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Strong Patterns of Intraspecific Variation and Local Adaptation in Great Basin Plants Revealed Through a Review of 75 Years of Experiments

Owen W. Baughman[1], Alison C. Agneray[1], Matthew L. Forister[1], Francis F. Kilkenny[3], Erin K. Espeland[4], Rob Fiegener[5], Matthew E. Horning[6], Richard C. Johnson[7], Thomas N. Kaye[5], Jeffrey E. Ott[3], J. Bradley St. Clair[8], Elizabeth A. Leger[1,2]

[1]Department of Natural Resources and Environmental Science, University of Nevada, 1664 N. Virginia St., Reno, NV 89557 USA; [2]Corresponding author, ealeger@gmail.com; [3]USDA Forest Service, Rocky Mountain Research Station, 322 E Front St. Suite 401, Boise, ID 83702 USA; [4]Pest Management Research Unit, USDA-Agricultural Research Service Northern Plains Agricultural Laboratory, 1500 N Central Ave., Sidney, MT 59270 USA; [5]Institute for Applied Ecology, 563 SW Jefferson Ave., Corvallis, OR 97333 USA; [6]USDA Forest Service Pacific Northwest Region, Deschutes National Forest, 63095 Deschutes Market Rd., Bend, OR 97701; [7]Washington State University, PO Box 646240, Pullman, WA 99164 USA; [8]USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis OR, 97331

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Running head: Local adaptation in Great Basin plants

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Abstract

Variation in natural selection across heterogenous landscapes often produces 1) among-population differences in phenotypic traits, 2) trait-by-environment associations, and 3) higher fitness of local populations. Using a broad literature search, we documented the frequency of these three signatures in plants native to North America's Great Basin and asked which traits and environmental variables were involved. We also asked, independent of geographic distance, whether populations from more similar environments had more similar traits. From 327 experiments testing 121 taxa in 170 studies, we found 95.1% of 305 experiments reported among-population differences, and 81.4% of 161 experiments reported trait-by-environment associations. Locals showed greater survival in 67% of 24 reciprocal experiments that reported survival, and higher fitness in 90% of 10 reciprocal experiments that reported reproductive output. Variation in eight commonly-measured traits was associated with mean annual precipitation and mean annual temperature at the source location, with notably strong relationships for flowering phenology, leaf size, and survival, among others. Although the Great Basin is sometimes perceived as environmentally homogenous, our results demonstrate widespread habitat-related population differentiation and local adaptation, suggesting that locally-sourced plants likely harbor restoration-relevant adaptations, and that certain key traits and environmental variables should be prioritized in future assessments of plants.

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Introduction

All plant species have limits to the range of conditions in which they can live, and all but the narrowest endemics grow across environments that vary in biotic and abiotic conditions. This natural complexity has significant impacts on individual survival and reproduction, and thus plant evolution (Loveless and Hamrick, 1984; Linhart and Grant, 1996; Ackerly *et al.*, 2000; Reich *et al.*, 2003). As plants are subject to different conditions associated with their local environment, populations of the same species will experience differential selection pressures (Turesson, 1922; Clausen, Keck and Hiesey, 1948; Antonovics and Bradshaw, 1968; Langlet, 1971), creating habitat-correlated intraspecific variation. When this intraspecific variation results in populations that are more fit in their home environment than foreign populations, these populations are considered to be locally adapted (Kawecki and Ebert, 2004; Blanquart *et al.*, 2013). The existence of local adaptation is well-established across different organisms and ecosystems, although our synthetic knowledge of this important topic rests on surprisingly few reviews of the subject (e.g., Leimu and Fischer, 2008; Hereford, 2009). Here, we focus on a particular region and ask if plant species share patterns of intraspecific variation and local adaptation, and, across taxa, what functional traits and environmental variables are most important for such patterns in this region. The regional focus provides a strong test of expectations generated from more heterogenous samples and provides an opportunity to link basic evolutionary patterns with applied concerns.

The detection of local adaptation ideally involves reciprocal transplant experiments designed to test for a local advantage across environments (Blanquart *et al.*, 2013; Bucharova, Durka, *et al.*, 2017). However, patterns associated with local adaptation (hereafter, signatures) can be detected in non-reciprocal comparisons of different populations of the same species

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(Endler, 1986). When populations are locally adapted to abiotic or environmental variables, we expect to see three basic signatures: 1) differences among populations in fitness-related traits, 2) correlations between these trait values and environmental or other habitat-related variables, and, if reciprocal transplants or common gardens have been conducted, 3) higher fitness of local over nonlocal populations in the local environment. Although population differences (signature 1) are necessary for local adaptation, they alone are not sufficient evidence for it due to factors such as genetic drift, high gene flow, and rapid environmental change, among other factors (Kawecki and Ebert, 2004; Blows and Hoffmann, 2005). While fitness differences in reciprocal transplant experiments (signature 3) are the "gold standard" for detecting local adaptation, there are experimental trade-offs between the number of populations sampled and the ability to do fully reciprocal transplants (Blanquart *et al.*, 2013). Thus, correlative approaches (signature 2) are popular alternatives that can sample many more populations to infer local adaptation (e.g. St Clair, Mandel and Vance-Borland, 2005), though spurious correlations, low sample sizes, or high variability in trait values could over- or under-predict the degree of local adaptation in wild populations using this approach. Given these considerations, separately reporting all three signatures can give an overall picture of the likelihood of within-species variation and potential local adaptation in a region, and is the first step towards a better understanding of variation in the strength and consistency of natural selection (Siepielski, Dibattista and Carlson, 2009).

The Great Basin Desert of North America is a ~540,000 km^2 cold desert landscape characterized by hundreds of internally-draining basin and range formations, which create high spatial and environmental heterogeneity and variability (Tisdale and Hironaka, 1981; Comstock and Ehleringer, 1992). While these are the kinds of conditions that would be expected to result in widespread local adaptation, the flora of the Great Basin is poorly represented in the relatively

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few reviews on the subject (Leimu and Fischer, 2008; Hereford, 2009), and this has resulted in uncertainty as to the prevalence, magnitude, and importance that local adaptation plays in this large and increasingly imperiled region (US House of Representatives Committee on Appropriations, 2014; Jones, Monaco and Rigby, 2015; Chivers *et al.*, 2016). Gaining a better understanding of potential fitness differences between populations of the same species is important in the Great Basin not only because it is a large, relatively intact floristic region in the Western US, but because it has direct impacts on conservation and restoration efforts. Large-scale, seed-based restoration has been very common in the Great Basin for many decades (Pilliod, Welty and Toevs, 2017), and trends in large destructive wildfires (Dennison *et al.*, 2014) and other disturbances (Rowland, Suring and Michael, 2010; Davies *et al.*, 2011) ensure even higher demand for restoration efforts in the future. Guided by the various national policies and strategies dating from the 1960s (Richards, Chambers and Ross, 1998) to the present National Seed Strategy (Plant Conservation Alliance, 2015) and Integrated Rangeland Fire Management Strategy (USDOI, 2015), a growing majority of these efforts are using native plant seeds or transplants. However, few of the widely-available sources of commercially-produced seeds of native species originate from populations within the Great Basin (Jones and Larson, 2005) or have been selected based on their success in restoring Great Basin habitats (Leger and Baughman, 2015), and demand for native seed has always exceeded supply (McArthur and Young, 1999; Johnson *et al.*, 2010). This has resulted in the prioritization of seed quantity and uniformity over population suitability and local adaptation (Meyer, 1997; Richards, Chambers and Ross, 1998; Leger and Baughman, 2015), and therefore it is still uncommon for restorationists in this region to prioritize or even have the option to prioritize the use of local populations, despite growing support of the importance of such practices (Basey, Fant and

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Kramer, 2015; Espeland *et al.*, 2017).

Though our understanding of the prevalence and scale of local adaptation in the Great Basin is far from complete, there is an abundant literature of peer-reviewed studies on the plants native to this region spanning over 75 years that have directly measured trait variation between populations via laboratory and greenhouse trials, common gardens, and reciprocal transplants. Many of these studies have also tested for correlations between intraspecific variation and environmental variables, and some were designed to detect local adaptation. This research includes common gardens (e.g. McMillan, 1959; Kramer, Larkin and Fant, 2015), studies of germination patterns (e.g. McArthur, Meyer and Weber, 1987; Meyer *et al.*, 1995), large genecology experiments (e.g. Erickson, Mandel and Sorenson, 2004; Johnson, Leger and Vance-Borland, 2017), and reciprocal transplants (e.g. Evans and Young, 1990; Barnes, 2009), among other types of studies. This rich literature provides an opportunity to summarize local adaptation and its associated patterns, or signatures (defined above), in this region, as well as describe which phenotypic traits have the strongest signatures of local adaptation.

