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# Extreme environments in a world of new extremes

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## Abstract

Extreme environments, whether defined by climate, soils, or disturbance, at landscape or micro-scales, are prevalent across Earth's surface and have long served as crucibles for ecological and evolutionary insights. Many foundational theories were developed in deserts, cliffs, ultramafic soils, and other harsh systems. Yet, these environments are usually studied in siloed, discipline- or ecosystem-specific contexts, rather than as part of a generalizable macroecological model. Here, we propose reframing extreme environments as a unifying framework for ecology, one that can explore the boundaries of ecological processes, detect the limits of functional trait strategies, and improve predictions of ecosystem responses to emerging global extremes. We also revisit key ecological concepts, including species coexistence, succession, spatial ecology, and functional trait theory, through the lens of extreme environments, and identify emerging research opportunities that arise when these systems are treated as central to, rather than siloed in, ecological theory. Rather than exceptions or outliers, these systems should be recognized as central to understanding the resilience, adaptability, and future trajectories of life on Earth.

KEYWORDS
atypical, extreme, extremophile, harsh, resilience, stress, tolerance

## EXTREME ENVIRONMENTS ARE PREVALENT

Extreme environments span a wide range of conditions, from rock cliffs, hot springs, and salt flats to arid woodlands, fire-maintained savannas, and glacial landscapes. However, what constitutes an extreme environment is inherently relative, making a precise and quantitative definition challenging (Boyd et al., 2016; Lortie et al., 2004). We therefore define extreme environments broadly as those where climatic, edaphic, or disturbance regimes impose conditions outside the tolerance of most

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neighboring species, severely limiting biomass accrual, reproduction, or survival (Grime, 1979; Rampelotto, 2013). For example, ultramafic soils, with their high concentrations of heavy metals, exclude most plants except for those with specialized adaptations for metal exclusion, tolerance, or hyperaccumulation (Brady et al., 2005). Although quantitative definitions are useful for defining climatic extremes (i.e., Rahmstorf & Coumou, 2011), they are less applicable across the diverse stressors and scales that characterize extreme environments. Furthermore, extreme conditions can arise from persistent edaphic properties (e.g., pH, salinity) or disturbance regimes (e.g., fire, avalanche) rather than climate alone, further complicating a singular definition of extreme environments. Nevertheless, extreme environments are widespread across the globe and have played crucial roles in the evolutionary history of Earth.

Extreme environments occupy nearly half of Earth's terrestrial surface (Figure 1) and occur within many biodiversity hotspots (Hulshof & Spasojevic, 2020). Even

