biomass), empirical studies report three different types of recovery (Figure 3): (1) species attain similar response values of control or nonextreme event period (full recovery) (Cheplick, 2017), (2) species exceed the control or nonextreme event values (overrecovery or overcompensation) (Hofer et al., 2017), and (3) species are unable to reach the control or nonextreme event values after several time units (underrecovery) (Jurburg et al., 2017; Thibault and Brown, 2008). We found several cases where species showed a strong population decline, often a decline exceeding 50% or more compared with controls, but their populations also fully recovered within few years after an extreme drought (Valliere et al., 2017; Xu et al., 2017a). For example, annual biomass production per unit of rainfall in grassland plants recovered to predrought levels within two growing seasons despite an 82% decrease during the extreme drought (Xu et al., 2017b). Such full and rapid recovery of grassland communities was often triggered by an increase in the abundance of nonnative plants (Valliere et al., 2017; Xu et al., 2017b). We also found evidence for a population decline of species during an extreme event followed by either over- (Pol et al., 2010) or underrecovery (Rondeau et al., 2013; Zwicke et al., 2013).

We address two questions related to ecological recovery in this review. First, what ecological factors can help predict three types of ecological recovery? Second, how can we scale-up species (or functional/taxonomic group) and community level recovery to ecosystem recovery? To address the first question, we include five ecological factors to obtain an integrative understanding of species recovery after any climate extreme (Figure 4): (1) population size and its characteristics, (2) the availability of resources, (3) the effect of neighboring species, i.e., competitors and facilitators, (4) the availability of mutualistic partners, and (5) the extent of enemy pressure. Although these factors are among the most fundamental biotic forces that structure ecological communities at the local scale, their interactive roles in determining the recovery of species and communities after climatic extremes has rarely been discussed (Hillebrand and Kunze, 2020). To address the second question, we discuss how three types of species recovery could shift aboveground-belowground interactions and thereby the recovery of terrestrial ecosystems. For instance, once we obtain the information on how various species within a community are recovering, can we then use this information to predict shifts in aboveground-belowground interactions? And can we then also use this information to predict recovery and potential changes in terrestrial ecosystems (Bardgett and Caruso, 2020; Ratajczak et al., 2018)? As an example, let us assume that a keystone species or an ecosystem engineer species (either from aboveground or belowground subsystem) is not able to attain a full recovery after an extreme drought. If so, will underrecovery of that species change biotic interactions between the aboveground and belowground subsystems? Will shifts in biotic interactions between the two subsystems then alter mass and energy flow between the two?

Population size and its characteristics

Population size characterized by genetic diversity, recruitment capacity, or dispersal ability is one of the most fundamental biotic features of a species that determines its recovery, as it directly influences its reproductive success and thereby its fitness (Capdevila et al., 2020; Oliver et al., 2015). Species become vulnerable to local extinction when their population size drops to the lower limit (Dennis, 2002; Oliver et al., 2015), even after climate extremes have stopped. For example, a butterfly species (*Cupido minimus*) went locally extinct after an extreme heat event that reduced its population size to an extremely low number (Piessens et al., 2009). However, when a population can recruit fast, it has a greater likelihood to recover after an extreme event (Lloret et al., 2012). Several examples of such recovery patterns exist for plants. For instance, despite population declines of a pine tree species (*Pinus pinaster*) during an extreme drought, it fully recovered in post-drought years by augmenting its recruitment across forest patches (Madrigal-gonzález et al., 2017). Also, greater genetic variability that allows for a greater intra-specific trait variability helps populations to resist during climate extremes (Allen et al., 2015). Yet, the loss of genetic diversity when climate extremes reduce population size can constrain species recovery (Jump and Peñuelas, 2005). Finally,

