

Forum

Cross-scale facilitation: a framework for microclimate moderation of climate change

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There is widespread evidence that plants can facilitate associated species through microclimate moderation. These effects can act locally, by increasing vital rates via direct effects on the conditions experienced by the beneficiary, or at the landscape scale, by enhancing population persistence via environmental heterogeneity and connectivity. Despite linkages between microclimate moderation and the consequences of climate change, few frameworks apply the concepts of facilitation, connectivity, and heterogeneity through this lens. We highlight the utility of expanding current research on facilitators to better understand how their ability to buffer abiotic conditions, promote heterogeneity, and enhance connectivity could shape beneficiaries' response to climate change at multiple scales. We additionally suggest tools and methods for enhanced incorporation of facilitators into models of species response, centered around the integration of facilitator-moderated microclimates and species responses with the goal of better defining the scenarios under which facilitators could mitigate the effects of climate change. As climates continue to change, the consequences of microclimate moderation at local and landscape scales will become increasingly important to predict, understand, and manage biodiversity response.

Keywords: climate change, connectivity, facilitation, heterogeneity, microclimate, scale

Introduction

Just as we appreciate the shade of a tree on a hot day, the importance of small-scale climatic modification experienced by organisms – microclimates – is becoming more appreciated as essential to predicting species responses to climate change (Maclean and Early 2023). Microclimates, the atmospheric conditions near the earth's surface shaped by abiotic (e.g. topographic) and biotic drivers (e.g. vegetation) (Geiger 1950), define the conditions such as temperature, vapor pressure deficit (VPD), solar radiation, and soil water availability experienced by organisms. Despite great progress in the study of microclimates over the past several decades (Bramer et al. 2018), the focus remains on abiotic microclimates. Microclimates moderated by vegetation are largely overlooked

despite their demonstrated importance and prevalence across the landscape (Suggitt et al. 2011, De Frenne et al. 2021, English and Wright 2021).

Microclimate moderation by vegetation is a key facet of facilitation. Facilitation is a positive interaction which results in enhanced performance of the beneficiary without harming the facilitator (Bertness and Callaway 1994). We focus here on direct facilitative effects where the facilitator ameliorates abiotic conditions for the beneficiary. Facilitators can act as an individual (e.g. a cushion plant) (Reid et al. 2010) or as an aggregated unit (e.g. a forest or grassland) (Liancourt and Dolezal 2020, Aguirre et al. 2021, Bernath-Plaisted et al. 2023), making them globally widespread.

The role of facilitation via microclimate moderation can influence the effects of climate change. The effects of facilitators on the microclimate vary temporally as the facilitator responds to climate change, both from a trait perspective and from a range perspective (Myers-Smith et al. 2011). As the effects of facilitators may be enhanced or degraded by climate change, understanding the role of facilitators in moderating climate change is paramount.

Perhaps most importantly, facilitators can act at a range of scales (Forey et al. 2009). At the biological scale of the organism, well-documented facilitative effects foster the survival and growth of particular species (Brooker et al. 2008), reducing their vulnerability to climate change (De Frenne et al. 2013, Wright et al. 2015). Scaled up, facilitative effects can result in greater environmental heterogeneity and landscape connectivity with consequences for species' responses to climate change (Sanczuk et al. 2023). Biotically-driven environmental heterogeneity is shaped by the variability in vegetation structure, composition, and arrangement (Stein and Kreft 2015) while landscape connectivity is defined by the number and arrangement of habitat patches (Forman 1995). Environmental heterogeneity and landscape connectivity could promote an array of microclimates experiencing moderated effects of climate change, enhancing the survival of beneficiaries through increased population persistence within the current range and hastened range shifts or expansions, respectively (Fig. 1a).

To promote further study of the role that facilitators may play under climate change, we highlight three related effects of facilitators: 1) they can ameliorate the abiotic environment; 2) they can foster asynchronous population response to stressors by adding to the heterogeneity of microclimates across a landscape; and 3) they can foster species migration and movement by forming connected networks of similar, buffered microclimates. We discuss the importance of facilitators across these scales (Table 1), provide an overview of how facilitator research has incorporated effects under climate change to date, and suggest tools and methods for progressing the field.