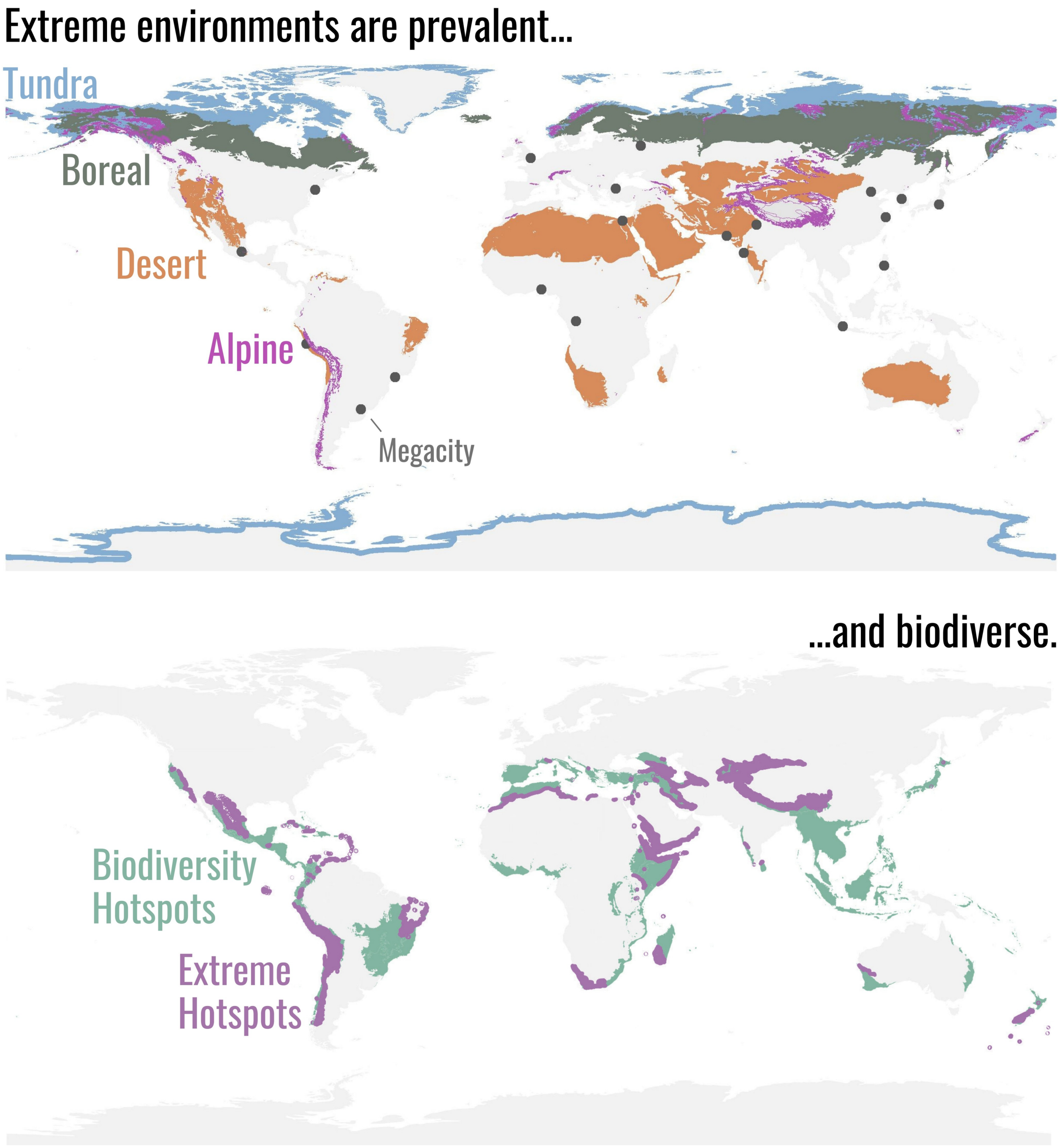

**FIGURE 1** Extreme environments are prevalent. Together, tundra, boreal, xeric, and alpine biomes encompass 45% of Earth's total land area (based on Olson et al., 2001; Testolin et al., 2020; and a total land surface area of 129,718,824 km$^2$ from Food and Agriculture Organization, 2025). The distribution of the world's 20 largest urban environments (megacities) highlights the global scale of a new type of extreme, usually embedded within non-extreme environments (city data from the *maps* R package; Becker et al., 2025). Extreme environments are also biodiverse. Many biodiversity hotspots occur in extreme environments (Hulshof & Spasojevic, 2020; hotspot data from Mittermeier et al., 2011).

within seemingly benign ecosystems, microenvironments can impose extreme local conditions (e.g., salt marshes, geothermal vents, cliffs, and urban heat islands). These extreme environments give rise to extraordinary hotspots of life. Yet, the organisms that flourish in these unusual environments find such conditions perfectly ordinary. This anthropocentric lens, shaped by our own physiological constraints, has influenced how we perceive environments and how we view the adaptability of life (Rothschild & Mancinelli, 2001). As a result, extreme environments have often been treated as exceptional rather than central to Earth's ecological and evolutionary theater (sensu Hutchinson, 1965). Moreover, extremophiles have arisen across most major lineages across the eukaryotic tree (Merino et al., 2019; Rappaport & Oliverio, 2023), underscoring that what we perceive as exceptional may in fact be foundational to understanding the origins, resilience, and fundamental processes of life on Earth.