Here, we present results of a broad literature search and subsequent meta-analysis using published studies that compared phenotypic traits of multiple populations of native Great Basin species in one or more common environments. Our first objective was to record the frequency and nature of the three expected signatures of local adaptation (population variation, trait-by-environment association, and greater local fitness) within grasses, forbs, shrubs, and deciduous trees native to the Great Basin, and ask how common these signatures are, and which phenotypic traits and environmental variables were most commonly associated with these signatures. We also present results by taxonomic group, lifeform, lifespan, distribution, and mating system. Our second objective was to examine links between the magnitude of trait and environmental (mean

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annual precipitation and mean annual temperature) divergence among populations across multiple taxa, asking whether populations from more similar environments were more similar in phenotypic traits. We also asked which traits and environmental variables showed the strongest patterns of divergence.

We expected to find widespread evidence of local adaptation and its signatures in the plants of the Great Basin, and we hypothesize that phenological and size-based traits, which show phenotypic variation in response to climate variation in both plants and animals (e.g. Sheridan and Bickford, 2011; Anderson *et al.*, 2012) and have been observed to be under selection in the Great Basin (Leger and Baughman, 2015), would be important indicators of adaptation in this region. We discuss our results both as a contribution to our general understanding of natural selection in plants, and as an example of evolutionary theory applied to the management and restoration of a large geographic region, where active and ongoing management can benefit from information on intraspecific variation and local adaptation.

Methods

Literature search

We began by using online search engines Google Scholar and Web of Science to search for combinations of key terms (see additional methods in Supporting Information Appendix S1). In order to be included in our review, a study had to meet all these criteria:

a) Examined a species that is native within the floristic Great Basin
b) Examined and compared more than one population of that species
c) Measured at least one phenotypic, physiological, phenological, or other potentially fitness-related trait (e.g. survival; hereafter, trait)
d) Measured the trait(s) of the populations in at least one common environment

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(including laboratories, growth chambers, greenhouses, or outside gardens; hereafter, garden).

Determination of nativity to the Great Basin was defined as at least one occurrence with native status within the floristic Great Basin according to occurrence information from the USDA Plants Database (USDA and NRCS, 2018) and/or the U.S Virtual Herbarium Online (Barkworth *et al.*, 2018). A total of 170 published studies published between 1941 and July 2017 were encountered that met these criteria.

Categorization and scoring of literature

All studies meeting our criteria were categorized and scored for each signature. The coordinates of all gardens and populations in each study were recorded or, if possible, generated from localities described in the studies (Supporting Information Appendix S1). For each study, we then noted these 15 characteristics: the year published, year(s) of plant material collection, year(s) of experimentation, number of years reported, taxa (genus, species, subspecies), life history traits (taxonomic status, lifeform, geographic range, life span, breeding system), experiment type (laboratory, greenhouse, common garden, reciprocal transplant), number of gardens, number of populations tested, which generation of material was used, and whether or not experimenters attempted to control maternal effects prior to testing (Supporting Information Appendix S1). Life history traits were compiled for each taxon from the USDA Plants Database as well as from published literature (Supporting Information Appendix S1). Each taxon (subspecies level, if given) was entered separately for studies addressing multiple taxa. In studies where more than one experiment was performed, and the experiments differed in the experiment type (defined above), the identity of the populations being compared, and/or the generation of material used, they were entered as separate experiments. In cases where the list of tested

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populations were identical among multiple published studies, and these materials came from the same collections, these experiments were entered separately if the garden type or location(s) differed among the studies or if authors separately published different traits from the same gardens, ensuring that no trait was recorded twice for the same set of populations in the same garden. In cases where the list of tested populations did not completely overlap between studies, even if some from each study arose from the same collections, they were entered separately. A total 327 taxa-specific entries (hereafter, experiments) were generated from the 170 published studies (Supporting Information Appendix S2).

The first two expected signatures of local adaptation were scored using a Yes/No designation for each experiment which considered all measured phenotypic traits. A score of "Yes", or, in the absence of supporting statistical evidence, "Authors claim Yes", was given when at least one measured trait significantly demonstrated the signature for at least two populations, and a score of "No" or "Authors claim No" was given when the signature was not detected between any pair of populations (Supporting Information Appendix S1). In addition, each of the measured and reported traits and environmental variables were scored (hereafter, trait scores) in the same way for each signature. Of the 327 experiments, 305 (93.3%) met the criteria to score for signature 1 and 161 (49.5%) met the criteria to score for signature 2. Pearson's chi-squared tests were used to determine if there were differences in signatures 1 and 2 among plants with different life-history traits, using totals from both "Yes/No" and "Authors Claim Yes/No" results, excluding any life history groups represented by less than 10 experiments.

To score whether there was higher fitness of a local population in a common garden (hereafter, signature 3), only experiments in which outdoor reciprocal transplants or common gardens were performed using a local population in at least one garden were considered

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(Supporting Information Appendix S1). Additionally, the experiment had to measure survival, reproductive output (number of seeds or flowers, or other reproductive output), a fitness index (a combination of several size and production traits), or total aboveground biomass. Each experiment was given a composite score to fully capture variation in the performance of each garden's local population, across multiple gardens as well as through multiple sampling dates. These scores refer only to those gardens within each experiment that each had their own local population. The five scores were "Yes for all gardens at all times", "Yes for all gardens at some times", "Yes for some gardens at all times", "Yes for some gardens at some times", and "No for all gardens at all times" (Supporting Information Appendix S1). Of the 326 experiments, 27 (8.3%) were appropriate for this scoring. This scoring provides an estimate of the frequency of higher local fitness, but it is not a measure of the importance of the difference per se. For example, a fitness difference could occur at a low frequency, but have a large impact on population trajectories (i.e. large differences in survival after a rare drought event).

Our dataset contained the possibility of bias associated with highly-studied taxa influencing patterns more than less-studied taxa. For example, some species were represented in our dataset more than once, and some widespread, community dominants (e.g. *Artemisia tridentata*, *Ericameria nauseosa*, etc.) were represented many times. To ask how this affected overall responses, we tallied all scores without correcting for multiple experiments per species as well as using an average score for each species for each signature. To generate these average scores for signature 1 and 2, we totaled all "Yes" and "Authors claim Yes" scores for each species and divided by the total number of scores (all Ys plus all Ns) for that species. For signature 3, all forms of "Yes" (all but "No for all gardens at all times") were totaled into a Y and divided by the total number of scores. Then, we averaged these per-species scores to re-

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calculate overall effects in which each species was represented only once.

Quantitative comparison of trait-by-environment associations

As a complement to the survey of author-reported results described above, we conducted a further, quantitative analysis of trait and climate values. This approach has the potential disadvantage of using data (trait values) for a purpose for which they were not originally collected, but the advantage of considering a standard set of environmental values. Specifically, to examine associations between the differences in trait values and the differences in environmental and geographic distance among population origins, we utilized experiments from which population-specific trait data and geographic coordinates could be extracted or obtained through author contact. Data from laboratory and greenhouse experiments were not considered for this extraction. First, we identified the most commonly measured traits across studies, which were then manually extracted from text, tables, or graphical data (Supporting Information Appendix S1). Next, we extracted trait data from the latest sampling date for which the most populations at the most gardens were represented, and if multiple treatments were used, we only extracted data for the author-defined 'control' treatment. However, if no control was defined, we used the treatment that was the most unaltered or representative of the garden environment (e.g. unweeded, or unwatered). Data from each garden within each experiment was extracted separately and considered its own sample (hereafter, garden-specific experiment). Finally, we generated 30-year annual precipitation and mean annual temperature values for each population's location of origin using the ClimateNA v5.10 software package based on methodology described by Wang et al. (Wang *et al*., 2016). Because studies took place at many times over the last 75 years, we extracted these climate data for each experiment for the 30-year climate normal that did not surpass the years during which the populations were collected

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(Supporting Information Appendix S2).

To reduce the likelihood of spurious correlations or false negative results, we limited this dataset to only include garden-specific experiments that measured a trait in at least 5 populations in a common garden, and to traits for which we had at least 20 garden-specific experiments (mean garden-specific experiments per trait: 34.4; range: 21-46), resulting in 81 garden-specific experiments (from 56 experiments) that measured at least one of eight frequently-measured phenotypic traits (Table 1). Within each garden-specific experiment, we calculated pairwise Euclidean distances (normalized) for each trait value, climate factor, and geographic distance for every possible pair of populations. Geographic distances were generated using the earth.dist function in fossil package (Vavrek, 2011) in the statistical computing environment R (R Core Team, 2017). Then, partial Mantel tests were used to compare pairwise trait and climate distances for each experiment while controlling for geographic distances, using the vegan package (Oksanen *et al.*, 2018) in R (R Core Team, 2017). We used the metacor.DSL function in the metacor package (Laliberté, 2011) to generate an overall effect size (partial correlation) and upper and lower confidence intervals for each combination of trait and environmental variable. Lastly, to better understand effect sizes, we ran regression analyses on each experiment, comparing pairwise changes in trait and environmental differences by generating a slope that estimated trait change per unit change in climate factors. Experiments with R^2 values of 0.2 or less were excluded, and the median slope from each trait by environment pair for remaining studies was used as an estimate. Due to limited sample sizes for factors such as lifeform, mating system, geographic distribution, etc., we did not include these factors in any of the quantitative analyses, but present lifeform (shrub, grass, or forb) information for each trait response as additional results in the Supporting Information Appendix S3.