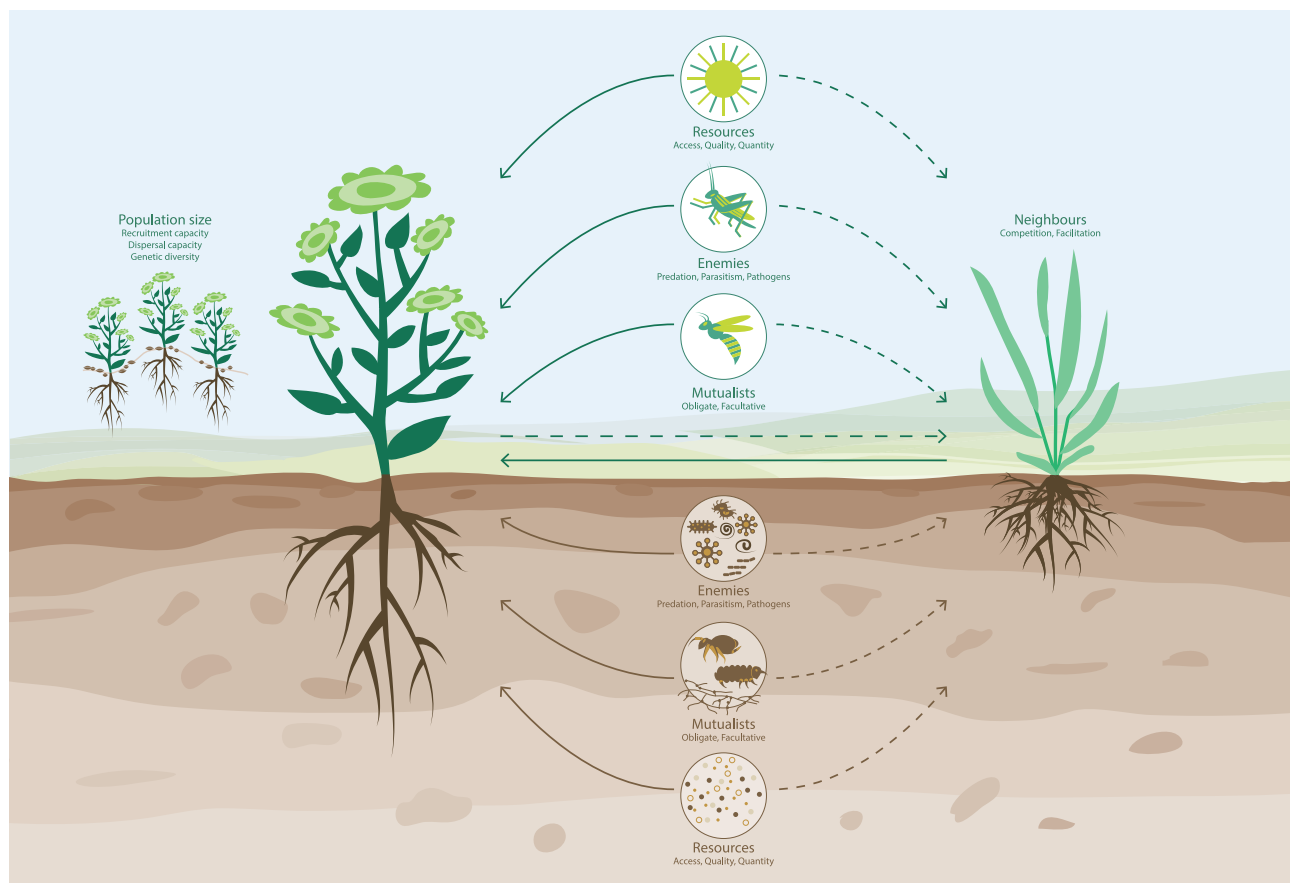


Figure 4. Five factors that affect species recovery in terrestrial ecosystems

(1) population size characterized by e.g., recruitment ability, or genetic diversity in population after climate extremes, and also the ability to disperse to favorable habitats; (2) the access, quality, and quantity of resources available for the recovering species; (3) the competitive and/or facilitative effects of the neighboring species; (4) the degree of positive effects from mutualists; and (5) the enemy effect from the predation and/or parasitism and/or pathogen infection on the recovering species. Interactive effects of these factors determine various type of species recovery (Figure 3). In the figure, we present the example of an herbaceous plant, illustrating that it interacts with both aboveground and belowground organisms during its recovery. Belowground resources for recovering plants are depicted via soil nutrients, whereas light availability is shown as an important aboveground resource. Thick arrows represent the “species recovery” perspective, whereas dashed lines represent the perspective of the “community recovery”, i.e., the same factor can have a different effect on two neighboring herbaceous species. For the sake of simplicity, community here refers to two plant species.

