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MINI REVIEW

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

A common garden super-experiment: An impossible dream to inspire possible synthesis

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Abstract

1. Global change threatens plant diversity and disrupts its interrelationship with ecosystem structure and function. This disruption in turn undermines confidence in the knowledge ecologists produce, and whether it will translate into multidisciplinary research settings or guide the effective management of natural lands.
2. To address this challenge, ecology needs to consider the interactions between different levels of biological hierarchy, especially how they feedback on, and are mediated by, plant diversity. Doing so will require conducting empirical work and developing theory that simultaneously considers multiple disciplinary perspectives and units of study.
3. Here we advocate the use of common gardens to integrate ecology, evolutionary biology and ecosystem science through an explicit focus on simultaneous measurement of response variables at multiple levels of biological organization. This approach will provide opportunities to evaluate assumptions important to prediction, such as space-for-time substitution, and tackle the integration of physicochemical and eco-evolutionary foundations to understanding plants and ecosystems.
4. *Synthesis*. We summarize the large body of research on Sonoran Desert winter annuals to demonstrate how experimental designs that employ common gardens to integrate processes across scales hold special promise. This includes refining trait-based theories of plant strategies, providing insight into ecosystem responses to global change and collaborating effectively with other scientific disciplines.

KEYWORDS

common gardens, ecosystem ecology, evolution, functional traits, global change, plant ecology

1 | INTRODUCTION

Global change—habitat modification, degradation and loss, along with anthropogenic climate change—challenges science to provide sound, synthesized and useful knowledge of our planet's future. Ecology is poised to contribute to solving this grand challenge, as a centuries-old research goal has been to explain processes driving the distribution of Earth's biodiversity at a range of scales including species localities (why are species not everywhere? e.g. MacArthur & Wilson, 1967), their population and community dynamics (what promotes coexistence? e.g. MacArthur & Levins, 1967), and variation in ecosystem-level processes deriving from differential species behaviour (why do some species define ecosystems? e.g. Paine, 1969). The need for theory that 'works' has never been greater, as it will provide both predictions and solutions for natural resource managers charged with conserving threatened and endangered species, restoring degraded systems and maintaining biological diversity, among others. One major issue is connecting the many different ideas concerning process across these different scales.

Our understanding of the spatial distribution of plant diversity has been supported by decades of work among organismal, evolutionary, population and community ecologists. The collective body of work has developed the mechanistic basis for understanding species performance, the consequences of life histories for population dynamics, conceptualizations of environmental space as filtering different species features and how interspecific interactions may shape realized plant diversity. Revealed by this venture are the emergent, fundamental axes of interspecific variation in plants that can provide prediction—from Grime's triangle (Grime, 1977) to the world-wide leaf economic spectrum (Wright et al., 2004), and more recently the 'fast–slow' trait conceptualizations (e.g. Reich, 2014).

A related issue, deriving from the question of why species are not found everywhere, is the issue of competitive exclusion—why do we not find more examples of single species dominating environments and what maintains the stable coexistence of diversity (Chesson, 2000)? The interspecific variation associated with the strategies above imply some species could out compete others depending on environmental context, yet we most often find groups of species stably co-occurring. Documenting how different features of the environment, time and disturbance interact with the trait-based conceptualization of species to promote diversity has led to effective prediction of community structure in time (Angert et al., 2009; Levine, 2000). The dynamics of coexistence in response to perturbation is fundamental to the management of natural resources and has many applied implications.

At the highest level of the biological hierarchy, ecology strives to understand how ecosystems exchange and transform material and energy to influence physical processes on the planet (Chapin et al., 2002). In this research, the local and regional distribution of species and their underlying traits dictate both the goods and services leveraged by society (Lavorel et al., 2011), and feedbacks to planetary conditions controlling the Biosphere (Green et al., 2017). Examples include such phenomena as woody plant encroachment and landscape water balance (i.e. Huxman et al., 2005) or forest die-off and carbon source/sink dynamics (i.e. Adams et al., 2015). Here, how biology has influenced hydrogeochemical features guides sophisticated hypotheses for Earth System Models and mechanisms that underlie their computation (e.g. Todd-Brown et al., 2012). An open question is how our trait-based conceptualizations provide insight into the biogeochemistry and energy balance issues that are manifest at these larger scales.

