Abiotic influences on intraspecific trait variation in montane species with varied life histories

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Abstract

Phenotypic plasticity and genetic adaptation are categorized as one of three main mechanisms that plants use to adapt to changes in their environment. Unlike genetic adaptation, which operates on the generational scale, plasticity can produce variation in traits within a single generation. Plasticity, often represented by intraspecific trait variation (ITV), may allow species to persist across a wider range of environments, resulting in greater resiliency. Higher temperature and moisture stress in montane communities related to the low snowfall of this past year presage the conditions that we expect to become more frequent in the future. Observing the reactions of plant species to these conditions is essential to advance our knowledge of the adaptation of vegetative communities. Across elevations, species may react to abiotic changes in different ways. By measuring the variability in plant height, leaf area, and specific leaf area for five species at ten sites across an elevational gradient in the Greater Crested Butte area, we investigate indicators of local adaptation and the potential climate resiliency within species. We conducted this study on five species - *Frasera speciosa* Douglas ex Griseb, *Linum lewisii* Pursh, *Erigeron speciosus* (Lindl.) DC., *Festuca thurberi* Vasey., and *Castilleja septentrionalis* Lindl – to assess ITV in plants with different growth habits, life cycles, and resource acquisition strategies. We assessed site and elevation differences in the three measured traits through separate analysis of variance (ANOVA). We also fitted 15 generalized mixed effects models to determine the relative effects of climatic, edaphic, and topographic variables on the three traits across the five species, accounting for site differences as a random effect. Our results showed that while there is significant trait variation between sites of the same species, elevation is not a significant driver of that variation. Edaphic variables had the most influence on trait values across the five species, but the intensity and direction of the relationship was species dependent. Precipitation had a more significant effect than other climatic variables. Within sites, precipitation seasonality had a significant positive effect on trait variance.

Introduction

In the context of a changing world–including rising temperatures, increases in drought frequency and intensity, and unpredictable weather patterns–scientists seek to explain how

ecosystems across the world will respond to these changes (Bjorkman et al. 2020). Earlier snowmelt timing, combined with increasingly arid conditions, is predicted to increase the risk of severe drought in Colorado (Bolinger et al. 2023). In the East River Valley near Gothic, CO, annual snowfall has been recorded since 1972. The winter of 2026 had the lowest snowfall on record (barr et al. 2026). Years such as this are becoming more frequent, forcing many plants to withstand conditions they are poorly adapted for (barr et al. 2026). Sitting at the base of food webs and ecological networks, plants are an essential part of every ecosystem and provide innumerable services. For many animals, the availability of food resources, shelter, and habitable climates, which determines their suitable habitat range, are mostly driven by plant distributions (Richman et al. 2020). Understanding the mechanisms that various plants use to react to climate change is crucial to predicting the future of ecosystems across the globe.

One of the main adaptive mechanisms at a plant's disposal is phenotypic plasticity: the ability for a genotype to produce multiple phenotypes in response to varying habitat and local environmental conditions (Henn et al. 2018). This mechanism is used by plants to react to shifts in abiotic and biotic conditions and is manifested as intraspecific trait variation. Variation in traits allows species to withstand stressful abiotic conditions (Helsen et al. 2017; Westerband et al. 2021). Research on the extent of plasticity within populations and individuals is necessary to estimate the conditions that communities will be able to withstand without changes to their genetic makeup. Since plasticity is strongly tied to intraspecific trait variation (ITV)– especially at the individual level–scientists use this as a metric to assess local adaptation which can be used to predict the response of plant communities to environmental stressors and climate change (Funk et al. 2017). For leaf traits in particular, plasticity allows individuals to react to changing abiotic conditions within a single growing season (Henn et al. 2018). Trait variation related to abiotic stress tolerance (i.e., drought tolerance) across populations is particularly successful at revealing the population’s capacity for local adaptation and persistence in changing and marginal environments (Westerband et al. 2021). Additionally, phenotypic plasticity has also been shown to help species persevere at the extremes of their range, which can promote range expansions (Van Nuland et al. 2020). Mounting evidence suggests that ITV is structured along abiotic gradients, but also driven by genetic foundations in trait development within species (Siefert et al. 2015; Westerband et al. 2021; Lammerant et al. 2025). Certain traits such as specific leaf area (SLA)–the area of a leaf divided by its dry weight– are particularly sensitive to abiotic factors (Helsen et al. 2017) and its variability has been shown to increase with elevation (Westerband et al. 2021). There is limited information on plasticity across species’ elevational range and the abiotic drivers that influence plasticity. This leads to a lack of information on how community composition will be altered by changes in abiotic conditions. Plasticity is an essential mechanism for range maintenance and expansion. Variation in leaf traits, or plasticity, increases fitness and facilitates adaptation in plant species (Shi et al. 2023). Further information on the abiotic conditions that influence variation in functional traits and how their influence changes between species is a remarkably underexplored avenue - one that is urgently in need of investigation (MacTavish & Anderson 2020).

Elevation has long been used as a proxy for varying environmental conditions, particularly in studies that predict plant responses to shifts in the climate (Blois et al. 2013; Sundqvist et al. 2013; Elmendorf et al. 2015). Altitudinal gradients are characterized by rapid changes in environmental conditions such as temperature, precipitation, geology, and exposure to solar radiation (Körner et al. 2007; Abbott & Brennan 2014). While some of these abiotic conditions vary predictably across elevation, water availability does not follow the same predictable patterns and is tied more closely to substrate (Sundqvist et al. 2013). Plasticity will become an increasingly important mechanism as plants are faced with rapidly changing environmental conditions. The influences of stressful abiotic conditions on plasticity are a notably under-researched topic. Although there is evidence that certain trees increase in plasticity at the extremes of their elevational range (Van Nuland et al. 2020), this phenomenon has not been explored for other species with different life histories and resource acquisition strategies. This research is increasingly urgent as some lower-elevation species shift upwards in search of the habitat they are best adapted (Zorio et al. 2016), encroaching on the habitat of sensitive alpine species. Many alpine species, in turn, seem to be shifting downwards to escape the stressful conditions found in their previous range - potentially related to water stress as aridity has been shown to be the predominant range-limiting factor (Zorio et al. 2016; Bjorkman et al. 2018). Understanding the abiotic mechanisms that are driving these range shifts may assist in preserving endemic montane species and predicting the composition of our future environments.

Increasingly unpredictable precipitation determines soil water availability with strong implications for nutrient mobilization and uptake in plants (Barber 1995; Nye & Tinker 1977). This, in turn, drives significant spatiotemporal variations in leaf traits such as specific leaf area (SLA) and leaf area (LA) (Emanuel & Campbell 2024; Westerband et al 2021). Plants with high SLA are often found in resource-rich environments; high SLA means thin leaves, associated with high photosynthetic rates and high leaf nitrogen and phosphorous content, but scaling negatively with leaf longevity (Joswig et al. 2021; Pérez-Harguindeguy et al. 2013). In contrast, plants with low SLA are connected to resource conservation strategies in water-limited habitats (Westerband et al. 2021). Plants subjected to environmental stresses such as heat, cold, drought, nutrient and high-radiation often produce relatively small and thick leaves, hence low LA and SLA values (Pérez-Harguindeguy et al. 2013). Plant height is a crucial trait as it is a major factor in their carbon gain strategy and ability to compete for light (Moles et al. 2009).

Functional trait variation is well established in the literature. Functional traits, or traits that influence performance or fitness, have been well studied as their variation is a useful indicator of species adaptability and resilience. ITV positively correlates with warm, dry range limits in *Populus angustifolia* (Van Nuland et al. 2020). While annual herbaceous plants respond quickly to environmental changes, climate responses often lag in perennial and long-lived species. Moreover, resource acquisition strategies vary widely among plants (Holz et al. 2024), leaving some species more vulnerable to drought, or more reliant on wet years, or on entirely different time frames. For example, *Frasera speciosa*, a monocarpic flowering plant, relies on temperature and precipitation cues three years prior to flowering (Evers et al. 2021). Hemiparasitic plants, like *Castilleja septentrionalis*, and epiphytic plants will likely react

differently to abiotic influences than plants that purely rely on photosynthesis and obtaining their own resources (Brown et al. 2020). Additionally, differing lifespans can change the priorities of a plant - whether they put more energy into fast, productive reproduction (that is, the r strategy plants) or into longevity (K strategy) may have impacts on the level of leaf plasticity that they display (Boyce 1984). Perennial species such as *Linum lewisii* may require higher levels of plasticity to react to the wider variety of environmental conditions they will experience over this time period.