The ubiquity of extreme environments is not just spatial but also temporal, extending throughout geological history. Earth's five major mass extinction events were driven by extreme climatic, geochemical, or disturbance events, fundamentally reshaping plant and animal evolution. For example, rapid environmental shifts during the Cretaceous–Paleogene period likely accelerated the diversification and expansion of angiosperms (Ramírez-Barahona et al., 2020) and insects (Peris & Condamine, 2024). As a result, many extant species descend from lineages that survived these extreme geological events (Grant et al., 2017). Today, the rising frequency and intensity of extreme events is contributing to phenological and behavioral shifts, local population collapses, and biodiversity loss (Bailey & van de Pol, 2016). This connection between the spatial prevalence of extreme environments and the increasing temporal frequency of extreme events highlights the need to better integrate extreme environments into ecological research and theory (Maček et al., 2016). As more than half of the global human population is projected to experience extreme climatic events (Doan et al., 2023), advancing our understanding of ecological processes in the context of extremes is ever more pressing.

## EXTREME ENVIRONMENTS WERE FOUNDATIONAL TO ECOLOGY

Ecological theory has disproportionately developed in mesic, high-productivity ecosystems (Martin et al., 2012). Yet, some of its most influential insights have emerged from extreme environments. Early experiments on ultramafic soils laid the foundation for research on plant phenotypic plasticity and local adaptation (Clausen et al., 1947), while alpine treelines and tundra ecosystems informed plant ecophysiology and stress tolerance (Billings & Mooney, 1968). In particular, arid and semi-arid ecosystems have yielded key advances in community and ecosystem ecology: competition–equilibrium models between trees and grasses were developed in African savannas (Walter, 1939), and species coexistence theory in deserts (Chesson et al., 2004). Global theories on nutrient cycling were inspired by work in tundra, heathlands, and deserts (Aerts & Chapin, 1999; Belnap et al., 2005; Chapin et al., 1980). Island biogeography was expanded through sky islands (Brown, 1971; Love et al., 2023), and state-and-transition models transformed rangeland ecology (Briske et al., 2005). Other landmark contributions, such as the keystone species concept (Paine, 1966) and the stress gradient hypothesis (Bertness & Callaway, 1994), were born from work in extreme environments. Even specialized substrates such as ultramafic (e.g., serpentine) and gypsum outcrops have become model systems in ecology and evolution (Escudero et al., 2015; Harrison & Rajakaruna, 2011; Moore et al., 2014).

There are no other concepts that better illustrate the contributions of extreme environments to ecological theory than competition and coexistence theory. Species coexistence is a cornerstone of ecological theory, often conceptualized through competition and niche partitioning, where species compete for limited resources and those with similar niches cannot stably coexist (Tilman, 1994). Foundational coexistence models were developed in temperate grasslands (e.g., Cedar Creek; Tilman, 1982) and forests (e.g., Hubbard Brook; Whittaker et al., 1974), environments where competitive exclusion is assumed to be a primary driver of community composition. However, extreme environments expand this competition-centric lens by emphasizing the importance of positive interactions (Bertness & Callaway, 1994; Delpiano et al., 2024). For example, in deserts and alpine environments, nurse plants facilitate the establishment of other species by buffering temperature extremes, reducing desiccation, or improving soil conditions (Cavieres et al., 2014; Delpiano et al., 2024). Facilitation can be particularly important for rare species in extreme environments, thereby enhancing diversity (Soliveres et al., 2015). Nitrogen sharing by species in gypsum outcrops, a largely unstudied mechanism, can also promote coexistence (Montesinos-Navarro, 2023). These insights into the importance of facilitation as a mechanism of species coexistence have been formalized in the stress gradient hypothesis (Bertness & Callaway, 1994), a key example of how extreme environments have advanced theory. This legacy of foundational insights from coexistence theory to the stress gradient hypothesis illustrates how focused research in extreme systems can yield broad theoretical advances.