Microclimates mitigate the effects of climate change via facilitation

Including the role of facilitation in a species' response to climate change may alter predictions based on macroclimate

or topographic microclimates alone (Lenoir et al. 2017, Haesen et al. 2023). The importance of facilitation under climate change depends on the match between the type of stressors facing the associated taxa and the type of stressors ameliorated, the magnitude and type of change offered by the facilitator, and the response of the facilitator to climate change.

Climatic match and magnitude of change

For a facilitator to moderate the effects of climate change for a focal organism, the relevant drivers in the relevant direction and magnitude must be affected. For example, forests have been found to decrease mean and maximum temperatures at a magnitude greater than that of global warming over the past century (De Frenne et al. 2019). Additionally, forests increased minimum temperatures, demonstrating decreased variance found under the forest canopy (De Frenne et al. 2019). This thermal amelioration has protected understory species acclimated to cooler temperatures from being replaced by species with a higher thermal optimum (De Frenne et al. 2013, Bhatta and Vetaas 2016). Microclimates can additionally be decoupled from the macroclimate (Fig. 2). For example, the microclimate experienced by the beneficiary is completely decoupled from climate change when a facilitator provides the same baseline climatic conditions (e.g. maximum daily temperature or VPD) despite continued climate change (Lenoir et al. 2017).

As organisms are exposed to multiple, often interacting, climate change drivers, facilitator-moderated microclimates may offer amelioration that is unique or of even greater magnitude than that provided by abiotically-driven microclimates. For example, global warming, in addition to increasing temperatures, can increase VPD (Dannenberg et al. 2022); plant mortality can be increased by exposure to extended periods at high VPD conditions (Will et al. 2013). However, facilitators can moderate temperatures and VPD through both biological (e.g. evaporative cooling via transpiration) and physical means (e.g. shading) making them uniquely poised to mitigate the effects of climate change.

Importantly, facilitators are able to not only moderate mean conditions but also extremes, from an hourly (Jucker et al. 2018, Sotomayor and Drezner 2019) to a seasonal basis (Myers-Smith and Hik 2013, Frey et al. 2016). For instance, during record high summer temperatures in the southern Sierra Nevada and San Bernadino Mountains, California spotted owls *Strix occidentalis occidentalis* preferentially roosted in cooler microclimates offered by denser forests with taller canopies (McGinn et al. 2023). These findings highlight the role that facilitators can play under extreme conditions, which is critical as extreme climate events are predicted to increase in frequency and intensity (Diffenbaugh et al. 2017, Ummenhofer and Meehl 2017). Because extreme conditions generally have a greater impact on survival and distribution than climatic means (Zimmermann et al. 2009), the buffering capacity of microclimates may play an important role in species' responses to climate change.