With the low levels of winter precipitation and snowpack this winter, plants may be pushed to the extremes of their adaptive ability. This sets the perfect environment to examine vegetative plasticity in five montane species: *Frasera speciosa* Douglas ex Griseb, *Linum lewisii* Pursh, *Erigeron speciosus* (Lindl.) DC., *Festuca thurberi* Vasey., and *Castilleja septentrionalis* Lindl. Through this study, we reveal:

1) What abiotic factors are behind changes in intraspecific trait variation both with and between populations?

2) Is trait variation driven by climatic, edaphic, or topographic influences?

3) Do different species have different reactions to the same environmental cues?

For functional traits, we expect LA, SLA, and plant height to decrease in response to lower soil moisture and in higher elevations, due to increased radiation and longer heat exposure. Height and SLA are expected to increase with increasing temperatures due to longer growing degree days. However, both heat and cold stress select for smaller LA, therefore as plants reach the edges of their elevational range, LA is predicted to decrease. ITV is expected to increase with increased stress – whether that is a result of temperature or moisture – in all species. By using plants in close proximity, we were able to remove geographical distance as a confounding factor in understanding ITV along elevational and hydrological gradients. As previous studies suggested, we expected that higher stress will promote higher levels of ITV as species reach the dry and hot outer limits of their elevational range and are exposed to increased environmental stress (Van Nuland et al. 2020). Overall, we expect to see a pattern of low to high ITV across the elevational gradient for each species as conditions become more stressful with higher elevation. This is correlated with temperature changes that elevation is used as a proxy for. Water stress muddles the correlation between ITV and elevation; sites with lower soil moisture will likely have higher ITV, but these sites are not distributed predictably across the elevational gradient.

Methods

Study Site

Our study sites are distributed in the East River Basin in Gunnison County and Crested Butte, Colorado, USA (38.8697°N, 106.9878°W), near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (Figure 1). In the East River Basin, the average annual minimum and maximum temperatures are -7 and 10 ℃, respectively. Average total precipitation

is 60.35 cm, and average snowfall is 515.32 cm. From September 1, 2025, to August 31, 2026, total snowfall was 459 cm–the lowest snowfall seen in 52 years. Precipitation totals are normally 90.63 cm; in 2026, there has been 57.86 cm from January-July. Soil water content was 38% below average for this time period (barr et al. 2026). We recorded coordinates and elevation of each population sampled. All locations sampled represented a meadow habitat with relatively the same environmental conditions. In total, 10 populations of each species were sampled, although some species were found at the same site.

Selected species

We selected five species - *Frasera speciosa* Douglas ex Griseb, *Linum lewisii* Pursh, *Erigeron speciosus* (Lindl.) DC., *Festuca thurberi* Vasey., and *Castilleja septentrionalis* Lindl. Our selected species represent different growth habitats, minimum generation time, and resource acquisition strategies. *Frasera speciosa* Douglas ex Griseb is a perennial, monocarpic herb in the Gentianaceae family ranging from 1800 m to 3800 m. *Linum lewisii* Pursh. is a perennial, long lived subshrub in the Linaceae family found from 1200 m to 3480 m. *Erigeron speciosus* (Lindl.) DC. is in the Asteraceae family, ranging from 1700 m to 3650 m. It is a rhizomatous perennial. *Festuca thurberi* Vasey., and *Castilleja septentrionalis* Lindl. are in the Poaceae and Orobancheceae families, respectively. *F. thurberi* is a large bunchgrass, ranging from 2000 m to 3800 m while *C. septentrionalis* is a hemi-parasite found between 2000 m and 3500 m. All ranges are specific to Colorado from Ackerfield (2022) and include populations across the state.

Field Methods

We sampled ten populations, five sites each in both low and high elevations, for each of the selected species (n = 50 populations total). The ten sites selected for each species represented an altitudinal gradient to allow for testing elevational differences in trait values. Populations are defined as individuals of a given species in close proximity or discrete patches in an area sharing the same environmental conditions (site). Sites are defined as the extent of a meadow and subdivided by ecosystem differences such as substrate type or microtopography. Five populations of each species were measured from high elevation sites (above 3000 m) and five from low elevation sites (below 3000 m). In each population, we measured leaf area and specific leaf area from 10 individuals, and plant height from 25 individuals of the species. Only reproductively mature individuals in full sunlight, with minimal signs of pests or herbivory, were sampled, while height was recorded as the distance between ground level and the tallest photosynthetic material of reproductive or near reproductive stems. Each individual was measured to the tallest photosynthetic material, excluding *F. speciosa* which was measured to the tip of the reproductive stem. Species-specific collection methodology is recorded in Appendix I. Functional trait collection methodology followed Pérez-Harguindeguy et al. (2013). All measurements are representative of the optimal growth state for that species in that location.

In all cases, leaves were collected from individual plants, excluding petioles, and preserved in plastic bags with a damp paper towel. The leaf samples were scanned in a flatbed scanner (Epson perfection V39 II) and the resulting scans were analyzed in image J software to

calculate leaf area. Leaf area was calculated using the wand tool with tolerance set at 60. A scale was included in each scan. Leaves were air dried for 48 hours before being transferred into the envelope and placed in an oven at 60 °C for a further 72 hours. The dried leaves were then weighed to calculate SLA using the formula:

SLA = leaf area (cm) / dry weight (g).

Dried leaves were stored in envelopes on silica beads for future reference.

Soil variables

For each sampled population, a measure of soil moisture was recorded with a handheld soil probe (Gouevn) at several points throughout the population and averaged. Substrate type at each population was recorded using Zorio et al. (2016) environmental data and personal observations. Additionally, we downloaded several other soil variables from the ISRIC World Soil database (Poggio et al. 2021), including soil pH, bulk density, coarse fragments, soil organic carbon, organic carbon density, silt content, clay content, and sand content, all at 5 cm depth and 1 km spatial resolution. These soil datasets were accessed using the soil_world function in geodata R package version 0.6-9 (Hijmans 2026). We extracted soil values associated with the 50 surveyed sites.

Climatic variables

We downloaded the 19 bioclimatic variables representing mean and variability of temperature and precipitation at 1 km resolution between 1970 and 2000 from the WorldClim database version 2.1 (Fick and Hijmans 2001). The dataset was downloaded in R using the worldclim_global function in geodata R package version 0.6-9 (Hijmans 2026). Thereafter, we extracted the climatic values associated with the surveyed site coordinates.

Site topographic variables

Elevation was recorded at each site and categorized into high and low categories. Using the site coordinates, we calculated the slope and aspect based on the digital elevation model (DEM; 305 m resolution) obtained from the elevatr R package version 0.99.1 (Hollister 2025). Slope and aspect were calculated using the terrain function in terra R package version 1.9.34 (Hijmans et al. 2026), with a neighborhood window of eight grid cells. Thereafter, the aspect and slope variables of the surveyed sites were extracted for downstream analysis.

Data analysis

All climatic, edaphic, and topographic variables were assembled and subjected to the variance inflation factor (VIF) analysis to remove highly correlated variables [VIF > 10]. This was done using the vifstep function in udsm R package version 2.1.7 (Naimi et al., 2014) separately for each species. Explanatory variables were grouped into three categories: topographic, climatic, and edaphic and analyzed separately to ensure we were able to infer the effects of each type of influence. The final shared variables among all species were elevation, precipitation seasonality (bio15), soil clay content, organic carbon density, soil organic carbon,

slope, and aspect. Several species also included precipitation of the warmest quarter (bio18), precipitation of the coldest quarter (bio19), soil silt content and soil pH. Annual precipitation (bio12), precipitation of the wettest month (bio13), mean temperature of the coldest quarter (bio11), soil coarse fragments, and bulk density were included for at least one of the species. We used separate one-way analysis of variance on each of the five species to determine if the three measured trait means were significantly different among the three sites and between elevation classes. We also conducted TukeyHSD post-hoc tests to determine pairwise significant differences within each explanatory variable.

We also fitted 15 separate generalized linear mixed effects models (GLMMs) to investigate the effects of elevation, soil moisture, soc, ocd, silt content, clay content, soil bulk density, soil coarse fragments, bio11, bio12, bio13, bio15, bio18, bio19, slope, aspect, and pH on leaf area, specific leaf area, and plant height of the five species collected, accounting for site as a random effect (Table 1). Coefficients of the GLMMs were approximated by maximum likelihood t-tests using Satterthwaite's method. Following the GLMMs, we determined the variation explained by both fixed and random effects using R^2 values.