## YET MANY PROMINENT ECOLOGICAL THEORIES FAIL IN EXTREME ENVIRONMENTS

Even though extreme environments were foundational to ecology, such systems are often treated in isolation, confined to ecosystem-specific case studies or dismissed as botanical curiosities (Bradshaw, 1971). As a result, many prominent theories are insufficient at explaining or predicting the patterns and processes that shape biodiversity in extreme environments. In this section, we revisit core ecological concepts (succession, spatial ecology, and functional traits) through the lens of extreme environments to explore their limitations and then propose ways in which to expand their relevance for anticipating ecological responses in an increasingly extreme world (Table 1).

### Successional theory

Classical succession theory proposes that ecosystems undergo predictable, directional changes in community composition driven by species replacement, competition,

**TABLE 1** Key research challenges and opportunities for integrating extreme environments into ecological theory and synthesis.

| Research challenge | Opportunity | Model systems for testing | Examples |
|---|---|---|---|
| Spatial identification of extreme environments | Integrate globally resolved soil, climate, disturbance, and biome maps | Atypical soils (ultramafic, gypsum, karst), high-salinity wetlands, and alpine summits | Hulshof (2024), Hulshof and Spasojevic (2020) |
| Underrepresentation of extreme environments in trait databases | Expand trait campaigns to target environmental extremes | Gypsum and ultramafic flora, coastal halophyte communities, deserts, cliff flora, alpine, and tundra | Gross et al. (2024), Samojedny et al. (2022), Thomas et al. (2020) |
| Lack of standardized trait protocols for stress traits | Develop protocols for measuring stress-tolerant traits relevant in extreme environments, (e.g., plant elementomes on atypical soils) | Desert Long Term Ecological Research sites (e.g., Jornada, Sevilleta), atypical soils | Pavanetto et al. (2024) |
| Inadequate phylogenetic analyses across extreme lineages | Employ phylogenetic comparative methods (e.g., multivariate phylogenetic variance decomposition, phylogenetic generalized least squares, and ancestral state reconstruction) | Asteraceae, Brassicaceae, Caryophyllaceae, and Saxifragales | Folk et al. (2020), Palacio et al. (2022) |
| Poor understanding of trait coordination under stress | Use phylogenetic comparative methods to test for coordinated trait evolution in extreme environments | Hyper-arid deserts, montane grasslands, and edaphic islands | Matesanz et al. (2018), Rodgers and Gomez Isaza (2023) |
| Underuse of extreme environments in predictive ecological models | Embed extreme environment variables in macroecological and Earth system models | All extreme environments | Groner et al. (2023) |
| Insufficient models linking abiotic stress to species interactions | Develop trait-based coexistence models that incorporate stress-mediated facilitation and asymmetric interactions | Coastal dunes, alpine zones, and rocky outcrops with patchy microhabitats | Hart and Marshall (2013), Takimoto (2020) |
| Poor understanding of whether extreme environments promote diversification via isolation | Use phylogeographic and genomic analyses to test for divergence and speciation | Sky islands, edaphic islands (ultramafic, gypsum), saline lakes, alpine summits, arid ecosystems, and cliffs | Folk et al. (2020), Guillory et al. (2024), Wootton et al. (2025) |

*Note*: Each row identifies a conceptual or methodological gap, proposes a solution or research direction, and provides ideal systems for testing along with example references. Examples span edaphic, climatic, and disturbance-driven extremes and illustrate how targeted work in extreme environments can advance predictive, trait-based, and macroecological frameworks.

