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EDITORIAL

What common-garden experiments tell us about climate adaptation in plants

What common-garden experiments tell us about climate responses in plants

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Abstract

1. Common garden experiments are indoor or outdoor plantings of species or populations collected from multiple distinct geographic locations, grown together under shared conditions. These experiments examine a range of questions for theory and application using a variety of methods for analysis. The eight papers of this special feature comprise a cross section of contemporary approaches, summarized and synthesized here by what they tell us about the relationships between climate-related trait spectra and fitness optima.
2. Four of the eight papers are based on field experiments in prairie, desert, Mediterranean and boreal biomes. Representative of many common garden experiments, these experiments reveal consistent evidence of traits varying with population climate provenance, but evidence of a tradeoff between growth and tolerance traits or of consistent fitness optimization at home is scant, in contrast to trait theory. Two synthesis papers highlight dominant patterns of trait divergence, including for an exotic invasive species. One theoretical paper warned that unknown kinship relationships between populations can result in the misidentification of adaptive trait divergence. A third synthesis paper formulated novel and ambitious goals for common-garden studies through including measurement of response variables at multiple levels of biological organization.
3. The featured papers discuss multiple avenues for improving common garden studies. Genomic analysis, together with the quantification of kinship relationships, will continue to reveal the influence of environmental drivers on gene selection. Measuring a more complete set of fitness traits, especially for traits related to regeneration, will permit the development of projection models to explicitly link trait spectra, climate patterns and fitness consequences. More standardized data reporting will additionally improve abilities to synthesize findings across experiments. Testing population performance in competition with other species will produce more robust fitness comparisons between genotypes, especially for slower-growing genotypes in higher-resource environments. Adding gardens in and beyond climatic edge locations will furthermore strengthen the understanding of population failure and species exclusion. Finally, there is unrealized potential in

adding ecosystem-level observations to common-garden studies that will enhance integrative analysis across scales of biological organization and scientific domains.

4. *Synthesis*. With novel, creative designs, data integration and synthesis, common garden experiments will continue to advance the understanding of trait ensembles interacting with climate across scales of biological organization, provide pivotal data for global change models and guide ecological applications such as restoration of habitats for rare and climate sensitive species.

KEYWORDS

climate change, demographic models, fitness optima, local adaptation, meta-analysis, population x environment interaction, synthesis

1 | INTRODUCTION

Global changes in temperature, seasonality, the frequency and intensity of extreme climate events and elevated atmospheric CO_2 will profoundly influence plant primary production, community structure and evolutionary processes (Peñuelas et al., 2013). The phrase 'adapt, move or die' summarizes the spectrum of possible outcomes for populations meeting novel climate regimes, but a comprehensive conceptual basis for predicting the response of plant species to climate change is still lacking (Chevin et al., 2010; Kearney & Porter, 2009; Parmesan & Hanley, 2015). Common garden research is a deep and extensive field of research that extends this knowledge. This collection of articles features a cross-sectional examination of the diverse experimental and theoretical approaches adopted by researchers in using common gardens to examine global change.

Common-garden experiments are indoor or outdoor plantings of species or populations collected from multiple distinct geographic locations and grown together under shared conditions (Berend et al., 2019). These experiments test how heritable traits and phenotypic plasticity determine the responses of populations to climate conditions and how they are shaped by natural selection to yield the best possible outcome for population persistence. A central assumption of trait theory is that climate adaptation is governed by tradeoffs, i.e., the hypothesis that increasing the fitness contribution of one trait inevitably leads to compromising the contribution of another trait (de Villemereuil et al., 2016; Shipley et al., 2016). Therefore, when populations are moved from their home climate to a different climate, tradeoffs and fitness optima should come to light, as the trait ensembles of translocated populations in new locations now fail to produce the best possible outcome (Kawecki & Ebert, 2004). Common garden experiments can thus address some of the critical complex and interrelated questions of climate adaptation: (1) Are there significant differences in persistence-related performance values between populations in the same garden? (2) Do local populations consistently outperform foreign populations translocated from a different climate zone? (3) What are the specific traits (and associated genes) responsible for mediating the climate responses of populations? (4) What are the dominant climate gradients that correlate with trait spectra and fitness optima? Jointly, these questions outline a global framework for the capacity for common garden experiments to examine species resiliencies and responses to climate change.

Climate itself is an interesting and complex agent of natural selection. Atmospheric conditions are variable and variably predictable across multiple time scales (Jiang et al., 2017; von der Heydt et al., 2021). Climate is composed of many variables, each with distinct effects on plant functions. Atmospheric conditions fluctuate on hourly (day/night), annual, decadal (El Niño/ENSO) to millennial time scales (glaciation), all of which could be relevant to observed patterns of plant adaptation (Moran, 2020). Thus, common garden studies examine the full scope of climate-mediated complexity embodied in modern coexistence theory (Barabas et al., 2018), and thus, we do not expect simple answers.

