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FEATURED REVIEW

COMMON GARDEN EXPERIMENTS AS A DYNAMIC TOOL FOR ECOLOGICAL STUDIES OF ALPINE PLANTS AND COMMUNITIES IN NORTHEASTERN NORTH AMERICA

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ABSTRACT. Alpine areas make excellent research sites for investigating questions of plant ecology due to harsh climatic filtering, compressed ecological/environmental gradients, limited species pools, and the presence of potentially isolated sub-populations on habitat islands. In northeastern North America, alpine areas are rare and potentially highly vulnerable to climate change. Despite a renewed focus by researchers on these ecosystems, much remains unknown about the environmental adaptations, species interactions, and dynamics of alpine species and communities in the region and how they may respond to future climate change. Here, we review the use of common garden experiments in alpine areas of northeastern North America and outline the many ways they can effectively address some of our region's most pressing questions in alpine plant ecology and conservation. We also present common garden research priorities, including investigating the influence of environmental conditions on plant trait variation, the response of populations and communities to environmental change, and identifying high-elevation ecotypes. Last, we present practical guidelines for future common garden research in the region, including discussions of experimental design, data collection and analysis, and interpretation and sharing of results.

Key Words: common garden, reciprocal transplant, alpine, plants, traits, plasticity, ecotype, adaptation, northeast, climate change

Alpine areas make excellent research sites for investigating fundamental questions of plant ecology. Harsh climatic filtering and compressed environmental gradients (e.g., elevation and temperature) limit the number of species, which allows scientists to create simple, focused

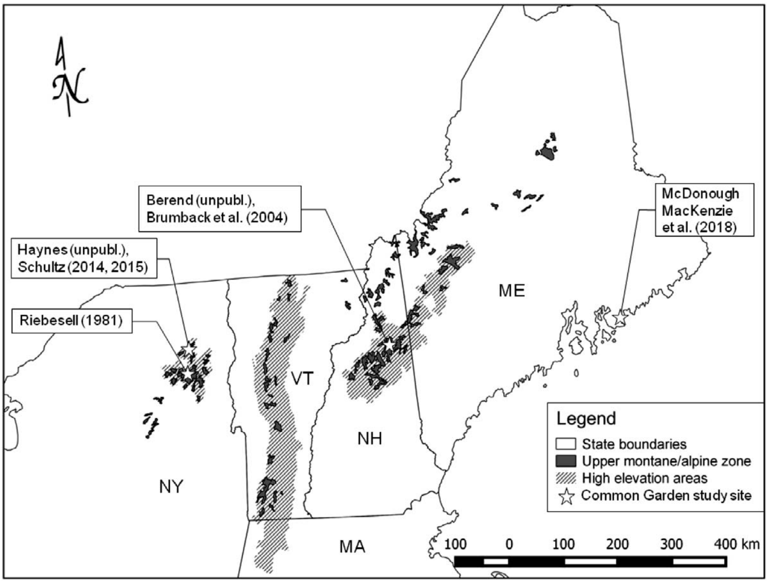

Figure 1. Map of alpine areas of northeastern North America discussed in this review (US only). Locations of common garden studies and alpine plant transplant work conducted to date indicated (see Table 1 for details). High elevation areas indicated are the Adirondack High Peaks (NY), Green Mountains (VT/MA), White Mountains (NH/ME). Upper montane/alpine zone is the ecoregion that includes land area above approximately 855 m a.s.l. One study site (McDonough MacKenzie et al. 2018) was located at Cadillac Mountain in Acadia National Park, which despite its lower elevation, is characterized by open subalpine vegetation species ubiquitous in Northeast alpine communities.

experiments and make direct linkages between environmental factors and plant growth and development. Second, the presence of potentially isolated sub-populations on high elevation "habitat islands" are well suited for research questions involving metapopulation dynamics, gene flow, and biogeography. Last, alpine areas worldwide are expected to respond sensitively and rapidly to alterations in temperature, precipitation, and other climate variables (Cannone et al. 2007; Grabherr et al. 2010; Rangwala and Miller 2012), making them an important ecosystem to investigate from the perspective of global change.

Alpine plant communities in northeastern North America (Northeast) are rare and sparsely distributed above ~1480 m elevation on the region's highest summits (Cogbill and White 1991; Kimball and Weihrauch 2000) (Figure 1). These areas, home to both relict populations of arctic tundra species and regional endemics, comprise an estimated 34 km^2 of land across New York, Vermont, New Hampshire, Maine, Quebec, and Labrador (Jones and Willey 2018; Kimball and Weihrauch 2000), and contain specialized habitats considered critically imperiled across much of this range (Edinger et al. 2014; Gawler and Cutko 2010; Sperduto and Nichols 2011) (here, we discuss only alpine areas in the United States, as some Canadian sites tend to grade into Arctic tundra). There exists an immediate research need to better understand these fragile, unique communities in light of the mounting pressures of climate change, invasive species, and increased public recreation in alpine areas of the Northeast (Capers et al. 2013).

In the Northeast, a long history of botanical exploration and collection provides a wealth of data on the distribution, morphology, phenology, and biotic interactions of alpine plants. The early botanical and geological explorations of the 18th century include the pioneering work of botanists Edward Tuckerman, Francis Boott, and Jacob Bigelow—names now associated with the region's famous landforms and species. Shortly following these early explorations, overcollection by amateur and professional botanists led to scarcity of several rare and/or highly desirable plant species that in some cases last to this day (Cogbill 1993; Sperduto et al. 2018). Several efforts to conserve or reestablish rare and/or endemic alpine plants have been undertaken in the region with varying results (Capers and Taylor 2014; Ketchledge et al. 1985; Schultz 2014, 2015), perhaps the most notable being the successful ex-situ propagation and transplant of *Potentilla robbinsiana* on Mt. Washington (Brumback et al. 2004). Modern ecological research in the Northeast alpine includes detailed descriptions of alpine communities (Bliss 1963; Capers and Stone 2011; Capers and Slack 2016; Carlson et al. 2011; Ketchledge and Leonard 1984; Robinson et al. 2010) and studies of gene flow and population dynamics (Riebesell 1982; Robinson and Miller 2013), phenology (e.g., Kimball et al. 2014), and community change (Capers and Stone 2011; Kimball and Weihrauch 2000; Robinson et al. 2010; Sardinero 2000), especially in response to a warming climate (Seidel et al. 2009). Despite the rich history of scientific exploration in Northeast alpine areas, many unanswered research questions remain. A recent paper identified six high priority research areas for the Northeast alpine: snowbed communities (location, composition, change), treeline limits (mechanisms and change), woody alpine species (extent and rate of change), alpha and beta diversity (change), climatic conditions (variation and change), and phenology (change and its consequences) (Capers et al.