aboveground organisms can have an advantage to disperse faster compared to belowground organisms (Bardgett and Wardle, 2010; Berg et al., 2010; Van der Putten et al., 2001). For example, when habitats become resource limited after climate extremes, aboveground organisms can recover by dispersing into areas with more abundant resources. We still know little about the dispersal of belowground organisms (Thakur et al., 2020b), particularly how it would contribute to their recovery after climate extremes. However, soils with sufficient moisture facilitate the dispersal of many belowground organisms, which could facilitate their recovery by increasing their access to food resources (Erktan et al., 2020; Yang and van Elsas, 2018). We speculate that belowground recovery, therefore, strongly depends on how soil water availability changes during and after climate extremes.

Resource availability

The availability and quality of resources such as food and water often change dramatically after climate extremes (Yang et al., 2010), which subsequently influence access of species to these resources (Maron et al., 2015). In general, the availability of resources during climate extremes in aboveground and belowground context may increase in two ways: first, by an accumulation of dead organic matter caused by increased mortality of species (e.g., forest dieback during extreme drought) for many belowground consumers (Frank et al., 2015) and aboveground scavengers (Tomberlin et al., 2017) and second, due to a reduced ability of

species (e.g., lowered population size during climate extremes) to consume surplus resources (Maron et al., 2015). In resource-rich environments, early colonizer species are likely to thrive and attain full recovery even in a short period of time. After an extreme flood, which nearly doubled the amount of dead organic matter in temperate experimental grasslands in Germany, fast-growing grassland species indeed showed a full recovery within a growing season (Wright et al., 2015). In another study, several non-leguminous species showed overrecovery following the extreme drought mainly due to excessive soil nitrogen that was not consumed during the drought (Hofer et al., 2017). Changes in resource quality further affects recovery. An extreme drought reduced crude protein content in several plant species that were consumed by White-tailed deer by nearly 30%, which in turn negatively affect their recruitment after an extreme drought (Lashley and Harper, 2012).

Climate extremes can also trigger resource shortages; this can be a problem for higher trophic level organisms when their prey items are eliminated. For example, a 44% reduction in the survival rates of pythons (*Liasis fuscus*) after extreme floods was caused by a nearly 100% mortality of their prey (dusky rats) during that extreme flood (Ujvari et al., 2016). This resource shortage strongly limited the python recovery afterwards (Ujvari et al., 2016). If the response during a climate extreme is a large decline in species population size combined with a simultaneous decrease in their resources, the underrecovery of that species is a more plausible scenario due to resource bottlenecks (Maron et al., 2015). Resource bottlenecks occur more often in fragmented landscapes where resources for recovering species could become patchier and thereby less accessible. Recovering populations with greater dispersal ability can overcome such resource bottlenecks by moving to patches with greater resource availability. Indeed, studies have highlighted the importance of dispersal corridors for facilitating ecosystem restorations (Aavik and Helm, 2018; Damschen et al., 2019; Perino et al., 2019). As mentioned earlier, many belowground organisms have lower dispersal ability (Ettema and Wardle, 2002; Thakur et al., 2020b). Thus, we hypothesize that belowground resource bottlenecks could hamper the recovery of belowground organisms much more compared to their aboveground counterparts.