Common-garden experimental designs range from single to multiple gardens and from few populations representing distinct ecotypes to numerous populations representing entire metapopulations. A specific design favoured by evolutionary biologists is the reciprocal transplant study, a symmetric design in which populations and gardens are co-located to decouple immediate climate effects from those of evolutionary climate history. The purpose is to detect signals of local adaptation operationalized as genotype-by-environment interactions (G × E) that favour genotypes at their homesites relative to foreigners at the same site or relative to genotypes away from homesites (Kawecki & Ebert, 2004). Common garden designs can thus provide a sense of the mechanics of natural selection under climate change and the coherence of evolutionary responses to climate drivers across species, space and time.

In this editorial, we synthesize the salient findings from the eight contributions to this feature starting with a comparison of methods used to detect signals of climate adaptation (Figure 1). Alongside, we present a concise overview of each paper and highlight their state-of-the-art contributions (Table 1). We then present a synthesis of perceived limits to current experimental approaches with suggestions for how they can be overcome and more generally, for the adoption of more integrative, interdisciplinary analyses of plant response to climate change.

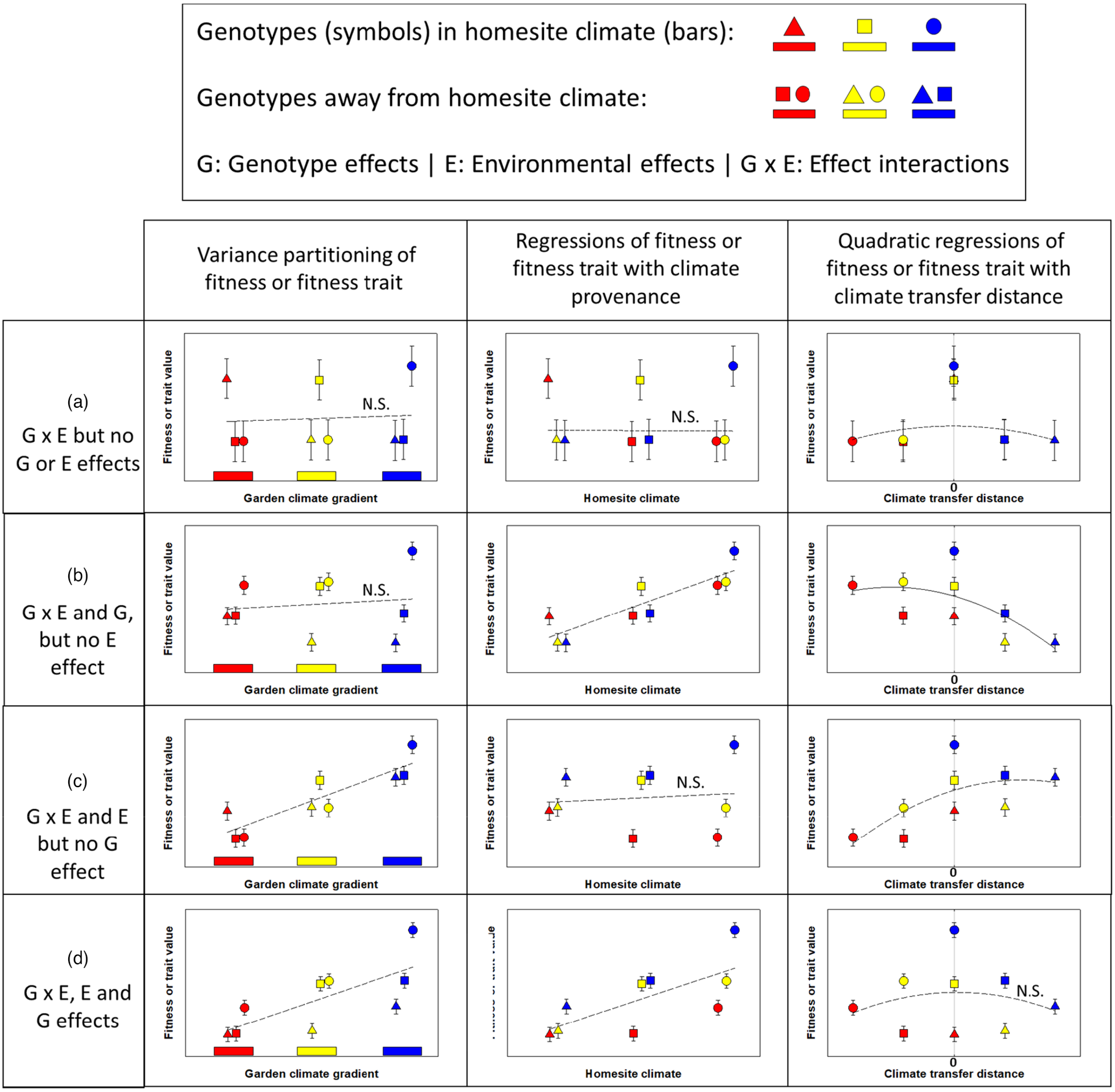

FIGURE 1 Four scenarios (a–d) consistent with local climate adaptation illustrated in terms of three commonly used analytical approaches to common garden experimental design. All have significant G × E interactions that boost the fitness of genotypes in homesite climate relative to genotypes away from home. Scenarios vary in the contribution of additive genotype (g) and environment (e) effects. Genotypes are distinguished by symbols; garden climate by colours. The legend illustrates genotype-homesite affiliations. (a) Without additive G and E effects, fitness optimization near zero climate transfer distance is most pronounced compared to all other scenarios. (b) Genotypes have consistent fitness and trait differences across climate gradients, suggesting that factors other than climate dominate trait divergence (soil, enemies). (c) Climate dominates fitness and trait values; all genotypes experience the same climate as 'best'. (d) Illustration of the fast-slow economics spectrum, where faster growth is an adaptation to more productive climate and slower growth is associated with harsher climate through tradeoffs (Chesson, 2000; Reich, 2014). A fitness trait is a component of lifetime reproductive success (R_0) such as growth, survival or reproduction. Traits are quantitative characteristics linked to fitness, such as leaf N content or xylem resiliency. Climate could be expressed in terms of one or more climate normals or the principal components of a matrix of climate normals. N.S. signifies non-significant regression curves shown for visual contrast

2 | REVIEW OF THE SPECIAL FEATURE CONTRIBUTIONS: METHODS AND INSIGHTS

2.1 | Quantitative signals of climate adaptation