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Results

Summary of reviewed literature

Our literature search revealed 170 published studies that measured trait responses from more than one population in at least one common environment, resulting in 327 separate experiments involving 121 taxa of 104 species of grasses, shrubs, forbs, and deciduous trees (Fig. 1). These experiments represent approximately 3,234 unique populations tested in approximately 208 outdoor garden locations (Fig. 2) and 154 indoor lab or greenhouse experiments. Grasses accounted for 21.0% of the taxa and 40.2% of the experiments, forbs composed 50.8% of the taxa and 30.7% of experiments, shrubs 26.6% of the taxa and 28.5% of experiments, and deciduous trees accounted for only 1.6% of taxa and 0.6% of experiments (Fig. 1A). Experiments were most commonly conducted in non-reciprocal outdoor common gardens (47.5%) or in the laboratory (31.9%), with fewer conducted in greenhouses (15.3%) or in reciprocal outdoor gardens (5.2%, Fig. 1B). For experiments in outdoor gardens, the average number of gardens per experiment across lifeform ranged from 1 (trees) to 1.8 (forbs) for non-reciprocal gardens, and from 2.2 (grasses) to 4 (shrubs) for reciprocal gardens (Fig. 1C). The number of populations tested in each experiment (range: 2 to 193) averaged 12.6 (Fig. 1D), with grasses (16.9$\pm$2.6 SE) higher than forbs (10.1$\pm$1.3 SE), shrubs (9.6$\pm$1.6 SE) and trees (7$\pm$2 SE).

Experiments took place between 1940 and 2015, with collections from native stands occurring between 1938 and 2013 (Fig. 3A). One quarter of the experiments (24.5%) reported only early germination and seedling stages of plants (generally less than 0.5 years), while the remaining experiments (75.5%) reported study periods ranging from 0.5 to 17 years, with an average of 2.1 years (Fig. 3B, C). Average pairwise geographic distance among populations per experiment for the 91% of experiments for which coordinates were available was 351 km$\pm$20

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SE, with a range from 610 m to 2,551 km. Most experiments were conducted with monocots, taxa with regional distributions, perennial species, and outcrossing species; very few annuals, endemic species, or selfing species were represented (Fig. 4). Over half of experiments (58.6%) tested plants grown directly from wild-collected seeds (or the seed of wild collected adults), 16.9% tested wild-collected adults, 13% tested materials with mixed generations since collection, 6.7% tested 1st or 2nd generation descendants of wild collected seeds, 0.3% tested only cultivars, and 4.3% did not provide enough information to determine.

Among-population variation

Of the 305 experiments appropriate for addressing among-population trait variation (signature 1), 290 (95.1%) experiments reported finding variation among populations in at least one phenotypic trait, with 230 (75.4%) of these 290 reporting significant variation, and 60 (19.6%) claiming such variation in the absence of any supporting statistics (Fig. 4A). Only 12 (3.9%) experiments reported no such differentiation in any trait after statistically testing for it, and 3 (1%) claimed no such variation without presenting statistical evidence. When categorized by basic life history traits, several differences appeared among groups. Non-monocots had significantly more population-differentiation than monocots ($X_1^2 = 7$, $P = 0.0081$), and forbs and shrubs had more population differentiation than grasses ($X_2^2 = 8.05$, $P = 0.0143$). There were no significant differences in signature 1 among plants with different geographic distributions, life span, or breeding systems.

A total of 1,465 trait scores were recorded from the 305 experiments appropriate for addressing signature 1. Frequently-measured traits (20 or more experiments) that had differences between populations in over 75% of experiments (with or without supporting statistics) were floral structure, vigor, emergence, plant size, number of leaves, plant structure, shoot biomass,

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leaf structure, and number of inflorescences (Fig. 5).

Trait-by-environment associations

Of the 161 experiments appropriate for testing trait-by-environment associations (signature 2), 131 (81.4%) reported associations for at least one comparison, with 81 (50.3%) supported by statistical tests and 50 (31.1%) supported by claims in the absence of statistics (Fig. 4B). Conversely, 13 (8.1%) of experiments reported no such correlations after having statistically tested for it, and 17 (10.6%) reported no such correlations but lacked any supporting statistics. There were no significant differences in the frequency of trait-by-environment associations for taxonomic status, lifeform, geographic distribution, or breeding system, but perennials (both long-lived and short-lived) had more frequent correlations between traits and environment than did annuals or short-lived perennials ($X_3^2 = 8.08$, $P = 0.0444$).

A total of 592 trait scores were recorded from the 161 experiments appropriate for addressing signature 2 (Fig. 6A). Frequently-measured traits (20 or more experiments) that were correlated with environmental variables in over 75% of experiments (with or without supporting statistics) were multivariate trait axes, floral structure, and germination date. Every remaining trait that was measured in >15 experiments was correlated with environmental characteristics in over 50% of experiments, and many were more frequently correlated, including leaf length, survival, and flowering date, and leaf structure, which were correlated with environmental variables in ≥70% of experiments.

A total of 426 environmental variable scores were recorded from the 161 experiments appropriate for addressing signature 2 (Fig. 6B). Of the variables most frequently reported as correlated with plant traits, many categorical variables or composite metrics made this list, with seed zones, ecoregions, multivariate environmental axes, and habitat classifications topping the

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list of important environmental variables (important in > 84% of experiments that reported them). Additionally, author-derived climate metrics, climate seasonality, and history of invasive species presence were correlated with plant traits in over 75% of studies that reported them.

Higher local performance in a local common garden

The 27 experiments that were suitable for detecting higher fitness of a local population in a local garden (signature 3) generated 39 scores (some experiments measured multiple fitness traits), with 27 scores (69.2%) reporting signature 3 for at least one fitness trait in at least one of the tested gardens during at least one sampling date, and the remaining 12 scores (30.8%) not reporting signature 3 at any point (Fig. 4C). Thirty-two of the 39 scores (82%) were generated from experiments with more than one garden. Survival was the most frequently measured fitness trait in these experiments, reported in 24 of the 27 experiments, followed by reproduction (10), biomass (3), and fitness indices (2). Incidence of local-does-best patterns was highest in experiments that directly measured reproductive output, with 90% reporting higher values for locals at some point in an experiment, followed by survival (67%), fitness indices that incorporated biomass (50%), and biomass measures (33%). For experiments in which only "some" gardens showed local-does-best patterns (Fig. 4C, hashed bars), the percentage of gardens showing this trend was 40%, 50%, and 40% for reproduction, survival, and biomass traits, respectively (not shown). For experiments in which only "some" sampling dates showed local-does-best patterns (gray bars), the percentage of sampling dates showing this trend was 56%, 47%, and 25% for reproduction, survival, and biomass traits, respectively (not shown).

Considering possible biases: highly-studied species and maternal effects

The average number of experiments per species in our dataset ranged from 1 (52 species) to 25 (*Artemisia tridentata*), with an average of 3.2 and standard deviation of 4.3. A given

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species was considered 'highly studied' if the number of experiments representing it was more than 1 standard deviation above the average (3.2+4.3=7.5), and 9 species met this criterion (*Artemisia tridentata*, 25, *Elymus elymoides*, 24, *Ericameria nauseosa*, 17, *Achnatherum hymenoides*, 17, *Krascheninnikovia lanata*, 13, *Pascopyrum smithii*, 11, *Atriplex canescens*, 9, *Leymus cinereus*, 9, and *Poa secunda*, 8). Results in which scores were averaged for each species were similar to uncorrected results: signature 1 was 4% higher when corrected (98% vs. 94%), signature 2 was 1% lower when corrected (79% vs. 80%), and signature 3 was 8% higher when corrected (78% vs. 70%).

Only 19 experiments (5.8%) used an experimental design that could control for maternal effects (e.g. growing all populations for a generation in a common environment before initiating an experiment). An additional 30 experiments (9.2%) were unclear on this point, and the remaining 278 (85%) experimented directly on populations differing in maternal environment. The incidence of population differences (signature 1) was 100% in the 16 experiments that moderated maternal effects, 95% for the 259 that did not make an attempt, and 97% for the 30 which were unclear. Too few of the experiments that attempted to control for maternal effects were appropriate for measuring signature 2 (4 experiments) and signature 3 (1 experiment) to compare incidences of these signatures.

Quantitative comparison of trait-by-environment associations

Overall, we recovered positive relationships between the magnitude of differences among populations in all eight phenotypic traits and the magnitude of differences between MAT and MAP at the collection locations (Fig. 7). The strongest relationship was observed between differences in flowering time and differences in MAT, and leaf size also showed a strong relationship with MAT. Multiple strong relationships were observed between trait/environment

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divergence for MAP, with leaf size, survival, shoot mass, inflorescence number, and flowering time all showing strongly positive relationships for grasses, forbs, and shrubs. (Fig. 7, Supporting Information Appendix S3). Regression analyses demonstrated that, for the 15 experiments in which strong flowering time and MAT relationships were observed, each degree change in MAT between population origins resulted in a median change of 4.4 days (IQR = 2.5, 5.7) in flowering time. Small sample sizes (few qualifying experiments) and challenges with interpreting changes in physical traits across species of various shapes and sizes precluded the presentation of estimates of this nature for the other strong trait-by-environment relationships we detected.