Effects of neighboring species (competitors and facilitators)

Neighboring species in this review refer to species living in closer spatial proximity of the recovering species (Figure 4). For a bacterium, closer proximity may be a few microns, whereas for a large vertebrate, it could be hundreds of meters. Closer spatial proximity essentially enhances the probability of biotic interactions of species with their neighbors. Such neighboring species can either constrain recovery through competition or promote recovery through facilitation. Competitive dynamics may shift during climate extremes, for instance by releasing sub-ordinate and rare species from strong competition by a declined abundance of the dominant species (Shi et al., 2015; Thibault and Brown, 2008). In those cases, release from competition promotes faster recovery of sub-ordinate and rare species. For instance, after an extreme flood in the Chihuahuan Desert, a previously rare desert pocket mouse (*Chaetodipus penicillatus*) turned into a dominant species mainly owing to flood-induced declines of the dominant rodent, the Merriam's kangaroo rat (*Dipodomys merriami*) (Thibault and Brown, 2008). Similarly, an extreme experimental drought in Australia promoted the establishment of a non-native grass (*Ehrharta erecta*) when the native grasses suffered from the drought (Manea et al., 2016). Climate extremes can, therefore, open windows of opportunities for non-native species to establish in habitats where native species either suffer more or are eliminated by climate extremes.

Although a release from competition may promote the recovery of competitively inferior species, facilitative interactions with neighboring species can boost species recovery particularly when competitive hierarchies remain unchanged after climate extremes (Saccone et al., 2009). For example, the presence of shrubs facilitated annual plant communities that are composed of fast-growing plant species with a one-year life cycle during an extreme drought in California, USA (Filazzola et al., 2018). These shrubs created favorable niches in which evapotranspiration was reduced (improved microclimate), which then led to annual plant dominance during the recovery period (Filazzola et al., 2018). As another example, a dung beetle species alleviated drought stress for a forb during an extreme drought by enhancing water retention in its burrows (Johnson et al., 2016). Such invertebrate ecosystem engineers (e.g. dung beetles, termites, ants, earthworms, etc.) (Byers et al., 2006) can therefore facilitate recovery of neighboring species via the creation of favorable microclimatic conditions (Thakur et al., 2020a).

Effects of mutualists

Ecological communities with higher numbers of mutualistic partners are often stable, particularly when the mutualistic interactions are specialized (Thibault and Fontaine, 2010). Accordingly, loss or gain in mutualist

interactions during climate extremes could influence species recovery (Angelini et al., 2016; Derksen-Hooijberg et al., 2018). Mutualism, both facultative and obligate, differs slightly from facilitation, as in mutualism both involved species must benefit (Bronstein, 2009). Species can negate abiotic stress by forming mutualistic partnerships with other species, which are often crucial for their persistence during climate extremes, and subsequent recovery. When abiotic stress of climate extremes disrupts mutualistic interactions (De Fouw et al., 2016; Harrison, 2000; Kiers et al., 2010), both survival and recovery of mutualistic partners are hampered, leading to biodiversity loss and deterioration of ecosystem functioning (Aslan et al., 2013). For example, drought events substantially reduced common grassland wildflower species with potential negative implications for their pollinators (Phillips et al., 2018).

Water availability in particular determines the strength of mutualistic interactions in aboveground and belowground subsystems, such as plant-pollinator interactions aboveground (Gallagher and Campbell, 2017) or plant-mycorrhizal interactions belowground (Bowles et al., 2018) (Figure 4). Plant-pollinator interactions may further depend on how water stress alters the functional composition of the pollinators. For instance, an extreme drought in the United Kingdom disrupted plant-pollinator interactions by reducing the abundance of specialist but increasing the abundance of generalist butterflies (De Palma et al., 2017). Mycorrhizal fungi in belowground subsystems often alleviate drought stress in their mutualistic partner plants (Begum et al., 2019; Jayne and Quigley, 2014; Ortiz et al., 2015), and thus can play an important role in the recovery of their partners. For instance, plants' adaptation to drought was assisted by belowground microorganisms that themselves adapted rapidly to drought (Lau and Lennon, 2012). For a better understanding of recovery patterns, we therefore need to consider how species involved in mutualistic partnerships co-respond during and after climate extremes.