Ecologists and evolutionary biologists design, analyse and use common garden experiments in different ways. Evolutionary studies have traditionally used variance partitioning and variance comparisons with neutral loci to demonstrate non-random genetic variation between populations that may (or may not) be the result of adaptive evolution. Ecologists, in addition, have used regression approaches to establish relationships between traits, function and climate, to potentially discover climate-driven selection processes. In a conceptual figure, we contrast three main analytic approaches (separated by columns) under four different scenarios (separated by rows) to provide common ground (Figure 1).

In analysis of variance, significant G × E effects are interpreted as necessary but insufficient support of local adaptation, because the interaction terms must also have the 'correct' structure, i.e., resulting in net-positive effects on fitness for genotypes at home relative to individuals grown away from home. In Figure 1, all genotypes have this homesite advantage, meaning that fitness trait values at their respected homesites *are higher than expected relative to purely additive genetic and environmental effects*. Thus, in scenarios A–D, we varied only the contribution of additive environmental and genetic effects to illustrate how local adaptation, as defined above, would present in other methods of analysis.

In scenario A, only G × E interactions are significant. For scenario B, genotype effects were added by shifting the trait values of genotypes up or down by the same amount across all gardens. For scenario C, environmental effects were added by shifting the trait values for all genotypes in the same garden up or down by the same amount. In D, both genetic and environmental effects were added.

The homesite advantage is most clearly expressed in scenario A, for example, by showing a fitness optimum at zero transfer distance across genotypes (third column). This can be a case of abundant phenotypic plasticity and climate gradients with weak effects of productivity. In scenario B, genotype effects establish consistent genotype fitness rankings within gardens, so that local genotypes do not outperform foreign genotypes in every garden. Here, the homesite advantage is expressed by each genotype performing better at home than at any away-site. This can occur when ecotypes have diverged for reasons other than local climate, perhaps because of habitat (including soil) specialization. Trait differences across genotypes are observed, but a homesite fitness optimum at zero transfer distance may not be, since more productive genotypes remain more productive across climate gradients. In scenario C, an additive environmental effect maintains within-garden fitness rankings, but the pattern of optimum fitness at zero climate transfer distance is also undone, since all genotypes profit from transfer into more productive climate regions (right of zero) and lose from transfer into less productive environments (left of zero). In scenario D, simultaneous additive environmental and genotype effects may obfuscate the signal of local adaptation the most, as neither within-genotype nor within-garden comparisons may consistently favour genotypes at home. Here, the analysis of G × E effects can be the only reliable method to detect local adaptation.