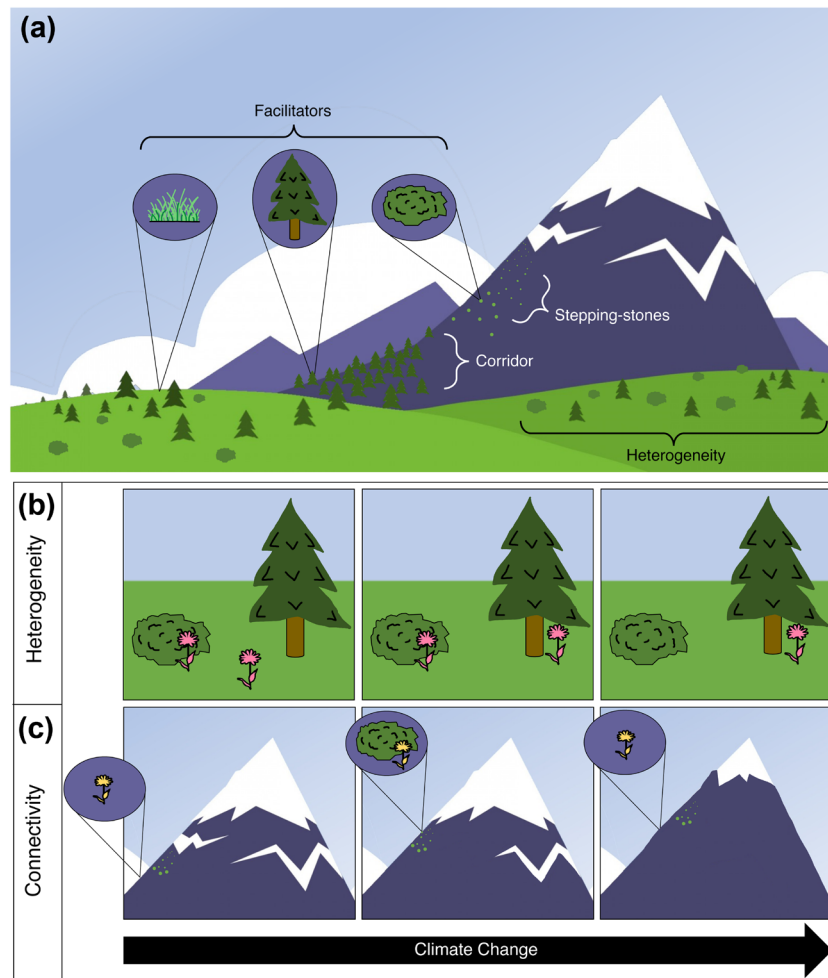


Figure 1. Examples of facilitators and the spatial arrangements likely to mitigate the effect of climate change on associated species. Heterogeneity is provided by a variety of patch types and structures while connectivity is enhanced by stepping-stones and corridors (a). Facilitators can shape a species response to climate change through facilitation, where the drivers of climate change (e.g. warmer temperatures) are moderated and potentially decoupled from the macroclimate and when scaled up, there are implications for environmental heterogeneity (b) and connectivity (c). Heterogeneity (b): the focal species responds to climate change differently in the different microclimates (tree, shrub, grassland), decreasing synchrony and increasing population persistence. Heterogeneity allows for the additional scenario where a focal species shifts its habitat preference to track its climatic niche under climate change (e.g. associating with the shrub and tree in the second panel as conditions in the grassland are no longer viable, and solely the tree in the third panel). Connectivity (c): the shrub acts as a stepping-stone, facilitating the range shift of the focal species into zones which are not currently suitable but will become suitable for the focal species under future climate change. Corridors would function similarly to enhance the rate of species movement in the face of climate change.

The facilitator's response to climate change

Because facilitators are living organisms, they can also amplify negative effects of climate change. For instance, previous research shows that when the limitation of a resource stressor (e.g. water availability) is exacerbated by climate change, association with a facilitator may no longer be beneficial as competitive dynamics start to dominate (Maestre et al. 2009, Michalet et al. 2014a, Butterfield et al. 2016). Whether the overall effect of the facilitator shifts to become competitive can depend on the other benefits provided by the facilitator. For example, the benefits of shade provided by a canopy-forming species (e.g. windbreak,

lower air and soil temperatures, lower solar radiation; Filazzola and Lortie 2014) may outweigh the increase in water competition (Chaieb et al. 2021). While it has been suggested that the transition from facilitation to competition under drought stress may be less likely when facilitators are woody species with a defined canopy, the performance of a focal species, *Poa secunda*, was higher in diverse and productive herbaceous communities under drought conditions due to the ameliorating effect of vegetation on VPD (Aguirre et al. 2021). This suggests that facilitators exhibiting a range of traits may provide microclimate amelioration even under climate change which results in limitation of a resource stressor.

Table 1. Directions for future research. Improving our understanding of the role that facilitators play in mitigating climate change depends on research in several key areas

1. Methods for identifying the most important facilitators so they can be incorporated into conservation and restoration applications, including an understanding of the differences amongst growth forms
 - Synthesis of the particular benefits and resiliency provided by different facilitator growth forms
 - Development of a workflow for determining the most promising facilitators across an area of interest
2. The impact of facilitators on local population dynamics under climate change
 - Develop models based on biological data collected with a consideration of relevant facilitators
3. The effect of facilitators on predictions of species' distributions under climate change, including the role of facilitators in promoting local climatic niche tracking under climate change
 - Through modelling and empirical work, test hypotheses regarding the role of facilitators in local species movement
 - Incorporate facilitator-moderated microclimates into models predicting species range responses to climate change
 - Develop models and empirically test the effect of facilitators on invasive, non-native species expansion