Ecology has also sought to understand the linkages among the population and organismal biology of trait evolution, the community-level processes driving 'diversity', and ecosystem-level 'function', frameworks for studying ecology as above, in part because stakeholders demand knowledge of each. However, research to tackle such linkages is challenged by the fact that we know this work has been challenging because organisms are driven by feedbacks from the environment and multiple levels within the biological hierarchy of life (populations, communities, ecosystems). This complexity suggests that understanding the behaviour of relatively small- and large-scale processes is simultaneously required to build useful knowledge. These facts highlight ecology's current experimental compromise—the constraint associated with controlling processes and making measurements are coupled to manipulation by scale, and the relative importance of either large-scale or low-frequency dynamics is restricted to observation (Pangle et al., 2015). For example, much of the trait-based, 'fast–slow' ecological theory has been developed with cross-system or taxa approaches that presume spatial patterns provide insight into temporal dynamics. Many ecologists currently employ 'fast–slow' theories to array traits in the context of resource acquisitive and conservative strategies to generalize the many functional and life-history approaches to organismal performance in an environment (Funk et al., 2017). On top of this, disciplines, such as genetics and biogeochemistry, have a history of employing different techniques on different units of study, constraining the integration of their foundational eco-evolutionary versus physicochemical approaches—the Darwinian/Newtonian divide (Harte, 2002).

Here we consider how evolutionary biology, ecology and ecosystem science can be coordinated to understand the future of plant diversity and ecosystem function using common gardens. We propose that this understanding requires a renewed focus on simultaneously documenting processes at multiple scales, helping evaluate long-held assumptions in the research enterprise. In addition, we suggest that with careful implementation and measurement, these gardens can be established to explicitly challenge divergent theory, such as through testing predictions emerging from physicochemical versus Darwinian foundations, or from theory as a function of spatial and temporal substitution. The need to create 'overlapping theory' across disciplines requires creating 'overlapping data' in the same system. The physical scale of common gardens, the duality of manipulation (biotic and abiotic) and the easy coupling of new gardens to existing research networks or in locations with deep research histories readily facilitate interdisciplinary interactions and provide a means for moving ecology forward as findings are interpreted through a common model.

2 | COMMON GARDENS IN ECOLOGY AND EVOLUTION

A common garden is a uniform setting where the traits of individuals can be characterized without the confounding influences of environmental variation. It is most frequently identified as an approach to understand genetic variation and adaptation (de Villemereuil et al., 2020). However, the intent, context and complexity of common garden use to understand how organisms work have varied significantly over the last 200 years (Figure 1).

Potato cultivation from the *Solanum brevicaule* complex by the Inca ~10,000 years ago (Spooner et al., 2005) perhaps represents the earliest common gardens. Or it might be maize varieties cultivated from teosinte (*Zea* spp.) by indigenous Mesoamericans ~9,000 years

