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Abstract

Global change is a multifaceted, unprecedented crisis hitting the life support system of our planet. Among global changes, climate change is regarded as one of the most grave threats to biodiversity because of its direct impacts on species and ecosystems integrity and because of its indirect consequences through synergistic effects with other global change factors such as biological invasions. The challenges presented to either reduce or mitigate this biodiversity crisis derived from climate change require novel synthesis and innovation in ecological and evolutionary theory. Positive species interactions within and between trophic levels can play a key role in the resilience of ecological communities. Depending on the tolerance of nurse species to different aspects of climate change, communities can be more or less resilient to those changes. This knowledge has important implications for both natural communities and agroecosystems. Further, our fundamental understanding of the role of positive interactions can also enable both effective conservation and restoration levers in space and time.

This special issue includes studies addressing the role of facilitative interactions on the response of ecological systems to climate change. Key concepts examined included stress, gradients, nurse species, spatial scale, translocation, phylogenetics alongside physiochemicals, and variation in the capacity of species to buffer changes. Alpine, tundra, drylands, and temperate forests were directly tested, but all salient principles were relevant to all ecosystems including a contribution on soil biota and also a call to more open data and collaborative science. Together, this corpus of work highlighted the significance of facilitative interactions in mitigating many of the effects of climate change on biodiversity.

Keywords

Facilitation, positive interactions, nurse, foundation species, climate change, restoration, resilience, biodiversity

Introduction

Since Darwin (1859), the study of the outcome of net interactions between individuals has been fundamental to the development of theories in ecology and evolution and the understanding of the mechanisms promoting biodiversity. This is a simple, yet profound starting point. Examining what happens, and why, when individuals of the same or different species co-occur, and how we can predict the outcome of these co-occurrences on emergent community properties such as productivity and resilience, still inspires many of the research agendas in the natural sciences today (Sandifer *et al.* 2015). The implications of these studies feed into complex theories that model and predict biodiversity through space and time and catalyze conceptual developments in resilience, conservation, and responses to large-scale changes (Diefenderfer *et al.* 2021). During the 20th century, ecology focused heavily on negative interactions including competition and predation as the principal mechanisms underlying ecological patterns and diversity (Agrawal *et al.* 2007) However, researchers began to document that not all species interactions were detrimental, and the realization that species can benefit from each other prompted a shift in understanding how communities are structured (Bertness & Callaway 1994; Bruno *et al.* 2003; Kinlock 2019).

Facilitative interactions are defined as non-trophic interactions between species that increase the average individual fitness of at least one of the species involved, with a myriad of mechanisms underlying these interactions (Callaway 2007). For example, in drylands, drought-adapted plants (so-called nurse or foundation species) allow more stress-sensitive ones to establish below their canopies, where the environmental conditions are improved (Franco & Nobel 1989; Valiente-Banuet *et al.* 2006). Similarly, in forests, thermal amelioration below the forest canopy protects understory species acclimated to cooler temperatures from being replaced by species with a higher thermal optimum (Bhatta & Vetaas 2016; De Frenne *et al.* 2013). In animals, grazing by one species can enhance the habitat or food availability for another as for example zebras that graze on tall grasses, which makes shorter grasses more accessible for gazelles (Dangles et al. 2018). Facilitation can also contribute to attenuating environmental stress among microbial strains (Jorna *et al.* 2024; Silveira Martins *et al.* 2016). Based on a solid foundation of experimental and theoretical work (e.g. Gross 2008; Kéfi *et al.* 2007; Lawrence & Barraclough 2016), contemporary facilitation studies have challenged our understanding of major ecological processes in community ecology and innovated our understanding of biodiversity and species specificities (Bruno *et al.* 2003; McIntire & Fajardo 2014).

Climate change is altering our world and the species and ecosystems therein (Intergovernmental Panel on Climate Change (IPCC) 2023), leading in some cases to hotter and drier conditions, with a higher frequency of extreme events (Diffenbaugh *et al.* 2017; Ummenhofer & Meehl 2017), threatening biodiversity, especially in vulnerable ecosystems, such as drylands or alpine ecosystems. When improved local environmental conditions are generated by nurse species, the microclimate experienced by the beneficiary species becomes more decoupled from the actual climate (Lenoir *et al.* 2017). Facilitative interactions can thereby potentially mitigate the effects of climate change and play a key role in the ability of ecological communities to cope with increasingly harsh or more stressful physical environments (Malhi *et al.* 2020). Understanding the relative capacity for facilitation to mediate the responses to climate change of different organisms and communities, as well as to inform models, is essential to advance biodiversity science and our understanding of their response to upcoming changes; This is especially important considering the tidal wave of changes that ecological systems are undergoing. Here, contributions were compiled that evaluated the role that facilitative interactions can play in climate change scenarios, where organisms, communities and ecosystems are experiencing drier and warmer climates.