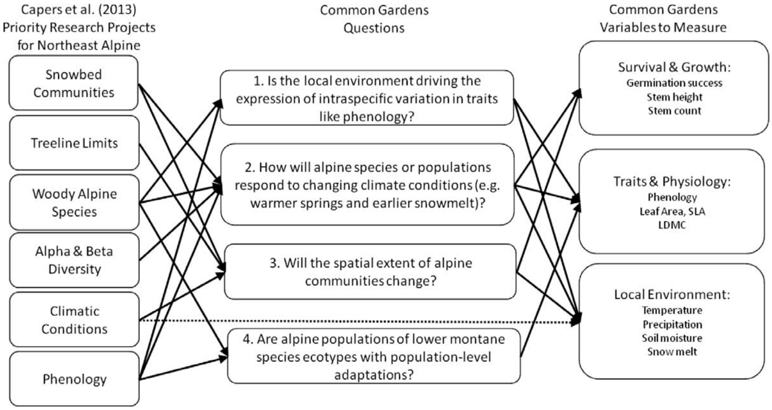

Figure 2. Concept map of links between Capers et al. (2013) Priority Research Projects, the research questions addressed through common garden or reciprocal transplant studies discussed in this review, and variables to measure for those particular questions. Arrow paths represent individual study approaches that could be taken, and links between categories shown are those that are primary, but others exist. Abbreviations: SLA = specific leaf area, LDMC = leaf dry matter content.

2013). Within these research priorities, we see four overarching questions and propose common gardens as a dynamic experimental method for plant ecologists pursuing these important projects (Figure 2).

Common Garden Experiments. The transplantation of species outside their native habitat and range is an ancient human practice. European botanists have been cultivating alpine plants at low elevation for over 400 years; however, the establishment of controlled experimental gardens for scientific study is much more recent (Correvon 1911). The earliest transplant experiments involving alpine species or habitats were conducted in the mid-19th century in Europe and involved moving low elevation plants upslope or alpine plants downslope into "common gardens" (Bonnier 1890, 1895; Kerner 1869).

"Common garden" can refer to a range of experimental designs in which organisms from different provenances are grown together under the same environmental conditions (Figure 3). Under this broadly-defined category, arboretums and botanical gardens can be viewed as adventitious common gardens, as in Zohner and Renner's (2014) study of leaf-out times at the Munich Botanical Garden. Clausen, Keck, and Hiesey (1940) popularized classic common garden transplant experi-

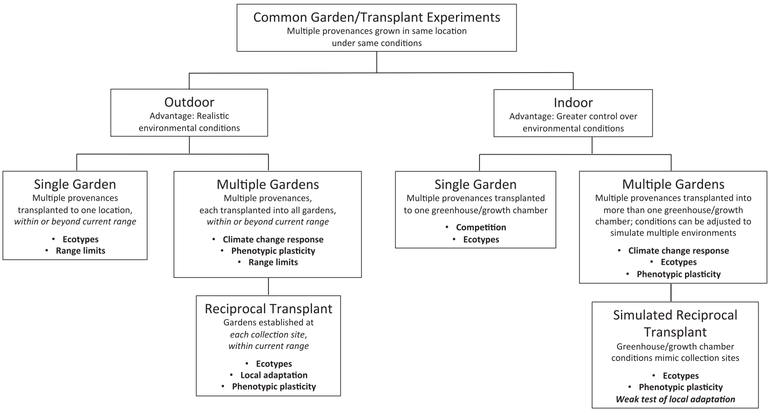

Figure 3. Definition tree representing the many types of common garden and reciprocal transplant experiments. Indicated are examples of the types of studies for which each design is most useful.

ments in American ecology with their ecotype research. Common garden experiments may compare traits across populations along elevational (e.g., Vitasse et al. 2009), latitudinal (e.g., Stevens et al. 2016), or environmental gradients (e.g., Ostaff et al. 2015), and may also include experimental treatments such as warming and drought (e.g., Bjorkman et al. 2017; Hamann et al. 2018). Often, multiple common garden sites are established within a single study and populations native to each location are represented in each garden. This experimental design, called reciprocal transplant, is common across elevation gradients in the European alps (e.g., Alexander et al. 2015; Körner et al. 2016; Scheepens et al. 2010; Vitasse et al. 2013) and the American West (Anderson et al. 2015; Stinson 2005; Wadgymar et al. 2018; Peterson et al. 2016).

The purpose of common garden experiments varies, including investigations of local adaptation (e.g., Halbritter et al. 2018; Hamann et al. 2016; McDonough MacKenzie et al. 2018) and ecotypes (e.g., Galen et al. 1991; Shimono et al. 2009), adaptive potential (e.g., Byars et al. 2007; Gonzalo-Turpin and Hazard 2009), phenotypic plasticity (e.g., Gugger et al. 2015; Kim and Donohue 2013; Vitasse et al. 2010), and species' climate change response (e.g., Alexander et al. 2015; Hamann et al. 2018). That one general experimental design has yielded such an abundance of diverse scholarship is a testament to the elegance of the design: researchers use common gardens to control for certain environmental factors while varying others in order to study the

Table 1. List of common garden studies conducted in alpine areas of northeastern North America to date. Brumback et al. (2004) and Schultz (2014, 2015) are listed as examples of successful transplant work not directly associated with a common garden study. See Appendix 1 for a list of exemplary common garden studies worldwide organized by research question. Abbreviations: SLA = specific leaf area, LDMC = leaf dry matter content, SRL = specific root length.

Study authors	Type	Seeds or mature plants	# of sp.	Species
Berend (unpubl.)	Greenhouse	Seeds	1	*Chamaepericlymenum canadense*
Brumback et al. (2004)	Greenhouse + transplant to alpine	Seeds + mature plants	1	*Potentilla robbinsiana*
Haynes (unpubl.)	Transplant	Seeds and seedlings	3	*Nabalus trifoliolatus* (var. *trifoliolatus* and var. *nanus*), and *N. bootii*
McDonough MacKenzie (2018)	Reciprocal transplant	Mature plants	3	*Kalmia angustifolia, Sibbaldiopsis tridentata,* and *Vaccinium angustifolium*
Riebesell (1981)	Greenhouse simulation of reciprocal transplant	Seeds and stem cuttings	1	*Rhododendron groenlandicum*
Schultz (2014, 2015)	Greenhouse + transplant to alpine	Seeds + mature plants	3	*Pyrola minor*, *Solidago leiocarpa*, and *Salix uva-ursi*

interaction of genes and environment (Blanquart et al. 2013; Clements et al. 1950; Merilä and Hendry 2014; Vitasse et al. 2013). However, common garden experiments are underutilized in the Northeast alpine (Table 1). Recently, our three research groups undertook independently designed common garden experiments in the White Mountains, Adirondack Mountains, and subalpine Acadia National Park (studies summarized below). Having met after completing these experiments, we determined that our experiences demonstrate the need for more regional collaboration and a general set of best practices for common garden experiments.

Northeast Alpine Common Garden Research. K. Berend examined ecotypic variation in alpine snowbed populations of lowland under-

Table 1. Extended.