Discussion

Our results represent the most extensive review of intraspecific variation and local adaptation for plants native to the floristic Great Basin, a region comprised of largely continuous but increasingly imperiled arid and semi-arid plant communities (Davies *et al.*, 2011; Finch *et al.*, 2016). Additionally, they represent a significant addition to the noteworthy though relatively small number of reviews investigating this topic in a manner that identifies individual traits and environmental factors involved. We found that Great Basin plant species contain large amounts of intraspecific diversity in a wide range of phenotypic traits, that differences in these phenotypic traits are often associated with the heterogeneous environments of origin, and that differences among populations are commonly relevant to outplanting fitness. The importance of intraspecific variation may equal or exceed the importance of species diversity for the structure and functioning of communities and ecosystems (Des Roches *et al.*, 2018), and our quantification of local adaptation and trait-environment associations should serve as encouragement to seriously consider intraspecific diversity in native plant materials used in restoration and conservation in this region throughout the selection, evaluation, and development process (Basey, Fant and

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Kramer, 2015). The results reported here should also serve as a cautionary note to restoration approaches that focus on only a few specific traits or the search for general-purpose genotypes. Our results suggest that, in the absence of species-specific information to the contrary, it is reasonable to assume that local adaptation is present in this region, and that locally-sourced populations would outperform non-local populations a majority of the time.

Our investigation encompassed 170 studies published between 1940 and 2017 in which over 3,230 unique populations of 104 native Great Basin plant species were compared in 327 experiments, ranging from laboratory germination trials to multiple-year common gardens and reciprocal transplants. The great majority (95%) found differences between populations (signature 1) in the majority of traits measured in a common environment, which indicates that a diversity of traits are variable among populations, at both small and large geographic scales. Additionally, a clear majority (81.4%) of experiments found trait-by-collection environment associations (signature 2), suggesting that intraspecific variation is frequently an adaptive outcome of natural selection in heterogeneous environments (Linhart and Grant, 1996; Reich *et al.*, 2003). In experiments suitable for detecting local performance advantages (signature 3), local populations had higher performance (measured by differences in reproductive output, survival, and biomass) than nonlocal populations more often than not (69.2%), and this was particularly true when researchers reported traits related to reproductive output (90%). The overall incidence of “local does best” in the Great Basin is similar to or higher than other reviews that have found local adaptation to be commonplace, but not ubiquitous. In a review of local adaptation in plants that compared survival, reproduction, biomass and germination traits in reciprocal transplants, Leimu and Fischer (Leimu and Fischer, 2008) found that local plants outperformed non-local ones in 71% of 35 published experiments. Similarly, Hereford (Hereford, 2009) quantified local

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adaptation in 70 published studies (50 of them plants), reporting only survival or reproductive traits, and found evidence of local adaptation in 65-71% of experiments. Our results indicated that the strongest indication of local adaptation came from experiments that directly measured reproductive output, and that using biomass as a fitness proxy may not be an effective way to compare relative performance in the Great Basin. This is consistent with a previous study that demonstrated selection for smaller, rather than larger, individuals in disturbed arid systems (Kulpa and Leger, 2013). Meta-analyses conducted across biomes may occlude regionally-important trait differentiation and mask patterns of local adaptation, as we might expect, for example, biomass to be more strongly linked to fitness in regions where light is a contested resource (Espeland, Johnson and Horning, 2017).

There are many processes that can reduce or prevent the development of local adaptation, such as the lack of divergent selection between sites, high gene flow, rapid or extreme environmental change, high phenotypic plasticity, and/or low genetic diversity (Sultan and Spencer, 2002; Kawecki and Ebert, 2004; Blows and Hoffmann, 2005). The high incidence of intraspecific variation, much of it habitat-correlated, that we found in the literature confirms that divergent selection by heterogeneous environments is the norm for species native to the Great Basin, presumably outweighing the balancing effects of gene flow and genetic drift. Key environmental factors in the Great Basin such as fire frequency, grazing regimes, resource availability, and climate are certainly being altered to varying degrees by invasive species introductions, changing land uses, and climate change, and it can be argued that such changes could outpace the ability of local populations to remain adapted to their surroundings (Jones and Monaco, 2009; Breed *et al.*, 2013; Havens *et al.*, 2015; Kilkenny, 2015). However, our analysis also demonstrated relatively high instances of trait correlations with relatively recent

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disturbances such as invasive species introductions. Rapid evolution in response to invasive species (Oduor, 2013) and other anthropogenic changes (Hoffmann and Sgrò, 2011; Franks, Weber and Aitken, 2014) has been documented for many species, indicating that local adaptation can evolve rapidly in some circumstances.

Some traits and environmental characteristics stood out as particularly important indicators of local adaptation and its signatures across the studied taxa. For example, in our quantitative comparison and regression of divergence in traits and environments, flowering phenology was strongly affected by mean annual temperature (MAT), with a median change of 4.4 days in flowering time per degree change in MAT of collection origin. Flowering phenology, along with germination phenology, were also in the top tier of frequently measured traits that showed significant correlations with environmental variables, consistent with other studies that have shown reproductive (Bucharova, Michalski, *et al.*, 2017) and germination (Donohue *et al.*, 2010) phenology to be an important response to environmental variation. Leaf size is also an important adaptive response to differences in temperature globally (Wright *et al.*, 2017), and in concert with this, we saw overall positive responses to MAP and MAT for leaf size in our analyses as well as frequent trait-by-environment associations in the literature. Floral structure, which has important adaptive significance for angiosperms (Harder and Barrett, 2007; Armbruster, 2014), was among the most frequent traits scored for among-population variation and trait-by-environment interactions. Seasonality of precipitation, which varies in this region depending on summer rainfall (Comstock and Ehleringer, 1992), was more predictive of trait variation overall than was mean annual precipitation (signature 2). In our quantitative comparisons, differences in MAP values were important for multiple phenotypic traits, including leaf size, shoot mass, reproductive output, and flowering phenology, in addition to being

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important for overall plant survival. Larger scale environmental descriptors, such as ecoregions and seed transfer zones, universally demonstrated signature 2, likely because they were developed based on climate/soil/vegetation associations or, in the case of seed transfer zones, developed based on trait-by-environment correlations. As found in other reviews (Geber and Griffen, 2003), physiological traits, phytochemical traits, and root traits were not measured as frequently as other traits, and though these did not show as frequent associations with environmental characteristics as other traits, they are known to vary across environments in some systems (Reich *et al.*, 2003). Additional studies of these traits in the Great Basin would be informative and could reveal different patterns than those observed here.

As in any review and analysis of published papers, there are elements of our design that were difficult to control. For example, consistent with other reviews (Gibson *et al.*, 2016), the vast majority of studies involved wild-collected plants or seeds, and thus maternal environment effects almost certainly affected some results (e.g. Bischoff and Müller-Schärer, 2010; Espeland *et al.*, 2016). Additionally, though the majority of populations tested in the literature were from western states, some of the populations compared in the literature were collected from well outside of the Great Basin, which increased the likelihood of observing local adaptation in these species. However, understanding patterns of intraspecific variation across the full range of the species native to the Great Basin is pertinent because it has been common (and for some species, ubiquitous) to utilize sources of native species originating from outside the Great Basin to use for restoration within the Great Basin (Jones and Larson, 2005). Finally, the scores and percentages for each of the signatures used throughout this study are uncorrected for phylogeny, as is our pairwise trait/environment analysis, and calculated such that each experiment is weighed equally. This introduces the possibility for phylogenetic biases, in which closely related taxa represented

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by many experiments affect the results more than less frequently studied taxa or groups of taxa. Though we did not conduct phylogenetic corrections for relatedness among taxa (Harvey and Pagel, 1991; de Bello *et al.*, 2015), our results were essentially identical for signatures 1-3 when we averaged results across species (scores differed by +3%, -1%, and +8%, respectively), suggesting that our lack of phylogenetic corrections are not unduly affecting our results. We present all species-specific information in Supporting Information Appendix S2 and available datasets section of the electronic supplementary material for further review.