If the stressor being exacerbated by climate change is non-resource (e.g. temperature, wind) then the facilitator should continue to benefit the focal species because the stressor changing is not one for which the facilitator and the focal species are competing. In fact, provided the facilitator does not experience degradation as a result of the shifting climate (i.e. a morphological change which decreases its capacity to offer a microclimate, Jones et al. 2010), then climate change should increase the potential for amelioration of those stressors if greater decoupling between the facilitator's microclimate and the macroclimate occurs (Michalet et al. 2014b). Loss or degradation of the microclimate through declines in the facilitator (e.g. as a response to climate change or land use change) could result in sudden increases in exposure, declines in microclimate heterogeneity, and negative consequences for associated taxa (Ellison et al. 2005, Thomsen et al. 2010, Hoffman et al. 2016). That being said, there are facilitators that are resilient to damage and which can have high ecological function following a relatively short recovery (e.g. a native shrub after aboveground damage; Lortie et al. 2018) as well as facilitators that can have beneficial effects after dying (e.g. juniper forests following drought mortality; Kane et al. 2011). Understanding the resiliency of facilitators and the range of benefits offered by different growth forms is important for predicting their effects on beneficiaries in the face of stressors (Table 1, Action 1).

Landscape-scale effects of facilitation

Microclimate heterogeneity increases population persistence

Sources of biotically-driven environmental heterogeneity can include land cover (e.g. the diversity and arrangement of

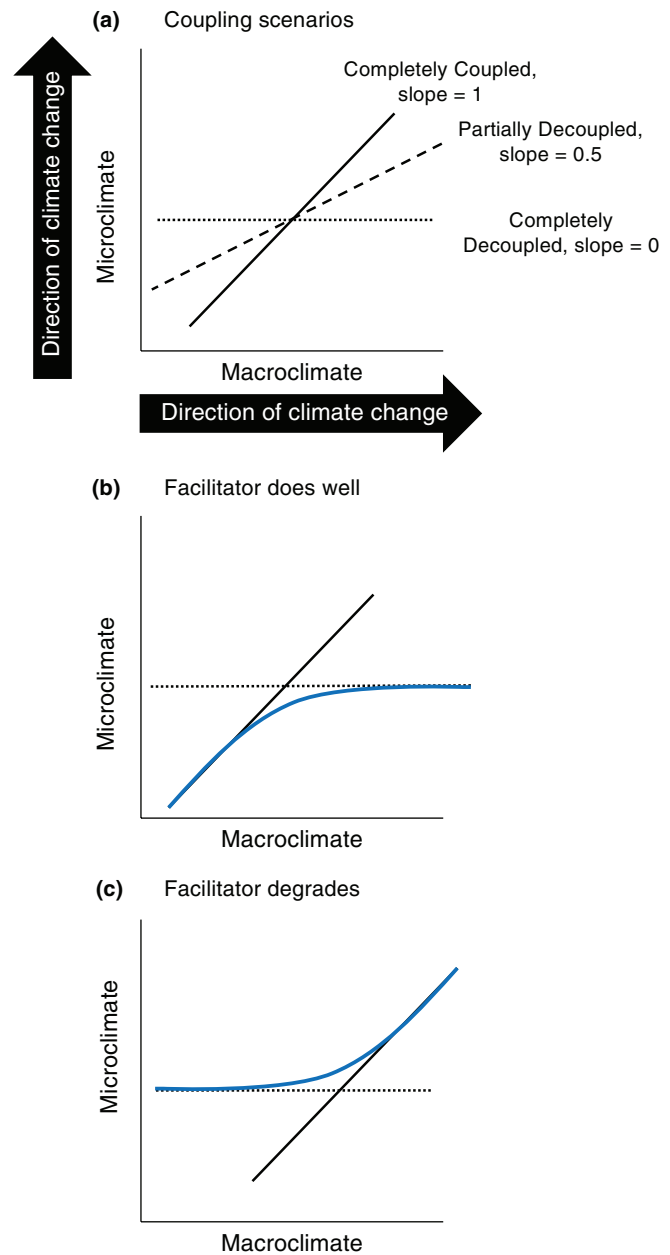


Figure 2. Facilitator-moderated microclimates have the capacity to mitigate the rate of climate change by promoting conditions decoupled from the macroclimate (a). If the facilitator performs well under climate change (e.g. the patch of grassland becomes denser with increasing carbon dioxide), its microclimate may respond by becoming increasingly decoupled from the macroclimate (b). If the facilitator is degraded by climate change (e.g. a tree sheds half its branches under drought stress), its microclimate may become increasingly coupled with the macroclimate (c). A tightly coupled micro- and macroclimate will result in a similar rate of change (though these conditions may be buffered) while decoupling will promote conditions which slow the rate of climate change.

