

REVIEW

Identifying ecological and evolutionary research targets and risks in climate change studies to break barriers to broad inference

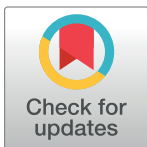
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Abstract

Understanding the responses of plants, microbes, and their interactions to long-term climate change is essential to identifying the traits, genes, and functions of organisms that maintain ecosystem stability and function of the biosphere. However, many studies investigating organismal responses to climate change are limited in their scope along several key ecological, evolutionary, and environmental axes, creating barriers to broader inference. Broad inference, or the ability to apply and validate findings across these axes, is a vital component of achieving climate preparedness in the future. Breaking barriers to broad inference requires accurate cross-ecosystem interpretability and the identification of reliable frameworks for how these responses will manifest. Current approaches have generated a valuable, yet sometimes contradictory or context dependent, understanding of responses to climate change factors from the organismal- to ecosystem-level. In this synthesis, we use plants, soil microbial communities, and their interactions as examples to identify five major barriers to broad inference and resultant target research areas. We also explain risks associated with disregarding these barriers to broad inference and potential approaches to overcoming them. Developing and funding experimental frameworks that integrate basic ecological and evolutionary principles and are designed to capture broad inference across levels of organization is necessary to further our understanding of climate change on large scales.

Introduction

Plants, microbial communities, and their interactions form the foundation of terrestrial ecosystems. Building broad inference, defined as the ability to apply and validate findings across a wide range of environmental, ecological, and evolutionary contexts, is fundamental for predicting global primary productivity, biogeochemical cycling, and ecosystem services under

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climate change [1–4]. Though climate change is drastically altering organismal fitness across the globe [5], we do not fully understand its consequences for the interactions between plants and microorganisms [6]. Several factors constrain our understanding of plant-microbial response to climate change, such as disjunct methodological approaches, limitations of experimental and observational study designs, and oversights common across studies and disciplines [7–9]. These factors have limited our ability to apply and validate findings across a wide range of environmental, ecological, and evolutionary contexts. We identify five high-impact barriers to broad inference in current global change research, using examples drawn from studies of plants, microbes, and plant-microbial interactions, but which are applicable across systems, and propose potential solutions to overcoming context dependency. Our review contributes to a global effort to understand the effects of climate change and mitigate species loss while preserving ecosystem function under global change.

Various approaches have been employed to quantify plant and microbial responses to climate change; namely, long-term observational experiments, manipulative experiments, resurrection studies, and space-for-time substitutions using natural gradients (i.e., elevation, latitude, precipitation, temperature; Fig 1; Box 1). However, there remain strong barriers to generalizing findings across study systems due to context dependency and experimental design limitations that are often overlooked [10–12] (Table 1). Many factors can significantly limit generalizability including lack of appropriate replication, failure to consider biogeographic context, absence of hierarchical genetic structure (nested levels of biological organization), and reliance on past experimental structures not specifically designed for the questions (Fig 1; Table 1) [7–9]. Although each approach has notable strengths, when employed in isolation, we only gain a limited, and thus potentially inaccurate, understanding of how climate change will influence plants and microorganisms [5, 13]. Empirical strength and biological inference both improve when multiple methods are used within a given study.

Box 1. Definitions and descriptions of primary methods used to study plant and microbial responses to climate change. The most widely used methods to study plant and microbial responses to climate change are paleoecological and resurrection studies, space-for-time substitutions, common garden studies, and experimental manipulations. Provided are definitions and descriptions for each, as well as caveats to using each method in isolation

Paleoecological studies: using fossilized organisms and historical climate data to study climate change over deep time. The inherent historical nature allows for observations of genotypic and phenotypic change across global spatial scales and across deep time (i.e., millennia). These data are also useful for predicting range shifts. However, these studies are generally observational, cannot account for population-level genetic variation or specific evolutionary mechanisms, and are not applicable to modern biotic systems. Climate change inference is dependent upon fossil or specimen age.

Resurrection studies: growing and studying preserved specimens, usually plants, from temporally separated populations or communities to study climate change over the last few hundred years. These studies provide powerful comparisons of evolutionary change across multiple generations, with inference for contemporary climate change from samples collected 200+ years ago. However, these studies are generally restricted to plant populations and may not accurately reflect historical or modern population genetic

diversity, depending on sample collection. Sample origin determines spatial scale, but most studies are restricted to inference at a local scale.

Relict studies: using populations or communities at geographic or climatic range edges, representative of isolated regions that are distinct from more connected regions at the range center, to study climate change in real time as it has progressed since the Last Glacial Maximum. Comparative studies of isolated relict populations and adjacent contiguous non-relicts directly test the effects of long-term climate change on populations across the globe. However, they are constrained to few species and issues may arise due to latitudinal variation present in specific cases.

Space-for-time over latitude or elevation: using populations or communities across latitude or elevation transects to measure responses to different climates. Gradient substitutions across latitude and elevation have been used for decades around the globe as a proxy for climate and other environmental variables, thus there is ample data across disciplines and taxa for long-term comparative studies. However, there are numerous confounding variables across each gradient, and few studies provide replication across populations or gradients, limiting inference. Further, elevational gradients are restricted to study organisms that have a notable elevational range.

Common garden studies: growing populations or communities in a common location or controlled laboratory setting to isolate genetically-based responses from responses driven by the environment. Experimentation in common gardens is useful for examining trait-based phenotypic responses over multiple generations, where controlling for phylogeny is ideal and replication is possible. These studies are able to reduce the effects driven by plasticity or epigenetic change and are useful where field-based studies are not possible. However, not all organisms are easily propagated, grown from seed, or cultured, in the case of microorganisms, thus limiting spatial scale. Further, long-term common garden studies are often unfeasible, though not impossible.

Experimental manipulations: exposing populations or communities to treatments representative of climate change such as increased temperature or CO₂, either in the field or in the laboratory. Often short-term, though long-term experimental manipulations do exist, these studies elicit rapid responses, are employable across all kingdoms of life, and are useful where field-based studies are not feasible. However, they are often single-factor, single-site manipulations that only represent highly artificial conditions over short durations, and therefore can produce false adaptive responses. Additionally, short-term manipulations don't capture long-term climatic pressures. Inference increases with time.

Though sparse, the research that has employed a combinatory approach has illuminated both convergent and contradictory patterns in plant and microbial responses to climate change. For example, in [14], two experimental manipulations (one warming and drying treatment, one snow removal treatment) were compared to a plot-scale natural snowmelt gradient, a landscape-scale elevational gradient, and a previous temporal study to determine the effect of climate change on the flowering phenology of 11 subalpine meadow plant species. Both manipulations advanced flowering phenology in parallel to the responses found across the natural and temporal snowmelt gradients [14]. Similarly, in [15], a 3-year snow removal