Current approaches to seed sourcing in restoration and conservation include genetic (e.g. Williams, Nevill and Krauss, 2014), genecological (e.g. Johnson, Leger and Vance-Borland, 2017), local-only (e.g. Erickson *et al.*, 2017), predictive (e.g. Prober *et al.*, 2015), and agronomic (e.g. United States House of Representatives Committee on Appropriations, 2014)) strategies, as well as strategies mixing several of these viewpoints (i.e. Rice and Emery, 2003; Rogers and Montalvo, 2004; Breed *et al.*, 2013; Havens *et al.*, 2015). These approaches vary in the degree to which they meet the needs of seed producers and land managers while balancing population differences that stem from adaptive evolution in different environments. The prevalence of local adaptation and its signatures found in our study justify and support incorporating existing best-practices (e.g. Basey, Fant and Kramer, 2015; Espeland *et al.*, 2017) for capturing and preserving important intraspecific variation into seed sourcing and plant production systems. For example, our results demonstrated a strong relationship between flowering time and mean annual temperature, so it would be wise to collect materials for research, evaluation, and testing from populations that vary in MAT, to collect seeds at multiple times to fully capture population variation in flowering time, and ensure that seeds are not transferred during restoration among sites that differ strongly in these characteristics. On the production side, best practices for seed

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harvesting should include methods that avoid inadvertent selection on flowering time, either for reduced variation or for a directional shift away from the wild condition. Similarly, emergence date was correlated with environmental variation in many plants, so testing in common gardens should involve seeding trials in place of or in addition to using transplants, and evaluation trials should guard against inadvertent selection on emergence timing by randomly, rather than systematically, selecting individuals to use in transplant experiments. These examples are not exhaustive, but demonstrate how evidence revealed by this study regarding which traits and environmental factors are generally involved in adaptation in this region can be used to improve approaches to seed sourcing and restoration. Finally, we acknowledge that ours is not the first review and meta-analysis to affirm an abundance of intraspecific variation and local adaptation in plants. However, its focus on the Great Basin is important, because the large and frequent yet commonly unsuccessful restoration efforts occurring in this region have lagged behind those of other regions with respect to recognizing the importance of intraspecific variation and local adaptation on outplanting success.

Conclusions

Reestablishing and maintaining native plant communities in arid regions has proven challenging (Svejcar *et al.*, 2017), and the lack of practical knowledge guiding more appropriate selection of seed sources is a major barrier (Friggens *et al.*, 2012; Gibson *et al.*, 2016). The forestry industry has long adopted the principles of local adaptation in their reforesting guidelines with great success (Matyas, 1996; Johnson *et al.*, 2004; Aitken and Bemmels, 2016), and similar approaches to restoration in the rangelands of the Great Basin may also increase success as our data support similarly high levels of population differentiation within grass, forb and shrub life history groups. Our results are in agreement with observations of local adaptation

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in plant populations world-wide, and further, we identified particular phenotypic traits (flowering and germination phenology, floral structures, leaf size, biomass, survival, and reproductive output), environmental characteristics (MAT, MAP, climate metrics, seasonality), and habitat classifications and site history (seed zones, ecoregions, history of invasive species) that were important predictors of local adaptation in this arid floristic region. Given the speed and severity with which natural communities are being altered by anthropogenic factors, the application of an evolutionary perspective to restoration ecology is more important than ever. Adjusting seed-selection priorities to account for the existence of locally adapted, intraspecific variation in the Great Basin will promote the maintenance and recovery of resilient, self-sustaining vegetation communities in this region (Meyer, 1997; Lesica and Allendorf, 1999; Rogers and Montalvo, 2004; Broadhurst *et al.*, 2008; Vander Mijnsbrugge, Bischoff and Smith, 2010).

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Dedication

We would like to dedicate this paper to the memory of our co-author, Dr. Erin K. Espeland, friend and collaborator to all of us who worked on this manuscript. Erin's light and life will never be forgotten by those who knew her, and we want to recognize her creative contributions to the field of plant ecology, including this effort. Erin is dearly missed.

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Data accessibility

Raw datasets and statistical code supporting this study (Baughman *et al.*, 2018) have been deposited at Dryad, [https://doi.org/10.5061/dryad.v73d5nd]

Authors' contributions

EAL, OWB, FFK, EKE, RF, TNK, and JBS conceived and designed the study; OWB conducted the literature search; OWB, ACA, FFK, JEO, RCJ, and JBS categorized, compiled and extracted data; OWB, EAL, FFK, ACA and MLF analyzed data; OWB, EAL, and ACA drafted the manuscript; all authors critically revised the manuscript for important intellectual content and approved of the version to be published.

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Table 1. Traits measured in outdoor common gardens or reciprocal transplants for at least 5 populations in at least 20 garden-specific experiments, with data available from text, tables, author contact, or extraction from figures. Note that in some cases, multiple highly similar measures were grouped, as indicated in footnotes.

Trait	**Units**	**Garden-specific experiments**
date – flowering[1]	# days	34
size – floral[2]	cm	22
height - plant	cm	46
size – leaf[3]	cm	30
mass – shoots[4]	g	43
number - inflorescence[5]	#	36
number – seeds[6]	#	21
survival	%	43

[1]Flowering date or any other floral phenology

[2]Any size measurement of a floral structure

[3]Most frequently, leaf length; occasionally leaf width

Any measure of aboveground biomass

Counts of flowers or flowering structures

Most frequently seed number, but also seed yield in mass and/or seed yield rating/rank

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Figure captions

Figure 1. Summary of reviewed literature that compared traits among at least two populations in at least one common environment, by lifeform. Total counts of published studies, species, taxa, and taxa-specific experiments (A); types of experiments (B); means and standard errors of duration of the experiments that measured more than germination traits (C); total counts of experiments that measured only germination traits, (D); means and standard errors of number of populations tested in each experiment (E), and garden sites per experiment for outdoor reciprocal transplant and common garden experiments (F).

Figure 2. Map of 129 different outdoor common garden locations (A) and 2953 unique population collection sites (B) for the 80% of outdoor gardens and 91% of experiments for which coordinates could be obtained or generated, from 170 studies reviewed. The size of the marker in panel A represents the number of experiments in which each specific garden location was used, with larger symbols indicating garden locations used in more experiments. Although all species represented are native to the floristic Great Basin (white outline), many populations were collected and tested outside this region.

Figure 3. Summary of the years in which the collections of each experiment were made (A, left), the year each experiment was performed (A, right), and the average geographic distance among population collections sites in each experiment. The percent of 327 experiments that reported this information were 99% and 88% (respectively) for panel A, and 80% for panel B. Collection year and experiment year represent the average for each experiment, as it was common for materials to be collected and tested over multiple years for each experiment. Geographic distance is the

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mean pairwise distance among populations in each experiment; note the noncontinuous vertical axis.

Figure 4. Frequency of among-population variation (A, signature 1) and trait-by-environment associations (B, signature 2) for any measured trait, grouped by five life history traits. Frequency of local advantage (C, signature 3) for reproductive traits, survival traits, fitness indices, or biomass. Data compiled from 327 experiments from 170 published studies on Great Basin plants (see Supporting Information Appendix S2 and available datasets in electronic supplementary material). For signatures 1 and 2, “Yes” and “No” represent statistical comparisons, while “Authors claim “Yes”” and “Authors claim “No”” represent textual, claim-based results where supporting statistics were not reported (common in older studies). For signature 3, most experiments had multiple gardens, and many evaluated performance at multiple sampling dates, leading to 5 different scores. These scores, from “All gardens, all times” to “No gardens at any time” represent a gradient of incidence and frequency of this signature. For all panels, numbers in parentheses, (x), indicate the number of experiments scored in a given category, and the dashed gray lines indicate 50%.

Figure 5. Summary of 1,465 trait scores from the 305 experiments appropriate for detecting signature 1 (differences between populations). Scores of “Yes” and “No” were supported by statistical comparisons, while the “Authors claim…” scores represent textual, claim-based results where supporting statistics were not reported (common in older studies). Numbers in parentheses, (x), indicate the total experiments that measured each trait or reported each factor, and dashed gray line indicates 50%.

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Figure 6. Summary of scores for associations between 592 traits (A) and 426 environmental factors (B) from the 161 experiments appropriate for detecting signature 2 (trait-by-environment association), expressed by trait/factors, and an example from the literature (C, redrawn with permission from (Meyer and Monsen, 1991)) in which date of germination for mountain big sagebrush is correlated with a measure of monthly temperature (treatment: 2-week chill). Scores of "Yes" and "No" were supported by statistical comparisons, while the "Authors claim…" scores represent textual, claim-based results where supporting statistics were not reported (common in older studies). For panels A and B, numbers in parentheses, (x), indicate the total experiments that measured each trait or reported each factor, and the dashed gray lines indicate 50%.

Figure 7. Results of comparisons of pairwise trait and environmental distances for eight frequently measured phenotypic traits and (A) the mean annual precipitation (MAP) or (B) mean annual temperature (MAT) at the original collection location. Values are effect sizes and 95% confidence intervals for each trait, averaged across all experiments for which data were available (number of experiments in parentheses). Examples of the two strongest relationships are shown for leaf size and MAP (C), where each line shows the correlation coefficient and confidence intervals for an individual experiment, for which we calculated the relationship between differences in percent survival and difference MAP at location of origin. Color indicates functional groups: Green = grasses, blue = shrubs, orange = forbs. Examples are shown for the two highest effect sizes: D), experiment 297A, (Kramer, Larkin and Fant, 2015), *Penstemon deustus* and E), experiment 297A,(Kramer, Larkin and Fant, 2015), *Eriogonum microthecum*.