patch types) and vegetation structure or composition (e.g. the vertical profile of a forest) (Stein et al. 2014). For example, a homogenous grassland of uniform height will have lower environmental heterogeneity than a savannah that is a mosaic

of trees and grassland from the perspective of both patch diversity and structural diversity. The heterogeneity created by facilitators and the microclimates they promote have implications for metapopulation dynamics and local species movement under climate change (Fig. 1b).

Heterogeneity provided by facilitators can increase metapopulation persistence in the face of climatic extremes. For instance, the bush cricket *Metrioptera bicolor*, experienced increased survival in patches of tall grass relative to short grass during a severe drought (Kindvall 1995), likely as a result of a lower VPD, lower air temperatures, and lower solar radiation offered by a denser canopy. Asynchronous responses of local populations to environmental perturbations due to differences in the presence or structure of facilitators could reduce the extinction risk of the metapopulation (Gilpin and Hanski 1991), particularly in the face of extreme events where microclimates (including patches and interstitial space) respond at different rates and magnitudes and thereby decrease environmental synchrony (Moran 1953, Hansen et al. 2020). Despite this important possibility, few studies have tested how heterogeneity provided by facilitator-moderated microclimates alter population dynamics under climate change (Table 1, Action 2).

Population persistence will also be buoyed by heterogeneity if there are a variety of microclimates available for colonizing as habitat preferences change (Davies et al. 2006, Suggitt et al. 2012). For example, while the population dynamics of *M. bicolor* were only assessed in tall and short grass habitats, the author noted the crickets were also found at the edge of nearby pine forest during the drought, a location typically unsuitable for this species (Kindvall 1995). Hence, heterogeneity in the types of available microclimates, which can be increased by the presence of facilitators (particularly a variety of facilitators), could be important for protecting populations from climate change because they buffer populations from extreme events under temporary changes in habitat preference and/or from directional climate change under long-term changes in habitat preference. While the role of abiotically-driven microclimates in facilitating more local, lateral climatic niche tracking under climate change has been explored theoretically (Graae et al. 2018), modeled (Luoto and Heikkinen 2008, Stark and Fridley 2022), and to a limited extent tested empirically (Suggitt et al. 2018, Virkkala et al. 2020), the role that local facilitator-moderated microclimates might play in buffering climate change is still unclear but highly plausible (Anthelme et al. 2014, Kim et al. 2022) (Table 1, Action 3).

Connectivity enables population expansion

If a species' response to climate change includes a range shift or expansion, then facilitators could increase the velocity of this shift by enhancing connectivity (Fig. 1c). Landscape connectivity can be promoted by corridors and stepping-stones, both of which can facilitate the movement of a species from its current to its predicted range in the face of climate change (Keeley et al. 2018). Corridors are large, continuous patches

of vegetation while stepping-stones are smaller patches scattered across the landscape at distances relevant to the organism's dispersal capabilities (Forman 1995). Landscape ecology and conservation ecology have a rich history of considering the role that habitat patches, often defined by facilitators and the microclimatic amelioration they offer, play in shaping migration scenarios.

By directly incorporating information about microclimates and various scenarios of coupling and decoupling from future climate change, the presence of important corridors and stepping-stones could be elucidated and may provide additional pathways for intervention and management. To track their climatic niche, species may shift their range through establishment in new suitable habitat (Chen et al. 2011). However, if the velocity of climate change (sensu Loarie et al. 2009) exceeds the speed of a species range shift, the species will not be able to shift their range fast enough to escape detrimental effects of climate change (Nathan et al. 2011). Facilitator-moderated microclimates may alleviate some of the challenges of range shifts by providing accessible microsites of suitable abiotic conditions. Corridors and stepping-stones with suitable microclimates can increase the velocity of range shifts by providing suitable habitat outside the current range of the species (Lembrechts et al. 2017). For example, the shrub *Rhododendron rupicola* enhanced the survival and growth rates of two treeline species (*Larix potaninii* and *Picea likiangensis*) beyond the current treeline, likely in part by buffering temperatures and increasing soil moisture (Chen et al. 2020). The inclusion of facilitator-moderated microclimates into predictions of species' distributions under climate change is key to more accurately predicting the required magnitude of species movement (Table 1, Action 3).