2.2 | The challenge of false positive and weak signals of climate adaptation

In reality however, not all G × E effects are necessarily adaptive. For example, recent arrivals can be in disequilibrium with the local environment (Alexander et al., 2018), and traits can be different for reasons other than climate (Phillips et al., 2010). Differences between populations could also simply be the product of random processes (Merila & Crnokrak, 2001). In quantitative genetics, divergent trait selection is tested by determining if standardized among-population variance in quantitative traits ('Q_{ST}') exceeds that of neutral loci ('F_{ST}') (Leinonen et al., 2013). In this feature, de Villemereuil et al. (2021) illustrate how complex meta-population structure can amplify evolutionary noise in purely neutral traits, thereby increasing the probability of Type I error—i.e., spurious detection of trait selection when in fact there is none for that trait. They advocate for the use of structured kinship models, calibrated from neutral markers, to assess more accurately local adaptation as variance excess.

Given the potentially high levels of uncertainty inherent to individual common garden studies, meta-analysis is a logical next step for examining the overall evidence for local adaptation across experiments. In this special feature, Lortie and Hierro (2021) report on a meta-analysis refined to reciprocal common-garden experiments. The effect size and metric of local adaptation was operationalized as the standardized mean difference between sympatric (genotypes at home) and allopatric (genotypes away from home) G × E interaction terms. There is a net-positive effect of sympatry relative to allopatry for almost all fitness components commonly reported: survival, reproduction, growth, germination, emergence and biomass for plants introduced as seedlings. The signature of local adaptation on fitness traits is indeed pervasive and consistent using these specific common garden designs. However, on the individual study level, significant G × E interactions are not always evident, even where they can be reasonably expected. High demands on sample size and a high noise-to-signal ratio, particularly in short-term studies, can make it challenging to detect local adaptation in performance related factors at statistically significant levels.

2.3 | Linking climate gradients to trait spectra

Analysis of variance approaches detect local adaptation, and if gardens are distributed across steep climate gradients, it is highly likely that observed adaptations include direct and/or indirect evolutionary responses to climate. Regression approaches, in which traits and genomic structure are related to variables of climate provenance (see Figure 1, middle column), get at questions of climate adaptation

TABLE 1 Summary of the eight papers in this special issue. Climate abbreviations: CVSP, mean coefficient of variation in monthly summer precipitation; MAP, mean annual precipitation; MAT, mean annual temperature; MTR, mean temperature range; T_{min}, average minimal winter temperature; WP, mean winter precipitation. Analysis abbreviations: ANOVA, variance partitioning; RCL, regression (single or multivariate) with climate factors; QRDist, quadratic or higher regression with home-garden climate distance

Reference/DOI	Research type	Biome or habitat	Climate variables	Duration (years)	Type of analysis
de Villemereuil et al., 2021; 10.1111/1365-2745.13528	Simulation model	General	n/a	n/a	ANOVA
Guo et al., 2020; 10.1111/1365-2745.13616	Single common garden	Boreal forest	MAT	4	ANOVA, RCL, QRDist
Montesinos, 2021; 10.1111/1365-2745.13616	Theory synthesis	Invaded habitats	n/a	n/a	n/a
Lortie & Hierro, 2021; 10.1111/1365-2745.13664	Meta-analysis of reciprocal transplant experiments	Global	n/a	Variable	ANOVA
Ramirez-Valiente & Robledo-Arnuncio, 2021; 10.1111/1365-2745.13730	Regional network of common-garden experiments	Mediterranean woodlands	MAP, T_{min}, MTR	48 (= span of multiple experiments)	ANOVA, RCL, QRDist
Johnson et al., 2020; 10.1111/1365-2745.13695	Reciprocal transplant experiment	Temperate grassland	MAP	6	ANOVA
Custer et al., 2021; 10.1111/1365-2745.13747	Three common gardens and multiple populations of two species	Warm desert	WP, T_{min}, CVSP	4	ANOVA, RCL
Huxman et al., 2021; 10.1111/1365-2745.13793	Commentary	General	n/a	n/a	n/a

more directly. Dominant 'drivers' of adaptive evolution are potentially identified, and theories of adaptive tradeoffs can be tested, such as those underlying the 'fast-slow' plant economics spectrum (Reich, 2014) or the notion of environmental filtering in community assembly (Cadotte & Tucker, 2017; Kraft et al., 2015).

The four experimental studies in this special feature all use climate regression approaches, three of them in addition to variance partitioning. Three studies come from biomes with seasonal drought and significant geographic aridity gradients: Mediterranean woodlands (Ramirez-Valiente & Robledo-Arnuncio, 2021), the Mojave Desert of North America (Custer et al., 2021) and the North American prairie (Johnson et al., 2020). One study reports on experiments in the boreal forest of Canada and focuses on temperature gradients (Guo et al., 2020). All four studies report significant trait correlations with climate provenance, equivalent to scenarios B and D developed here (Figure 1). This is also consistent with recent meta-analyses (Baughman et al., 2019; Caruso et al., 2020; Matesanz & Ramirez-Valiente, 2019), including the meta-analysis on Mediterranean pine and oak trees in this feature (Ramirez-Valiente & Robledo-Arnuncio, 2021), documenting strong correlation between traits and provenance.