Effects of enemies

The strength of trophic regulation during the recovery of species can vary depending on how climate extremes affect their natural enemies. Like competitive release from species of the same trophic level, species may also be released from their enemies (between trophic levels) during recovery. This is the case when predators, parasites, or pathogens suffer more from climate extremes than their prey or host does, as we found for both vertebrate predators and parasitoids in aboveground subsystems (Figure 2). Although we suggest that temporary enemy-free space can promote recovery of prey species (Lindmark et al., 2019), such habitats may also promote non-native enemy species. Such invasive enemies can have dramatic negative effects on recovering prey species, by altering their competitive interactions, for example by driving the local exclusion of competitively inferior native prey species (Doherty et al., 2016; Pringle et al., 2019). The eradication of invasive predators such as American mink (*Mustela vison*) from the British Isles substantially increased the recovery of a native otter (*Lutra lutra*) population, i.e., otter signs increased up to 80% when mink signs decreased from 80% to 20% (McDonald et al., 2007).

In some cases, enemy pressure may also increase after a climate extreme. For example, when recovering prey species are poorly defended against their enemies, and enemies are starved and/or are higher in numbers after the extreme event, the recovery of prey species can be severely constrained. Although empirical evidence of such scenarios is still lacking, it was shown that a generalist herbivore induced greater stress on a grass species in the period following extreme drought (Walter et al., 2012). It is well known that pathogen infections increase in forests after extreme drought, particularly when dry environments can substantially suppress tree defense against pathogens (Allen et al., 2015; Jactel et al., 2012). The role of both non-native and native enemy release and escalation after climate extremes needs more attention in empirical studies for improving our understanding of species recovery.

ABOVEGROUND-BELOWGROUND INTERACTIONS AND TERRESTRIAL ECOSYSTEM RECOVERY

Applying the information of species and community level recovery to understand the recovery at the ecosystem level is often challenging. These challenges mainly arise due to scaling problems, i.e., that information at lower-level hierarchy may not always be transferred to higher-level ecological hierarchy (Velend, 2010). In addition, it is a challenge to use the right metric to estimate ecosystem recovery. For example, if the density of all species within a community reaches the same pre-extreme event value after a few months or years, this full recovery could still lower certain ecosystem functions, such as decomposition rates, due to shifts in functional traits of the decomposer species; this often leads to shifts in organisms' functional impacts on ecosystem processes and an ecosystem recovery debt (Moreno-Mateos et al., 2020).

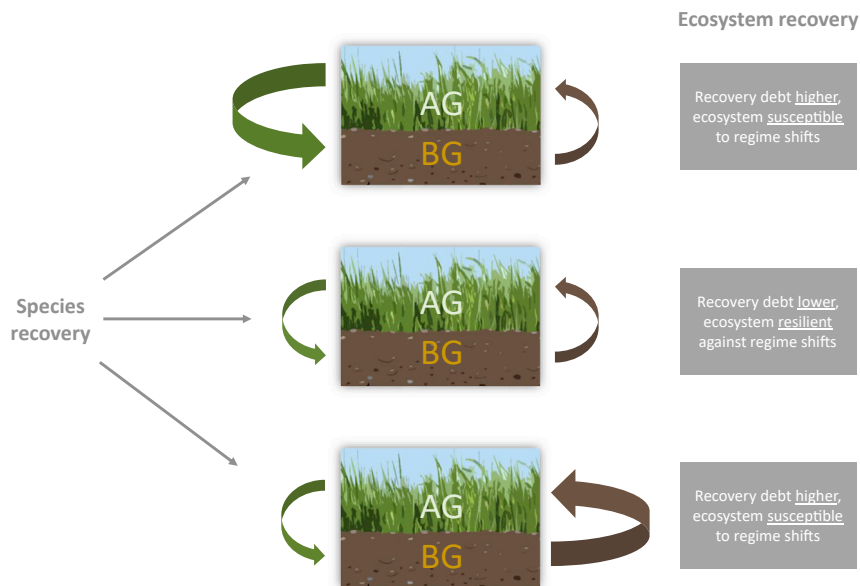


Figure 5. Species recovery can alter aboveground-belowground interactions in three possible ways (thicker arrows indicate higher flow of mass and energy from one subsystem to the other), which has various implications for (terrestrial) ecosystem recovery

When aboveground and/or belowground species (or community) recovery causes an imbalance in mass and energy flow between aboveground (AG) and belowground (BG) subsystems, recovery debt is likely to become higher. This increases the susceptibility of an ecosystem to dramatic changes in ecosystem functions, thereby pushing them toward tipping points and regime shifts. AG to BG mass/energy flows shown by green arrows and BG to AG mass/energy flows shown by brown arrows.