Location	Elevation gradient	Variables measured	Molecular analysis
Mt. Washington, NH	Base to alpine snowbed (620-1650 m)	Survivorship, functional traits (height, leaf area, SLA, LDMC)	No
Mt. Washington, NH	Greenhouse to Monroe flats, Mt. Washington, NH (1550 m)	Germination success, post-transplant survivorship	n/a
Whiteface Mt., NY	Base to summit of Whiteface (375-1398 m)	Survivorship, functional traits (height, SLA, SRL, LDMC, leaf pigmentation)	Yes
Cadillac Mt., ME	Base to summit of Cadillac (100-466 m)	Leaf-out phenology, survivorship, height	No
Algonquin/Whiteface Mt., NY + Roakdale/ Fish Creek Bog, NY	Bogs to summits (469-1539 m)	Net photosynthetic rate, diffusion resistance, internal leaf CO_2, leaf chlorophyll conc., leaf area	No
Whiteface Mt., NY	Sub-alpine to alpine (along Whiteface Mt. auto road)	Post-transplant survivorship	n/a

story species, which are able to survive above treeline due to the insulating protection of prolonged spring snow cover. He performed a common garden experiment in which he collected ripe fruits of *Chamaepericlymenum canadense* (L.) Asch. & Graebn, *Clintonia borealis* (Aiton) Raf., and *Maianthemum canadense* Desf. from eight alpine snowbed and three low-elevation sites on Mt. Washington, New Hampshire (Figure 4). He germinated and grew the plants under uniform conditions in the greenhouse at the College at Brockport, SUNY, and compared phenotypic traits (plant height, leaf area, specific leaf area [SLA], and leaf dry matter content [LDMC]) between the alpine and low-elevation source populations. There was substantial mortality of *C. borealis* and *M. canadense* plants, and seedlings from one alpine and two lowland sites did not produce sufficient numbers of

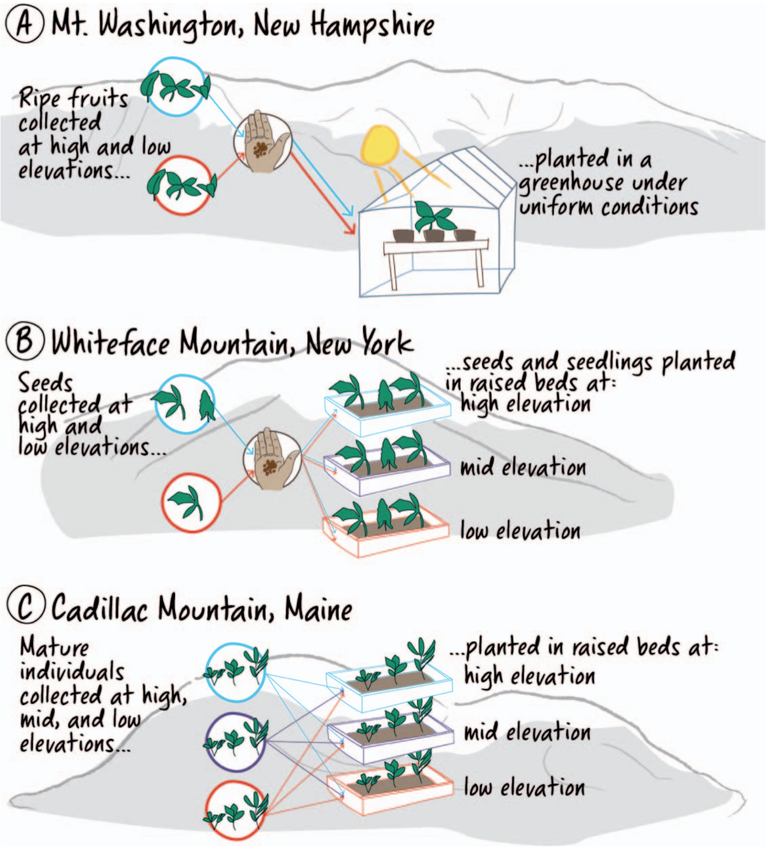

Figure 4. Schematic drawing of the authors' common garden experimental designs. A) K. Berend's (unpubl.) common garden greenhouse study of alpine snowbank plants on Mt. Washington, NH; note high mortality of two species (empty pots). B) K. Haynes's (unpubl.) multiple-common garden study of *Nabalus* spp. on Whiteface Mt., NY. C) C. McDonough MackKenzie et al.'s (2018) reciprocal transplant study of subalpine plants on Cadillac Mt., ME. See section titled Northeast Alpine Common Garden Research for details on study design and Supplementary Figures 1, 2, and 3 (available at https://researchgate.net/profiles/Kevin_Berend/publications) for sample results. Artwork by Bonnie McGill.

mature *C. canadense* plants (n<15) to be included in data analyses. *Clintonia canadense* plants grown from the lowland source population tended to grow taller, have lower LDMC, and higher SLA compared to plants from alpine source populations (Supplementary Figure 1), but limited replication among low-elevation plants restricted the ability to make definitive statistical comparisons (Supplementary figures are available at https://researchgate.net/profiles/Kevin_Berend/publications).

K. Haynes initiated a common garden study at Whiteface Mountain in Wilmington, New York involving two rare alpine taxa, *Nabalus boottii* DC. and *Nabalus trifoliolatus* var. *nanus* (Bigelow) Weakley and one common non-alpine taxon, *Nabalus trifoliolatus* Cass. var. *trifoliolatus*. The purpose of the study was twofold: first, to investigate the response and vulnerability of the alpine taxa to forecasted climate warming by planting individuals at warmer lower-elevation sites; second, to evaluate whether or not the two varieties of *N. trifoliolatus* remain morphologically distinct when grown in the same environment and thus constitute distinct ecotypes worthy of separate conservation. K. Haynes planted seeds and seedlings of the three taxa into raised beds at low, mid, and high elevation and monitored them for survival (Figure 4). After two months, she removed plants from the field for functional trait measurement, focusing on traits of presumed importance for climate change response (Nicotra et al. 2010). Overall, the results revealed strong functional trait plasticity according to temperature (elevation) across all three taxa (Supplementary Figure 2), suggesting that phenotypic plasticity will help buffer populations of these taxa from the threat of climate change. The results additionally suggested ecological distinctiveness in functional traits between the two varieties of *N. trifoliolatus*, but these differences were not significant.

C. McDonough MacKenzie et al. (2018) established common gardens in Acadia National Park, Maine to disentangle the general pattern of temperature-induced shifts in spring phenology—in which populations at cooler locations tend to flower and leaf out later than populations at warmer locations—from population-level variation in phenological sensitivity. Mature individuals of *Kalmia angustifolia* L., *Vaccinium angustifolium* Aiton, and *Sibbaldiopsis tridentata* (Aiton) Rydb. were transplanted into three raised beds across a compressed environmental gradient from the base to the summit of Cadillac Mountain (Figure 4). While Acadia does not include true alpine habitat, the summit of Cadillac is characterized by open, subalpine vegetation species ubiquitous in Northeast alpine communities. The plants in these gardens experienced low mortality; however, a majority of the plants did not produce flowers, thus statistical analysis was limited to leaf out phenology. Over three years of monitoring, evidence for local adaptation of leaf out response to temperature varied among the species, but was weak for all three (McDonough MacKenzie et al.

2018). Instead, the variation in phenological response to temperature appeared to be driven by local microclimate at each garden site and year-to-year variation in temperature; this pattern is also visible in reaction norms for flowering in *V. angustifolium* (Supplementary Figure 3).

Other common garden or transplant experiments that have been conducted in the Northeast include Riebesell's (1981) comparison of plant physiology between alpine and bog populations of *Rhododendron groenlandicum* (Oeder) Kronn & Judd in the Adirondacks, Schultz's (2014, 2015) transplant of *Pyrola minor* L., *Solidago leiocarpa* DC., and *Salix uva-ursi* Seem. on Whiteface Mountain, and Brumback et al.'s (2004) ex-situ propagation and transplant of *Potentilla robbinsiana* (Lehm.) Oakes ex Rydb. on Mt. Washington (Table 1). Although scant in the Northeast, alpine common garden experiments are common across many regions of the world. We have listed some illustrative examples organized by research topic in the Appendix, which we hope will help guide researchers in our region.