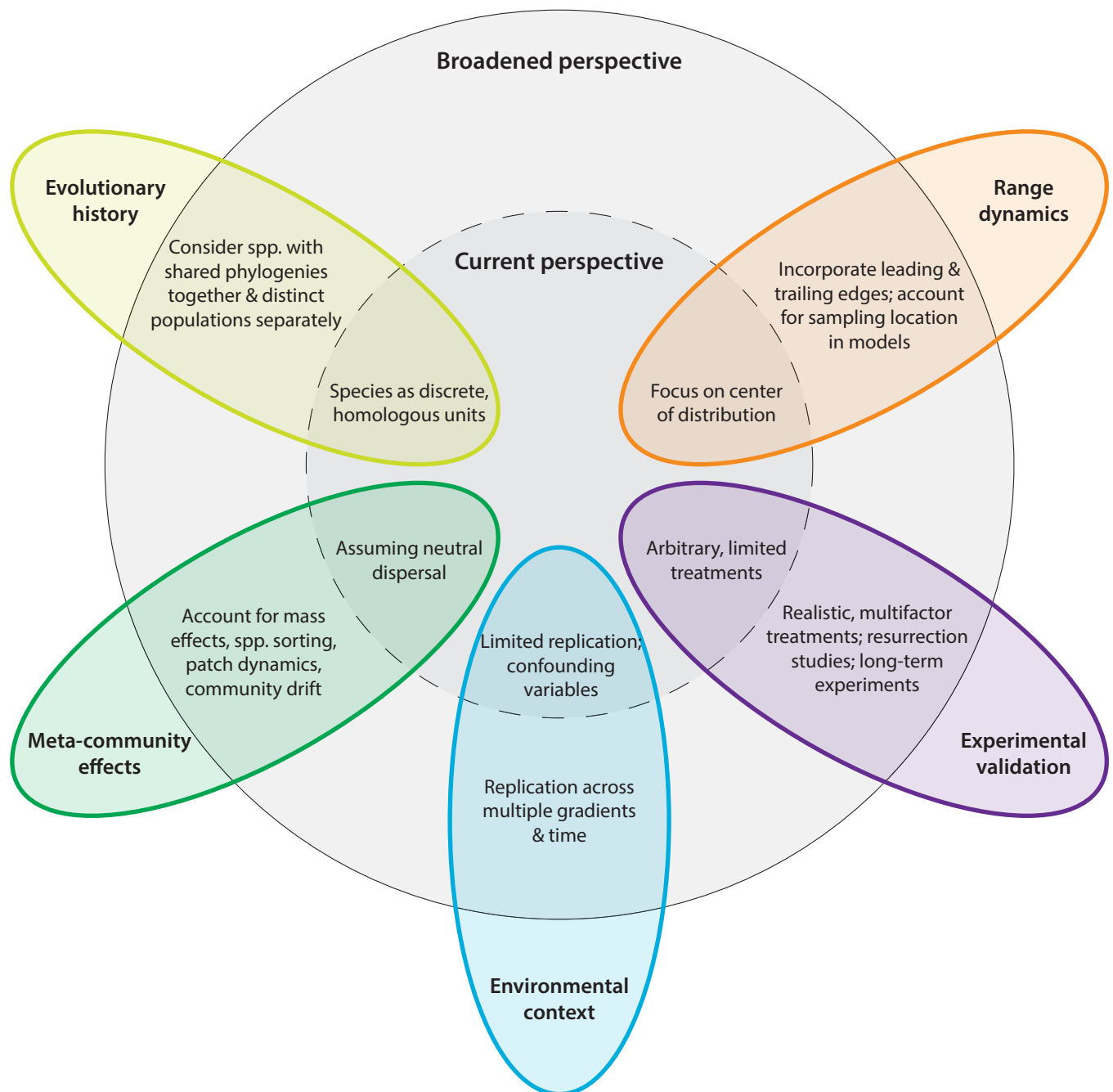


Fig 1. Considerations for broadening inference in plant, microbial, and plant-microbe interaction studies. The center circle (“current perspective”) describes current perspectives on each methodological component. The larger circle (“broadened perspective”) provides additional considerations that would help broaden inference across climate change studies.

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manipulation experiment was compared to a 43-year record of flowering phenology to determine the effect of climate change on six subalpine species in a similar geographic region to [14]. Broadly, they also found support for earlier phenological timing due to climatic warming and earlier snow melt, with both methods supporting the findings from the other. However, the support found by cross-validating methods in plant studies is, to our knowledge, not as common in studies that examine microbial responses to climate change.

Table 1. Evaluation of the primary methods used to study plant and microbial responses to climate change in the context of five common barriers to broad inference. Common methods (rows) were qualitatively evaluated for the incorporation of each barrier (columns); “explicit” indicates that the method inherently incorporates or addresses the barrier, “possible” indicates that it is possible for the method to incorporate or address the barrier based on the experimental design, “no” indicates that, to our knowledge, the method cannot incorporate or address the barrier. References were chosen based on applicability, impact, and novelty.

Method		Does the method explicitly or possibly incorporate ___?					References
		Evolutionary history	Range dynamics	Environmental context	Meta-community effects	Experimental validation	
	Paleo studies	Explicit	Possible	No	No	No	[19–22]
	Resurrection studies	Explicit	Possible	Possible	No	Possible	[19, 22, 23]
	Relict studies	Possible	Explicit	Explicit	Possible	Possible	[24–30]
	Space-for-time: Latitude	No	Explicit	Explicit	Possible	Possible	[31–35]
	Space-for-time: Elevation	No	Explicit	Explicit	Possible	Possible	[10, 36–41]
	Common garden studies	Possible	Possible	Possible	Possible	Possible	[42–47]
	Experimental treatments	Possible	Possible	Possible	Possible	Explicit	[16–18]

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The lack of methodological cross-validation is particularly concerning because studies of microbial responses to climate change have often resulted in contradictions between observational work and experimental manipulations. For example, when responses of microbial respiration to experimental manipulations of rainfall were compared to those along nearby natural precipitation gradients, the experimental manipulations did not reflect the locally adapted respiration responses observed under historical environmental precipitation regimes [16]. Additionally, when microbial composition was directly altered across this same rainfall gradient [16], respiration was a function of the active members present in the microbiomes regardless of origin, indicating a weak correlation between microbiotic function and sampling origin [17]. Similarly, a long-term warming experiment generated different plant-associated microbiome assemblages than those observed in their “natural” proxies at nearby elevations approximating the same temperature regimes [18]. These discrepancies indicate that responses to climate change are unique emergent properties generated by the specific combination of space, time, environment, and community composition, as well as focal species. Though the reasoning for why cross-validation is inconsistent in plant versus microbial studies may seem intuitive—microbes respond at significantly faster timescales, their dispersal is challenging to study, community composition and function is likely as vital to responses as it is complex—the question of what causes these inconsistencies has yet to be addressed qualitatively or quantitatively. Moving forward, we must find a way to unify the scientific concepts underlying plant and microbial responses to climate change so that they can be examined within a single study.

Unfortunately, we must rely on reductionist approaches like manipulative experiments and space-for-time substitutions (*i.e.*, the approximation of organismal responses to climate change over time using climatic variation present across a geographic space), which often generate different results along the same environmental gradient. Issues arising from reductionist approaches are exacerbated at larger scales as dispersal limitation and spatial variation in communities and abiotic factors also create differences between local and regional responses to climate change. Given the temporal, financial, and practical constraints to observing climate change at one location across time, much less at multiple locations across time, there is likely no “one-size fits all” experimental approach. The variation seen in the examples above showcase the necessity of cross-validating results by using multiple methods before deducing broad patterns from a representative sample.

The need to understand organismal responses to climate change at large temporal and spatial scales is at the forefront of global change biology. Yet, unique challenges present themselves when empirically moving beyond local ecosystems. One such issue is that the strength and direction of climate change and the distribution of genetic, phenotypic, and phylogenetic variation is geographically variable. Ideally, organismal responses to climate change would be studied directly as changes in genotypes and phenotypes in response to known environmental variables over time and space. Similarly, the ecosystem consequences of changes to organismal phenotypes would be measured in natural and controlled settings with known differences in environmental parameters. Yet, due to logistical and financial challenges, long-term manipulations of global change factors that capture direct responses to environmental selection are rare and direct inference is therefore limited to organisms with short generation times and often to a single location [48–50].