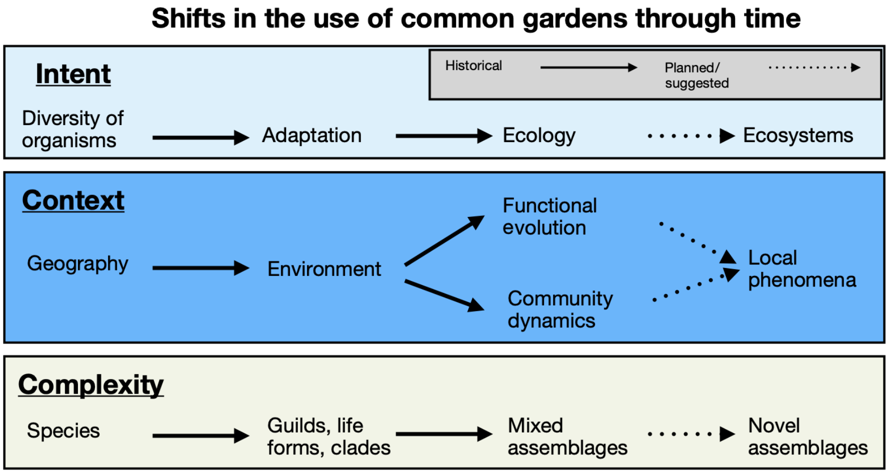

FIGURE 1 The change in application and intent of common gardens in the contemporary history of science. Efforts using common gardens can be categorized as varying in **intent** (from understanding diversity as driven by environment, to a Darwinian tool, to questions in ecology and ecosystem science), in **context** (from understanding the nature of geography, to environmental influence, to use as a tool to investigate process), and in terms of **complexity** (where the unit of study or the inclusion of biotic and abiotic variation is considered). Explicitly considering the interactions among these histories highlights potential areas of novel experimentation and opportunities to connect disciplines in ecology and related fields. This is especially true for structure/function relationships and feedbacks among the hierarchies of life (genotype–phenotype divide; life–environment coupling) and experiments to explicitly challenge the Darwinian/Newtonian divide (see Figure 2)

ago (Matsuoka et al., 2002). In both cases, and likely similar to many pre-colonial breeding experiments, multiple species, seed sources and forms of artificial selection were used in terraced gardens and fields intentionally designed along elevation gradients to breed desired traits (Cleveland & Soleri, 2007; Hodge, 1951). Some forms of these common gardens exist today (e.g. maize landraces in Mexico; Perales et al., 2003). Of course these efforts predate the Enlightenment and the challenges to notions of immutable species that inspired Darwin.

Common gardens evolved in form during the 18th century when Europeans, oftentimes commissioned by royal societies and governments, travelled the world procuring/stealing species as potential medical remedies, beauty products, crops, and novelties for collections and displays (Schiebinger & Swan, 2007). Botanic gardens and collections intensified European desires for further exploration as species of potential economic value were identified, which rationalized further colonial expansion (Brockway, 1979). Along the way, challenges to transporting and establishing species in novel environments essentially led to the amalgamation of modern botany, shifting the common garden as a place for exotic novelties towards a tool to understand plants in relation to environments (e.g. Baber, 2016). These efforts included early approaches to explain the spatial distribution of biological diversity and rectify competing, pre-Darwinian evolutionary theory (Osborne, 1997).

Gregor Mendel may have been the first to employ common gardens with a modern scientific approach to develop transferable theory, using hybridizing peas *Pisum sativum* to understand generational transmission of traits (Mendel, 1986). While common garden sensu *lato* refers to a uniform environment to study plants, the designs and principles are also consistent with animal studies (e.g. Bassar et al., 2010). Resurrecting the approach of 10,000 ybp, common gardens has been replicated across environmental gradients to study genotype-by-environment interactions (e.g. Clausen et al., 1941). Some view reciprocal transplant experiments as fundamentally different from traditional common gardens (de Villemereuil et al., 2016), citing that such experiments aim to identify local adaptation while common gardens aim to uncover the genetic basis of traits. With a few important exceptions (i.e. de Villemereuil et al., 2018), most common garden attempts to understand the genetic basis of adaptation to the environment have documented broad-sense heritability, the proportion of phenotypic variation attributed to genotypic variation. However, the inclusion of additive genetic effects or dominance (narrow-sense heritability) is critical to selection and breeding programmes, which often employ common gardens. These have had tremendous applied impact, especially those rooted in agriculture and forestry.