Research Priorities. As outlined above, common garden experiments have great potential to explore a variety of topics related to ecology and evolution, with implications for conservation and management. Looking forward, we outline four major research questions for our region that can be addressed through common garden experiments, building on Capers et al.'s (2013) Priority Research Projects for Northeast alpine areas (Figure 2). We also highlight specific research directions and priorities for each question.

1. Is the local environment driving the expression of intraspecific variation in traits?

A central question for all common garden experiments is to what extent the local environment drives expression of traits such as growth and phenology. Capers et al. (2013) recognized two alpine research projects closely related to this question: 1) analyzing the extent and rate of change in woody species occurrence and abundance and 2) investigating changes in phenology. Both projects involve the relationship of a plant's physical environment to its growth and development; changes in these relationships may have far-reaching influences, possibly affecting species persistence and turnover (or beta diversity) in alpine plant communities.

Plant traits are measurable morphological, physiological, or phenological characteristics of an individual plant that reflect the evolutionary responses (or "ecological strategy") to particular environmental conditions (Pérez-Harguindeguy et al. 2013; Wright et al. 2004). Because they are plastic (to varying degrees), plant traits vary both within and among species along common mesotopographical gradients of sunlight, temperature, precipitation, soil moisture, nutrients, substrate, and elevation (e.g., Choler 2005; Fonseca et al. 2000; Milla et al. 2008; Nicotra et al. 2010; Schöb et al. 2013), all of which play especially important roles in structuring plant communities in alpine environments (Sultan 1995; Westoby and Wright 2006; Violle et al. 2007; Yan et al. 2012).

Phenotypic variation in plants can be caused by both trait plasticity and evolutionary divergence (Franks et al. 2014). Clones and closely related plants from a single population grow and develop differently when raised under different environmental conditions in a phenomenon known as phenotypic plasticity. Phenotypic plasticity is a response to locally-varying environmental conditions that, when adaptive, can increase an individual plant's fitness (Ågren and Schemske 2012; Bradshaw 1965) by optimizing its response to the specific growing conditions it encounters during growth and development, as well as later in life (Beaman et al. 2016).

Plasticity is important in alpine environments in several ways. The structure of alpine landscapes is complex and shaped primarily by small-scale topographic and climatic conditions, creating a mosaic of habitat types above treeline. Such heterogeneity in microhabitat conditions may have a sorting effect on certain plant trait values relative to individuals' tolerance of those conditions, thereby determining the structure of those communities. The condensed environmental gradients (e.g., elevation and temperature) of alpine landscapes may also select for plastic responses in plants that could disperse into different microhabitats (Levins 1963; Bradshaw 1965; Matesanz et al. 2010). The plasticity of morphological and phenological traits in alpine plants can have cascading effects on alpine communities, including insect pollinators and their predators or threatened or endangered species that rely on alpine habitat (Levesque and Burger 1982; McFarland 2003; McFarland et al. 2017). Also, recently noted increases in the occurrence and abundance of woody species in alpine environments (Capers and Stone 2011) may be facilitated by plasticity in their morphological and phenological traits in response to climate change (explored in more detail in Question 2).

Because common garden study designs almost always incorporate some physical measure of plant traits, physiology, or phenology, they offer a straightforward and practical way to explore trait responses to environmental variables in alpine plants. These experiments are a relatively economical way to begin to answer some of the most pressing questions we have about how trait plasticity and expression is related to species persistence or community structure in the Northeast alpine. For example, multi-species studies could be used to investigate if Northeast alpine plants display greater plasticity in more heterogeneous environments, or how spatial versus temporal environmental heterogeneity influences plasticity. Research priorities should be directed toward species inhabiting a range of environments or those that already exhibit substantial intraspecific variation.

2. How will alpine species or populations respond to changing climate conditions (e.g., warmer springs and earlier snowmelt)?

In the Anthropocene, documenting and predicting ecological responses to climate change is vital. The high-priority research projects that Capers et al. (2013) highlight address this question at multiple levels, from communities (species richness, particularly in snowbed communities) to populations (phenology) to species (habitat expansion/contraction). Research on the ecological effects of warmer temperatures, earlier snowmelt, and more variable precipitation can improve our understanding of abiotic filters on biodiversity, allow us to identify the species, populations, and communities most vulnerable to climate change, and inform managers as they allocate limited resources. Common garden studies provide a way to directly assess the response of organisms to a change in climate and thus provide a critical tool for informing conservation in the face of rapid change (Nooten and Hughes 2017).

Global climate change threatens to drive one sixth of the world's species extinct (Urban 2015) and has already caused local and global declines and extinctions (Cahill et al. 2013; Freeman et al. 2018; Panetta et al. 2018; Wiens 2016). Mountaintop species and communities, including those of the Northeast alpine, are highly vulnerable to climate change as they cannot advance to higher elevation and may be out-competed by invading lower-elevation species (Marris 2007; Freeman et al. 2018; Urban 2018). In addition, high-elevation species may face a faster than average rate of warming in some locations (Pepin et al. 2015; Rangwala and Miller 2012). The Northeast is the fastest warming region in the contiguous United States (Karmalkar and Bradley 2017), and while contrasting evidence has been found regarding the rate of warming at high elevations in the region (Seidel et al. 2009 vs. Wason 2016), undoubtedly Northeast alpine species will face warming rates unprecedented for at least the past 50 million years, (Jansen 2007). This rapid change poses a serious threat to the persistence of Northeast alpine communities, which represent a significant part of our region's natural and cultural heritage and include several endemic plants (e.g., *Geum peckii* [White Mountain avens], *Potentilla robbinsiana* [Robbins' cinquefoil], and *Nabalus boottii* [Boott's rattlesnake-root]) and animals (e.g., *Boloria montinus montinus* [White Mountain fritillary]).

We may see three potential responses in species impacted by climate change: (1) range shift, (2) adaptation, and (3) phenotypic plasticity/acclimation (Chevin et al. 2010; Davis et al. 2005; Jump and Peñuelas 2005). Of these, phenotypic plasticity may be the only mode available to Northeast alpine species. Alpine plant populations are usually small, isolated, and often clonal (Capers et al. 2013; Körner 2003), and may therefore lack the genetic diversity needed to adapt. Additionally, given their isolated position at the highest points of the region's landscape, range shift may also be highly unlikely (Theurillat and Guisan 2001). Determining the plasticity of traits related to growth, allocation, and phenology can help us predict Northeast alpine species' responses to ongoing climate change.

Arguably the most important plant traits to investigate in light of climate change are phenological traits, which provide insight into organismal, community, and ecosystem processes (Funk et al. 2017). Phenological traits mediate a species' ability to persist at a location or shift its range, and mismatches in phenology between an organism and its environment or between two interacting organisms can drive species to extinction (Cahill et al. 2013; McLaughlin et al. 2002). Common garden experiments can uncover local patterns in phenological plasticity; in a reciprocal transplant experiment in Switzerland, Gugger et al. (2015) found that populations from colder locations have more constrained phenological responses (less plasticity) than populations from warmer locations. In contrast, a study of observational records of tundra species from high-latitude sites concluded that plants at colder sites had greater phenological sensitivity (Prevéy et al. 2017).