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Similarly, flowering time and MAT (F) is shown, with examples of G) experiment 271A, (Larsen, 1947), *Schizachyrium scoparium*, and H) experiment 245A, (Ward, 1969), *Deschampsia caespitosa*. Full results for each trait/environment relationship are shown as additional results in Supporting Information Appendix S3.

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Figure 1.

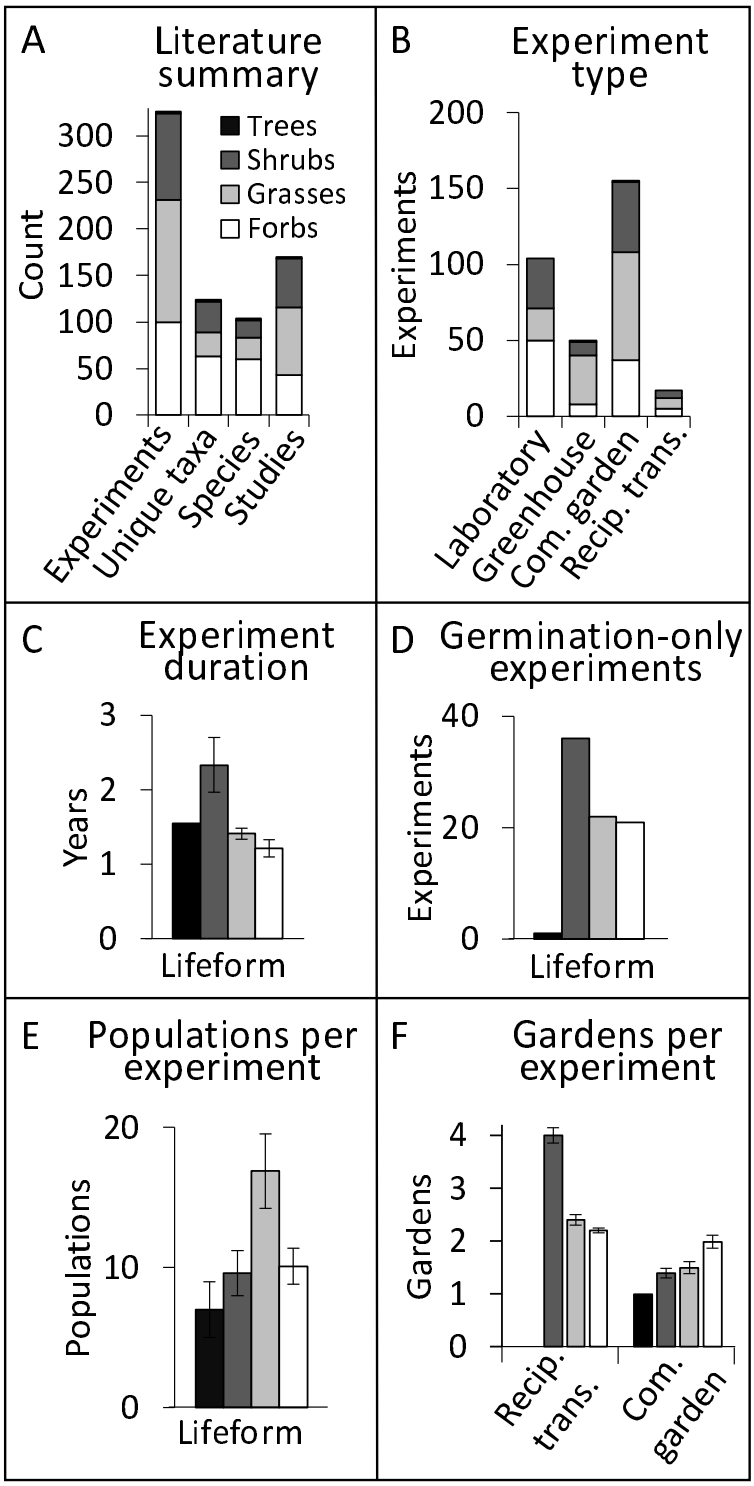

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Figure 2.

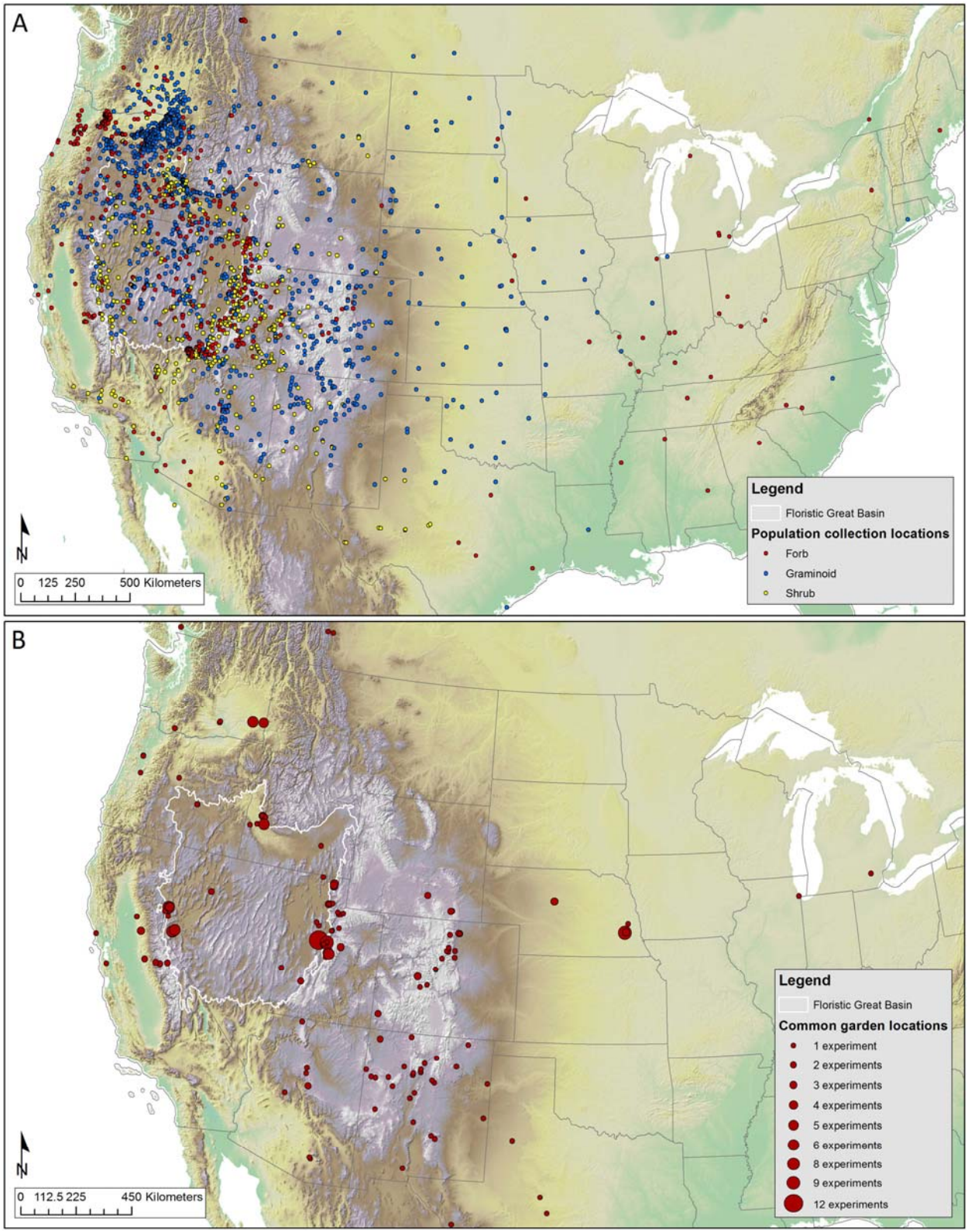

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Figure 3.