and environmental modification (Poorter et al., 2023). These models were developed primarily in forests and grasslands, where biomass accrual and resource availability increase over time. However, extreme environments often deviate from these expectations. Harsh abiotic conditions like nutrient-poor soils, drought, salinity, or temperature extremes can arrest succession, slow down community turnover, or shift the mechanisms driving assembly. For example, deserts exhibit slow primary succession due to limited water and nutrient inputs (McAuliffe, 1994), while gypsum outcrops show decoupling between time since disturbance and community development (Martínez-Duro et al., 2010). In Arctic ecosystems, extreme conditions prevent classic successional replacement, resulting in long-term persistence of early pioneer species (Svoboda & Henry, 1987), defying classical models. In extreme ecosystems, facilitation, resource-use, microhabitat buffering, and stochastic colonization may outweigh competitive exclusion as drivers of community structure (Caccianiga et al., 2006; Flores & Jurado, 2003). Rather than exceptions, these patterns suggest that extreme environments can help refine successional theory by expanding it to encompass systems where resource scarcity, stress tolerance, and disturbance frequency dominate.

## Island biogeography and spatial ecological theory

Although extreme environments were central to broadening island biogeography theory (through the study of sky islands), they challenge core assumptions due to strong environmental filters, infrequent colonization, and the resulting importance of historical and evolutionary processes. Classical models assume that species richness in discrete habitats, such as islands or habitat patches, results from a balance between immigration and extinction rates shaped by patch size, isolation, and spatial configuration (MacArthur & Wilson, 1967). However, extreme environments often violate these assumptions. Despite being fragmented and isolated, harsh abiotic conditions in extreme environments, like extreme temperatures, poor soils, and water scarcity, limit species dispersal and establishment regardless of spatial proximity or patch size. For example, across ultramafic outcrops, colonization and community assembly are constrained more by physiological tolerance and evolutionary history than by spatial proximity (Harrison et al., 2006), accumulating highly adapted species in situ over millions of years (Anacker et al., 2011; Kruckeberg, 1991). This contrasts sharply with classical metacommunity frameworks, which often assume frequent dispersal among patches and predictable source–sink dynamics (Leibold et al., 2004). The evolution of sky island flora does not meet the basic assumptions of island biogeography theory either. Like edaphic islands, sky islands lack a clearly defined mainland and thus a colonization source. Furthermore, their floras are shaped by lowland lineages rather than by in situ diversification or island-to-island dynamics. In the European Alps, nearly 50% of sky-island flora are derived from non-alpine taxa, while only 6% represent in situ cladogenesis (Wootton et al., 2025), underscoring the limited temporal and taxonomic scope of classical models.

Improved spatial and temporal data resolution can enhance our understanding of these systems, but the mismatch between classical theory and extreme environments reflects deeper structural limitations. We suggest that advancing theory for these systems requires modifying fundamental assumptions about species pools, community assembly, and turnover dynamics (Vanschoenwinkel et al., 2025), rather than just adjusting for scale. Integrating non-equilibrium dynamics, trait-based filtering, and phylogenetic frameworks offers a more realistic approach that recognizes the outsized role of abiotic filters and deep evolutionary constraints in structuring biodiversity in extreme systems (Harrison & Rajakaruna, 2011; Schrader et al., 2021).

## Plant ecophysiology and functional ecology

A foundational assumption in plant ecophysiology is that plant fitness is determined by carbon gain, and water use maximizes photosynthetic returns (Blonder et al., 2023). However, plants in extreme environments challenge this carbon-centric paradigm. For example, desert plants sustain high transpiration to cool leaves and avoid heat damage (Aparecido et al., 2020), while mangroves expend energy to exclude salt and maintain osmotic balance (Reef & Lovelock, 2015). These examples illustrate that in extreme environments, water use strategies are multifaceted, often decoupled from photosynthetic efficiency, and better understood through a framework of stress tolerance rather than carbon maximization (Roddy, 2023).