Current phenology research in the Northeast tracks the impacts of warming climate on species' life history events (Everill et al. 2014; Gallinat et al. 2018) and provides valuable trait data for managers assembling climate change vulnerability assessments (Cleland et al. 2012; Enquist et al. 2014). However, almost all current investigations of phenology in the Northeast alpine are limited to long-term observations rather than manipulative common garden experiments; the latter are arguably more powerful at predicting species' responses to future change (see Wolkovich et al. 2012). Indeed, despite the wealth of questions surrounding plasticity in phenology and other organismal traits with regard to climate change, only two experimental studies have been undertaken to examine trait plasticity in alpine species in northeastern North America (K. Haynes, unpubl.; McDonough MacKenzie et al. 2018). Unfortunately, given the species- and trait-specificity of phenotypic plasticity, we cannot fully grasp the likely response of Northeast alpine communities to continued change from these two studies alone. Furthermore, neither of these studies examined abiotic or biotic changes associated with climate change apart from temperature.

We are left with an urgent need for studies investigating Northeast alpine species' responses to abiotic (e.g., Hamann et al. 2018) and biotic community changes (e.g., Alexander et al. 2015) to more fully understand the vulnerability of these communities to climate change and to identify species at the greatest risk. Common gardens could be used to study variation in phenology and identify potential mismatches in plant/pollinator relationships in alpine areas as well as the influence of seasonal events (such as snowmelt) on the phenology of entire plant communities. Other studies could investigate the role of functional trait plasticity in buffering plant communities facing ongoing climate change. As priorities, we suggest investigating phenotypic plasticity of phenological and functional traits for regionally endemic alpine species, followed by rare non-endemics, using common garden experiments spanning wide elevation gradients. Researchers should concurrently monitor the survival and reproductive consequences of induced abiotic or biotic changes to provide managers with a more complete picture of the threats posed by ongoing climate change.

3. Will the spatial extent of alpine communities change?

Alpine habitats worldwide are deemed vulnerable to climate change in large part because the extent of their mountain habitat is likely to shrink as forests encroach—the geometry of mountain topography means that there is usually diminishing area available for species migrating upslope (Elsen and Tingley 2015). In northeastern North America, where alpine habitat is already sparsely distributed across low peaks, advancing treeline could quickly reduce available habitat or eliminate it from a mountain altogether. Within remaining alpine habitat, the extent of individual alpine plant communities will likely shift as demographics change. For example, an increase in growth rates for woody alpine species ("shrubification") might increase the extent of heath communities at the expense of herbaceous or cushion plant communities (Capers and Stone 2011). This risk of lost spatial habitat extent has led to assessments of high climate change vulnerability for alpine species here (Whitman et al. 2014), and for these reasons, Capers et al. (2013) ranked monitoring treeline and woody alpine species as two top priority projects for alpine researchers in the region.

At a coarse scale, the spatial extent of alpine communities depends on the location of treeline (Griggs 1942). Treeline could advance upslope in two ways: first, existing krummholz trees currently growing in horizontal mats above treeline could grow more vertically, or second, seedlings could recruit above treeline. While the location of treeline is generally correlated globally with the 10 ° C isotherm for the warmest month of the year, there is evidence that in the Northeast, this may not be an accurate delineation (Kimball and Weihrauch 2000). Exposure to other climatic factors, including wind and rime ice, seems to play a large role in determining the treeline here (Cogbill and White 1991; Kimball and Weihrauch 2000). At a finer scale, there is evidence that shrubification is already impacting the composition and size of alpine plant communities within available alpine habitat. A repeat photography study in New Hampshire's White Mountains found local evidence of increased forest cover and tree islands expanding into alpine habitat in the past century (Beale 2009); at lower elevations in the Green Mountains, the northern hardwood-boreal forest ecotone has also shifted upward (Beckage et al. 2008). Similarly, resurveys of alpine vegetation plots in Maine and New Hampshire report more abundant trees and shrubs (Capers and Stone 2011; Sperduto et al. 2018). This trend is expected to continue in response to warming temperatures (Bjorkman et al. 2018).

Common garden experiments can be leveraged to study the impact of climate change on treeline and shrubification. Some work has been done on this topic elsewhere in the world, including studies of the advancing northern hardwood-boreal forest ecotone (Beckage et al. 2008; not a common garden), the plasticity of transplants across elevation ranges (Körner et al. 2016), and seedling recruitment beyond the extent of current treeline (Kueppers et al. 2017). Common garden studies at treeline could additionally expose patterns of plasticity (see Best Practices) for traits like plant height when mature individuals are transplanted into different microclimates, shedding light on the interaction of plant traits and ecosystem functions. Shrubs are underrepresented in common garden literature, as experiments generally focus on herbaceous/forb species (Alexander et al. 2015; Bjorkman et al. 2017) or tree seedlings (Ostaff et al. 2015; Körner et al. 2016), but shrubification trends in the alpine should be further explored through common gardens.

The Northeast is well-suited for common garden studies related to treeline and shifting community boundaries, given the complex interaction of forces that determine treeline in the region. Studies could include growing treeline species above their current elevational extent (potentially coupled with experimentally warmed gardens) to anticipate change in spatial extent of communities. Additional studies involving transplants among other alpine communities could help reveal the relationship between microclimates and community composition and predict changes in these communities under climate change. Priority should be given to particularly rare or suspected climate-sensitive communities, such as snowbed communities, or species/communities that might invade from lower elevation, such as treeline species.

4. Are alpine populations of lower-montane species ecotypes with population-level adaptations?

The alpine habitats of the Northeast support plant species with different ranges, from endemics (*Geum peckii* and *Potentilla robbinsiana*) to alpine-restricted (*Diapensia lapponica* L.) to wide-ranging (*Chamaepericlymenum canadense* and *Sibbaldiopsis tridentata*). Populations of lower-montane species existing above treeline could represent morphologically and genetically distinct ecotypes, differing in their phenological and physiological responses to environmental change compared to their alpine-restricted neighbors (Winkler et al. 2018). Understanding the existence of alpine ecotypes for wide-ranging species and their likely response to ongoing change is important for managers assessing climate change vulnerability and for identifying source populations for restoration projects (Buisson et al. 2017). Both identifying ecotypes and understanding their response to change (as discussed in Research Priority 2) can be accomplished through common garden studies. We see our fourth research question as a reflection of three of the Capers et al. (2013) priorities for Northeast alpine research projects: 1) snowbed communities, which comprise many lower montane species, 2) woody plant species, and 3) phenology, which may be more (or less) plastic in alpine ecotypes.

Northeast alpine areas are highly fragmented and topographically diverse, creating a complex web of interactions between populations and sub-populations of species across their range. Individual communities or populations may therefore act as "habitat islands" (MacArthur and Wilson 1963, 2016; Riebesell 1982), separated from each other by local topography (on a single peak) or discontinuous habitat (such as lowland hardwood forest across adjacent peaks), with separation ranging from meters to hundreds of kilometers. Under such conditions, individual populations may act as their own evolutionary units, driven by both the particular conditions on the island (i.e., peak or sub-habitat) and gene flow (or lack thereof) with their closest neighbors (Whittaker and Fernandez-Palacios 2007). Thus, a cline of genotypes (and potentially phenotypes) can develop across populations over time. Ecotypic variation is usually evidenced by trait variation, and there are many examples of ecotypes emerging in alpine environments worldwide on that basis (e.g., Galen et al. 1991; Oleksyn et al. 1998; Scheepens et al. 2010; Shimono et al. 2009; Shimono and Kudo 2003, 2005). However, trait variation observed in wild populations is not sufficient for establishing ecotypes, as variation may be due to plasticity alone rather than genetically fixed trait differences. By raising individuals from different populations in common gardens, researchers can identify the existence of fixed morphological differences indicative of ecotypes.