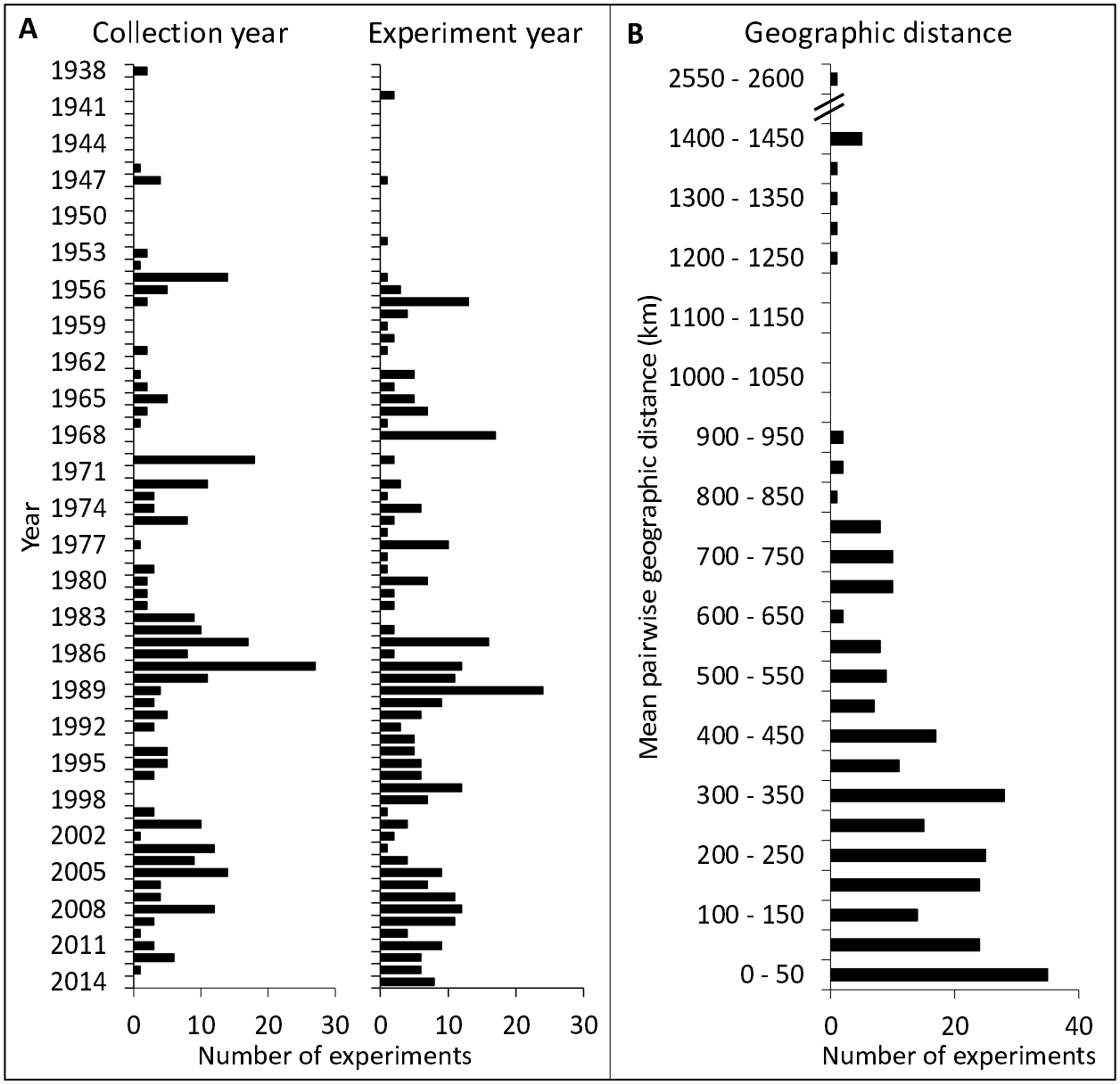

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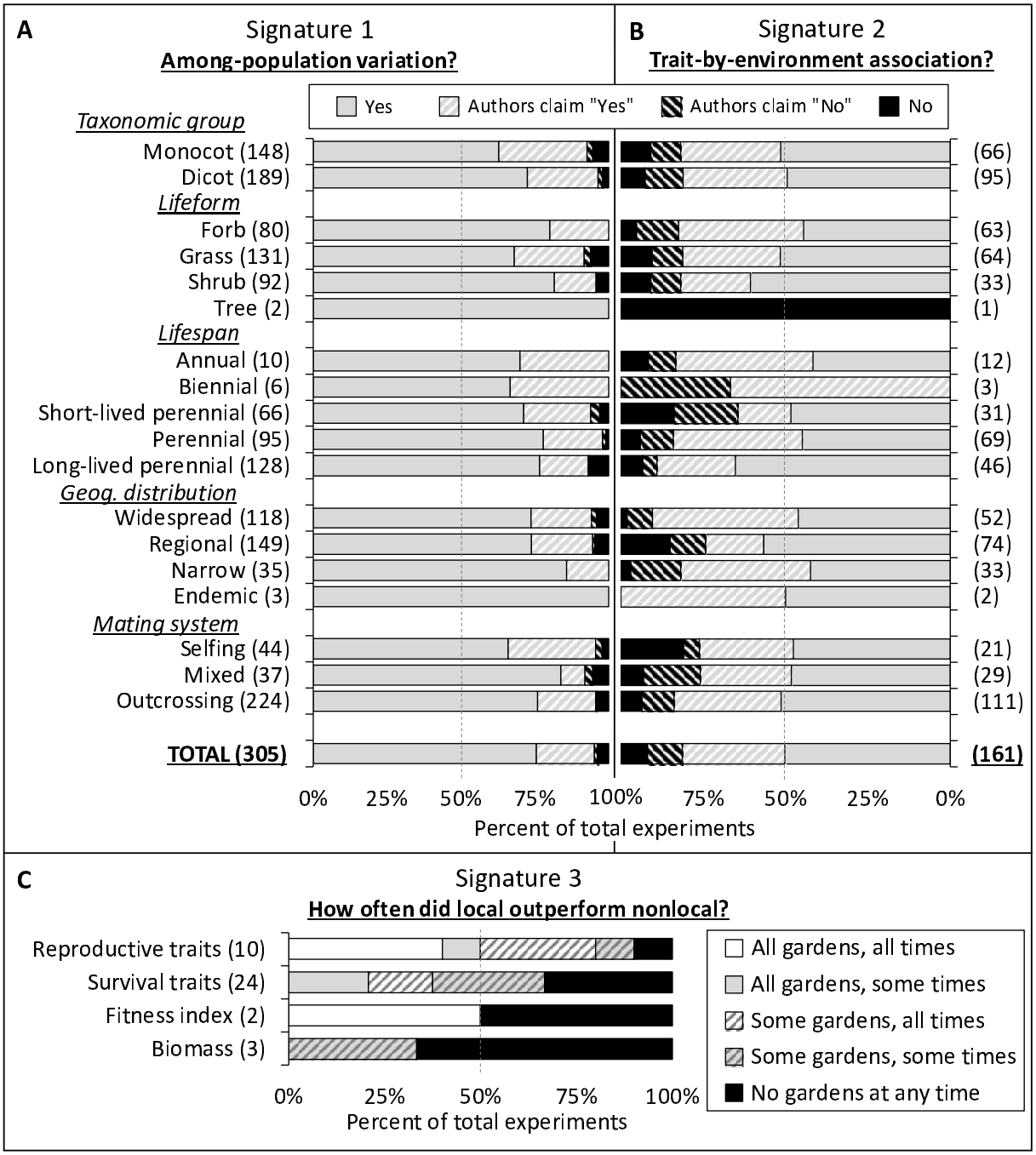
Figure 4.



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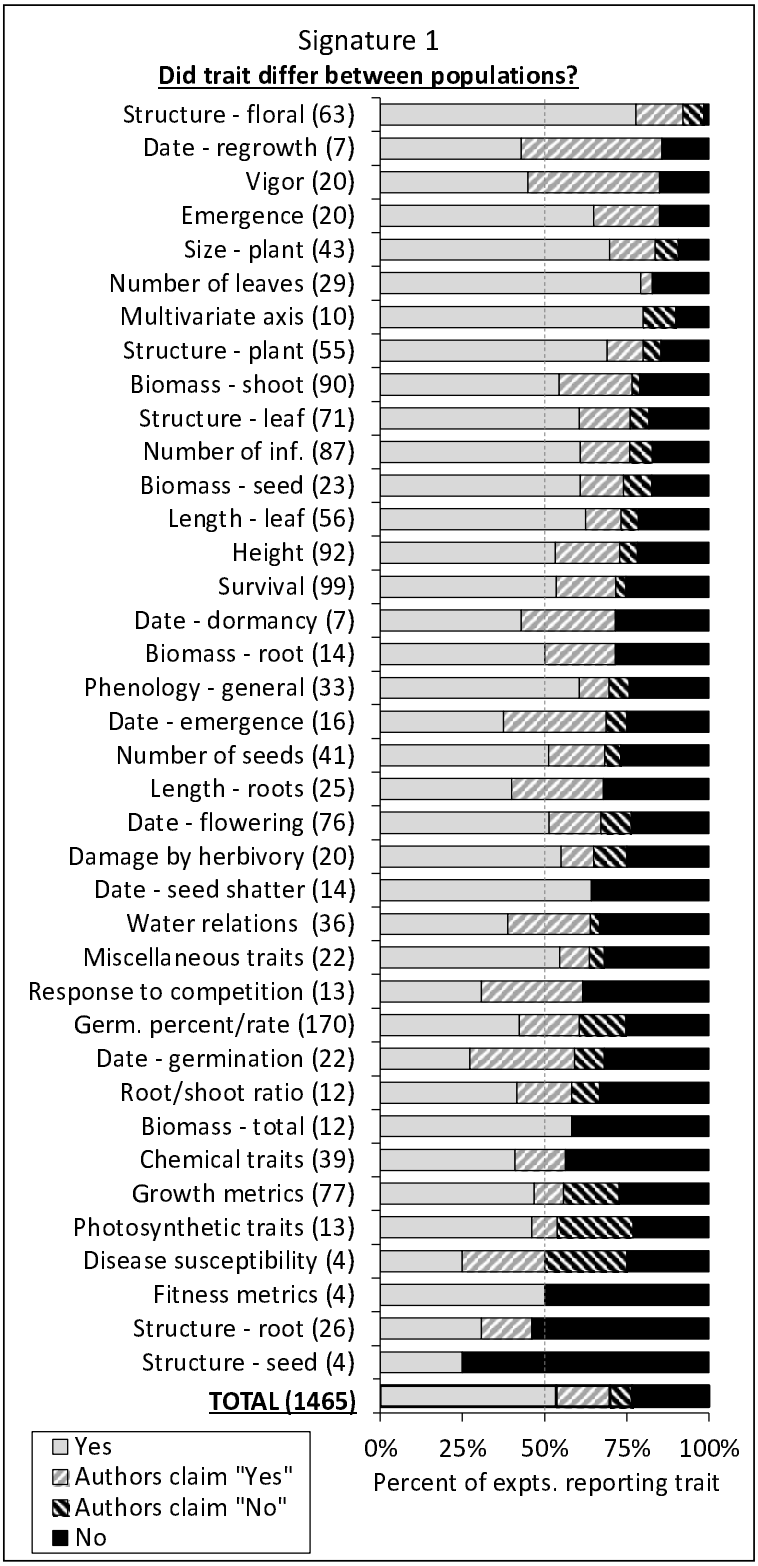