Barriers to broad inference

In this review, we provide examples of, methodological concerns for, and ways to address five barriers to broad inference present in climate change research on plants, microorganisms, and their interactions:

- 1. Evolutionary history/Genetic hierarchy.** Does shared evolutionary history predict organismal response to climate change?
Consideration to broaden inference: Are data about individual organisms, populations, and species hierarchically structured and was ancestry taken into account in the analysis [51]?
Risk if excluded: Incorrect results via inflated effect sizes and high probability of false positives (type 1 error) when evolutionary history is not incorporated into statistical models. Possible interpretation that responses to climate change are occurring at the wrong level of organization (e.g., population instead of species), incorrectly informing management practices.
- 2. Range dynamics.** How does organismal response to climate change vary across a species' range and are individual responses at leading edges more predictive than the core or trailing edges?
Consideration to broaden inference: Where in a species' range were samples collected and how many populations were used [11, 51]?
Risk if excluded: Frequent bias toward sampling the center of species distributions—typically, the zone of admixture—will produce different results relative to leading and trailing edge populations with reduced genetic variation and unique traits. For example, if a study failed to report that sampling took place only at the leading edge, a plant species could be misinterpreted as “stable” when it is actually in decline.
- 3. Environmental gradients and replication.** How variable are similar climatic gradients (e.g., different mountainsides)?
Consideration to broaden inference: Has the experiment thoroughly sampled replicate climate gradients and described relevant environmental variation [52]?
Risk if excluded: Unobserved geographic variation in organismal response to the gradient and missing genetic by environmental interactions leads to poor statistical inference. Could lead to generalizations regarding microbial function to different temperatures, for example, from one mountainside that do not apply to others.
- 4. Meta-community dynamics.** How do dispersal and environmental filtering separately and jointly affect organismal response to climate change?

Consideration to broaden inference: How do meta-community effects differently influence climate adaptive responses of plant and microbial communities?

Risk if excluded: Unidentified microbial dispersal could be responsible for positive or null effects in studies of climate change factors on microbiomes; misleading important scientific conclusions.

5. **Experimental validation.** What is the tempo, mode, and severity of global change?

Consideration to broaden inference: To what extent do experimental approaches incorporate multiple global change factors and represent realistic future scenarios?

Risk if excluded: Unrealistic treatments and outcomes over limited geographic or temporal range could produce irrelevant answers to contemporary questions.

While comprehensively addressing each of these questions and limitations is difficult, we must overcome these challenges to reduce bias in the data, accurately estimate effect sizes, and increase the power and reliability of organismal response to climate change forecasts [53, 54].

Evolutionary history/Genetic hierarchy

Over the last 20 years [55, 56] it has become apparent that genetic structure needs to be incorporated in studies that estimate organismal responses to climate change to account for the influence of individual variation on the patterns and drivers of evolution and to control for non-independence among individuals and species. Over time, evidence demonstrating the critical importance of genetic variation in establishing broad inference across levels of organization has continued to grow [53, 54]. However, the omission of data related to genetic structure is still common.

Species are non-independent units but maintain shared variance in traits at a variety of hierarchical levels that should be included in statistical models. When genetic structure is not considered, significant issues with the qualitative and quantitative estimates of effect sizes can arise and impact overall conclusions about the primary drivers of phenotypic variation [12]. Previous research using both simulation models and common garden trials of *Eucalyptus*, *Populus*, and *Picea* species confirmed that without controlling for genetic structure in models examining trait data, species-level effect sizes can be overestimated by 20–50%, and often in the wrong direction [53]. Further, when model simulations did not incorporate hierarchical genetic structure, there was a 20–60% chance of incorrectly attributing organismal response to species-level influences rather than correctly identifying genetic structure as the primary driver. In many instances, when genetic structure is not considered as a confounding factor, findings obtained from these studies may be akin to random chance [53].

Integrating genetic structure is fundamental to correctly identifying the climatic drivers that underlie the distribution, fitness, and performance of populations, community structure, and ecosystem processes on the landscape. Phenotypic variation among species, or populations of a species, drives organismal responses to climate change [57]. Recent studies have clearly shown that the climatic drivers of species ranges and phenotypic variation vary depending upon whether or not genetic structure was incorporated into statistical models (for example, see bud break phenology in *Populus* species [54, 58], and distribution and survival models in *Pinus* species [59]). More importantly, when species-level models were subsequently applied to populations within species, predictions of species responses to climate change varied by up to 50% compared to population specific models [59].

Accounting for non-independence, or phylogenetic relatedness, among species due to shared ancestry is also important to the biological relevance of a study. For example, shared

phylogenetic lineage was a more powerful predictor of plant response to increasing nitrogen deposition than functional traits of scarlet monkeyflower, *Mimulus cardinalis* [22]. However, without controlling for phylogeny, leaf economic traits and species identity indicated a diverging pattern [22]. When studies that exclusively consider species-level differences without accounting for phylogenetic distance or hierarchical genetic structure are used in subsequent meta-analyses, the observed species' effect sizes are likely to be inflated, compounded, or potentially incorrect [50], making it difficult to place much confidence in their conclusions.

Incorporating phylogenetic relatedness and genetic structure into experimental design and statistical models is an important step towards building broader inference regarding organismal responses to climate change and the drivers shaping them. Without accounting for genetic structure, there is a high probability of generating inflated effect sizes, of type 1 error, and of poor model selection. Studies excluding this information compound negative impacts on their inferential power. Additionally, it is important to recognize that the phenotypic variation underlying organismal responses to climate varies across any given species' range. Therefore, studies should also consider the effect that sampling locations, with respect to the species distribution, might have on our understanding of organismal responses at large spatial scales.

If genetic structure is not incorporated into statistical and spatial models appropriately, and the environmental variables used are not the most biologically important, not only do we run the risk of incorrectly identifying the primary drivers of phenotypic variation, but we may be compounding the resultant errors [60].

Range dynamics

Range dynamics are fundamental to broad inference for many reasons including: 1) genetic variation underlying phenotypic traits vary throughout a species range; 2) phenotypic traits differ between leading edge and trailing edge populations and likely vary within leading and trailing edge groups; and 3) associated communities vary geographically. A species' natural range describes where the species has been, where it is going, and to what degree it can withstand external stressors and change (Fig 2A). Inferring species' responses without considering where in the range individual or population samples originate is a conclusion without context due to numerous population and community level differences in diversity metrics (Fig 2B and 2C). In order to build broad inference, it is important to sample multiple individuals from many populations across a species range, when possible, to ensure that a representative population sample is not skewed by local diversity.

One common bias in ecological and evolutionary research is that studies and experiments often use species collected from or observed at the center of their natural range. This is often simply due to the abundance of target organisms or populations at range centers and the logistical ease of reaching those organisms. However, phenotypic traits and their genetic underpinnings are influenced by where in the species' range samples were collected [51] as are associations between plants and microorganisms [61]. When we fail to take into account genetic structure within and among populations across a species range, there is a risk of overinterpreting the factors driving organismal response to climate change (type 1 error) and inflating effect sizes. Generally, the core, or middle, of a species' distribution is considered the zone of admixture where species' abundances and within-population genetic variation are the highest, and demographic stochasticity, or population fluctuations due to chance birth and death rates, is lowest [51] (Fig 2). Previous research used both simulation and experimental systems of *Populus*, *Eucalyptus*, and *Picea* with varying levels of genetic variation to examine the effect of including or ignoring genetic variation across a species' range in statistical models [53]. When genetic variation was high, representative of the middle of the distribution, there