Beyond water, extreme environments highlight additional plant resource strategies that challenge conventional functional trait approaches. For example, secondary metabolites and non-structural carbohydrates are often considered nonessential, yet are emerging as a universal plant response to stress in many extreme habitats (Fernández-Marín et al., 2020). The elementome can also provide insights into plant functioning on atypical soils where nutrient imbalances are a major limiting factor for growth and survival (e.g., Hocedez et al., 2024; Palacio et al., 2022). Despite their importance, such traits and extreme ecosystems remain underrepresented in global trait databases, which tend to focus on core axes of variation (e.g., specific leaf area, wood density) from mesic environments (Gross et al., 2024). Recent efforts to measure plant-specific leaf area in ultramafic systems revealed an unexpectedly wide range of values, including some of the lowest values ever recorded (Samojedny et al., 2022), suggesting that systematic inclusion of extreme systems in trait sampling initiatives could expand the known global trait spectrum (i.e., Gross et al., 2024) and uncover unique trait combinations, increasing the accuracy of trait shift projections under future climates. While it is technically possible to contribute any trait data to repositories, many stress-tolerance traits critical for extreme environments, like salt exclusion efficiency, metal tolerance capacity, foliar nutrient balances or water storage strategies, are rarely measured across taxa at macroscales. This underrepresentation reflects the fact that such traits are not yet considered part of the standard trait toolbox in functional ecology. As a result, the breadth of plant strategies in extreme environments is poorly captured in large-scale syntheses (Gross et al., 2024; Rajakaruna, 2018).

Moreover, stress tolerance itself encompasses a variety of mechanisms (e.g., avoidance, tolerance, and -philic strategies) that are often conflated in traditional trait frameworks, such as Grime's (1979) CSR model. For example, both metal hyperaccumulation in ultramafic plants (Manara et al., 2020) and sulfur accumulation in gypsum plants (Palacio et al., 2022; Ruiz et al., 2003) can evolve through multiple independent pathways, each with distinct physiological underpinnings. Sulfur accumulation in gypsum plant specialists seems further linked to lineage-specific metabolic pathways (Moore et al., 2014; Palacio et al., 2022). Functional trait approaches that do not explicitly differentiate these mechanisms and their phylogenetic basis risk oversimplifying the diversity of adaptive strategies in extreme environments.

To improve predictive models of plant responses to environmental extremes, we argue for a targeted expansion of trait-based approaches (Table 1). This includes prioritizing traits linked to abiotic stress tolerance, limiting resources, and biotic interactions under extreme conditions, as well as integrating phylogenetic and evolutionary perspectives (Craine et al., 2012). By doing so, we can build a more complete understanding of the functional strategies that enable persistence and resilience in a world of increasing extremes.

# EXTREME ENVIRONMENTS OFFER WORLDS OF INSIGHT IN A WORLD OF NEW EXTREMES

Extreme environments have long served as natural laboratories (e.g., Merino et al., 2019; Picó et al., 2022; Rajakaruna et al., 2014; Rappaport & Oliverio, 2023; Rothschild & Mancinelli, 2001; Vanschoenwinkel et al., 2025), yet their insights remain siloed across systems and disciplines. We propose that reframing extreme environments as a unifying axis of abiotic stress, spanning climatic, edaphic, and disturbance gradients, offers a path to synthesize fragmented insights and extend ecological theory (Table 1). In this section, we highlight how extreme environments offer powerful opportunities to test ecological theories related to stress tolerance, facilitation and succession, to develop innovative, nature-based tools for anticipating ecological responses to global change, and to provide Earth-based analogs for understanding the potential for life on other planets.

Extreme environments are particularly well suited for studying stress tolerance and resilience under current and future conditions of intensified global change (Doerner, 2020). Research on extreme environments has already uncovered novel metabolic pathways and phylogenetically diverse stress-tolerant microbes (Rappaport & Oliverio, 2023). Plant lineages thriving in extreme environments such as Asteraceae, Brassicales, Caryophyllales, and Saxifragales possess traits essential for chronic abiotic stress, traits increasingly important under scenarios of prolonged drought, heat, and salinity. Yet, many adaptive mechanisms remain poorly understood. Expanding trait-based ecology to include resilience to multiple, interacting stressors, traits often found in extreme environments but underrepresented in global databases, can fill critical knowledge gaps. Targeting lineages dominant across extreme environments is a promising place to start.