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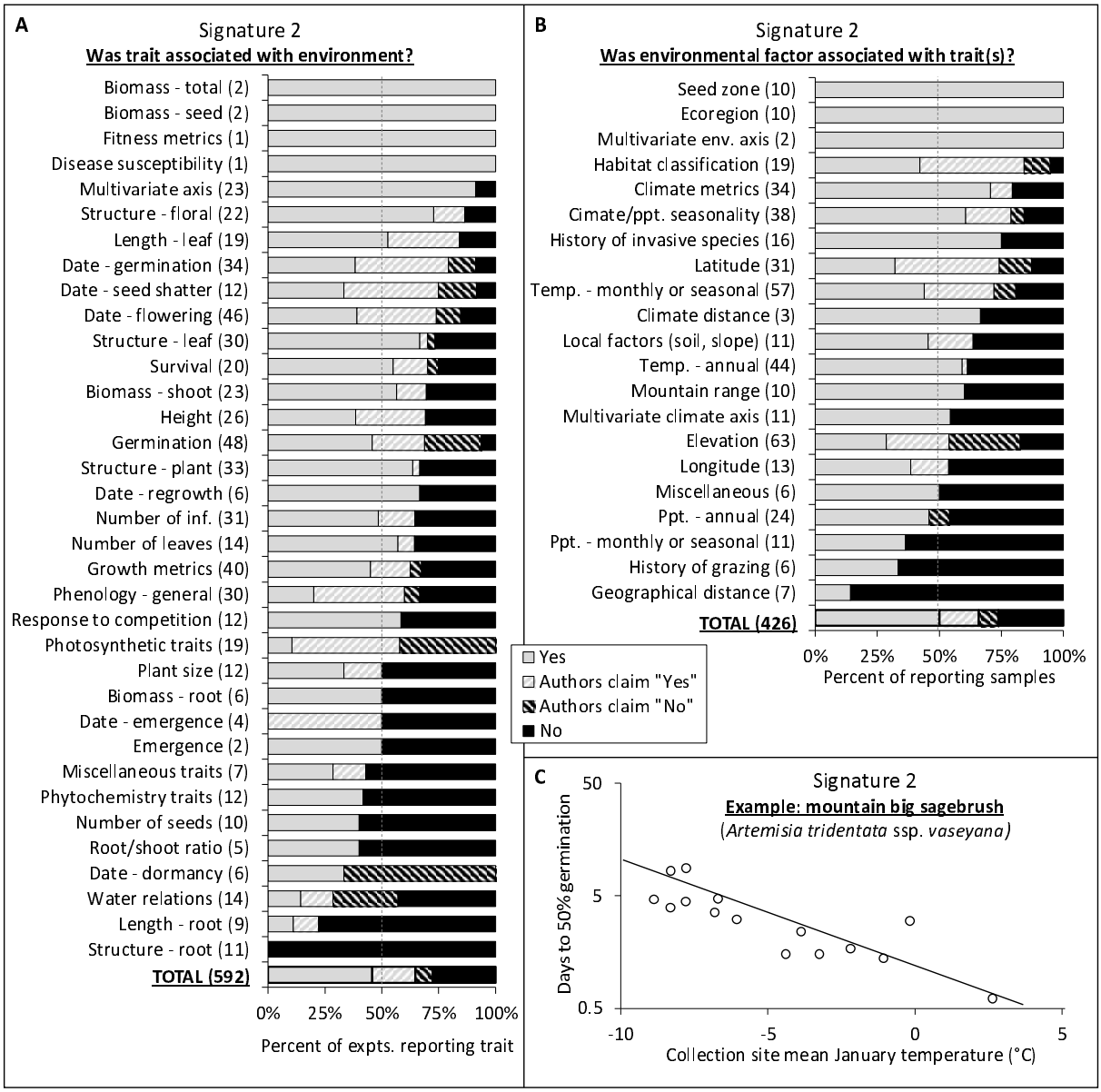
Figure 6.



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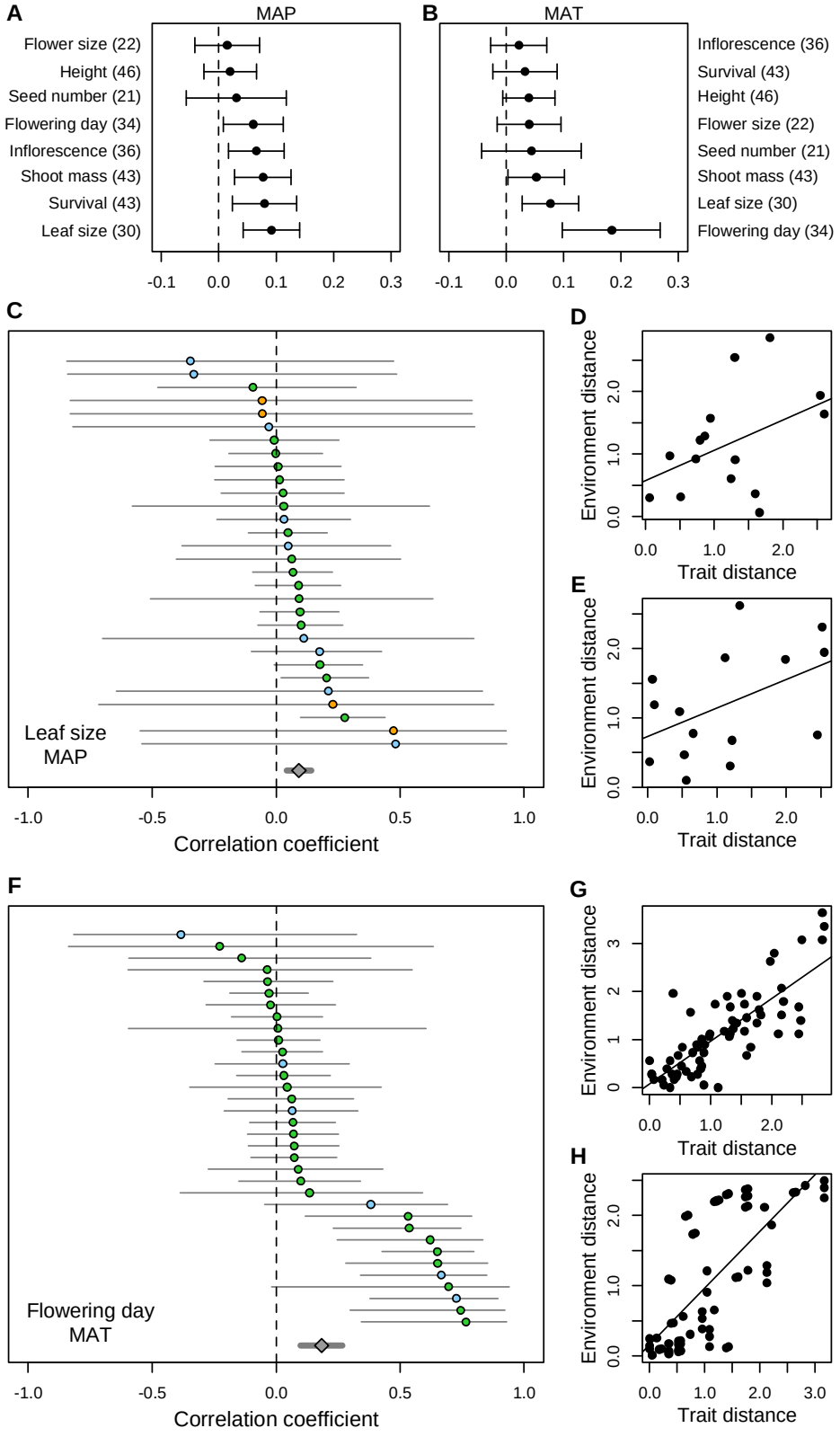
Figure 7.