In the three studies from seasonally dry biomes, drought survival decreased, and growth potential increased with precipitation provenance, although not across all species examined and not in all common gardens (Custer et al., 2021; Johnson et al., 2020; Ramirez-Valiente & Robledo-Arnuncio, 2021). The studies from the Mediterranean Basin (Ramirez-Valiente & Robledo-Arnuncio) and the Mojave Desert (Custer et al., 2021) additionally identify minimal winter temperature as having effects on key trait sets. In the Mediterranean, the variable is related to freezing tolerance (Ramirez-Valiente & Robledo-Arnuncio, 2021); in the Mojave Desert, winter temperature and precipitation have similar effects on traits, possibly mediated through their joint positive effect on soil water storage. Measures of intra-annual climate variability also correlate with fitness traits; for example, the average annual

Scenario supported (Figure 1)	Concept reported	Message	Notable techniques applied or suggsted
Neutrality by assumption	Not all trait differences between populations are the product of selection	Common-garden experiments need to consider kinship among populations	Evaluate trait divergence relative to the kinship structure of meta-populations
Figure 1c: Minor genotype effects on fitness	The interplay pf phenotypic plasticity and development regulation reduces fitness variability between genotypes	Complex genetic/environmental control of phenology can produce surprising climate responses	Separate seed collections by half-sib families to estimate the heritability of traits
Figure 1d: All factors significant	Ruderal invaders evolve to become 'faster' than their ancestors within a few hundred generations	Translocation across provinces strengthens productivity traits	Inclusion of a most-closely related, exotic conspecific or congener
Potentially Figure 1a–d	Homesite advantage is observed in many traits	The signal of local adaptation is particularly strong for seed germination and emergence	Standardize reporting to facilitate future synthesis
Figure 1d: All factors significant	Mediterranean oaks and pines vary in cold hardiness and drought tolerance along climate gradients	There is no tradeoff between tolerance and growth rate in Mediterranean pines and oaks	Network approach to facilitate generalization and lengthen effective observation periods
Figure 1a: G × E effects dominate	Ecotypes from the climate extremes maximized fitness at home, not the intermediate ecotype	Ecotypes differentiate from the level of the genome to their interactions with local communities	Genotypes tested alone, in community plots and in selection plots; Genomic analysis; Long-term experiment
Figure 1b,c for different species	Two desert shrubs differentiate along the same gradients of WP and T_{min}, but vary in patterns of trait divergence	Proximate causes of death (hydraulic failure or carbon starvation) shape species adaptive response to aridity	If used, effects of initial transplant size need to be carefully accounted for
n/a	Common garden experiments are poised to become hubs for interdisciplinary research, hypothesis testing, and research network building	Traditional focus on Darwinian feedbacks (through selection) should be expanded to include Newtonian feedbacks (through constraints of mass and energy balance)	Experimental design limits can be overcome with external, supplementary data and ad-on experiments

temperature range in Mediterranean woodlands (Ramirez-Valiente & Robledo-Arnuncio, 2021) or, in the Mojave Desert, summer precipitation variability (Custer et al., 2021; Shryock et al., 2015). Because climate factors are linked by various degrees of co-linearity across a region, it is difficult to associate population performance to specific climate factors beyond one or two major axes of climate variation. Nonetheless, it is clearly established that temperature extremes and seasonal precipitation, in biomes where precipitation limits productivity, are in fact the major drivers of trait selection.

Guo et al. (2020) provide compelling evidence of how phenological plasticity interacts with climate provenance. In general, adaptive plasticity is expected to lower fitness and trait differences between genotypes (Figure 1a,c). Genotypic differences are instead expressed in the sensitivity of phenology to environmental cues. Guo et al. (2020) examine genotype effects on the timing of bud burst and bud set in a 'warm' common garden in Southern Canada, simulating potential future conditions for *Picea mariana*. Bud burst timing is most strongly affected by interannual temperature variation. Population effects are minor in comparison, advancing bud burst by only about 1 day for every 1°C increase in temperature transfer difference. However, bud set was advanced at a similar rate, following *daylength* cues. Together, these responses produce minor population differences in the timing of the growing season and even smaller differences in growing season length. They concluded that complex genetic and environmental effects on phenological timing can produce surprising responses to climate change.