Common garden studies range in form and focus so as to confound easy synthesis on individual processes. They also present opportunities for connecting insights into ecological and evolutionary processes across disciplines, by simply inspiring diverse research in co-occurring settings. Differences in scope include field-based common gardens to identify phenotypic variation within species (e.g. Kimball et al., 2013), between native and introduced genotypes (as in Colautti et al., 2009), in competitive interactions among species (Levine et al., 2017), and for biodiversity–ecosystem function experiments (Cardinale et al., 2006). Common gardens can be implemented in controlled environments—greenhouses (e.g. Winkler et al., 2018), growth chambers (Pelini et al., 2012) or field manipulations of abiotic variables such as the Free-Air Carbon Dioxide Enrichment (FACE) studies (e.g. Reich et al., 2018). There are designs evaluating relationships spanning from species traits up to guild-level variation focused on ecosystem function. At a level of intraspecific variation, there is relatively little biodiversity–ecosystem function equivalent research, except that emerging from microbial experimental evolution (e.g. Rillig & Antonovics, 2019).

It is interesting that despite a long history of common garden use, there are few syntheses. A key issue may be how researchers identify plant traits on which to document variation. If the goal of a researcher is to evaluate local adaptation, simple documentation does not necessarily require congruent variables across species or context. Yet when implementing questions to compare species, diverse assemblages, behaviour of related species or additional features such as those related to life history, it is essential to carefully select response variables to allow comparison. A ripe area for synthesis is to evaluate the different trait theories that have produced simplifications for comparing species from macroecological patterns that array species by traits along a growth–survivorship continuum (e.g. the world-wide, 'fast–slow' plant economic spectrum; the CSR, or competitor, stress tolerator, ruderal theory; the leaf economic spectrum; Grime & Pierce, 2012; Reich, 2014; Wright et al., 2004). Effectively employed, common gardens can use time to then evaluate the predictions of spatial knowledge and contribute to producing novel, robust knowledge.

3 | MOVING FORWARD—INTEGRATING WITH COMMON GARDENS

Evans (1956) reminded us that while we are free to choose a unit of study specific to a relevant process, such designations are necessarily arbitrary, and response variables vary with questions. At the same time, Velland (2016) suggests many of the processes we are interested in at one level of organization may be in play, analogous to or coupled with related phenomena at another level. The earth sciences have rapidly advanced an understanding of integrated life-environment systems by explicitly integrating hydrology, geochemistry, geomorphology and biogeochemistry in the context of the critical zone (Lohse et al., 2009), while evolutionary ecologists (authors of this paper included!) pedantically point to tradition and Tansley (1939) as gatekeepers of scholarship. In comparison, the