Coefficient of variance (CV) was calculated for each site to determine within-site trait variance. We assessed differences in CV between species and elevations using separate one-way analysis of variance for each of the three traits. A pairwise tukeyHSD post-hoc test was performed on significant ANOVAs for within-site variance. Following that, GLMMs were fitted for each of the three traits to investigate the effects of elevation, soil moisture, ocd, silt content, clay content, bdod, bio11, bio12, bio13, bio15, bio18, bio19, slope, aspect, and pH on CV, accounting for site and species as a random effect. Trait variation was not separated by species due to a lack of sufficient datapoints. GLMMs were fitted similarly to between site variance measures using functions in the lme4 R package version 2.0.6 (Bates et al. 2015).

Results

Observed intraspecific trait variability among the five species

There were clear differences in trait values related to topographic, climatic, and edaphic factors in each of the five plant species. Between elevation classes, leaf area (LA) values were higher at lower sites for several species, except for *Festuca thurberi* and *Linum lewisii* (Figure 2). Plant height was higher at low elevations for all species while specific leaf area (SLA) values were slightly lower at low elevation sites for all species except *Erigeron speciosus* (Figure 2).

Sites also had clear differences in trait values within each species (Figure 7). The coefficient of variance for each site in each species also appeared to vary between sites (Figure 7).

We observed an inverse relationship between SLA and precipitation seasonality for all species; plant height showed a similar relationship with precipitation seasonality for *F. thurberi* and *Erigeron speciosus* but was positively correlated in the three other species (Figure 3). Bio11 and bio13 were only included in the analysis for *Linum lewisii* and *Festuca thurberi* per the variance inflation factor. Mean temperature of the coldest quarter (bio11) appeared to have a positive effect on specific leaf area for *Linum lewisii* while precipitation of the wettest month

(bio13) seemed to have slight positive effects on both leaf area and specific leaf area for *Festuca thurberi* (Figure 8).

Most of our edaphic variables showed visible correlations with the measured plant traits. Soil pH had notable correlations with specific leaf area and plant height, although the direction of the relationship depended on the species (Figure 4). Leaf area appeared to have less of a relationship with soil pH, although *F. speciosa*, *F. thurberi*, and *C. septentrionalis* do show varying relationships to soil pH (Figure 4).

Is there significant among-site and elevation trait variations across the five species?

Our analysis of variance (ANOVA) showed no significant differences between elevation classes for any of the traits in any of the species (Figure 2). However we observed significant site differences in SLA, LA, and plant height for *Castilleja septentrionalis* ($F=2.32$, $df=9$, $p=0.02$; $F=7.54$, $df=9$, $p=0.00$; $F=18.96$, $df=9$, $p=0.00$, respectively). We observed pairwise significant differences in LA, SLA, and height among several sites (Table S1).

SLA, LA, and plant height were all significantly different amongst the ten sites for *Erigeron speciosus* (ANOVA: $F=5.61$, $df=9$, $p=0.00$; $F=9.12$, $df=9$, $p=0.00$; $F=32.25$, $df=9$, $p=0.00$, respectively). For each trait, several sites showed pairwise significant differences when run through a TukeyHSD post-hoc test (Table S2).

For *Festuca thurberi* and *Frasera speciosa*, similar results were obtained with SLA being significantly different among the ten sites (ANOVA: $F=2.22$, $df=9$, $p=0.03$; $F=7.89$, $df=9$, $p=0.00$, respectively). LA was significantly different among sites (ANOVA: $F=9.56$, $df=9$, $p=0.00$; $F=5.55$, $df=9$, $p=0.00$, respectively), as was plant height (ANOVA: $F=5.67$, $df=9$, $p=0.00$; $F=30.61$, $df=9$, $p=0.00$, respectively). We observed pairwise significant differences amongst several sites for each trait (Table S3 and Table S4)

Significant differences were found across the ten sites for *Linum lewisii* for SLA, LA, and height ($F=12.45$, $df=9$, $p=0.00$; $F=2.654$, $df=9$, $p=0.01$; $F=19.11$, $df=9$, $p=0.00$). Pairwise significant differences were observed between several sites for each trait (Table S5).

What are the abiotic drivers of ITV within populations?

Significant differences were found in trait variation between species for plant height (ANOVA: $F=6.63$, $df=4$, $p<0.01$). Pairwise significant differences were observed between *L. lewisii, F. speciosa, F. thurberi,* and *C. septentrionalis* ($p<0.01$, $p=0.03$, $p=0.05$, respectively). Elevation was not significantly different between species for any trait. Within species, significant differences were found between all sites for SLA, LA, and plant height (Figure 7; Table S6).

For within population ITV, we used coefficients of variance (CV) to standardize trait variances between species. Sites and species were included as random effects to control for unaccounted differences between sites and species. For all models, site and species both had significant effects on within population variation (Table S7).

Our GLMM showed the plant height was significantly affected by bdod and ocd (Figure 5a). Bdod had a positive effect on plant height variation within populations while ocd had a negative effect. For SLA, bio13 and soil moisture both had significant negative effects on trait

variation (Figure 5b). Conversely, bio15 had significant positive effects on SLA variance within populations (Figure 5b). Leaf area was affected by more of our fixed variables than both of our other two traits. Bio11, bio19, and soil clay content all had significant negative effects on variance in leaf area within populations (Figure 5c). Soil moisture content had significant positive effects on leaf area variance, as did bio15 (Figure 5c).

What are the abiotic drivers of ITV between populations?

In our generalized linear mixed models, we included site as a random effect to control for unaccounted differences between sites. The site did not have a significant effect on any traits for any of the five species (Table 4).

Our GLMM showed significant effects of different climatic and edaphic predictor variables on the measured traits for *C. septentrionalis*. Organic carbon density has significant positive effect on both LA and plant height, as did clay, soil bulk density, and precipitation seasonality (Table 3, Figure 6b, 6c). Both soil pH and silt content had significant negative effects on LA and plant height (Table 3, Figure 6b, 6c), but none of the fixed effect variables had significant effects on specific leaf area. In this GLMM, site, the random effect, had no contribution to the variance explained (R^2 for fixed effects was equal to R^2 for both fixed and random effects for all traits - SLA: 0.19, LA: 0.43, Height: 0.42).

For *Erigeron speciosus*, only organic carbon density had a significant positive effect on plant height for this species (Table 3, Figure 6f). Both LA and SLA were not significantly affected by any of the variables. Similarly to in *C. septentrionalis*, the random effect did not have any contribution to the variance explained in the models (SLA = 0.34, LA = 0.48, Height = 0.55).

Plant height showed no significant relationships for *Festuca thurberi*, however, SLA and LA were significantly affected by six variables. Soil pH, organic carbon density, clay content, and precipitation of the wettest month all had significant positive effects on the two leaf traits (Table 3, Figure 6g, 6h). Soil silt content and bulk density showed a negative effect on leaf traits in *F. thurberi* (Table 3, Figure 6g, 6h). Variance explained in the models (SLA = 0.18, LA = 0.49, Height = 0.36) were contributed solely by the predictor variables.

Organic carbon density had significant positive effects on SLA in *Frasera speciosa*, as did bio15 (Table 3, Figure 6j). In the same species, soil pH had positive effects on leaf area, but negative effects on SLA (Table 3, Figure 6j, 6k). Moisture and silt also displayed negative effects on *F. speciosa* specific leaf area (Table 3, Figure 6j). In this species, model variance was explained exclusively by the predictor variables (SLA: 0.44, LA: 0.36, Height: 0.54).

In *Linum lewisii*, organic carbon density had a significant effect on plant height (Table 3, Figure 6o). The effects were positive. Specific leaf area and height trait values were both significantly affected by pH, although the relationship was negative for plant height and positive for SLA (Table 3, Figure 6m, 6n). Two other variables had significant effects on specific leaf area: bio15 and bio11; the effects were negative and positive, respectively (Table 3, Figure 6a). Plant height was also positively affected by soil clay content, soil bulk density, and soil moisture

content (Table 3, Figure 6o). The random effect of site had no significant effect on the variance explained by our models (SLA: 0.56, LA: 0.21, Height: 0.42).

Discussion

In our analysis, we confirmed that there was significant intraspecific variation for the three traits in each species by analyzing differences between sites of the same species (Tables S1:S5). Contrary to what we expected, there was no elevational gradient in the intraspecific trait variations across the five species; this is likely due to the fact that all variance in the measured traits have been explained by site-level differences. Similarly, slope and aspect, our other topographic variables, had no significant effect on any traits. Due to the universal lack of significance for these two variables, we decided to exclude them from the final between-site analysis. In this analysis, soil organic carbon density (ocd) had significant effects on at least one trait for all species (Figure 6). However, the direction of that relationship varied depending on the trait and species. A negative effect of soil ocd on plant height was the only significant effect observed for the species *Erigeron speciosus* (Figure 6f). The other four species were all significantly affected by pH and at least one climatic variable; similarly, the direction and trait involved in the relationship varied by species (Figure 6). Multiple other effects of edaphic variables on trait expression were observed as well. In terms of within-site trait variation using the coefficient of variance, elevation was again found to be non-significant, but several precipitation related variables and soil moisture content significantly affected leaf traits (Figure 5). Within-site variance in plant height was only affected by soil traits (Figure 5).