2.4 | The evidence for tradeoffs between climate-correlated trait values

Evolutionary theory predicts that environmental factors select genes with favourable effects on trait expression, and never just one trait, but a host of traits linked by tradeoff or constraint (Reich et al., 2003;

Shoval et al., 2012). For example, the assumption of a tradeoff between growth (favoured in productive climates) and tolerance (favoured in stressful climates) looms large in vegetation and community models but has been surprisingly difficult to demonstrate directly (Adler et al., 2014; Merila & Hendry, 2014). In this feature, two contributions tackled the tradeoff question directly. Ramirez-Valiente and Robledo-Arnuncio (2021) review the evidence for Mediterranean oak and pine species, and while finding ample evidence for a negative correlation between annual precipitation and traits associated with drought tolerance (e.g., rooting depth, xylem embolism tolerance, sclerophyllous leaves, capacity for osmotic adjustment), negative correlations of these traits with growth potential are not generally significant. One potential reason is that tolerance traits support the continuation of net carbon gain as conditions get drier; thus drought tolerance and growth may not be in conflict in Mediterranean trees. Custer et al. (2021) took a different approach to the same question by correlating the growth rates of genotypes in the most productive garden with survival in the harshest garden, thus selecting different gardens for different traits to amplify trait divergence, provided it exists. Contrasting one evergreen and one drought-deciduous shrub species, they find a negative correlation between growth and survival only in the evergreen shrub *Larrea tridentata*. In this species, both growth and mortality are correlated with the same functional trait at the population level, time-averaged leaf cover. Possibly, greater year-round average leaf cover simultaneously increases the potential for growth and the risk of dying by hydraulic failure.

A different approach to examining evolutionary tradeoffs is presented by Montesinos (2021) in a mini-review of evolutionary change undergone by recent invaders compared to their old-world relatives. According to the enemy-release hypothesis, introduced species can become invasive in their new homes, when translocation resulted in relief from attack by specialized enemies (Heger & Jeschke, 2014; Keane & Crawley, 2002). Montesinos (2021) concludes that ruderal invaders almost always reallocate internal resources from defence (thus tolerance and survival) to growth and competitive traits within a few hundred generations of arrival. Thus, ruderal species, already considered fast on the fast-slow spectrum, are becoming even faster during invasion. Furthermore, species did so idiosyncratically, amplifying different traits to enhance competitiveness. Common garden studies that contrast ecotypes of invasive species as well as their old-world relatives generate phylogenetic context for climate adaptation that may improve the prediction of species responses to climate change. This powerful approach need not be limited to the study of invasive species. For example, Ramirez-Valiente and Robledo-Arnuncio's (2021) analysis is based on examining multiple species across two tree genera (oaks and pines), all native to Spain.

2.5 | The evidence for fitness optimization in home climates

At last, we turn to the question of fitness maximization. Figure 1 illustrates that a monotonic (clinal) response of fitness traits to either genotypic climate provenance or experienced climate can interfere with the emergence of an adaptive optimum at zero climate transfer distance, i.e., where the garden climate is most like that at the population's collection site. In this feature, only one paper tests the quantitative relationship between trait values and climate transfer distance explicitly on four Mediterranean pine and one oak species (Ramirez-Valiente & Robledo-Arnuncio, 2021). Using height (as a proxy for growth) and survival as fitness traits, the study finds significant negative quadratic terms in regression with climate transfer distance in only one species (*Pinus pinaster*) and only for survival. Even so, the predicted maximum survival is not located near zero climate transfer distance, suggesting that additive environmental effects dominate survival traits (Figure 1c).

Counter to this finding, Johnson et al. (2020) report that ecotypes of *Andropogon gerardii* from wet and dry regions of the North American prairie each attained maximal cover in gardens near their respective climate origins. (The exception is the intermediate genotype, which performed similarly across all gardens). At least two factors may contribute to this contrary result: First, the fitness metric used in this study (cover) is a composite of potentially several demographic processes, e.g., growth, sexual and clonal reproduction, mortality or die-back. Some of these processes could be linked by tradeoffs, increasing the likelihood of complex, non-linear responses to environment (Laughlin et al., 2020). Second, genotypes compete against local community members, which can amplify effects of maladaptation in ecotypes far from home. Johnson et al.'s (2020) brilliant common garden design includes three testing stages: genotypes growing alone, genotypes growing in local communities and genotypes competing against one another. Together, they offer complementary perspectives on climate adaptation and a more comprehensive understanding of relevant selection processes.