Many ecosystems feature lower functioning during the species (or community) recovery phase. For instance, a global synthesis revealed that ecosystem under recovery is characterized by annual deficits in species densities (up to 51%), diversity (up to 33%), and in ecosystem functions like elemental cycling, such as carbon cycling (up to 42%) and nitrogen cycling (up to 41%) (Moreno-Mateos et al., 2017).

Understanding shifts in aboveground-belowground interactions during the recovery phase can provide insights to link species to ecosystem recovery (Figure 5) (Kardol and Wardle, 2010) in broadly two ways: (1) ecosystems will have a higher recovery debt and will become more prone to dramatic shifts in ecosystem functioning when the species recovery alters the mass and energy input from aboveground to belowground ecosystems or vice versa; (2) ecosystems will have a lower recovery debt and greater resilience when the species recovery does not alter the balance of mass and energy flow between aboveground and belowground subsystems (Figure 5). Alteration in mass and energy balance between the two subsystems would mainly occur when recovery rates of aboveground and belowground species vary by a great margin (Thakur, 2020). For instance, when extreme drought results in a higher mortality of trees or aboveground vertebrates, their dead biomass enters belowground subsystems as mass and energy. Slower recovery of consumers of such inputs would result in an excess of nutrients in the belowground system. Similarly, when extreme temperatures increase decomposition rates and subsequently nutrient availability in belowground subsystems, but plants and aboveground organisms are unable to exploit these resources, it may then cause an imbalance of mass and energy flow between aboveground and belowground subsystems. A recent study even showed that photosynthetic supply from plants to their roots and thereby to soil microorganisms substantially decreased after the drought period, further indicating a drought-induced imbalance in energy flow between the two subsystems (Chomel et al., 2019).

Alterations in mass and energy flow between the two subsystems during species recovery can have multiple consequences for ecosystems. For instance, it is possible that non-native plant species become more successful, given that more resources remain unexploited by native plant species (Davis et al., 2000). Greater success of non-native plants could further hamper the recovery of native plants and their aboveground consumer species (Didham et al., 2005; Zavaleta et al., 2001), which in turn would increase the recovery debt. If

such recovery debts persist over longer time periods, terrestrial ecosystems will become more susceptible to dramatic alterations in their biodiversity and ecosystem functioning and therefore more susceptible to regime shifts (Berdugo et al., 2020). Such mass and energy imbalances between aboveground and belowground subsystem could be included in Earth system models to better predict ecosystem dynamics in a world with increasing climate extremes. Also, long-term experiments in different biomes with simultaneous measurements of aboveground and belowground biodiversity and ecosystem functions would allow to understand mass and energy flows and can thereby shed insights on which ecosystems are likely to have higher recovery debts.

LIMITATIONS OF THE STUDY

Although our review has several limitations, such as lack of quantifying the species- or functional/taxonomic-group-specific responses to a given climate extreme using meta-analytic techniques and restricting our review to only three climate extremes, we mainly caution readers about our arbitrary threshold (the 50% or more change relative to control conditions) to quantify an extreme or rare response to climate extremes. For example, a 50% reduction in bacterial population size and a 50% reduction in mammalian population size to climate extremes cannot be considered as the same extreme response, given their different pace of life and subsequent interactions with their environments. Indeed, the challenge is whether there can be a unified way to quantify a rare response to climate extremes across life forms. Our review is an attempt to provide a very simple overview of ecological responses to climate extremes across a variety of taxonomic/functional group, and in doing so, we certainly miss to provide a detailed overview of how a rare response within one group may have less severe implications on their fitness relative to another group where even a moderate response to climate extremes can have much severe consequences on their fitness.