The lack of consistency in effects between our species was in line with our hypothesis that the different life history strategies of these species would become evident in their resource use and reactions to abiotic influences. However, the significant effect of abiotic conditions on intraspecific trait variation of *C. septentrionalis* was unexpected, as was the lack of reaction by *E. speciosus*. The influences of abiotic factors seem to be magnified in *C. septentrionalis* - potentially due to secondary effects of host plants. In water limited environments, hemiparasitic species have been shown to have increased fecundity as they benefit from both their own photosynthetic abilities and their connection to host plants (Adler 2003; Těšitel et al. 2015). Considering our sampling was conducted in a severe drought year, it is likely the same interaction influenced our results.

Topographic and climatic effects

Precipitation and edaphic variables have significant effects on intraspecific trait variations measured in our study, while temperature-related variables have little to no significant effect. Elevation is highly correlated with climatic variables, especially temperature. Since temperature is strongly correlated with elevation, it is not surprising that elevation is a relatively insignificant driver of functional trait variation in these five species. Therefore, the significance in intraspecific variation between sites is driven by variance in soil features and other climatic conditions. Variability is explained by the joint influence of climatic and edaphic variables, rather than any one variable – a pattern that is observed on both larger and more specific scales

(Těšitel et al. 2015; Joswig et al. 2021). A particularly influential climatic variable both between and within sites was precipitation seasonality. Increased variability in precipitation, often captured as years with extreme drought effects and other years with excessive flooding, has been shown to increase productivity in shrub species, while decreasing productivity in grass (Gherardi & Sala, 2015). None of our species were shrubs but the perenniality and deep root structures of most of our species may provide them the same advantages. Increases in seasonality of precipitation likely increase stress in plants, aligning with our predictions of increased ITV with increased stress (Zeppal et al. 2014). For certain species, precipitation of the wettest month and the mean temp of the coldest quarter had influential effects on SLA as well. These variables both reflect conditions in the extreme season for precipitation and temperature, reflecting the climatic tolerances that species exhibit.

Edaphic effects on plant functional traits

For all species, soil organic carbon density seems to be one of the major drivers behind trait variation between populations. Our findings showed that soil ocd has a positive effect on leaf area and plant height in *C. septentrionalis, F. thurberi,* and *L. lewisii*, but a negative effect on plant height in *E. speciosus*. Soil organic carbon density supports soil microbial communities which are linked with soil aggregate formation, overall soil health, nutrient cycling, stress mitigation in plants, and nutrient availability for the aboveground vegetation (Lefevre et al. 2017; He et al. 2019). Negative effects on E. speciosus are likely due to the reduced soil nitrogen content associated with high soil carbon, limiting vegetative growth (Reed 1952; Rawls et al. 2003). Soil composition was also highly influential across species. Higher soil clay content increases nutrient availability and water retention capacities - particularly for nitrogen and carbon (Johannes et al. 2017; Kome et al 2019; Kjær et al. 2026) by reducing leaching. Our findings of a positive effect of soil clay content on both plant height and leaf area align with these properties of soil clay content. Soil silt content had a negative effect on plant traits across the five species. Although increased silt content can promote water filtration and aeration of soils, silt particles do not have the same nutrient holding capacity as clay particles – some studies have suggested that low SLA is an adaptive response to nitrogen stress (He et al 2019). The decreased water holding capacity and increased erosion risk in drought and flooding events respectively for soils with high silt content have adverse effects for plant persistence (Usaborisut & Ampanmanee 2015). Several other soil variables had significant effects on our three traits in all species. Soil traits also had significant effects on trait variation within populations, with increased variation seeming to correlate with increased stress. The influence of edaphic conditions on plant traits heavily overshadowed the influences of both climatic and topographic variables, leading us to infer that soil quality is the most important driver of trait variation across-sites in our five species.

Intraspecific trait variation has broad implications for species' survival and resiliency. The study of functional traits and their influences inform our knowledge of their survival strategies and thus our ability to predict climate responses. The ability to react to varied

environmental conditions for plants is highly dependent on the flexibility of their trait expression. Increased variability in traits is an essential mechanism for plant persistence – particularly in cold biomes where change is occurring at a faster rate (Henn et al. 2018). Incorporating intraspecific trait variation into climate models not only makes them significantly more relevant to real-world ecosystems but also improves the accuracy of model predictions (Verheijen et al. 2013). This is particularly useful for generating reliable future predictions of species and community shifts under climate change with greater uncertainty.

For each of the five species, we expected slightly different reactions to the same abiotic influences. Each of them has a different nutrient acquisition and use strategy that defines how they utilize the resources available to them. A complex interaction of climatic and edaphic influences plays a primary role in determining trait variation in all of the observed species. This has significant implications for the future of plant populations. This study highlights the necessity of having a set of study organisms that accurately represent the variation found within ecosystems.

Limitations

This study was conducted over the course of two months in the summer of 2026. Collection occurred within a limited timeframe and thus may not have captured the extent of variation in these populations. Trait sampling was conducted within a smaller portion of the elevational ranges of these five species, which we also broadly categorized into “high” and ‘low’ elevation within a limited elevation gradient. This may have oversimplified the system we were sampling and thus limited the extent of elevational effects on the study species. Future research should attempt to sample across the entire altitudinal extent of the species to fully capture variations across the entire species ranges. We also suggest sampling more populations at each elevation as our collection of five populations at each elevation may have failed to capture the full range of trait values. Larger patterns in trait variation may have been obscured by the lack of populations and the limited number of replicates for each variable. The scale of our extracted climate and edaphic variables was 1 km; this may have obscured fine scale differences in environmental conditions within sites. Moreover, our data analysis and considered variables did not account for biotic interactions which is important for a hemi-parastitic plant like *Castilleja septentrionalis*, for example, is a hemi-parasitic plant that extracts water, sugar, and mineral nutrients from a host plant (Heckard 1962). Failure to capture other influential factors for this species including host plant identity, proximity to other hemi-parasitic species, and variation in individual plant reliance on parasitism is an oversight of this study.

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Data Availability Statement

As part of the RMBL Data Archiving, Curation, and Vouchers, I participated in workshops and training for spatial and non-spatial metadata and archiving. My Data Management Plan includes a description of the datasets being archived, the dissemination methods, and the timeline for data-sharing. I used the RMBL template metadata form. I used the default data repository Environmental Data Initiative (EDI), https://environmentaldatainitiative.org/.

Appendix I

Species-specific methodologies

Linum lewisii

An individual is one cluster of stems, clearly extending from the same central point
Height: measured on the tallest stem to highest photosynthetic material; 25 replicates
Collection: only collect flowering stems - ensuring they have grown to maturity; when scanning, collect 2 of the highest mature leaves, 4 of the middle leaves, and two of the lowest healthy leaves and scan as one; calculating the individual leaf metrics later.

Frasera speciosa
One individual is one flowering stem
Height: measured to top of flowering stem. This is more easily standardized between plants as highest photosynthetic material was often unclear; only flowering, non-broken, and erect individuals
Leaf collection: leaf under the lowest flower is collected; 1 from each individual

Castilleja septentrionalis
An individual is one cluster of stems, clearly extending from the same central point
Height: to tallest photosynthetic material, one measure per individual of the tallest stem
Leaf collection: 2 per individual but scanned as one

Erigeron speciosus
As this is a rhizomatous species, an individual is defined as one cluster of flowering stems. A new individual is delineated by a gap of 20 cm or more.
Height: to tallest photosynthetic material, one measure per individual of the tallest stem
Leaf collection: 2 per individual but scanned as one

Festuca thurberi
An individual is defined as one continuous bunch of vegetative material, with gaps of greater than 20 cm delineating a new individual
Height: to tip of flag leaf, without straightening the plant
Leaf collection: The blade directly below the flag leaf is collected from just above the ligule.