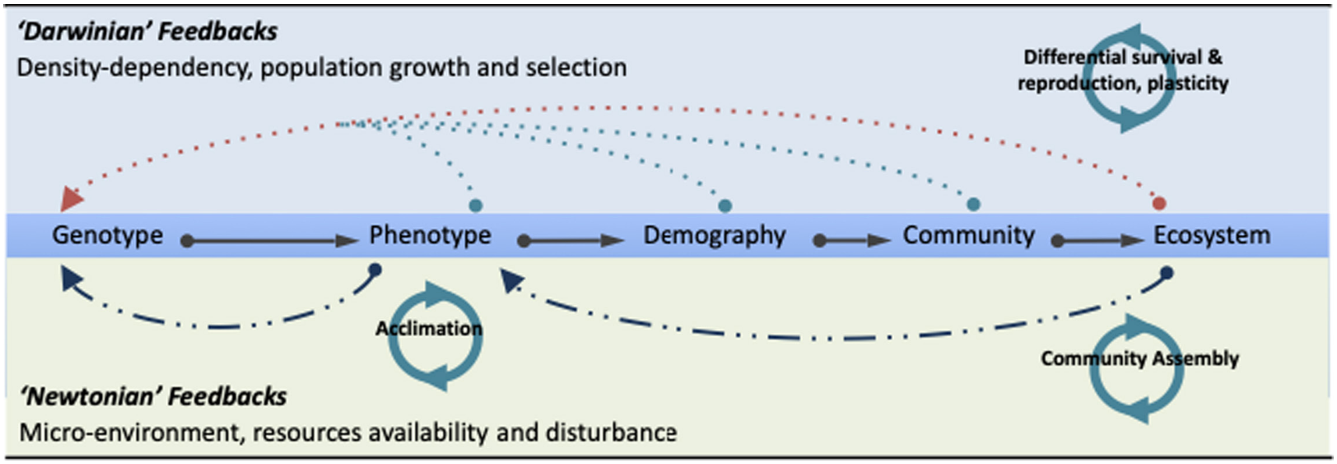

FIGURE 2 Frameworks for potential multi-scale and disciplinary experimentation illustrating units of study and feedback processes important to understanding how biological diversity may be influenced by environmental variation and connected to material and energy transformations and fluxes. The performance of any given genotype is a function of the differential forces applied to the system and feedbacks from other levels in the biological hierarchy. Darwinian feedbacks associated with differential survival and reproduction (dotted lines above the scale sequence) can be separated from Newtonian feedbacks (dashed-dotted lines below the scale sequence) associated with energy, mass and space/time through careful contrasts in linked designs. Creative use of studies that explore manipulation and measurement at multiple scales of biological organization provides us the opportunity to differentiate between the relative importance of different feedback processes on the scale sequence. For example, using the Sonoran Desert annuals system, past research has extensively explored feedbacks and linkages between genotype and community from a Darwinian perspective (blue dashed feedbacks; Huxman et al., 2013 and citations in main text), but the research exploration has not extended to the idea of the ecosystem as a measurement or experimental entity. In including that scale, we can use this framework to isolate any potential Darwinian feedbacks (**Conceptual Experiment 1**—red dotted line) emergent from properties associated with that hierarchy in living systems. An additional example of an area of study (**Conceptual Experiment 2**—lower left dash-dotted line) would be isolating the relationship between genotype and phenotype explicitly to contrast Darwinian and Newtonian dynamics, again using Sonoran Desert annuals. We have extensively studied phenotypic plasticity and the quantitative structure of traits within this system, and the climate features associated with genotype and species performance. However, we know that physical features of biochemical systems have to adhere to mass balance, stoichiometric and continuity constraints (Newtonian features). Careful manipulation of the environment to change such features as the time duration of soil moisture availability with respect to temperature would allow us to explore the role of acclimation (the reversible adjustments individuals undertake integrating variable environmental factors with the function processes contributing to survival, growth and reproduction). Additional conceptual experiments can be constructed as to the above using this framework, such as evaluating how ecosystem effects on resource availability, etc., influence community assembly through a similar research approach

earth sciences reorganized as a community to force an interaction among disciplines into overlapping experimental units, promoting new areas of thought (Waldron, 2020). We advocate a similar approach to understanding the response to climate change by explicitly considering multiple units of study in the biological hierarchy from genotypes to ecosystems in common gardens and manipulating the presence/absence of presumed feedbacks among the levels (Figure 2). This approach also may help bridge incongruence among the physicochemical foundations of ecosystem science and the eco-evolutionary dynamics relevant to population-based biology. Such incongruence is ubiquitous, such as the simplistic dose–response ecophysiologists employ to understand phenotype, given a genotype, as compared to the contrasting approach leveraging the concept of phenotypic plasticity used by evolutionary ecologists. Studies in the context of our proposed common garden framework, with overlap of measurement and manipulation allow for many designs that can isolate concepts and guide the development of theory (see conceptual experiments in Figure 2 and below).

The common garden experimental approach would be more powerful in tackling the above research issues if we consider the potential for manipulation, integration with other research efforts, the explicit use of assumptions in the design and the potential axes of variation possible associated with any system in an inclusive matrix (Table 1). This integration includes considering variation in the oft-biological dependent variables (individual (traits) to ecosystem (plots)), the level of diversity studied (genotypes to species to guilds), the structural dynamics (with or without species interactions), the temporal dynamics (manipulations of recruitment and mortality) and environmental coupling (environmental manipulation in space or time, or driver 'replacement' studies, i.e. Knapp et al., 2001). This comprehensive design concept is essentially an unachievable 'super-experiment' that would enable plant ecology to provide explicit guidance, offering knowledge and prediction to different stakeholders. At one extreme, global change modellers need to understand how matter (water, carbon, nutrients) flows among ecosystems compartments and through ecosystems, and how such flows will be mediated by a diversity of responses to global change. At the other extreme, land managers need to understand how to protect species of concern and preserve biodiversity, or prevent undesirable change to ecosystem services within a particular system. For practitioners across scales, understanding process emerges from a mechanistic understanding of system dynamics at one or more embedded levels of organization.