In addition to the microclimatic effects of facilitators which benefit associated species, the physical structure of some facilitators can contribute to connectivity (Filazzola and Lortie 2014). For example, greater seedbank density and diversity was discovered in the center and upslope edge of a leguminous cushion plant *Onobrychis cornuta* in a degraded subalpine grassland (Niknam et al. 2018). Similarly, seed deposition of two dwarf shrubs was several-fold greater next to allospecific shrubs compared to nearby short grass (Bullock and Moy 2004). In addition to trapping seeds that are dispersed by wind or surface water flow, facilitators can enhance seed deposition by acting as a perching site for birds (Debussche and Isenmann 1994).

It is important to take a species-specific approach when determining the effects of facilitators on increased connectivity between currently suitable habitat (Raath-Krüger et al. 2019). First, the microclimates must be accessible given the migrator's dispersal capabilities (Hodgson et al. 2009). Second, for those species that reproduce by seed, the requirements of the seedling need to be taken into consideration (Walck et al. 2011). Third, provided a focal species can reach a facilitator, it will also be important to consider novel species interactions, which could exclude the focal species from establishing (HilleRisIambers et al. 2013, Alexander et al. 2015, Losapio et al. 2021). Hence, for upward or poleward

movement of species to be successful, the benefits of niche expansion must exceed the detrimental effects of greater niche overlap with potential competitors in the new areas (Bulleri et al. 2016).

Material and methods

Methods for understanding the role of facilitators have largely relied on observational or experimental data from the field, without the use of loggers for measuring the microclimate. For example, long-term observations have been used to assess how facilitators enhance species persistence under climate change via habitat amelioration, increased heterogeneity, or increased connectivity (De Frenne et al. 2013, Bhatta and Vetaas 2016, Kim et al. 2022). Seed and transplant experiments (Batllori et al. 2009, Greiser et al. 2021), as well as correlative studies which measure seedling association (Akhalkatsi et al. 2006, Bonanomi et al. 2021), have been used to determine whether facilitators foster uphill or poleward migration. These approaches are valuable because they demonstrate the importance of facilitators, but an explicit consideration of the microclimate will improve our mechanistic understanding as well as allow us to project these impacts into the future.

On the other hand, detailed microclimate measurements are often collected without the incorporation of species data. For example, an intensively logged forest with smaller canopy heights and lower canopy density had higher temperature and VPD extremes compared to old growth forests and less intensively logged forests, indicating a lower capacity to buffer a focal species from climate change (Jucker et al. 2018). This information suggests that old growth forests will be superior in buffering a species from climate change in situ and will act as better corridors for range shifts compared to intensively logged forests. While logger arrays can enable the description of microclimate heterogeneity and unveil the potential for localized or larger-scale species movement in response to climate change, the incorporation of species data enables more specific predictions.

While measuring facilitator effects on species and facilitator-moderated microclimates on their own can allow for development of restoration and conservation priorities, the intersection of observational and experimental data with microclimate measurements would be powerful for enhancing our understanding of species' responses to climate change.

Integration of species responses and facilitator-moderated microclimates

Microclimate data can be combined with occurrence, physiological, and demographic data to predict species' responses to climate change. When endeavoring to understand the potential need for a range shift or expansion, species distributions models (SDM) are a commonly used tool. These models, also called environmental niche models, use occurrence data (or presence-absence data) paired with environmental data to

statistically predict suitable habitat and can be additionally modeled under future conditions to assess the role of climate change (Elith and Leathwick 2009). Currently, SDMs rarely use climate data which accounts for the microclimates created by facilitators (but see Lenoir et al. 2017, Haesen et al. 2023, Stickley and Fraterrigo 2023).