Figures and tables

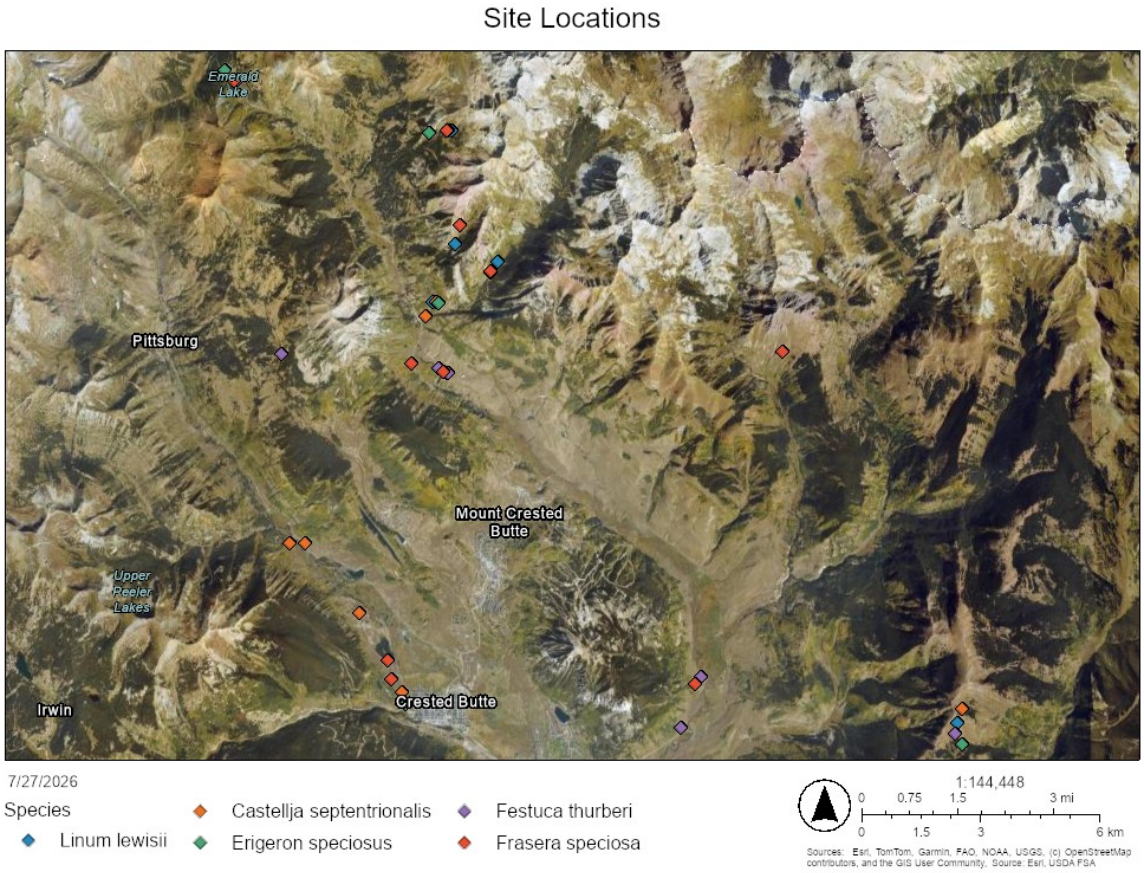


Figure 1. Site location for each species marked and differentiated by color. When possible, multiple species were collected at the same site and thus may overlap on the map. Sites of each species were a minimum of 1 km away from each other to minimize redundancy of climatic data. The study was conducted in the East River Basin, near Crested Butte, Gunnison County, Colorado.

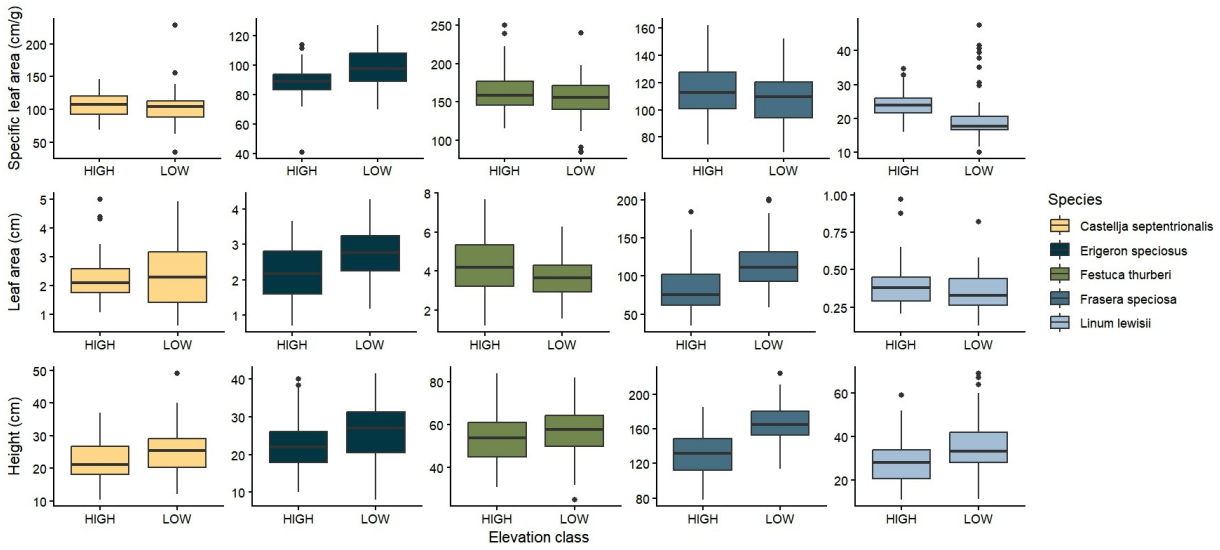


Figure 2. Differences in mean trait values for the two elevation classes. Sites at greater than 3,000 m elevation are considered high sites while sites at less than 3,000 m elevation are considered low sites. Predictably, low elevation sites displayed higher overall height and larger leaf area in most species.

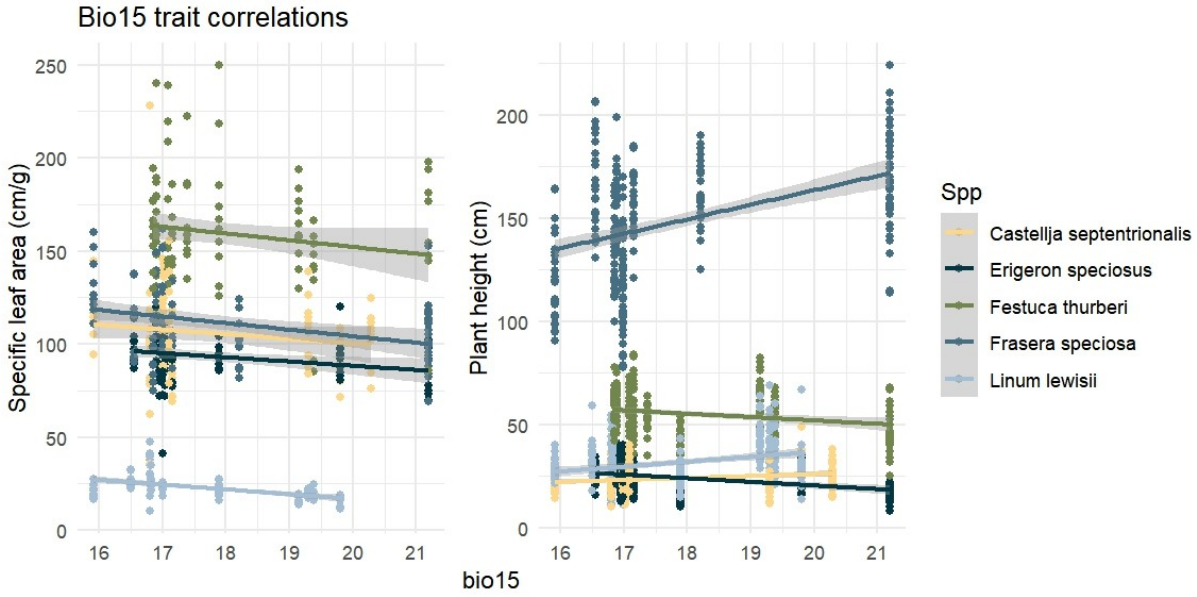


Figure 3. Plot of the correlation between bio15 (precipitation seasonality) and traits values (specific leaf area and height). Mean temperature of the coldest quarter (bio11) and precipitation of the wettest month (bio13) were excluded by variance inflation factor for all species except *L. lewisii* and *F. thurberi*, respectively.