Extreme environments also provide powerful natural experiments for testing hypotheses about the evolution and coordination of stress-tolerance traits (Anacker et al., 2011; Kühn et al., 2021), especially as global change intensifies abiotic stress worldwide. Phylogenetic comparative methods, such as multivariate phylogenetic variance decomposition (MPVD), can reveal whether particular traits have enabled success under harsh conditions (e.g., Palacio et al., 2022). Traits that confer advantages under rarity, resource scarcity, long-distance dispersal, or pollinator limitation (Astegiano et al., 2015; Grubb, 1998; Nogales et al., 2012) may be increasingly favored, much as the Cretaceous–Paleogene extinction event favored fast-growing angiosperms (Blonder et al., 2014). Extreme environments offer obvious test cases for understanding how stress-tolerance traits evolve and confer resilience to novel stressors because they encompass all types of stress at all spatial scales. Specifically, theory predicts that tolerance to one stress may confer resilience to others (Chapin, 1991; von Wettberg et al., 2014). Indeed, calcium tolerance appears to be a prerequisite for gypsum tolerance (Moore et al., 2014; Palacio et al., 2022), and tolerance to bare and open habitats appears to be a prerequisite for ultramafic soil tolerance (Armbruster, 2014). These examples suggest that stress-tolerance traits may act as preadaptations to emerging environmental extremes (Rodgers & Gomez Isaza, 2023). Additionally, some stress-tolerance traits appear to confer dual advantages. Metal hyperaccumulation in ultramafic plants, for example, also deters herbivores (Strauss & Cacho, 2013). Such trait syndromes, whether shaped by shared selection, evolutionary constraint, or both, may define ecological resilience and reveal coordinated trait complexes that are critical under future stress (Ackerly et al., 2000; Craine et al., 2012). By explicitly leveraging extreme environments for phylogenetic and functional comparisons, it may be possible to forecast which lineages and trait strategies are likely to persist in a rapidly changing world.

Gradients of environmental stress provide a critical axis for theoretical innovation, especially under global change. The stress gradient hypothesis and related work (e.g., Holmgren & Scheffer, 2010; Maestre et al., 2009) suggest that facilitation becomes more important than competition as stress increases. Many extreme environments also exhibit structurally distinct interaction networks, such as asymmetric facilitation (e.g., nurse plants), keystone mutualisms, and strong reliance on microhabitat refugia (Soliveres et al., 2015), challenging assumptions of symmetrical competition or resource partitioning in classic coexistence theory. Conversely, stress may reduce competition but simultaneously select for species that are less tolerant of competition, maintaining competitive exclusion in harsh environments even under weak interactions (Chesson & Huntly, 1997). By systematically incorporating extreme environments across diverse geochemical and hydrological stressors (e.g., Lima et al., 2022; Randé et al., 2024), we can better understand when and why positive interactions dominate (Michalet et al., 2014), how competition shifts to facilitation under chronic stress (and when and why it does not), and how these dynamics evolve under increasing environmental extremes (Brooker et al., 2008).

The generally slower rates, and sometimes absence, of succession in extreme environments provide valuable analogs for ecosystems increasingly impacted by both acute and chronic disturbances (e.g., floods, droughts, hurricanes). Identifying species and traits that confer resilience in extreme systems could inform restoration strategies, assisted migration, and ecosystem management under global change (Mota et al., 2004; Rajakaruna & Boyd, 2014). The naturally patchy structure of extreme environments resembles the fragmented landscapes resulting from habitat loss and modification, offering insights into persistence, connectivity, and adaptation (Matesanz et al., 2018). Extreme environments, like deserts, saline landscapes resulting from sea-level rise, and urban heat islands, are projected to expand (Reynolds et al., 2007), making it necessary to understand the traits and strategies of the species that already thrive there (see Kühn et al., 2021). These stress-tolerant species are likely to be the evolutionary pioneers of the world to come. Identifying the traits that predict success under these emerging conditions is thus key to forecasting ecological change.