The above approach may seem especially *unhelpful,* as it seems to suggest plant ecologists should 'do everything, everywhere'. This super-experiment may nevertheless provide a straw person for understanding the purpose of any design and effectively communicating constraints on inference from different required assumptions (Table 1). An example of where ecology may have 'done some things, in enough places' to build reliable assumptions while tackling integrated questions in a simplified design is the Sonoran Desert winter annual system. First, in a demographic study, the specific environmental cues governing survival and fecundity were illustrated when rainfall manipulated within a common garden shifted phenology and root/shoot allocation leading to year-to-year changes in abundance between contrasting annual species thereby supporting species coexistence and demonstrating significant variation in strategies for a group of plants commonly considered to be the same functional type (e.g. Angert et al., 2010). Second, where we have knowledge gaps, we can consider the grand challenge as bite-sized chunks that contribute to the development of generality and reliable assumptions in the future. This is illustrated in the Sonoran Desert annuals in how a community-scale trade-off in traits that balances growth capacity (relative growth rate) with low-resource tolerance (intrinsic water-use efficiency) was fundamental to long-term species coexistence and appeared consistent with a 'fast–slow' continuum (Angert et al., 2009). Yet, the fundamental assessment of trait evolution required careful quantitative genetic approaches using fewer species (Kimball et al., 2013), where species did not necessarily adhere to the predictions from the world-wide leaf economic spectrum relating leaf nitrogen to photosynthetic capacity (Huxman et al., 2013). Finally, we can also consider where existing understanding and tools may provide imperfect, but adequate substitutes for ideal information. Tests of competitive ability by pairwise species contrasts validate assumptions underlying the long-term coexistence, including how species with rapid growth withstand competition in years with frequent rainfall but species with high water-use efficiency are more competitive under drier conditions (Gremer et al., 2013). Together, common gardens, coupled to other experiments, historical data or simplifying assessments have illuminated how diversity dynamics are linked to the evolution of desert annual plant traits (Huxman et al., 2013).

Our framework for using common gardens can be employed to evaluate the relative importance of different feedback processes associated with physicochemical versus eco-evolutionary forces. Using the Sonoran Desert annuals as an example, past research has extensively documented the relationship between traits (genotype) and species coexistence (community) from a Darwinian perspective (Figure 2; Conceptual Experiment 1), but the role of ecosystem properties has not been explored. Explicitly including that scale allows this framework to isolate potential Darwinian feedbacks emergent from properties associated with that level in life's hierarchy. Another additional example would be to contrast Darwinian and Newtonian forces linking genotype and phenotype, where our lack of understanding of physical rules of acclimation would complement our deep eco-evolutionary understanding (Figure 2; Conceptual Experiment 2). This area of research may be extremely fruitful in understanding how the system can array as a function of 'fast–slow' dynamics but still appear to not follow the predictions of the world-wide leaf economic spectrum, as has been shown in other annual systems from the Mediterranean Basin (Kurze et al., 2021). While these research avenues are attractive, many more conceptual experiments could be designed leveraging the common garden framework we promote.