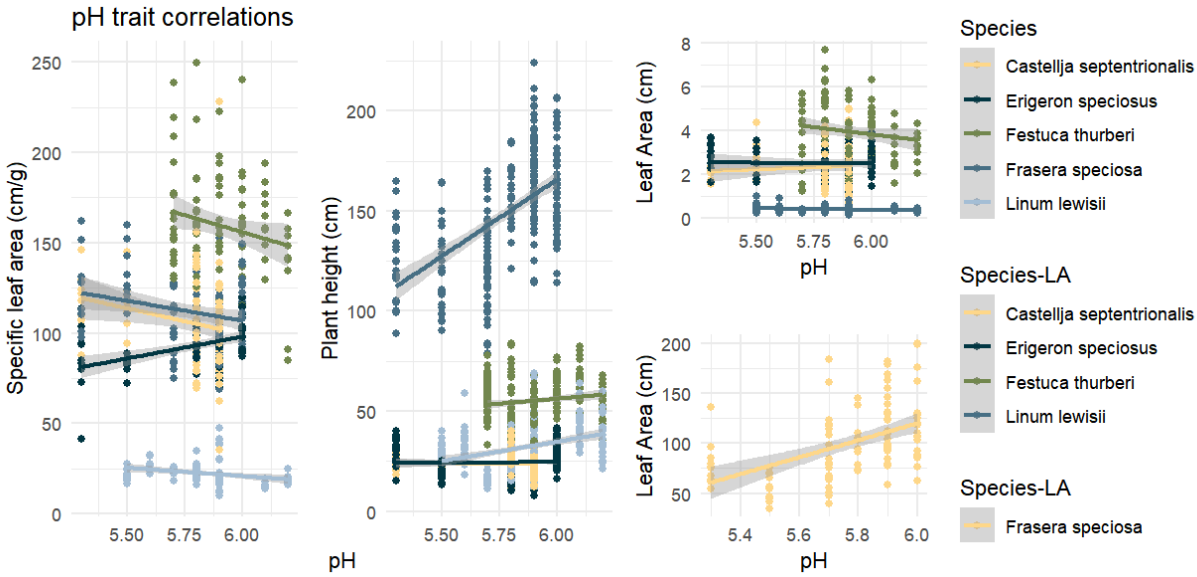


Figure 4. Plot of the correlation between pH and the three traits. Leaf area is separated into two graphs to account for the difference in scale between *Frasera speciosa* and the other four species.

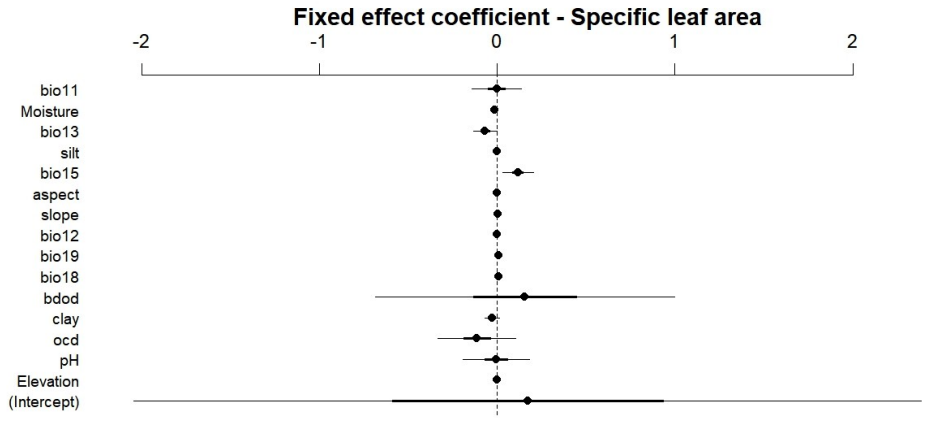
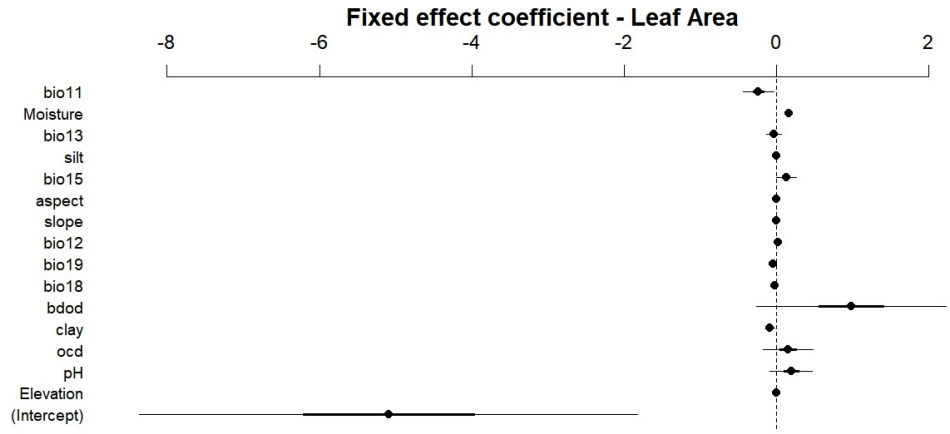
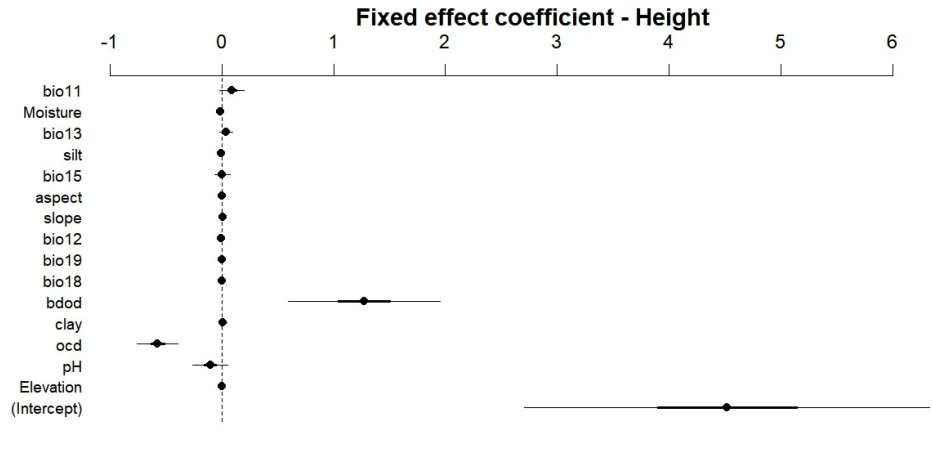
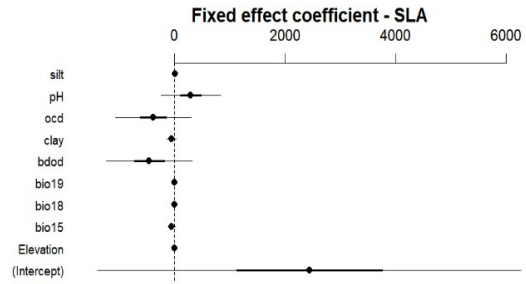
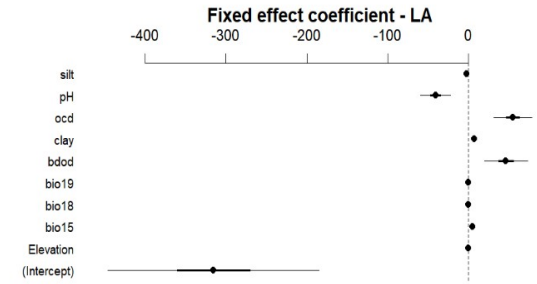
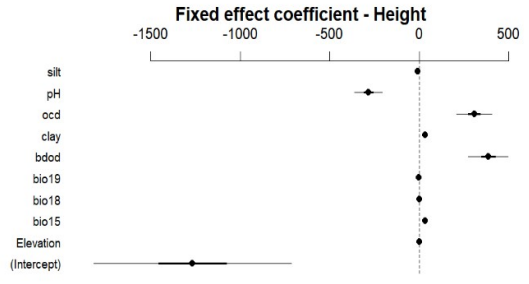
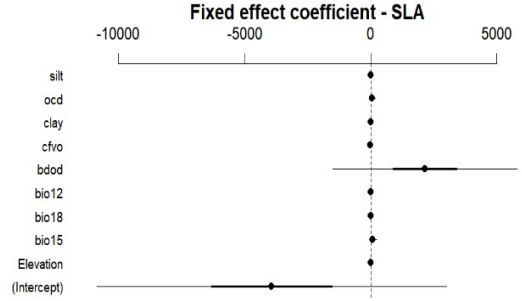
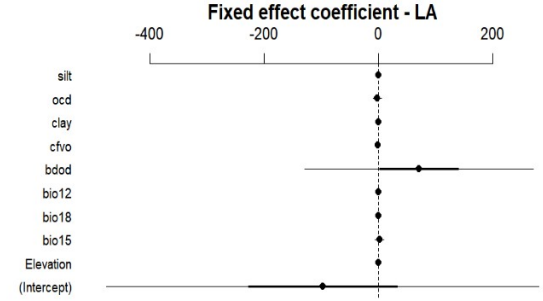
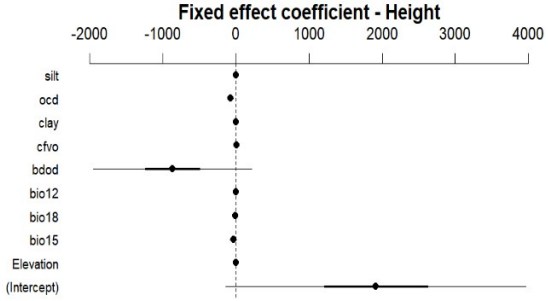
Trait	
Specific leaf area	
Leaf area	
Height	

Figure 5. Fixed effect coefficient plots for within-site variation analysis. The coefficient of variation of each site for each species was calculated separately before analyzing with a generalized linear mixed effects model. Center dots represent mean values and bars represent standard deviations.