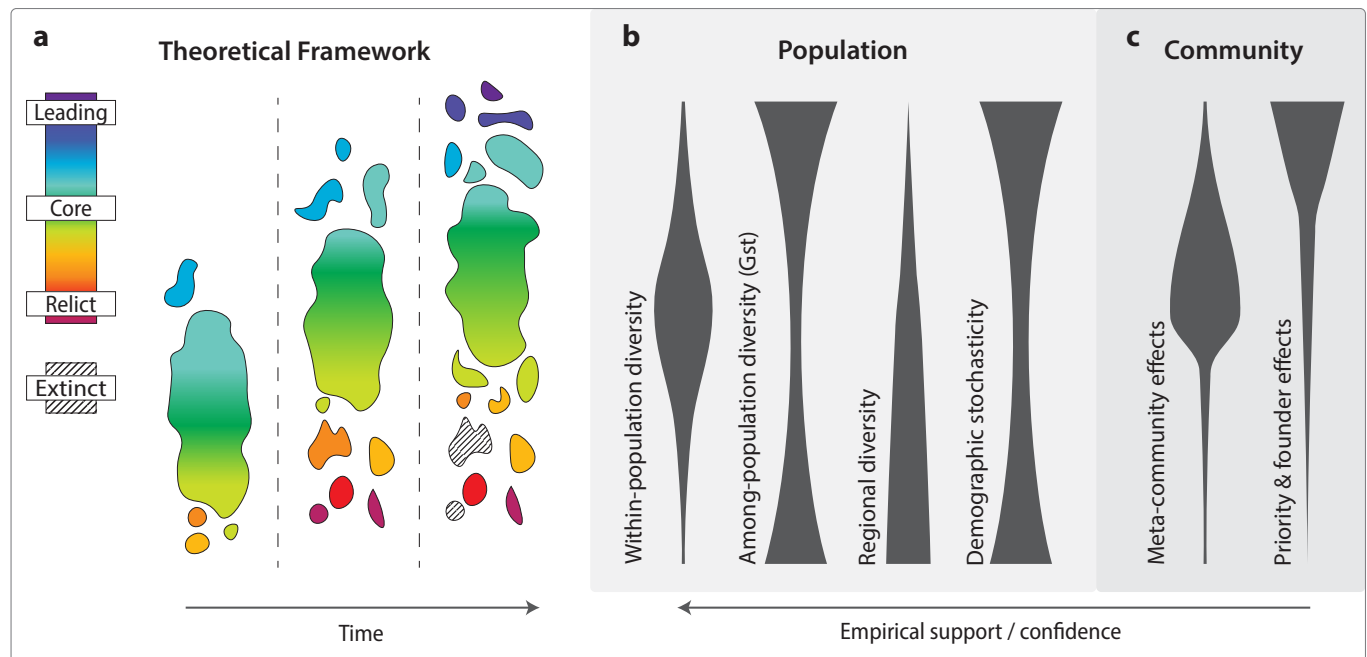


Fig 2. Framework for understanding organismal responses to climate change. (A) Proposed theoretical framework whereby three vignettes (meta-community theory, range dynamics, and resurrection studies) are employable across the entire range of a species or communities. As time increases (x-axis), range shifts move leading, core, and relict populations across the landscape, exposing relict populations to extinction risks. (B) Dominant population-level processes and dynamics that vary in prevalence across the natural range of a species, sorted by empirical support. (C) Hypothesized community-level processes and dynamics should also vary across the natural range of a species. (B, C) Y-axis is the density of each process and dynamic relative to the rightmost natural range in (A).

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was a 60% chance of concluding that higher levels of genetic organization, *e.g.*, species, were primarily responsible for organismal responses to climate when these responses were actually driven by genetic variation at the population level [53]. Conversely, there was a 20% chance of reaching this conclusion when genetic variation was low. Equally important, the effect size attributed to species was inflated relative to models with genetic structure included. Overall, if selected field sites and experiments are non-randomly distributed with respect to a species' distribution, there is likely inherent bias that is a barrier to broad inference. Further, including genetic structure in statistical models is vital to accurately estimating the genetic level at which biological responses are patterned and meaningful.

In addition to the expectations driven by genetic variation across a species' range, the leading and trailing edge populations are vital to predicting species responses to climate change, as well to as identifying influential traits for population persistence [51]. Importantly, from a population perspective, there are many leading and trailing edges. Populations at the leading and trailing edge of species' ranges often have lower within- and higher among-population diversity than populations at the core of the range [51, 62] (Fig 2). Because the environmental challenges that organisms face vary depending on where an individual is within the range, population range edges can provide better estimates of the adaptive capacity, the phenotypes, and the function of the species within a given ecosystem [33] that allow it to persist and colonize new habitats. For example, a recent study comparing replicated trailing edge sky islands to adjacent core population mountain chains found a pattern of convergent evolution across sky island populations [30]. Overall, sky island populations were hotter and drier and sky island trees from a common garden produced more asexual ramets than adjacent mountain chain populations. The observed trait divergence and the position of these populations across

the species' natural range supports the overall hypothesis of differing responses to climate change as a result of range position.

Lastly, range dynamics are not simply a population level process, but may involve key interactions with organisms that respond to climate uniquely across their own ranges. When considering how interactions among organisms will shift with climate change, one must consider that interacting partners may diverge in climate change responses [63]. Observations of plant-microbial symbioses across plant species' ranges provide ample evidence that plant-microbial interactions are not static across space [64, 65]. Carefully examining these dynamics across different portions of a plant species' range could provide evidence for which interactions may be beneficial for persistence under global change (*e.g.*, leading and trailing edge symbioses). For example, extant communities present at the leading and trailing edges of a species range can dictate whether expansion or persistence is possible [66, 67]. These communities may alter resource availability or occupy space needed for expansion into a given site, making it inhospitable for colonization by new migrants [68]. Alternatively, these communities could facilitate migrant colonization by creating favorable habitat through alterations of the biotic and abiotic landscape [68]. The intraspecific variation of the leading edge is also a determinant or driver of successful expansion; higher variation increases the likelihood for the occurrence of traits facilitating expansion into a new site [69–72].

Climate and climate change, biotic communities, and genetic variation all drive organismal responses across a species range. Building broad inference in this context is difficult, however doing so is impossible if we do not take range-based factors into account. As studies that have incorporated these factors are rare (but see [73, 74]), it is critical that we undertake this challenge in future experiments and experimental designs.

Environmental context

As climate and climate change velocity (*i.e.*, the rate and direction of change) varies across a species range, it is critical to have adequate replication of populations and gradients to build broad inference. Climatic gradients across latitude or elevation are longstanding experimental proxies for climate change studies. However, past experimental designs using gradients to infer organismal response to climate are commonly limited in scope of their study to a single gradient from which larger scale conclusions are extrapolated (*e.g.*, studying the effects of elevation using one gradient on a single mountain). Previous research suggests that studies implementing elevational gradients had an average and median of $n = 1$ for replication [52]. When studies have used replicated gradients, they commonly find interaction effects which indicate that the gradients are not uniform in their effects, the underlying genetic variation within and among populations differs on the gradients, or the surrounding biotic community varied along the gradients of interest.

Gradient replication also limits effect size inflation and increases the probability that the results reflect the central tendency, or average responses, of the population's genetic structure and phenotypic variation across the gradient. Among-population genetic variation across a gradient can lead to nonlinear responses to global change, complicating modeling efforts to predict these responses without replicated gradients across an organism's range [75]. Comparisons across populations that span gradients demonstrate that 77% of populations exhibit differing levels of phenotypic plasticity in 1/3rd of functional traits measured [60]. Gradient diversity within populations and species provides insight into the precise mechanisms driving organismal responses to climate change [76], making it an important independent consideration for future research efforts.

Gradient-based approaches offer prime opportunities to incorporate evolutionary history with range dynamics to build broad inference to organismal response to climate, but only with

sound experimental design [77]. For example, elevation is often used as a proxy for climate, yet there are many ways in which an elevational gradient also interacts with species range, evolutionary history, or metacommunities, expanding the environmental context beyond climate alone. A population found higher on a mountain is more likely to be on the periphery of a species' range (either leading- or trailing-edge) than one at lower elevation, thus likely has lower overall genetic diversity for traits representative of climate adaptation [78, 79]. Similarly, populations at higher elevations are likely to have specific adaptation for dispersal and survival in these conditions which may differ from their counterparts closer to sea level or in the middle of their natural range [66, 67]. We might also expect non-linear patterns in overall community diversity as elevation increases [80, 81], making the influence of random ecological drift or other meta-community dynamics more idiosyncratic in these communities.