When there are sufficient biological data on the focal species, process-explicit range models can enhance predictions of range dynamics (reviewed by Evans et al. 2016 and Briscoe et al. 2019). For instance, the coupled SDM-population approach (Keith et al. 2008, Brook et al. 2009, Franklin et al. 2014) is relevant for more localized population dynamics, providing information on population growth rate and different demographic parameters across the landscape. Demographic studies which capture climate extremes or variability, and studies with experimental manipulations, have been occasionally used to determine the role of facilitators in shaping population dynamics under climate change (Kindvall 1995), but should be more extensively conducted (Table 1, Action 2). These data could be deliberately collected to include habitats defined by facilitator-moderated microclimates (Godfree et al. 2011 [for an abiotic microclimate example], Kindvall 1995). Additionally, where physiological tolerances are known, process-explicit range models which incorporate these data can be used to identify areas where physiological tolerances of a species are met under future climate change scenarios (Kearney and Porter 2009, Buckley et al. 2023, Gong et al. 2023). To our knowledge, just one study has developed process-explicit range models that include microclimate data which accounts for facilitator-moderated microclimates (Table 1, Action 3, Sanczuk et al. 2023).

Microclimate data availability

While it is currently uncommon to incorporate facilitator-moderated microclimate data into models of ranges, it is becoming more feasible as the methods and data become increasingly accessible to researchers (Bramer et al. 2018, Lembrechts et al. 2019, Zellweger et al. 2019). While the primary focus has been on characterizing temperatures at small scales (Haesen et al. 2021), fine-scale predictions of soil moisture, VPD, and wind are active areas of research (Bramer et al. 2018). For instance, several sensors can measure relative humidity in addition to temperature (e.g. DS1923 Hygrochron iButton), providing the opportunity to calculate fine-scale VPD across a landscape. In addition to statistical modelling approaches using in situ data, there are mechanistic approaches to estimating a suite of microclimate variables. There is a mechanistic model, 'microclim,' available as an R software package (www.r-project.org) which estimates temperature, relative humidity, and wind profiles, above, within, and below a canopy (Maclean and Klimes 2021).

In addition to estimating current microclimates, a key part of understanding the role of facilitators under climate change is projecting microclimate conditions into the future. To move from the current microclimate to the future

microclimate there are two main approaches at this time: use the offset between the current microclimate and free-air conditions to determine future buffering (Schooler et al. 2020, Haesen et al. 2021) or use the slope between the current microclimate and free-air conditions to determine both the buffering and decoupling effects of the future microclimate (Lenoir et al. 2017, Jurgens et al. 2022). Because the relationship between the microclimate and the macroclimate can be variable on a daily and seasonal basis (e.g. during the leaf-off and leaf-on period, Gril et al. 2023), incorporating the slope is preferred and can alter expectations (Lenoir et al. 2017). The slope can be determined using time-series data, either measured directly or modelled, or taken from the literature. It may also be useful to test multiple coupling scenarios as the strength of coupling may change over time due to alterations in facilitator quality (e.g. the forest grows or degrades).

Conclusion

We urge researchers to consider the role that facilitator-moderated microclimates could play in shaping species' responses to climate change. Because facilitators, and their effect on microclimates, could be lost or degraded by climate change, it is important to determine when and where ameliorated or decoupled effects occur. Due to their large impact on biodiversity dynamics across scales, it will be paramount to make a concerted effort to protect those facilitators from, for example, degradation brought on by land use changes. This goal is made more possible by integrating facilitation at various scales with recent advances allowing explicit microclimate measurement. High-resolution microclimate data that describes the microclimate effects of facilitators, as well as abiotic drivers, will enable researchers to model range dynamics and more localized population dynamics with greater precision.

Thus, to better understand how facilitators shape local and regional population dynamics as the climate changes, we suggest developing models and conducting empirical tests that 1) incorporate biological data under the influence of facilitators; 2) investigate several microclimate variables; and 3) test multiple scenarios of future macro- and microclimate coupling. With these advances we can move closer to understanding how to best leverage facilitator-moderated microclimates, in addition to abiotic microclimates, in conservation and restoration.

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Author contributions

Laurel M. Brigham: Conceptualization (lead); Writing – original draft (lead); Writing – review and editing (equal).

Katharine N. Suding: Conceptualization (supporting); Writing – review and editing (equal).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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