Species	SLA	LA	Plant height
Castilleja septentrionalis	a) 	b) 	c) 
Erigeron speciosus	d) 	e) 	f) 
Festuca thurberi	g)	h)	i)

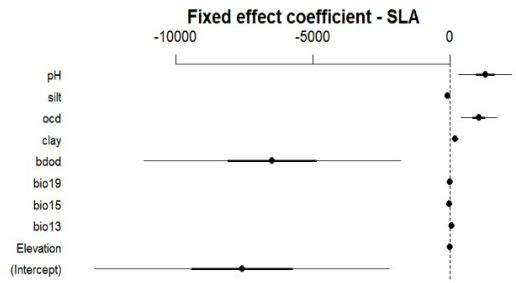
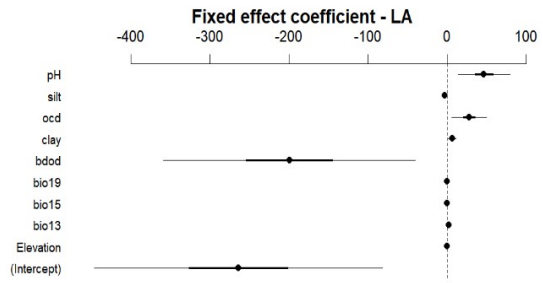
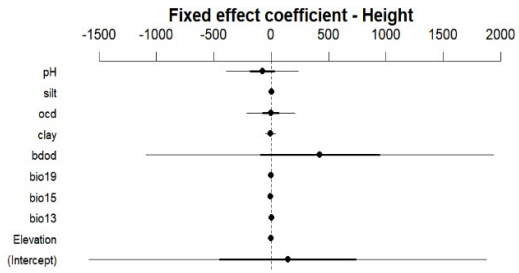
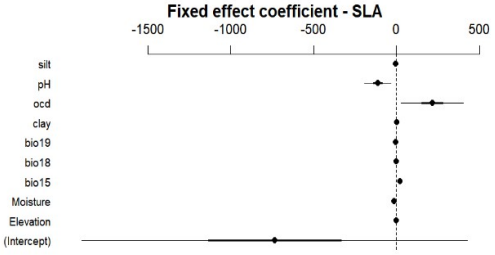
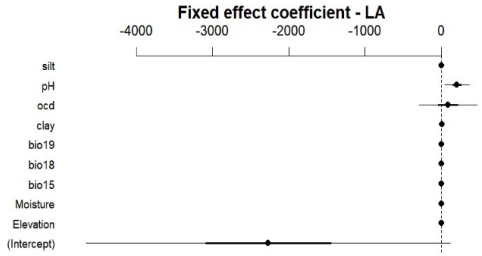
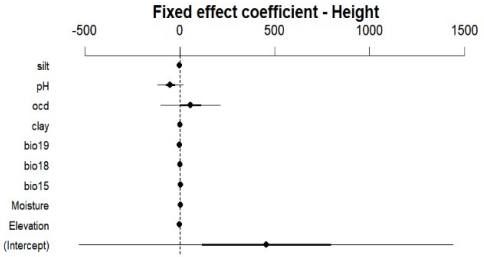
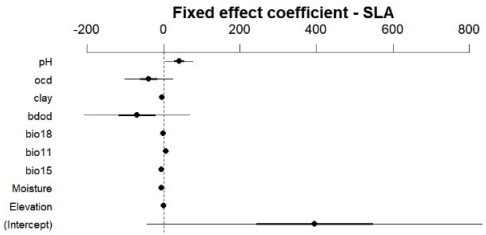
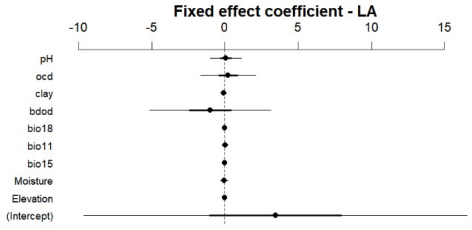
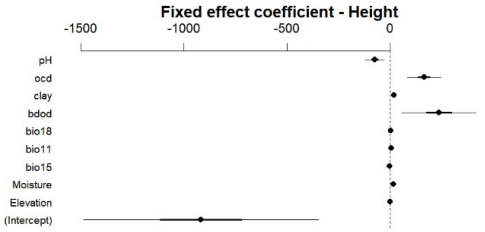
			
Frasera speciosa	j)	k)	l)
			
Linum lewisii	m)	n)	o)
			

Figure 6. Plots of the coefficients for the fixed effect variables used to fit GLMMs for the five studies species. Center dots represent mean values and bars represent standard deviations.

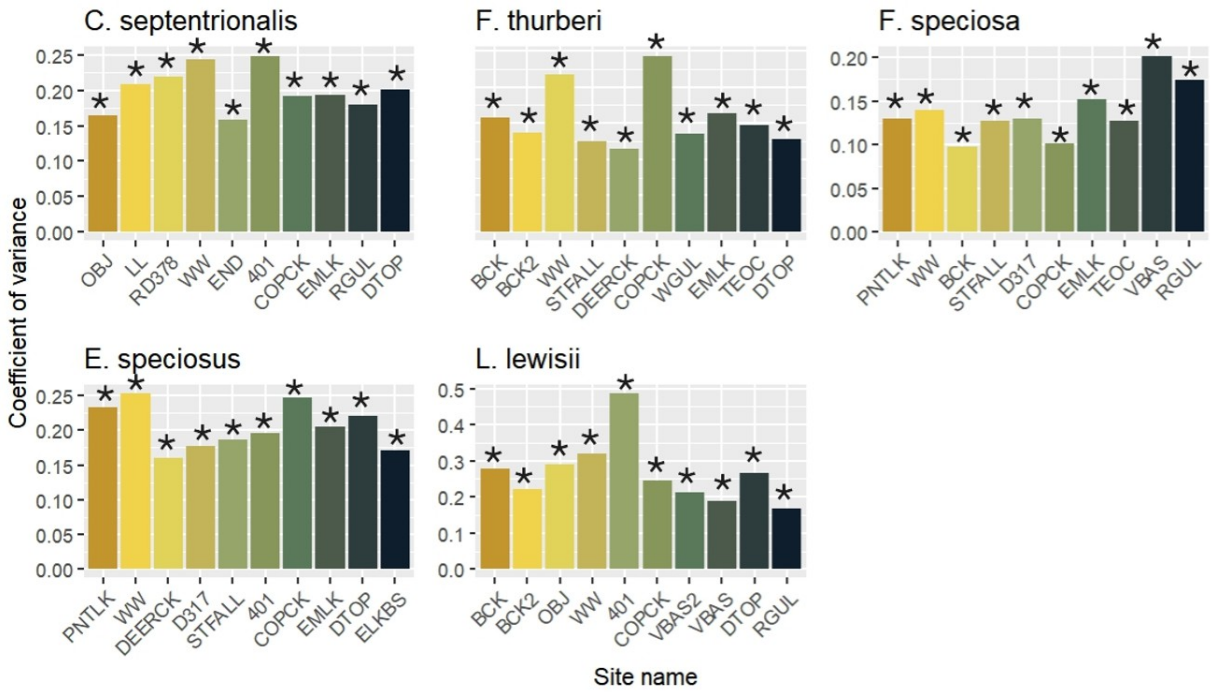


Figure 7. Plots of significant differences in trait variation within sites for each species. Within-site variation was calculated as the coefficient of variance for each site to standardize the scale between species. Every site for each species was significantly different from each other.