Further, climatic and environmental predictor variables used in ecology and evolution are not always the most proximate cause of the response variable in question. Though there are valid reasons for why temperature and precipitation are the most used variables in general ecological research addressing global change (temperature and precipitation were two of the earliest and most widely available climatic data available for analyses, organisms possess a critical temperature past which life-sustaining functions are no longer possible, and all organisms require water), they are often not the most precise variables to examine differences in response [82, 83]. Though many ecological studies include interaction terms in statistical models, thus theoretically addressing the interaction between temperature and water, there is significant geographic variation across ecosystems that affects the way that temperature and water interact [5, 84, 85]. Variables such as potential evapotranspiration, actual evapotranspiration, and aridity, for example, have been referred to as “functional” global change factors as they determine how energy and water function on the landscape. These indices represent the reality of biologically “available” water and energy and are thus “biologically meaningful” [86].

All of these considerations must be taken into account when attempting to extrapolate the effects of environmental variation and when comparing environmental gradients to experimental manipulations of the same abiotic factors. Many experimental manipulations do not replicate organismal response to climate along nearby abiotic gradients and thus fail to identify the most important environmental drivers of organismal response to climate change [16, 18, 87]. Changes in community composition, species richness, genetic diversity, and plasticity all vary across environmental gradients and associated species ranges. Careful consideration of the outcome of a multitude of interacting biotic and abiotic factors across environmental gradients will place experimental manipulations in the correct environmental context.

Meta-community effects

Communities of organisms are embedded in a matrix of linked communities across the landscape (*i.e.*, the meta-community [88]). Yet, most global change studies focus on individual communities and therefore do not incorporate the effects of differential dispersal among patches, variation in patch quality, or neutral dynamics. This oversight could result in misleading inference, especially in cases where dispersal is high. For example, in a given global change manipulation, treatments (*e.g.*, warming, drought, nitrogen deposition, *etc.*) are often embedded in a matrix of surrounding habitat that mirrors that of control plots (Fig 3). If dispersal from the surrounding matrix (mass effects) dominates community assembly relative to environmental selection (species sorting) imposed by the global change treatment, the experimental results would lead one to assume that the community is resistant to the global change driver. Similarly, if neutral processes or random dispersal (patch dynamics) are occurring, sparse treatment patches being embedded in a matrix of many control-like patches may lead

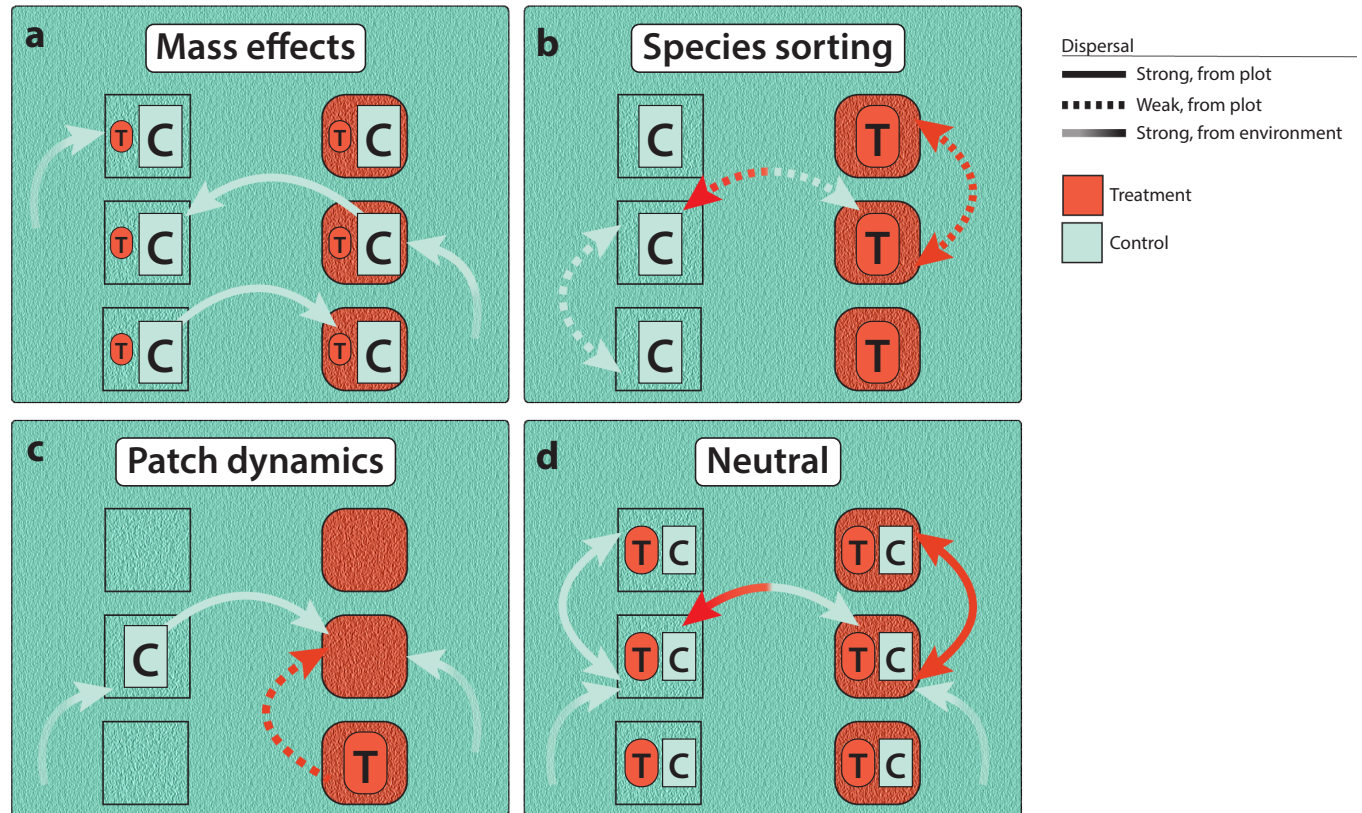


Fig 3. Influence of four meta-community effects on community assembly in experimentally warmed plots. All panels are representative of a single experimental design whereby warmed plots are embedded in an un-warmed control matrix; individual panels represent different effects from four types of meta-community dispersal. Dark green background indicates the surrounding matrix, from which the control plots (light green boxes) originate; dark red plots indicate experimentally warmed plots, and light green boxes indicate control, un-warmed plots. Light green boxes (labeled “C”) indicate the control community (treatment or control), as determined by dispersal strength and ability. Strong dispersal is indicated by solid arrows; weak dispersal is indicated by dashed arrows. Gradient arrows indicate dispersal from the surrounding matrix environment. (A) Mass effects are present when dispersal from the surrounding matrix dominates community assembly; if propagule pressure is strong enough, dispersal could mask treatment effects. (B) Species sorting is present when environmental selection or differential niches prevent dispersal from influencing plots. (C) Patch dynamics are present when one community (here, the control) is a better colonist, and the other (here, treatment) is a better competitor, resulting in random dispersal. (D) Neutral processes are present when the communities are ecologically equivalent; random dispersal and chance outcomes neutralize any community dominance.

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to communities in treatment patches resembling control patches by chance alone. While these four major areas do not encompass the entirety of potential metacommunity dynamics [89] they do represent a compelling place to further expand and more fully integrate the perspectives of ecological and climate change research.

While dispersal dynamics may be easy to observe for plants and animals because newly established propagules are morphologically distinct from established adults, this may not be the case for microorganisms such as bacteria and fungi [90]. For example, numerous multi-year global change studies have failed to find a consistent effect of the manipulated global change factor on microbial communities [16, 18, 87, 91]. While often unmeasured, differential dispersal may be contributing to these null results. Other dynamics, such as priority effects, where the baseline community prevents reassembly of a new community following imposition of the global change factor could also influence our global change inferences [92]. Thus far, relatively little unified theory has developed relating to how and when various microbial meta-community dynamics manifest [93, 94]. However, two major factors appear to be key drivers: baseline community heterogeneity [95] and dispersal mechanisms of various microbial

propagules [96]. In more heterogenous environments, we may expect greater niche partitioning [97], potentially lessening the influence of mass effects while strengthening species sorting and patch dynamics. Further, less diverse communities are more likely to experience ecological drift [98], making the elucidation of broader patterns more difficult. Variation in the dispersal mechanisms of microbial propagules also drive metacommunity dynamics [99]. Yet, we do not know how these dispersal modes correlate with other traits that would relate to microbial responses to climate change. Trait-based models can effectively predict microbial dispersal in arbuscular mycorrhizal fungi (AMF) [100], thus further investigation of these patterns across a broader swath of microbial domains will likely provide greater evidence of how dispersal traits influence metacommunity dynamics. Greater and more critical consideration of how microbial metacommunity dynamics influence their response to climate change is necessary to delineate broader patterns across experiments and study systems.