Tundra species inhabiting alpine areas in the Northeast have been separated from their source populations for ∼10K years due to Pleistocene glaciation (Billings and Mooney 1968; Ikeda et al. 2008; Spear 1989). There is evidence that genetic bottlenecks caused by geographic isolation have led to genetic and/or trait differentiation among some tundra populations, including *Carex bigelowii* Torr. ex Schwein (Scheepens and Stöcklin 2011; Schönswetter et al. 2008). In fact, research has shown that most alpine species are ecotypically different from their congeners in the Arctic (Billings 1974; Mooney and Billings 1961), and it is likely that a similar pattern is driving divergence among isolated alpine plant populations in our region. However, the current degree of genetic isolation for most Northeast alpine species and communities is unknown, as is the ecotypic uniqueness of geographically separated conspecifics.

Just as alpine plant communities in the Northeast are separated from their tundra source populations, some specialized alpine plant communities harbor lowland plants where conditions allow. For example, some herbaceous species normally found in the hardwood forest understory at low elevations in the Northeast are able to persist in alpine snowbed communities (Björk and Molau 2007; Bliss 1963; Capers and Slack 2016), where they are sheltered from spring frosts and high winds by late-lying snow that collects in topographical depressions, usually on the leeward side of peaks. *Chamaepericlymenum canadense*, *Clintonia borealis*, *Maianthemum canadense, Veratrum viride*, and other lower-montane species thrive in these environments alongside alpine-restricted species despite substantial ecological displacement. There seems to be considerable discontinuity in many of these species' local ranges—they are filtered out at higher elevations by the increasing harshness of the alpine environment yet thrive in snowbed communities well above treeline.

We know little about the degree of connectivity between lowland and alpine populations of such herbaceous snowbed species, and whether or not snowbed populations represent alpine-adapted ecotypes meriting separate conservation concern. Researchers should identify alpine populations of typically lower-elevation species that exhibit trait differences, then raise plants representing both alpine and lower-elevation populations from seed in a common garden to see if trait differences are fixed (Figure 3). A reciprocal transplant design could be used to establish the existence of local adaptation of high-elevation populations to the alpine environment. These two lines of evidence—fixed morphological differences and local adaptation—would provide strong support for the existence of a distinct alpine ecotype meriting separate conservation concern from low-elevation populations. In addition, common gardens could be utilized to investigate whether naturally observed intraspecific variation in morphology or phenology is due to local adaptation, informing conservation actions like population augmentation or seed banking. We recommend targeting charismatic, easy to cultivate lower-montane species that occur across microclimates and communities, for which larger-scale studies may be more feasible.

The research environment in the Northeast alpine region is poised to tackle these four questions. Many plant communities and populations are well mapped and monitored (Kimball and Weihrauch 2000; Carlson 2011), source populations are readily accessible, and natural environmental gradients are easy to co-opt for field experiments. Additionally, extensive literature is available on collection, germination, and growth of many common alpine species (see Best Practices, below) and many regional resources exist (e.g., New England Botanical Club, New England Wildflower Society, state natural heritage programs, etc.). Last, while we focus in this review on alpine areas of the northeastern United States, most of these research directions apply equally to the alpine and sub-alpine habitats of Québec, Labrador, and Newfoundland (Jones and Willey 2018). Incorporating those locations into work described here will be valuable to our understanding of alpine ecology in the region.

Best Practices and Research Suggestions. Finally, we present a list of best practices and suggestions for researchers undertaking common garden research in the Northeast alpine. A review of the global common garden literature (see Appendix) reveals large variation in experimental design and in the level of reporting on methodological details, rendering cross-study comparisons difficult. We encourage researchers and land managers in the Northeast to explicitly state their project goals and transparently report on experimental design, data collection and analysis, and interpretation of results to facilitate future meta-analyses and provide guidance for future studies.

Experimental Design. As a part of experimental design, researchers must make decisions to meet their project goals; this involves matching the research question with the appropriate type of common garden (Figure 3). Here, we offer some advice on site selection, life stage selection, and transplant care, as well as recommendations for minimizing environmental impact.

Researchers should work with land managers to identify the best sites for in-situ common gardens. Depending on the project goals, gardens may need to be located across environmental gradients that span elevations, slopes, or aspects, or may require researchers to hold some of these variables constant (see Interpreting Results, below). In all cases, it is important that researchers clearly report the slope, aspect, elevation, and microtopography of gardens in publications. Methods for planting in the literature range from placing potted plants into arrays (Gugger et al. 2015; Körner et al. 2016; Stevens et al. 2016; Vitasse et al. 2013) to planting individuals or cuttings directly into local soil (Alexander et al. 2015; Scheepens et al. 2010; Stinson 2005; Ostaff et al. 2015; Vitasse et al. 2009, 2010) to planting individuals into raised beds (McDonough MacKenzie et al. 2018). Brumback et al. (2004) found that smaller pots were easier to transport and plant in the field and that pot size did not affect growth or survival of *P. robbinsiana* transplants; however, species with more extensive root systems may be detrimentally affected by small pots. Ultimately, the appropriate planting method will depend on the goals of the project, the sampling strategy, and the species.

The choice of species and life stage to use in transplant experiments will be driven by research questions and the availability of material. Typically, the younger the individual, the greater its capacity for plasticity. Many common garden experiments use seeds collected from source populations, either directly transplanted into gardens or first germinated to the seedling stage. Researchers requiring greater precision (i.e., full knowledge of genetic relatedness among study individuals, control for maternal effects, etc.) may decide to raise a generation in a greenhouse and hand-cross individuals to produce seed for use in their planned experiment. However, germinating seeds and/

or raising a greenhouse generation requires time and resources, and the resulting plants may take years to display reproductive traits or set seed. On the other hand, mature transplants obtained from wild populations provide a time-efficient and cost-effective alternative for studies on the effects of environmental changes for long-lived perennials when full knowledge of genetic relatedness is not necessary (Alexander et al. 2015; Ostaff et al. 2015; Stinson 2005; Vitasse et al. 2010).

Whether transplanting seeds or plants, researchers must decide how to collect these samples to ensure proper coverage and replication because selection of any particular sampling strategy involves tradeoffs (Richards et al. 2006). For example, an evolutionary biologist comparing the plasticity of genotypes within a single population might favor choosing multiple clones (or full- or half-siblings) of several genotypes, while an ecologist comparing plasticity among several related species might reduce genotype-level replication in favor of sampling a greater number of populations (Richards et al. 2006). It is critical that no matter the strategy chosen, a suitable number of replicates is obtained from each source population to avoid misinterpretation of results due to sampling errors such as pseudoreplication and to sufficiently represent inherent variation both within and among populations. Researchers can find information regarding experimental design, replication, sample sizes, etc. in quantitative genetics textbooks, such as those by Falconer and Mackay (1996), Lynch and Walsh (1998), or in Conner and Hartl's (2004) accessible introduction. Although writing in the context of ex-situ conservation, Guerrant et al.'s (2014) discussion of sampling methodology—covering individuals to species and topics like timeframe, propagule type, and sample size—may also be useful.