One key challenge in this venture is recognizing when and where pieces of the straw person can be re-assembled (i.e. where dynamics are additive). Modelling with big data may be able to address some of these needs but this is a still-emerging frontier, limited by theoretical

TABLE 1 The complete common garden design elements—the super-experiment—that would be required to comprehensively tackle questions of genes to ecosystems. Using the complete matrix allows for explicit consideration of how to manage the experimental compromise of being unable to control all aspects of the system and explicitly consider assumptions associated with factors unmanipulated. Features of experimental design associated with different questions (What) affect how the experiment is ideally designed (Ideal), or the potential for inference may be gained from an additional approach (Substitutes). Such substitutions and leverages are, of course, non-comprehensive

What	Ideal	Substitutes
Spatial environmental variation	Replicate gardens in different climatic settings	Space-for-time coherency in climate drivers; long-term data; leveraging ecosystem manipulations
Temporal variation	Long-term study of cohorts (of individuals, species, communities) initiated over multiple years to separate ontogeny from inter-annual variation in climate	Historical data, experimentation of inter-annual variation
Key life-history stages driving ecosystem responses	Demographic models to infer sensitivity of lambda to different transitions	Assumptions of controls on population dynamics; disturbance experiments
Species filtering	Gardens with multiple foundational species competing	Removal experiments
Evolutionary processes	Gardens with multiple genotypes of foundational species competing (experimental evolution)	Model organism use; leveraging controlled environment experiments
Species traits variation	Gardens with multiple foundational species	Constraining biological variation to a single guild
Genetically based intraspecific trait variation	Gardens with multiple genotypes of foundational species	Genotype–phenotype associations from sequencing of wild-grown individuals
Potential for response to evolution	Greenhouse studies to distinguish broad- and narrow-sense heritability	Meta-analysis of past studies to arrive at context-specific associations
Local adaptation	Tests for home versus away advantage in fully reciprocal transplants	Historical monitoring of restoration experiments; long-term ecological research sites
Climatic factors	Climatic manipulations	Gradient analysis

and infrastructural challenges (LaDeau et al., 2017). Though empirical approaches may share similar challenges, the super-experiment described above may be the catalyst that promotes different researchers to contribute to synthesis, provides data for further exploration or leverages existing research networks (e.g. NEON, the National Ecology Observatory Network; Keller et al., 2008).

Despite the monumental nature of this super-experiment, it could in fact be feasible if scientists pooled biodiversity across scales (genotypic, community richness) into plots and observed their responses to climatic variation in space and time. The design template could also be manipulated. Climatic manipulations could be imposed within one or more sites to definitively characterize the effects of weather separate from observed patterns driven by spatial and temporal variation. Similarly, plots with varying levels of genetic or species variation could be constructed to definitively document the importance of species filtering or evolution in driving higher level processes. Finally, whole-plot assessments of ecosystem processes can be documented to provide data supporting overarching structure–function questions at larger and larger spatial scales. For example, much of the research agenda surrounding plant response to rising CO_2 concentration over the past three decades focused on how biochemical, organismal, population and community processes may constrain the well-known stimulatory effect of CO_2 on photosynthesis and feedback on anthropogenic climate change. We now know that there are processes at all these levels of life's hierarchy that demonstrate important response. As such, documenting their individual behaviour in overlapping contexts is essential to predicting the large-scale response. Through such efforts, ecology may then be in a position to directly tackle important or oft-ignored questions, such as the role of plasticity in relating species behaviour to population, community and ecosystem processes, which can only be accomplished through combinations of the experiments described above.

4 | CONCLUSION

Predicting plant diversity's future while also understanding ecosystem process response is a challenge that stresses our research approaches. Global change also stresses our fundamental understanding of linkages among the structure and function of ecosystems because it explicitly challenges the assumptions we have held in much research to date. Integrating disciplines with non-overlapping theory by employing common gardens will spur opportunities, research questions and synthesis to move ecology forward. Combined with the thought experiment underlying our 'super-experiment' and imagining the impossibility of manipulating '*everything, everywhere*' highlights where connecting processes provides opportunities for new science and connections to large-scale research networks. This is especially true if we commit to simultaneously documenting process across multiple levels of biological organization and tackling the differences among our disciplines.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors equally developed the ideas presented in this paper, the manuscript drafts and the major conclusions presented.

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This paper does not include data.

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