Experimental validation

The vast array of manipulative global change experiments have contributed to our understanding of organismal responses to varying environmental factors and provided projections of severe disruptions to biological communities in the future. Warming experiments have been used extensively to study the impacts of climate change on plants and microbial communities [63, 101, 102]. Plant responses to warming vary by species but these experiments show that we should expect shifts in phenological events, altered growth and reproduction [103, 104], and changes to plant community composition [105]. Long-term (> 15 years) warming experiments on microbial communities have led to decreases in microbial biomass and reduced respiration rates due to both reduced biomass in organic soils and thermal adaptation in mineral soils [106] and shifts in microbial community composition [107]. However, these studies overwhelmingly describe patterns in organismal responses to environmental factors rather than illustrating the processes that drive responses to climate change writ large, have not or cannot incorporate genetic structure, are non-randomly placed with respect to range, and often reflect treatments that are beyond the range of expectation in natural systems. In other words, broad inference drawn from these studies should be avoided or treated with caution.

The emerging reality is that global change is a complicated, multi-factor phenomena, with significant disruptions to historic patterns and increases in the frequency of extreme climatic events. Experimental treatments are often single-factor manipulations (*e.g.*, only heat, drought, or nutrient limitations) that are much more severe than the expected reality of global change [108]. For example, nitrogen addition studies often apply orders of magnitude more nitrogen than predicted for increased atmospheric nitrogen deposition [109]. These studies, by necessity, also take a reductionist perspective to climate change, limiting the number of factors included in studies and limiting the effects of climate change to essentially “hotter and drier” conditions. These issues demonstrate a need to think critically about how well experimental climate change studies represent realistic future scenarios and validate the findings of these studies *in situ*. Ultimately, any artificially imposed climate treatment is arbitrarily based on what might be expected to reflect a future scenario or produce a response in the study at hand.

In order to build broad inference, new experimental approaches that integrate many of the points mentioned above with global change manipulations are necessary. It is important that we implement realistic experimental designs (multi-factor, realistic conditions) specifically designed for broad inference to optimize applicability. Designing and implementing experiments that integrate genetic structure, environmental gradients, organismal range dynamics, and associated communities and species interactions with global change manipulations is an exciting challenge that should be the central question of future research.

Data currently available that could address all five barriers are scarce. However, as an example, we provide the following data to show how invoking genetic hierarchy and environmental context affects statistical output and broadens inference for a given study.

An example of establishing broad inference

The effects of global change impacts individuals, and evolution occurs within populations. Yet, most modeling frameworks only account for species-level responses to changing climates. This oversight may obscure the true drivers of organismal response to climate change and lead to spurious results about the synchrony of these responses across populations and genetic provenances. As mentioned above, temperature and precipitation are not always the most biologically meaningful environmental predictors of organismal response to climate change, and variables such as potential evapotranspiration (PET), actual evapotranspiration (AET), and aridity may be better suited for these models.

From an organismal- and ecosystem-level perspective, functional variables such as PET, AET, and aridity describe a more nuanced environment in determining, for example, the atmospheric demand for water from plants or the availability of water in the soil [110]. Potential evapotranspiration represents the atmospheric demand for water from plant vascular systems and the earth's surface and depends on temperature, solar radiation (proxied by latitude and the month of the year), percent cloud cover, wind speed, atmospheric surface pressure (proxied by elevation), and the latent heat of vaporization which describes the amount of energy required to break liquid water bonds to create water vapor. Actual evapotranspiration represents the amount of water being recycled to the atmosphere through plant transpiration and depends on the amount of available water to plants, PET, and functional adaptations of plant species vascular systems for dealing with water resources [82]. Using metrics like these that are more precise determinants of plant functional traits can be particularly useful when considering the evolutionary history of plant populations that have evolved across variable landscapes with different histories of energy and water balance [83]. However, this perspective has rarely been considered or tested, especially in concert with varying degrees of genetic hierarchy in statistical models.

To test the validity of species (no genetic structure), provenance (broad-scale genetic structure), and population (fine-scale genetic structure) models of organismal responses to climate change, we re-analyzed 23 plant and soil traits measured in the common garden and field, of the riparian tree *Populus angustifolia* [30, 41, 58, 73, 74, 85] to determine the influence of accounting for nested population genetic structure and different environmental variables on selecting models with the highest predictive power [53]. We used standardized predictors and traits to run linear models with no population structure (species-level) with temperature and precipitation as additive predictors, then with dryness index and evaporative index as additive predictors. Linear mixed effects models were run following the structure of the linear models above but including population structure with either genetic provenance or population as random effects. We compared models using Akaike Information Criterion (AIC), and present the lowest AIC model as the “best” (S1 File).

When no population structure was included in models (“species” models, Fig 4B), temperature and precipitation models were selected as better (lower AIC values) for 16 of the 23 examined response variables. Of the 16, nine were traits measured in the field (Fig 4C), seven in the greenhouse (Fig 4D), twelve were plant traits (Fig 4E), and two were soil traits (Fig 4F). However, when population structure was included, the overall trend shifted to dryness and evaporative index being better predictors for 17 and 15 of the 23 examined response variables, depending on whether provenance or population were included. Importantly, this pattern