Care of plants during germination and growth varies widely by species, but there are several good resources available. Cullina (2000) provides instructions for germination and care of seedlings and plants for most common species found in the region, and Baskin and Baskin (1998) is comprehensive regarding the germination requirements of taxa worldwide. In order to germinate, seeds may require cleaning, scarification, warm and/or cold incubation/stratification, or light adjustments. Researchers attempting to germinate species for which no guidelines exist should consult related species; some degree of trial and error may also be needed. Treatment with gibberellic acid (GA_3) may increase germination success (Brumback et al. 2004) but may also affect plant morphology; our recommendation is to use the minimum concentration of GA_3 needed to achieve germination success and to forego its use altogether when possible.

Proper care of greenhouse or outdoor common gardens depends on the nature of the study and garden location. Greenhouse gardens should be kept at consistent (or cyclical) day/night temperatures and light regimes with plants watered and rotated regularly. Outdoor gardens require additional care, possibly including weeding, watering, or protection from herbivory (K. Haynes had success using bird netting). In both experiment types, we recommend using a standardized soil mix with a composition as close to the natural setting as possible, such as a mix of potting soil, peat, sand, and perlite. In areas where gardens will be visible to the public, educational signage may help inform visitors of the purpose of the study and dissuade tampering with plants or equipment (Clarin et al. 2014; Jacobi 2003; Kidd et al. 2015).

Alpine habitat is fragile. When both sampling natural populations and caring for outdoor gardens, it is important to minimize impact to the surrounding alpine environment, and special care should be taken to avoid detrimental impacts to the populations being studied. In the Northeast and globally, mountains are overrepresented in protected areas and have some of the longest conservation histories (Elsen et al. 2018). Acadia National Park, the White Mountain National Forest, and Adirondack Park are over a century old. These parks and their agencies have long histories of management and have permitting processes in place to reduce the environmental impact of ecological research. The common garden research priorities we outline above will support the conservation mandates of these protected areas and support management decision making.

Special care should be taken during collection and garden siting in order to minimize impacts. In deciding on a sampling scheme for collection, researchers should consider not only what is optimal for their experimental design, but also what is reasonable for avoiding negative effects for wild populations. As a rule of thumb, researchers should collect no more than 50% of seeds in 50% of years for large populations (>500 plants) or 10% of seed in 10% of years for small populations (<500 plants) in order to avoid detrimental genetic or demographic effects due to overcollection (Menges et al. 2004; Vitt et al. 2010). Collection should only take place after consulting with regional botanists/biologists and obtaining permission from land managers. Gardens sites should be selected so as to reduce impact on native vegetation communities. Utilizing already-impacted sites, such as those near existing infrastructure (e.g., summit areas or paved roads of Whiteface Mountain, Mount Washington, or Cadillac Mountain) may be a way to address this concern. Gardens and collection sites could be located at existing pedestrian routes, trails, and other already-disturbed areas. Regardless of location, researchers should use non-visible/non-impactful markers such as magnetic markers, small stakes, or dull colors to delineate plots or gardens in order to keep off-trail sites hidden and reduce the impact of visible gardens on the wilderness experience for hikers. To avoid introducing new species or genotypes from garden propagules or soil mix, consider lining beds with plastic (such as landscape fabric), covering inflorescences or germinating seed with nylon mesh, and weeding regularly. Again, any disturbance to alpine habitat, including the creation of experimental gardens, should be planned in coordination with regional managers and biologists to minimize negative environmental impacts and should only move forward once permission is secured from land managers. As a single garden setup can provide the opportunity for multiple studies (concurrently or in succession), we believe researchers and managers can find ways to undertake conservation-focused research without extensive impact to existing habitat.

Data Collection & Analysis. The types of environmental and plant data collected will depend on the project goals and research question. Here, we outline common variables, measurement tools, and analyses for common garden experiments, as well as resources available for researchers.

We consider three types of measurable variables in common garden experiments: plant survival and growth, plant functional/phenological traits, and local environment (Figure 2). Plant survival and growth includes measurements of mortality and germination success, as well as size-related traits such as stem height and stem count that are immediately visible and straightforward to measure. Classic plant functional traits such as specific leaf area (SLA) and leaf dry matter content can be measured with fairly basic equipment such as a flatbed scanner and electronic balance. Functional traits related to physiology (such as light-saturated photosynthetic rate, leaf water potential, and leaf dark respiration) may require specialized instruments, while phenology traits (such as leaf out, flowering, and fruit development) are relatively simple to monitor but need standardized definitions. Local environment variables (temperature, precipitation, soil moisture, etc.) can be measured using data loggers, weather stations, or by taking repeated measurements with appropriate instruments. Standardized measurements for plant traits have been established (Denny et al. 2014; Pérez-Harguindeguy et al. 2013), and researchers should adhere to those methods whenever possible.

To meet the unique challenges of gardens located in remote and wild alpine habitats, researchers need rugged and lightweight equipment. The Appalachian Mountain Club has successfully implemented a network of time-lapse cameras to monitor alpine plant phenology above treeline for the past eight years (D. Weihrauch, pers. comm.), and the PhenoCams Network (Richardson et al. 2018) has been highly effective in monitoring seasonal phenology in the region more broadly using remote sensing. A similar approach using mounted cameras in alpine common gardens may be an efficient and reliable way to remotely capture key phenophases like bud break, leaf emergence, flowering, and senescence, especially when access to alpine sites is limited by weather or terrain or when high-frequency monitoring is not possible. Portable instruments (such as those made by LI-COR Biosciences, Lincoln, NE) can be used to measure in-situ physiological traits relating to photosynthesis, respiration, and water use, and do not require harvesting or removal of plant material.

For trait measurements from scanned leaf/plant images, ImageJ (National Institutes of Health, Bethesda, MD) is an open-source image analysis software that is able to digitally measure some physical or morphological traits using digital images of specimens collected in the field. The software, which can be calibrated to any standard desktop scanner, accurately measures leaf area, perimeter, circularity (and traits derived from them, such as SLA) and more in a user-friendly interface.

Differences in morphological, phenological, physiological, or fitness-related traits in common garden studies are best analyzed through ANOVA or linear models to parse variation due to genetics (e.g., for establishing ecotypes), the environment (e.g., for establishing plasticity), and their interaction (e.g., for establishing genotypic differences in plasticity; Falconer and MacKay 2009; Lynch and Walsh 1998; Valladares et al. 2006). The use of mixed models and/or nested study designs is encouraged to account for additional sources of variation such as pot position and population of origin (e.g., Gelman and Hill 2007).

Quantifying and visualizing differences in plasticity among species or provenances can be achieved through the use of reaction norms (DeWitt and Scheiner 2004; Schlichting and Pigliucci 1998; Stearns 1989), which represent the slope of differences in mean trait values among sites (such as in Supplementary Figure 3). Reaction norms allow for the comparison of mean trait responses, the degree of plasticity, and the direction of response among groups. One disadvantage, though, is that they are study-specific and that individual traits are often measured on different scales, making cross-comparisons challenging.

Therefore, we also strongly encourage reporting plasticity indices (especially those that are environmentally standardized) to allow for comparisons of plasticity across traits and differently sized environmental gradients (e.g., Valladares et al. 2006). Cross-trait and cross-study comparisons of plasticity indices can be made with statistical confidence using a Wilcoxon signed rank test (e.g., Gugger et al. 2015).

Common garden studies investigating local adaptation or climate change response often involve investigations of survival. As a binary response variable (alive/dead), a slightly different analysis technique is necessary. To compare survival over time, we recommend Cox regression analysis of proportional hazards models (as implemented in the R "coxme" package [R Core Team, 2018]; Kim and Donohue 2013).