Contributions

A total of seven unique contributions examined the relative importance of facilitation in mediating climate change impacts on biodiversity in different communities. The authors explored plant communities in arid and semi-arid systems, mountains, and temperate forests as well as soil communities. A summary of the key themes and high-level findings is displayed in Table 1.

At local scales, well-documented facilitative effects foster the growth and survival of other species (Brooker *et al.* 2007; Callaway 2007). For example, in this special issue, Lortie (2024) shows that, in drylands of California, direct effects of nurse species buffer diversity losses to a changing climate. In the same vein, in experiments conducted in a Mediterranean semi-arid site, Danet *et al.* (2024) found that facilitation by nurse plants improved the performance (biomass and survival) of species diverse ben-eficiary communities under water stress conditions. Interestingly, in that study, the species richness of the beneficiary communities was found to play a major role in the net effects that nurses have on the survival and biomass of the beneficiaries, suggesting that facilitative interactions are more likely to occur in species-diverse communities (Danet *et al.* 2024).

More is not always more beneficial however in ecology, and we need to examine the relative importance of non-linearity in buffering capacities, and whether facilitation interactions function consistently across biotic and abiotic gradients. Facilitation is expected to be maintained as long as the nurse is itself not duly impacted by the change (Jones *et al.* 2010). There is certainly no guarantee that this is the case, and novel research must examine this potentially critical limitation in facilitation as a conservation and restoration tool. In an alpine ecosystem, Cavieres *et al.* (2024) experimentally demonstrated that warmer temperatures were beneficial for the nurses thereby maintaining the ecological impor-tance of facilitative interactions for native species, but not for the non-natives. The absence of need for facilitation for non-native species with warmer conditions calls attention to potential synergistic effects between global change drivers (i.e. biological invasions and climate change) in the already vulnerable alpine habitats. Thus, sensitivity of nurse species to environmental change and the provenance of the associated species in a community are key themes highlighted in this research contribution.

Facilitation is expected to increase in frequency and importance as the environmental harshness level increases (Stress Gradient Hypothesis or SGH, Bertness & Callaway 1994). Lortie (2024) predicted that positive effects of the two shrub species studied on species richness increased with increasing local temperatures. Climate change could thus reverse the sign of plant–plant interactions for shrub species that currently have a negative RII on richness as warming temperatures reduce competitive pressures and increase the importance of shrub facilitation effects. Conversely, as stress decreases, facilitation is expected to decrease in importance. Danet *et al.* (2024) found that the positive effect of nurses on beneficiaries shifted to a negative one when stress was lowered (i.e. under watered conditions). Both alpine and dryland research in this special issue (and beyond) directly test the relative importance of variation in the effects of stress on gradients on the resilience and stability of nurse species in mitigating climate effects on biodiversity. Novel research could thus scale-up even further as previous syntheses have done

(He *et al.* 2013) to explore similarity in trends and even more importantly tipping points on gradients across multiple ecosystems in the buffering capacity that nurse species in plant and in animal communities provide to anthropogenic change. We must also move from populations to communities in our studies to advance novel syntheses (Hart 2023) and expand the scope of the species tested to better integrate plant-animal interactions in a changing climate and also soil biota (Jorna *et al.* 2024) and other organisms that can underpin entire networks of different taxa. This call for diversity in thinking and collaboration is both implicit and explicitly invoked in this special issue. We echo this critical sentiment. Open science in facilitation research will further and enable next-generation and more rapid syntheses (Strømme *et al.* 2022). There is significant complementarity in not only the concepts but also the experimental designs, importance of scales tested in different studies, and data that can better and more directly test connectivity within and between species and heterogeneity in the climate that species experience (Brigham & N. Suding 2024).