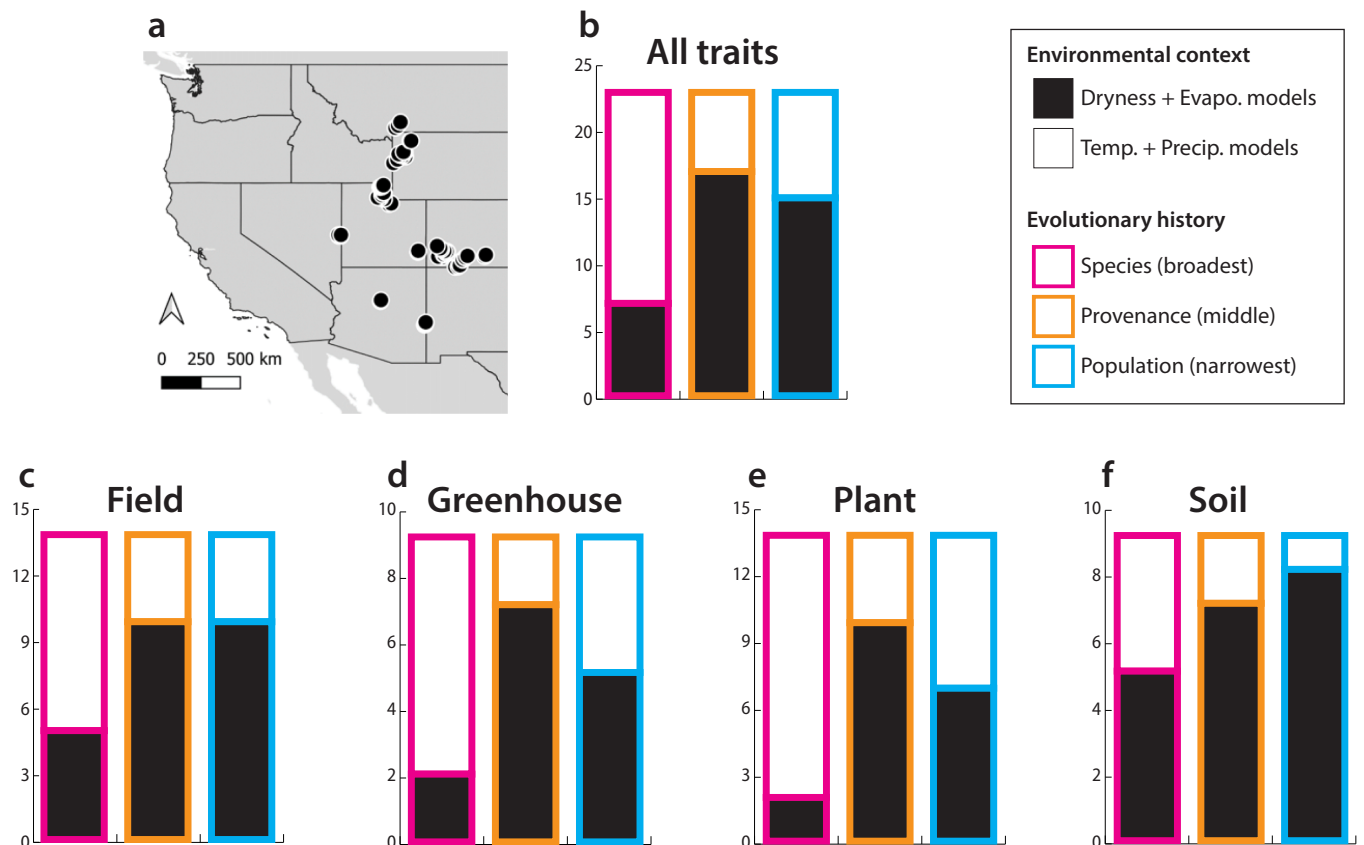


Fig 4. Model selection depends on genetic and environmental precision. Representation of model selection for the best environmental variables to explain trait variation determined by AIC model selection across species-level, provenance-level, or population-level analyses. Panel (A) shows a map of data collection sites. In panels (B-F), white bars represent models where the dryness index and evaporative (evapo.) index were selected as the best predictors while black bars represent models where temperature (temp.) and precipitation (precip.) were selected as the best predictors. Panel (B) represents all examined traits and panels (C-F) split all trait into those measured in the field (C), greenhouse (D), and into plant (E) or soil (F) traits. Base map shapefile downloaded from: https://gadm.org/download_country_v3.html. Base map license information: <https://gadm.org/license.html>.

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held in all subsequent analyses. Ten of fourteen trait models measured in the field were better predicted by the dryness and evaporative index (Fig 4C). Seven of nine greenhouse traits (Fig 4D) were better predicted by the dryness and evaporative index at the genetic provenance level while this was true for four of nine at the population level (Fig 4D). Four and seven of the 14 plant traits were better predicted by dryness and evaporative index at the provenance and population-levels (Fig 4E). Finally, seven or eight of the nine soil traits were better predicted by dryness and evaporative indices with provenance and population as random effects, respectively (Fig 4F).

This example demonstrates how these barriers to broad inference interact in selecting appropriate statistical models. We show that by incorporating hierarchical genetic structure from populations distributed across the western US, functional global change factors are better at explaining variation in functional plant traits, soil microbiomes, and soil nutrient pools than traditional metrics of temperature and precipitation. Without considering base population level genetic structure: 1) the effects of species are inflated; and 2) climate models are based on poor metrics. Both outcomes represent barriers to broad inference in the effects of global change across levels of organization.

Overcoming barriers to broad inference

As climate change progresses and we continue to seek a broadened understanding of its biological impacts, it is imperative that we reduce context dependency in scientific research that aims to uncover and predict the patterns and processes underlying organismal responses across the global landscape. We have discussed the limitations from common methodologies used in climate change research that fail to account for evolutionary history and genetic structure, range dynamics, meta-community effects or environmental context, or do not apply realistic treatments or validate experiments with multiple methods or sufficient replication. To increase the resolution and realism across eco-evo climate change studies of plants, microbes, and their interactions, we can go “deep” by replicating gradients across multiple environmental contexts, for example, or “wide” by combining multiple approaches. To explore these concepts further, below we provide potential ways forward.

Evolutionary history/Genetic hierarchy

Diverging organismal responses to climate change will ultimately rely on functional differences (*i.e.*, gene mutations, adaptations, behavioral differences, *etc.*) that may be conserved across species but not among populations, or vice versa [84]. Focusing efforts to study the mechanistic underpinnings of organismal divergences, as well as the phylogenetic hierarchies underlying the differences, will provide a stronger framework to predicting the effects of future climate change rather than simply identifying population-level differences alone (Fig 5A). This approach will also likely allow for greater curation and conservation of overall biodiversity than a strictly species-centric model [77]. Considering the sources of variation in organismal traits, rather than their distribution and presence/absence among species will improve future efforts to understand how climate change will impact individuals, populations, and communities [5]. Thanks to advances in genomic sequencing, we are rapidly developing a sophisticated understanding of inter- and intra-species differences at various levels of phylogenetic hierarchy. This perspective must be incorporated into future attempts to understand how organisms will respond to climate change, as well as how they have responded to changes in the past.

Range dynamics

Barriers due to range dynamics can be bridged by sampling across the full range of a species, utilizing the leading and trailing edges to examine priority effects and range shifts, and examining relict populations to better predict future changes within a given population (Fig 5B). Future studies of species response to climate change should describe where in the range sampling has occurred and use this knowledge to dictate the scope of inference applied to findings. Range-wide studies, as opposed center-focused studies (*i.e.*, the zone of admixture) should be more frequently implemented to capture the full range of standing genetic variation for a given species, thereby broadening the study’s scope of inference. If the full range is not sampled, studies should explicitly choose portions of the range to compare isolated effects of environmental change (*e.g.*, relict populations versus central populations).

Environmental context

Un-replicated gradient approaches only provide anecdotal evidence of specific phenomena without generalizability at larger scales [52, 65, 85]. Without gradient replication, inference is significantly limited and biased towards the specific gradient observed. Accordingly, some populations may respond strongly to gradients while others may show little or no response