Interpreting Results. Finally, we offer best practices for placing garden studies in a broader context and interpreting the results of these experiments. Understanding and accounting for the sources of variation and the limitations of short experiments can improve experimental design at the beginning of a project and bring nuance to conclusions at its end. One challenge associated with common garden experiments is accounting for sources of variation that are not of experimental interest. Poorter et al. (2012) discuss eight variables that exert a strong influence on plant growth: light (quantity and quality), CO_2, nutrients, humidity, soil water, temperature (see Körner and Hiltbrunner 2018), and salinity. Measuring and reporting levels of these variables and accounting for their variability is critical for ensuring reproducibility of results and for avoiding erroneous experimental conclusions, especially when comparing growth chamber/greenhouse and field studies.

Care should also be taken to minimize variation in non-focal environmental variables within and among gardens. For single-garden growth chamber and greenhouse experiments, pot/tray position can be rotated systematically in a chamber or along a bench to equalize exposure of plants to the temperature, light, and humidity gradients (Poorter et al. 2012). For single-garden field experiments, it may be impractical to rotate plant position; rather, a position covariate can be included in analyses (e.g., shade; Haynes, unpubl. data).

Similar strategies can be employed for multi-garden experiments. For multiple growth chambers or greenhouses, plants should be rotated between available spaces. In field experiments, where plants cannot be rotated among gardens, researchers must measure environmental variables, control them as best as they are able, and/or account for differences in statistical analyses. For investigations of local adaptation among provenances, researchers are usually interested in plants' overall response to a suite of environmental conditions and may wish to maintain all environmental differences between gardens. Researchers investigating the response of plants to climate change, on the other hand, will need to control for non-climatic variables like soil nutrients or salinity that may differ among gardens. All researchers will likely be interested in controlling variables like slope, aspect, pot size, and shading, unless variation in these are of experimental interest.

Researchers using multiple gardens should consider using more than two gardens whenever possible. For example, Kim and Donohue (2013) located gardens at three paired sites of low and high elevation, enabling them to account for garden-to-garden variation at a given elevation. Another strategy involves establishing more than two gardens along an environmental gradient so that trends in plant growth, phenology, fitness, and more can be related with the gradient rather than to any of the many differences that could exist between just two gardens (as in McDonough MacKenzie et al. 2018).

Most common garden experiments in the literature (see Appendix) were limited to one or two years of observation by the time of publication; we found only a single common garden study with a continuous five-year monitoring scheme (McMillan and Winstead 1976). The short lifespan of common gardens may bias interpretations of phenotypic plasticity in plants (e.g., see Hamann et al. 2018) and limit the suite of traits that can be studied. Many alpine plants will not reproduce sexually their first year, so multi-year studies are necessary to investigate fitness or reproductive phenology. However, even with adult transplants, flowering may be suppressed, or "perceived mortality" may occur, wherein plants appearing dead re-grow new stems or leaves in subsequent years. A relatively long monitoring scheme (three years) allowed McDonough Mackenzie et al. (2018) to make year-to-year corrections for perceived mortality, but they were unable to find comparable experiences in the literature. We recommend strategic partnerships with appropriate regional, state, or federal land management agencies and conservation organizations to facilitate the creation of more permanent common garden plots and allow longer time spans for studies.

Sharing Results. Conservation-based research is not complete until it is shared with the scientific community, land managers, and the public, and we encourage researchers undertaking common garden experiments in Northeast alpine areas to make their findings available through scientific publication or by making theses/technical reports publicly available. Sharing scientific findings with land managers is equally important, as land ownership in the Northeast alpine can be complex and management decisions must often be made with the input of many stakeholders with differing priorities or goals. We expect that common garden studies like the ones proposed under our "Research Priorities" will have much to offer managers of Northeast alpine areas tasked with species or habitat conservation, and hope they will help to focus monitoring and conservation efforts on the species and sites most at risk. Finally, public outreach is critical for conservation success, especially given the high volume of recreational users—sometimes several thousand per day—that frequent our alpine summits. Transplant gardens could provide an excellent means of engaging with public visitors about the biota of alpine areas and the consequences of climate change for this unique ecosystem.

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APPENDIX.

List of representative common garden and reciprocal transplant studies conducted in alpine areas worldwide. Research questions addressed include phenology, trait plasticity, treeline/range, competition, and ecotypes. See Literature Cited for article references.

Research question	Study authors	Type	Seeds or mature plants	Location	Elevation gradient	Variables measured	Molecular analysis
Phenology	Olsson and Ågren (2002)	Common Garden	Seeds	Sweden	n/a (studied latitudinal gradient)	Plant height, winter bud count, winter bud length, survival, flowering phenology, corolla width, petal length, calyx length	No
	Gugger et al. (2015)	Reciprocal transplants of congeneric species pairs	Seeds	Switzerland	1050-2000 m	Reproductive phenology, flowering phenology plasticity	No
	Vitasse et al. (2010)	Common Garden	Seedlings	Pyrenees, France	131-1533 m	Leaf out and senescence	No
Trait Plasticity	Byars and Hoffmann (2009)	Greenhouse + reciprocal transplant	Seeds	Alpine National Park, Victoria, Australia	1700-1877 m	Leaf morphological traits (length, width, number)	No
	Michalet et al. (2011)	Greenhouse + common garden at altitude	Mature plants	Humphreys Peak, AZ	collected from 3650-3800 m; common garden at 2800 m	# leaves, # flowers, leaf/stem/root size	No
	Sedlacek et al. (2015)	Reciprocal transplant	Turfs	Davos, Swiss Alps	2320-2355 m	Phenology, morphological/fitness traits, herbivory	No
	Oleksyn et al. (1998)	Common garden	Seeds	Carpathian/Sudety Mts., Poland	(lowland) - summit/treeline (~1400m)	Height, diameter, root/needle/stem dry mass, root length, SLA, net photosynthesis, needle dark respiration, pigments, N content	No

APPENDIX. Continued.

Research question	Study authors	Type	Seeds or mature plants	Location	Elevation gradient	Variables measured	Molecular analysis
Treeline/Range	Vergeer and Kunin (2013)	Reciprocal transplant	Seeds	Northern Europe (Iceland, Sweden, Scotland, Wales)	n/a (studied latitudinal gradient)	Leaf and flower physical traits, “biomass index"	No
	Halbritter et al. (2015)	Reciprocal transplant	Seeds	Swiss Alps, Germany, and Scandinavia	(Not given)	Aboveground biomass, lifetime fitness	Yes
Competition	Kimball and Campbell (2009)	Common garden	Mature plants (cuttings)	Sierra Nevada, CA	2400-3800 m	Water potential, SLA, phenology, gas exchange, photosynthetic physiology	No
	Alexander et al. (2015)	Reciprocal transplant	Mature plants and “lawns"	Swiss Alps	1400-2600 m	Survival, biomass, flowering	No
Ecotypes	Shimono et al. (2009)	Greenhouse	Seeds	Taisetsu and Tateyama Mtns., central Japan	1800-2650 m	Flowering phenology, morphological traits, allozyme electrophoresis	Yes
	Frei et al. (2012)	Greenhouse + transplant	Mature plants (cuttings)	European Alps	1532 m	Traits: growth, reproductive, and morphological; RAPD genetic fingerprinting	Yes
	Galen et al. (1991)	Greenhouse + reciprocal transplant	Seedlings	Pennsylvania Mt., CO	3500-4250 m	Survival, no. leaves, leaf size, trichome density/length	Yes