2.6 | Thinking bigger: Common gardens as platforms for theory integration

In this feature, Huxman et al. (2021), discuss how scientific progress in ecology, and particularly in climate change ecology, has been constrained by separate and largely independent research traditions and theories; one focused on levels of biological organization amenable to short-term, small-scale experiment, and the other on examining only patterns shaped by slow and/or extensive processes. This leaves a gap in understanding consequences of multi-scale feedbacks on ecological function and evolution. Huxman et al. (2021) advocate for common garden studies to facilitate this kind of synthesis by generating scale-overlapping data for scale-overlapping theories and to test predictions emerging out of competing eco-evolutionary ('Darwinian') and physicochemical ('Newtonian') world views.

Amid painting a vivid picture for a common-garden 'super-experiment', Huxman et al. (2021) remark that the key challenge is to recognize which areas of research are 'ripe for synthesis'. They see one such opportunity in attempting to merge the macroecologial theory of strategic trait continua and concepts of community assembly (Grime, 1977; Reich, 2014; Wright et al., 2004), with process-understanding of physiological function, population and community dyamics in the context of a fluctuating and changing climate (Chesson, 2000; Funk et al., 2017; Gremer et al., 2013). The fast-slow trait continuum is a conceptual framework that arrays plant taxa by their tradeoff between resource-acquisitive and -conservative traits, but it is unclear if or how this macroecological pattern relates to eco-evolutionary processes, including growth, survival, and response to climate change from the level of acclimation to natural selection (Adler et al., 2014; Merila & Hendry, 2014). Notably, Montensinos' (2021) analysis of 'fast plants becoming faster' during exotic plant invasion, is a fitting example of a multi-scale synthesis that leverages past events and known histories to develop a broader conceptual context for common-garden studies. In general, Huxman et al.'s (2021) message is that common-garden studies, if conceived in the spirit of scale-integration, hold special promise for developing theory, as well as pragmatic solutions to the thorny problems of ecosystem management in the face of rapid climate change.

3 | SYNTHESIS: WHAT MAKES A COMMON GARDEN EXPERIMENTS WELL SUITED TO TEST AND GENERALIZE PLANT RESPONSE TO CLIMATE CHANGE?

Common garden studies play a central and crucial role in the study of climate adaptation in plants, by disentangling the three-way interactions between environment, phenotype, and genotype—provided they are adequately framed, designed and reported (de Villemereuil et al., 2016). In general, common garden experiments have successfully linked the climate provenance of genotypes to traits or differences in the sensitivity of plastic traits to environment, in concordance with what we know about trait function. They have shown that relationships between climate and traits are almost always clinal; both functional traits (e.g., xylem resistance to embolism) and their related fitness traits (e.g., drought survival) tend to change monotonically with relevant climate gradients (e.g., mean precipitation or minimal temperature). The importance of this linkage for forecasting and prediction in global change ecology, including ecological restoration, cannot be overstated (Brudvig & Catano, 2021).

However, common garden studies have been mostly unsuccessful in explaining the selection of trait combinations that presumably optimize fitness at the scale of populations, particularly for long-lived species. Direct observation of population fitness is possible only for some species with short generation times and even then—because short-term climate patterns do not represent long-term climate patterns—multiple years of observation are required to estimate long-term, average population fitness.

In that respect, Lortie and Hierro's (2021) meta-analysis provides a glimpse into the importance of recruitment traits by showing that germination and emergence produce the largest overall effect size for local adaptation (compared to e.g., growth and survival). This suggests that common garden studies must pay greater attention to the earliest life history stages, i.e., regeneration niches (Grubb, 1977; Schwinning & Kelly, 2013). In common-garden experiments, regeneration traits are reported chiefly for annual plants and short-lived perennials, but long-lived, woody perennials also have highly specialized germination requirements (Bowers et al., 2004; Gutierrez & Meserve, 2003; Meyer & Pendleton, 2005). Unfortunately, the practice of transplanting greenhouse-grown yearlings into common gardens (to ensure uniform establishment) often eliminates early responses to climate (for further discussion, see Custer et al., 2021; Ramirez-Valiente & Robledo-Arnuncio, 2021).

Climate sensitivities of long-lived plants are typically studied on juveniles or recently matured plants but interpreted to be representative of the entire life cycle. In fact, ontogeny itself can be subject to climate adaptation and a seedling's earliest response to climate can set the stage and influence climate response in later ontogenetic stages (Donohue et al., 2010; Laughlin et al., 2020). For species with short generation times, common-garden experiments can be designed to obtain direct estimates of population growth, or as in the prairie study in this feature (Johnson et al., 2020), cover dynamics over a period long enough to have included plant turn-over. This is not an option for long-lived species. Ultimately, demographic models will be needed to determine how adaptations at every developmental stage will pay off over a lifetime.