OUTLOOK AND CONCLUSION

Climate extremes will continue to increase and get more severe in coming decades (Fischer and Knutti, 2015; IPCC et al., 2018a). Our literature review shows that taxonomic/functional groups of aboveground and belowground subsystem respond negatively to climate extremes, and occasionally their performance could decline as much as 50% and more. Despite the negative effects of climate extremes, most functional and/or taxonomic groups also show recovery over time. However, our current ability to predict how species, communities, and ecosystems recover remains limited.

We conclude that contemporary approach of considering population perspective alone will likely be insufficient for understanding and predicting species recovery. Identifying how the recovering species interacts with various biotic and abiotic factors will be crucial for a mechanistic understanding of recovery and hence for predicting the structure of ecological communities in a future world with more climate extremes. This approach, as well as the capacity of species to evolve (Grant et al., 2017), needs to be tested in their native habitats, on species that shift range under climate change (Chen et al., 2011; Wallingford et al., 2020), as well as on species that are (anthropogenically) introduced into new habitats (Essl et al., 2018; Ricciardi et al., 2017). Species or community recovery can inform ecosystem recovery by quantifying aboveground-belowground interactions during species recovery. The mass and energy flow between aboveground and belowground subsystems can be used as an indicator of terrestrial ecosystem recovery, for which methodological tools are already available, such as isotope labeling to quantify nutrient flow across trophic levels (Morriën et al., 2017; Potapov et al., 2018). Moreover, tools that combine empirical data and food web theory, such as energy flux in food webs (Schwarz et al., 2017), will play an important role in quantifying alterations in energy flow between the two subsystems. Both theoretical and long-term experimental studies are required to quantify how species density, diversity (including genetic), and processes (e.g., photosynthesis and decomposition) affect the overall mass and energy flow between the two compartments after a climate extreme. The species diversity of an ecosystem is often considered as a key determinant of its robustness against climate extremes (Isbell et al., 2015; Oliver et al., 2015). We stress that it will be further important to combine within-species diversity (e.g., intra-specific variability in traits) (Bolnick et al., 2011) along with between-species diversity in an ecosystem to predict species' responses to climate extremes both in aboveground and belowground subsystems.

Long-term experimental studies that cover large spatial scale (e.g., landscape level) would be particularly important for integrating species and community recovery to ecosystem recovery in relation to different dispersal and recolonization capacities of different groups of organisms. These approaches may provide relevant insights into the vulnerability of ecosystems for changes during and after the occurrence of climate

extremes and will be crucial for informing conservation and restoration strategies. Understanding species responses to climate extremes will accordingly be relevant for rewilding (Perino et al., 2019) and reforestation (Kemppinen et al., 2020) programs, as it will be crucial to restore species and systems that may perform well under changed conditions, and may further foster the recovery of other species (Thakur et al., 2020a). In fact, our conceptual framework aligns well with recent suggestion to quantify resilience for successful restoration and conservation projects (Pimm et al., 2019). For instance, restoration and/or conservation through identifying the main stressors (e.g., which climate extreme?), the characteristics of a system (e.g., quantifying aboveground and belowground diversity), the scale of management (e.g., spatial and temporal scale of ecosystem under study), and finally also the relevance to social and ecological metrics of success (Aslan et al., 2018) could be informed by measuring how climate extremes alter biotic interactions in terrestrial ecosystems. We believe that our proposed framework to incorporate aboveground-belowground interactions by acknowledging some of the key ecological interactions during and after climate extremes is an important step toward effective conservation and restoration in terrestrial ecosystems in a world where climate extremes are going to become more common and severe.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.104559>.

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AUTHOR CONTRIBUTIONS

MPT, ACR, and WHvP conceived the idea. MPT performed the literature search and wrote the manuscript with inputs from ACR and WHvP.

DECLARATION OF INTERESTS

The authors declare no competing or financial interests.

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