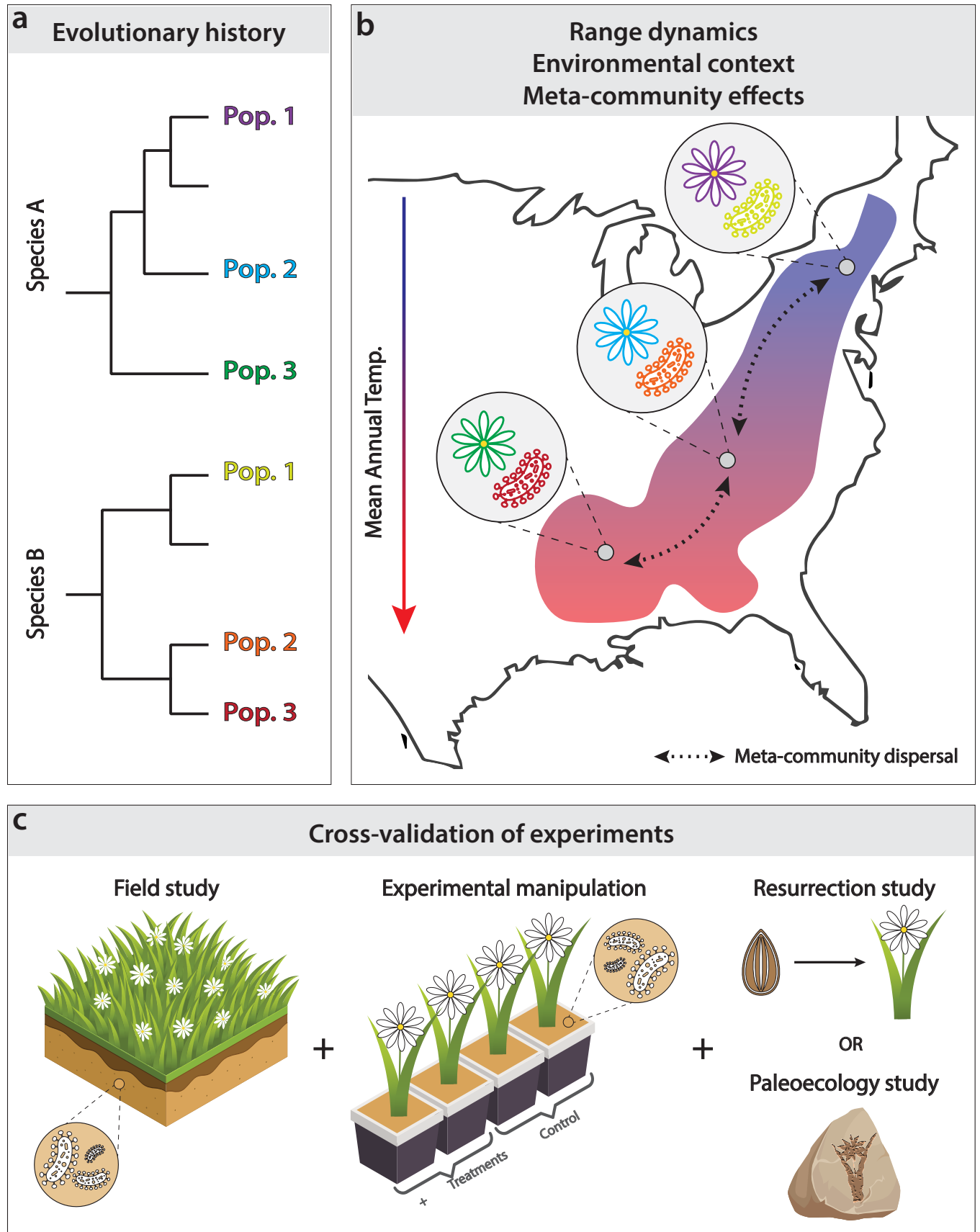


Fig 5. Conceptual framework for maximizing broad inference in climate change studies on plants, microbes and their interactions. To optimize the robustness of a study, each of the following components should be considered, measured, or incorporated. (A) Especially in studies across multiple species or populations, accounting for evolutionary history or genetic hierarchy reduces the possibility of effect size inflation due to phylogenetic relatedness and informs the researcher of the effect of genetic variation on phenotypic responses. (B) Ideally, sampling should take place across the entire range of the species examined. At the very least, where in the species' range sampling took place should be noted and accounted for in analyses. Here, we are assuming that Species A (flower) and Species B (microbe) have overlapping ranges (blue and red background) for graphical simplicity. Across the range, multiple environmental variables should be assessed for analyses (again, only one, mean annual temperature, is shown for simplicity). Sequencing and genotyping field samples can assess the strength and type of meta-community effects driving population and community patterns. (C) Examples of cross-validating experimental methods. Field observations can validate or inform experimental manipulations, as well as resurrection or paleoecological studies. Note that to our knowledge, resurrection and paleoecological studies are only possible for plants and not microorganisms at this time. Base map shapefile downloaded from: https://gadm.org/download_country_v3.html. Base map license information: <https://gadm.org/license.html>. <https://doi.org/10.1371/journal.pclm.0000320.g005>

[86]. Thus, it is vital to implement multiple, randomly-selected gradients within global change studies to ensure accurate estimates beyond the study system.

Further, identification of the most biologically meaningful environmental predictors is necessary to understand the influence of climate change on plants and microbes writ large. As an example, utilizing functional variables such as PET, AET, and aridity could help to predict whether plant traits may buffer or exacerbate feedbacks to the water cycle. Water returns to the atmosphere through plants and changes to atmospheric water cause climate feedbacks such as increasing temperatures with increasing atmospheric water. Thus, modern and historical supply and demand for water on the landscape, and the interaction of such with standing genetic variation across the species' range, informs us of the reciprocal relationship between plants and climate.

Meta-community effects

Meta-community dynamics may be better accounted for with baseline measurements prior to beginning experiments and controlling for dispersal into experimental plots throughout the duration of the experiment (Fig 5C). Future studies could account for meta-community dynamics in at least two ways. First, baseline measurements should be taken in all plots and potentially the surrounding habitat. In doing so, one could account for the starting community and how plots may naturally vary from one another before treatments are imposed. Second, dispersal into experimental plots should be tracked by active and passive air collectors or other methods (*e.g.*, sequencing dust or scat) when appropriate. While it is unlikely that all dispersal events will be captured, understanding the magnitude of inputs will allow researchers to understand if species sorting on environmental factors versus other meta-community mechanisms are at play. Finally, appreciation for and, if possible, attempts to measure the more "random" aspects of meta-communities (*i.e.*, patch dynamics and drift) should be cultivated to more fully verify whether climate change-associated effects are correctly attributable to this mechanism or background community variation.

Experimental validation

Environmental gradients provide insight into plant and microbial responses to multiple varying abiotic factors [74, 111]. However, a single gradient insufficiently represents the complexity of any climate-based phenomena in question. Future use of climate gradients as a proxy for climate change must incorporate multiple gradients, preferably varying in multiple variables of interest, to produce results that are more consistent and broadly generalizable (Fig 5B). Additionally, validating the observations made along environmental gradients with experimental manipulations will provide a robust understanding of the causal mechanisms behind phenotypic or genetic variation (Fig 5C). Further, we must recognize that these gradients do not

exist within a vacuum. We must be more considerate of the ecological and evolutionary phenomena that may differ between individuals, populations, species, and communities found on opposite ends of a gradient. Incorporating range dynamics, evolutionary histories, and meta-communities into future investigations of organismal performance over a climate gradient will make interpretations of precise climate effects more accurate and, hopefully, more applicable across systems.

Paleoecological and resurrection techniques are a promising avenue that allow for a direct investigation of evolutionary responses to climate change across a continuum of past and present ranges (Fig 5C) [108, 112–114]. Resurrection studies have demonstrated evolutionary change in various plant traits related to drought and heat tolerance and have shown that these changes are often adaptive and can occur over relatively rapid timescales [23, 114]. These studies provide evidence for phenological shifts in plants (*e.g.*, earlier flowering and seedling emergence times) after periods of warming and drought [115]. Resurrection studies naturally mimic the manipulation of multiple climatic factors to understand ecosystem response to global change. We suggest a complete and continuous collection of samples from different microbial communities and their plant associates over long periods across species' climatic and geographic ranges. The collection should maximize the number of source locations and communities while recording the historical microbiomes and associated plant communities. We also recommend storing and preserving samples in the best laboratory or natural conditions (see [116]). Such precautions enrich the archive stocks and facilitate resurrection studies that directly test the differential in response to climate change (performance, fitness, and adaptation) between ancestors and descendants. For an even more informative species resurrection, we advocate for microbial inoculations across multiple plant populations and across the continuum of historical and contemporary ranges to improve our understanding of ecosystem response to global change.

We have addressed barriers to accuracy and broad inference and propose additional ways to implement these studies at the global scale with the intention of furthering climate change studies of plants, microbial communities, and their interactions. Previous methodologies have provided an invaluable, yet sometimes contradictory, preliminary understanding of responses to climate change from the organismal- to ecosystem-level. Accordingly, we have provided guidance to circumvent the hidden challenges faced by meta-communities, range dynamics and the use of resurrection studies. Through the consideration of these overlooked challenges and implementation of the suggestions provided here, we can gain better insight into patterns and processes determining organismal (*i.e.*, plant, microbe, and plant-microbe) responses to climate change across the globe. We hope that this work is employed alongside similar literature that aims to improve our understanding of the influence of climate change, and improves scientific, management, and conservation practices [117].

Supporting information

S1 File. Supplementary information for Fig 4 and S1 Table. This file includes data, methods, and results from the meta-analysis reported in Fig 4 and S1 Table, as well as a comprehensive list of the traits measured in the analyses.

(DOCX)

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