Extreme environments have long served as crucibles of biological innovation. Elevated and sustained speciation rates (Harvey et al., 2020) and rapid evolution under abiotic stress (Grant et al., 2017; Li et al., 2014) suggest that extreme environments can act as evolutionary hotspots. This aligns with broader concepts of ecological and evolutionary insurance (e.g., Loreau et al., 2021) where biodiversity in extreme environments may provide novel adaptations that enhance resilience to emerging stressors. This evolutionary potential has already inspired a range of nature-based solutions. Applications span agriculture, design, and biotechnology: stress-tolerant crops (Rajakaruna et al., 2006), plants to extract precious metals and rare earth elements (Rylott & van Der Ent, 2025), passive cooling strategies inspired by Indigenous desert architecture, cliff plants as analogs for vertical urban gardens (Lundholm, 2006), and PCR technology developed from thermophilic bacteria enzymes, to name a few.

Finally, extreme environments provide important analogs in astrobiology. Many of the abiotic stressors that define Earth's extreme habitats, like high salinity, desiccation, extreme temperatures, and nutrient scarcity, closely parallel conditions on Mars, and natural satellites of Jupiter (Europa) and Saturn (Enceladus) (Schulte et al., 2006; Thombre et al., 2020; Vance & Melwani Daswani, 2020). For example, serpentinization, a chemical reaction between water and ultramafic rocks, produces hydrogen and methane which are considered a possible energy source for microbial life on Mars and early Earth (Schulte et al., 2006; Vance & Melwani Daswani, 2020). Similarly, crystallization water in gypsum supports plants (Palacio et al., 2014) and microbes (Huang et al., 2020), pointing to an alternative Martian water source. These examples push ecological theory beyond carbon- or photosynthesis-centric models to include chemosynthesis and sulfur or methane metabolisms. Far from speculative, such research has underpinned major funding programs by the National Science Foundation, National Aeronautics and Space Administration, and the European Union (Rothschild & Mancinelli, 2001) where extreme terrestrial environments underpin models of habitability and life-detection technologies (e.g., Higgins et al., 2024). Rather than a departure from ecology, this perspective underscores the value of extreme environments as fundamental systems for evaluating the limits of life.

# EXTREME ENVIRONMENTS ARE EMERGING FRONTIERS

Extreme environments are not outliers, but fundamental components of Earth's biosphere. Historically, they have been central to advancing ecological and evolutionary understanding, whether through foundational work in plant physiology, coexistence, or island biogeography. These systems have repeatedly revealed processes and mechanisms that generalize beyond their harsh settings but also reveal limitations of current models. Extreme environments thus offer powerful test cases for expanding ecological theory to new frontiers, from understanding stress tolerance mechanisms to informing planetary habitability models. Their unique conditions challenge assumptions, reveal alternative strategies, and underscore the adaptability of life. A deliberate, systematic, macroecological focus on extreme environments as a unified framework is both timely and necessary to equip ecology with conceptual tools and models for a world of new extremes.

## AUTHOR CONTRIBUTIONS

**Catherine M. Hulshof:** Conceptualization (lead); analysis (supporting); visualization (lead); writing—original draft (lead); writing—review and editing (equal). **Pablo Tejero Ibarra:** Conceptualization (supporting); writing—review and editing (equal). **Nishanta Rajakaruna:** Conceptualization (supporting); writing—review and editing (equal). **Sara Palacio:** conceptualization (supporting); analysis (supporting); writing—review and editing (equal).

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Mittermeier et al., 2011; Olson et al., 2001; Testolin et al., 2020) are available as follows: https://databasin.org/datasets/23fb5da1586141109fa6f8d45de0a260, https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2, and https://doi.org/10.6084/m9.figshare.11710002.

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