The expected increasing importance of facilitation with increasing stress has positive consequences: it can help communities survive through time despite climate change, especially species-diverse ones (Danet *et al.* 2024). However, this increased facilitation also comes at a cost: communities are becoming more dependent on facilitation, especially since species are pushed to the boundary of their optimal niche by climate change (Verdú *et al.* 2024), meaning that there are more maladapted species in the community (and beneficiaries shift to lower stress profiles; (e.g. Danet *et al.* 2024)). So, facilitation and its benefits hold provided that the nurses themselves can cope with the environmental changes experienced. If nurses suffer from climate change and/or are targeted by land-use change, dramatic cascading effects can be expected at the community level (Losapio & Schöb 2017). This is the well-known 'double-edge sword' effect of facilitation, where facilitation increases productivity and species richness but also comes at the cost of increased fragility for the corresponding ecological communities (Danet *et al.* 2021; Gross 2008; Kéfi *et al.* 2007, 2016). It can also come at the cost of facilitating exotic, invasive species (Lucero *et al.* 2019) thereby indirectly shifting communities.

A deeper understanding of how nurse effects are affected by climate change is likely fundamental to the development of more robust facilitation theories. If climate change exacerbates a main stressor of the community (e.g. water availability), it is expected to eventually outweigh other possible benefits of the facilitator as stress increases because there are less resources available, and therefore more competition for resources: facilitation can vanish and even switch to competition (Garcia-Fayos *et al.* 2020; Maestre & Cortina 2004; Tielborger & Kadmon 2000; Zhang *et al.* 2018). Along these lines, Verdú et al. (2024) found that *Quercus ilex* (a beneficiary species) was pushed out of its climatic optimum in stressful habitats in semi-arid and sub-humid Mediterranean drylands in Spain. Further, spatial association between nurses and facilitated species disappeared in the semi-arid but not sub-humid populations, suggesting an erosion of the facilitated signal under stressful conditions (extinction of the interaction) and the possible expected extinction of the facilitated and less adapted species. This strongly supports the emergent theme in this special issue that direct study of nurse species is a critical research priority. If these specific species can withstand change, then we have a solid indicator and starting point for understanding and managing communities, at least in plants, but likely in many other systems as well. This short-cut is common in many facilitation studies, and we do not mean to imply that this is the only path forward at all. Nonetheless, theory and experiments that consider plant-plant interactions, at least in some dimensions, and their ecological roles in responding to climate change and to one another will engender connecting different studies and systems and hence synthesis. Harmonizing terms, data, and some of the experimental designs including explicit tests for the importance of scale and multiple-taxa will promote restoration and translocation practices that are evidence-informed based on the relative likelihoods that some species can hold on and facilitate other species - preferably natives.

The importance of nurse species does not underscore the importance of scale. The effect of facilitation on ecological communities is often thought of at the scale of the individual, but, in this special issue, Brigham (2024) stressed the consequences of micro-environmental modifications at other spatial scales since local changes affects the landscape connectivity and heterogeneity, with important consequences for persistence, metapopulations dynamics and species movements. In particular, facilitation can help species shift their range. Including such effects is important for e.g. species distribution models. This is a novel contribution to both theory and how we can instrument and test for climate effects at scales relevant to the challenges and species at hand.

With the ongoing climate change, we are conducting a global experiment on all the species and ecosystems on the planet. Global change is a reality that is clearly echoed and amplified by changes in biodiversity. This raises the challenge of predicting the future of biodiversity and of unveiling the mechanisms that allow nature to cope. Altogether, the studies of this special issue highlight a number of mechanisms by which facilitation can mitigate the effect of climate change:

amelioration of the abiotic environment (which leads to complementarity, change in competitive dominance, and trait plasticity; Danet *et al.* 2024), fostering asynchronous response by adding heterogeneity (Brigham & N. Suding 2024), and fostering species migration via landscape connectivity (Brigham & N. Suding 2024). These results highlight that maintaining and supporting nurse species is a potentially pivotal approach in the face of projected increase in drought conditions for many drylands across the world. At the minimum, we must use what we know about the species we still have in all systems - in particular drylands and the alpine show that some species have a demonstrated capacity to buffer change. Leveraging these species can will help preserve biodiversity (Danet *et al.* 2024; Lortie *et al.* 2024) and maintain this role potentially even under harsher environmentally conditions (Cavieres *et al.* 2024), although not forever (Verdú *et al.* 2024). Thus, nurses can be seen as a set of powerful nature-based solutions (Lortie *et al.* 2024). Nonetheless a note of caution is pointed out in Michalet *et al.* (2024) on the consequences of assisted translocation: because the current accelerating pace of climate change prevents long-lived tree species from responding fast enough to changing environmental conditions, translocation of conservative tree species could help them reach more suitable site but it would also reduce the buffering capacity of forests and decrease facilitation, leading to potential negative cascades in biodiversity and increases in fire frequency in temperate forests. Also, the important role of facilitators in modifying micro-climatic conditions should be considered to predict future species distributions (Brigham & N. Suding 2024). More generally, we need to further include facilitation and its consequences in contemporary theories of ecological communities, also beyond plant communities, as highlighted by Jorna *et al.* (2024) for soil bacteria communities.