Demographic modelling does require all vital rates to be known (they cannot), but generic models of suitable life history structure could be used to develop a prediction range. This approach is routinely used in population viability analysis (Fordham et al., 2012; Jaffre & Le Galliard, 2016; Jeltsch et al., 2019; Keith et al., 2008) and could be explored for common garden experiments to compare population persistence probabilities within and across gardens, or indeed by interpolation for any population-climate scenario. Demographic modelling has the capacity to finally bridge the gap between trait spectra and fitness optima (Laughlin et al., 2020).

Stronger focus on trait data integration suggests several other design improvements for common garden experiments, such as routinely measuring a larger array of fitness traits (germination, seedling survivorship, age of first reproduction or reproduction size thresholds) and characterizing juvenile traits (growth and survival) as a function of age and size. Adding common-gardens in more extreme locations on or beyond the trailing and leading edges of current ranges or manipulating climate factors by experimentation would also be very useful. This would capture plant responses to a wider range of climate conditions, perhaps more representative of future conditions (Huxman et al., 2021; Johnson et al., 2020; Ramirez-Valiente & Robledo-Arnuncio, 2021).

Common garden experiments have traditionally focused on questions of trait variation among ecotypes and how they function to improve population performance in their respective climate zones. For example, many contemporary common garden experiments are conducted to establish seed transfer zones for restoration, i.e., map locations in a species range within which plant materials can be transferred with minimal risk of maladaptation. Common garden experiments have not fully seized on the opportunity to map limits of adaptability and to document associated traits that may doom populations, for example through low seed production or germination, poor seedling establishment, excessive juvenile mortality, or simply negative long-term population growth (Allen et al., 2010; Anderegg et al., 2015; McDowell et al., 2008; Stevens-Rumann et al., 2018). Common garden experiments, especially when they include edge environments, are well suited to tackle where local populations would become non-viable if they stayed in place or which populations would have the best chance to survive as immigrants elsewhere.

A second track for next-generation common garden experiments is to establish stronger ecological context in genotype testing (see Johnson et al., 2020). Though not the only ecological interaction relevant to genotype success, competitive interactions will likely amplify effects of trait variation on population growth (Chesson, 2000). Johnson et al. (2020) documented elemental competitive dynamics among prairie grasses, in which stress-adapted 'slow' ecotypes at their dry homesite gain space vacated by 'fast' ecotypes during drought periods, and 'fast' ecotypes at their wet homesite overtop and displace shorter-statured 'slow' ecotypes. These dynamics along stress gradients may be universal among members of similar niches, and even in long-lived species should be observable in juvenile stages (Kelly et al., 2008). To date, competitive arenas, such as those described by Johnson et al. (2020) are not routinely implemented in common garden experiments, a lost opportunity for testing foundational theories of trait evolution and community assembly.

At last, there is further unrealized potential for comparing and synthesizing the outcomes of many common-garden experiments, so that we can begin to develop a generalized conceptual framework for plant response to climate change (Huxman et al., 2021; Lortie & Hierro, 2021; Ramirez-Valiente & Robledo-Arnuncio, 2021). Publications based on common garden studies sharply increased in the first decade of this century, and this trend will likely continue as scientists across the world prioritize climate change preparedness (Strassburg et al., 2020; Turney et al., 2020). Data integration will benefit from more standardized research techniques, including a set of priority traits, guidelines for garden selection, and reporting standards that facilitate quantitative synthesis. Comparing the climate responses of different species across similar climate gradients as well as species responses to different stress gradients (aridity, frost duration, flooding) will be critical to answering the ultimate questions of plant response to climate change; which species have sufficient genetic variation to adapt, which can move or should be moved, and which are destined to disappear.

4 | CONCLUSIONS

This feature was motivated by one question: What can common garden experiments tell us about climate responses in plants? The contributors addressed this question though field study, meta-analyses and conceptual innovation. We built upon their contributions to frame heuristic scenarios (Figure 1) and to highlight key messages (Table 1) to synthesize an integrated vision for next-generation climate studies using these tools and theories. Common garden experiments can become global research hubs that promote conceptual syntheses by teasing apart the contributions of multiple confounding factors such as climate, genotype, phenotype, life history stage, biotic and abiotic feedbacks from short to long timescales. Climate gradients and related trait spectra are a common thread through this field of research, but weaving connections to population fitness and persistence under ecologically realistic conditions remains an ambition and a challenge. With novel, creative designs that cut across scales of biological organization and with continuing data integration and synthesis, common garden experiments will continue to be an important tool for investigating the ecology and evolutionary biology of adaptation and to generate crucial information for global change modelling and planning mitigation of climate change impacts on society.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest. S.S. is an Associate Editor of the Journal of Ecology, but took no part in the peer review and decision making process for this paper.

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This study does not include or use any data.

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