Conclusion

Facilitative interactions among species play a critical role in mitigating the impacts of climate change on biodiversity, enhancing the resilience of ecological communities by improving local environmental conditions, fostering species coexistence, and supporting ecosystem functions. The studies presented in this special issue highlight the multifaceted benefits of facilitation across various ecosystems, including arid and semi-arid lands, temperate forests, and alpine regions. Future research must continue to explore the mechanisms and extent of facilitation across different ecological contexts, including soil microbiomes and other less-studied systems. When possible, leveraging nurse or foundation species is a prudent staring point. Species traits, provenance, and other key factors that play into more long-term, and at times indirect effects of facilitation will advance novel theory development. By integrating facilitative interactions into ecological and evolutionary theory, we can also better predict and manage the impacts of climate change on biodiversity, fostering more resilient and sustainable ecosystems.

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Table 1. A list of salient findings from contributions in facilitation mediating climate change impacts.

title	Authors DOI	objective/question	key contribution	ecosystems	future directions
Warming had contrasting effects on the importance of facilitative interactions with a cushion nurse species on native and non-native species in the high-Andes of central Chile	(Cavieres *et al.* 2024) 10.1111/oik.10296	Test the effect of nurse species loss under warmed and control conditions on both native and non-native species beneficiaries.	Warmer conditions benefited the growth of the nurses. Under warmed conditions, the importance of facilitation (for survival) was maintained for the native but not for the non-native species.	alpine	Warmer trends expected in mountains could promote the presence of more non-native species at high elevations.

Cross-scale facilitation: a framework for microclimate moderation of climate change	(Brigham & N. Suding 2024) 10.1111/oik.10241	Highlight the importance of local facilitation (micro-climate moderation) at the landscape scale	Importance of facilitation (micro-climate moderation) for connectivity and spatial heterogeneity	forum, alpine examples	Facilitator-moderated microclimate can contribute to better model the effect of climate change on species distributions
Species diversity promotes facilitation under stressful conditions	(Danet *et al.* 2024) 10.1111/oik.10303	Explore the role that facilitation will play in buffering changes associated with increasing droughts as well as the role of the species diversity of the beneficiary community	Net facilitation from the nurse happened when the beneficiary community is species-diverse and under drought	drylands	Facilitation by nurses contributes to mediating climate change through three mechanisms: complementarity, competitive dominance, and trait plasticity
The underground network: facilitation in soil bacteria	(Jorna *et al.* 2024) 10.1111/oik.10299	Discuss the impact of climate change on facilitation in soil bacteria, which underpin assembly of other biota	Phylogenetics, physicochemicals, and species-specificity is needed for soil biota experimentation to best support theory advances relevant to change and natural soil communities	forum, relevant to grasslands and forests *and all terrestrial ecosystems	FAIR data to support microbial synthesis science, connecting nurse species to soil bacterial communities, and upscaling the links between all levels of organizations to assess function and vulnerability

Patronus charm: a comparison of benefactor plants and climate mediation effects on diversity	(Lortie *et al.* 2024) 10.1111/oik.10292	Investigate the effect of nurse plants on biodiversity under changing climate	The positive effects of shrubs in drylands increased with increasing local temperatures or warming in trained models	Drylands	The direct effects of nurse plant species, native shrubs, can mitigate diversity losses to climate variations Role of nurse species as nature-based solutions (to offset climate change effects on other species)
Assisted migration in a warmer and drier climate: less climate buffering capacity, less facilitation and more fires at temperate latitudes?	(Michalet *et al.* 2024) 10.1111/oik.10248	Investigate the ecological and societal costs of translocated species (assisted migration from drier to wetter climate)	translocated species of more conservative tree species will reduce buffering capacity of forests and decrease facilitation leading to potential negative cascades in biodiversity and increases in fire frequency	temperate forests	diversify vertical structures of forests and increase heterogeneity in forest canopies to promote more sustainable balances in interactions and buffer these systems from change with implications for many systems including Mediterranean systems and concepts such as buffers and resilience