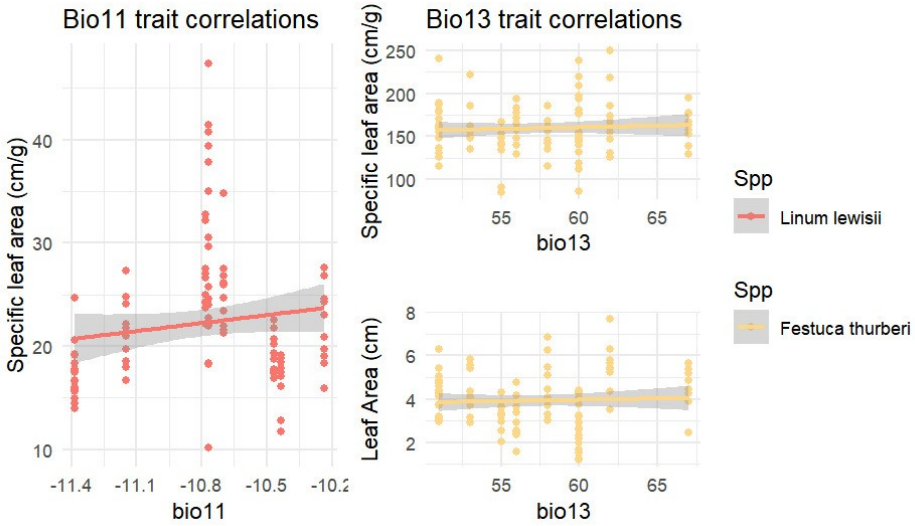


Figure 8. Correlations of specific traits with temperature of the coldest quarter (bio11) and precipitation of the wettest month (bio13). These variables were only included in the analysis for *F. thurberi* and *L. lewisii*.

Table 1. A summary of abiotic variables at each site. Elevation and moisture were collected at location. All other values were extracted from the ISRIC World Soil database (Poggio et al., 2021), at a depth of 5 cm.

Site code	Site name	Elevation (m)	Soil organic Carbon	Soil silt content	Organic carbon density	Soil bulk density	Soil clay content	Soil moisture	Soil pH

401	401 trail	2995.13	155.29	40.67	4.77	1.17	20.00	1.00	5.90
BCK	Brush creek	2739.67	137.43	47.33	4.87	1.17	20.67	1.00	6.10
BCK2	Brush creek 2	2731.00	142.30	47.00	5.00	1.20	20.00	1.00	6.10
COPCK	Copper creek	3064.00	146.30	38.00	4.52	1.10	19.00	2.00	5.76
D317	Down RD317	2856.00	134.90	42.00	4.90	1.20	22.00	4.00	6.00
DRCK	Deer creek	2859.50	114.60	43.00	4.80	1.20	23.00	1.00	6.00
DTOP	Double top mtn	3532.00	137.80	37.00	4.80	1.10	17.25	1.25	5.80
ELKBS	Elk basin	3426.00	147.20	37.00	4.50	1.10	18.00	1.00	5.50
EMLK	Emerald lake	3227.25	128.28	53.25	4.45	1.00	21.25	1.75	5.40
END	Enders cabin	2906.00	154.40	41.00	4.70	1.20	20.00	1.00	5.90
LL	Lower loop trail	2734.00	125.30	44.00	4.90	1.10	19.00	1.50	5.90
OBJ	Oh be joyful campground	2733.00	141.55	44.00	4.90	1.10	20.00	2.00	5.85
PNTLK	Peanut lake	2708.00	122.60	45.00	4.90	1.20	19.00	2.00	5.90
RD378	County rd 378	2739.00	133.80	45.00	4.90	1.10	20.00	4.00	5.90
RGUL	Rustlers gulch	3535.33	112.20	33.00	4.40	1.10	16.00	1.00	5.50
STFALL	Stupid falls	2849.33	114.60	43.00	4.80	1.20	23.00	1.00	6.00
TEOC	Teocalli mtn	3365.00	107.60	34.00	4.50	1.10	15.00	2.00	5.70
VBAS	Virginia basin	3481.00	130.70	37.00	4.30	1.10	17.00	3.00	5.70
VBAS2	Virginia basin 2	3341.00	156.50	39.00	4.60	1.10	19.00	1.00	5.80
WGUL	Washington gulch	3052.00	159.70	40.00	4.80	1.10	20.00	1.00	5.90
WW	Wild woods trail	2739.80	112.76	44.40	4.78	1.20	19.60	1.40	5.90

Table 2. A list of definitions and sources for our variables. All except soc, aspect, and slope were included in the model for at least one species. These three were tested for significance separately and none was found for any species

Variable abbreviation	Meaning	Source
Elevation	Meters above sea level	Garmin inreach
Moisture	Soil moisture	Goueven garden soil probe
Bio11	Mean temperature of coldest quarter	World_clim database
Bio12	Annual precipitation	World_clim database
Bio13	Precipitation of wettest month	World_clim database
Bio15	Precipitation seasonality (Coefficient of variance)	World_clim database
Bio18	Precipitation of warmest quarter	World_clim database
Bio19	Precipitation of coldest quarter	World_clim database
Bdod	Bulk density of fine earth fraction (kg dm^{-3})	ISRIC World Soil database
Cfvo	Volume fraction of coarse fragments (%)	ISRIC World Soil database
Clay	Mean soil clay content in fine earth (%)	ISRIC World Soil database
Ocd	Organic carbon density (kg m^{-3})	ISRIC World Soil database
pH	Soil pH	ISRIC World Soil database
Silt	Soil silt content in fine earth (%)	ISRIC World Soil database

soc	Soil organic carbon (g kg^{-1})	ISRIC World Soil database
Slope	Slope	Terrain tiles database
Aspect	Aspect	Terrain tiles database

Table 3. Summary of the 15 generalized linear mixed models fitted for the five species. Significant values are highlighted in red. The coefficient plots for fixed effects were used to decide the final significant effects. *See Table 2 for the full name of the abbreviated variables*

Species	Variables	Specific leaf area			Leaf area			Plant height		
		Estimate	t value	p	Estimate	t value	p	Estimate	t value	p
Castilleja septentrionalis	(Intercept)	2439.30	1.25	0.21	−315.46	−4.73	>0.01	−1266.35	−4.50	>0.01
	Elevation	−0.08	−0.81	0.42	0.02	5.98	>0.01	0.05	3.64	>0.01
	bio15	−49.85	−1.38	0.17	5.38	4.38	>0.01	33.05	6.38	>0.01
	bio18	−3.44	−1.30	0.20	0.31	3.45	>0.01	2.12	5.56	>0.01
	bio19	2.08	1.43	0.15	−0.14	−2.81	>0.01	−1.46	−6.99	>0.01
	Bulk density	−455.70	−1.14	0.26	46.58	3.42	>0.01	385.04	6.72	>0.01
	Soil clay	−51.85	−1.22	0.23	7.43	5.10	>0.01	32.61	5.31	>0.01
	Soil ocd	−384.82	−1.10	0.28	55.32	4.62	>0.01	307.92	6.10	>0.01
	Soil pH	291.01	1.05	0.29	−40.71	−4.32	>0.01	−283.79	−7.14	>0.01
	Soil silt	14.49	1.28	0.20	−1.95	−5.05	>0.01	−9.62	−5.91	>0.01
Erigeron speciosus	(Intercept)	−3934.14	−1.11	0.27	−97.70	−0.51	0.61	1915.89	1.83	0.07
	Elevation	0.63	1.19	0.24	0.02	0.68	0.50	−0.22	−1.41	0.16
	bio15	84.11	1.14	0.26	1.75	0.43	0.67	−34.79	−1.59	0.11
	bio18	12.37	1.12	0.26	0.29	0.48	0.64	−5.49	−1.69	0.09
	bio12	−6.25	−1.14	0.26	−0.15	−0.51	0.61	2.47	1.52	0.13
	Bulk density	2159.93	1.15	0.25	70.81	0.69	0.49	−865.66	−1.56	0.12
	Soil coarse fragments	−25.08	−1.23	0.22	−0.78	−0.70	0.49	8.18	1.35	0.18
	Soil clay	−7.78	−0.73	0.47	−0.56	−0.97	0.33	5.09	1.61	0.11
	Soil ocd	55.39	0.82	0.42	−2.58	−0.70	0.49	−71.12	−3.54	>0.01
	Soil silt	1.80	0.66	0.51	0.17	1.17	0.24	−1.51	−1.86	0.06
Festuca thurberi	(Intercept)	-7584.15	-2.77	0.01	−263.76	−2.84	0.01	144.25	0.16	0.87
	Elevation	-1.00	-2.89	>0.01	−0.03	−2.43	0.02	0.00	0.02	0.98
	bio13	72.76	2.90	>0.01	2.22	2.61	0.01	3.36	0.41	0.68
	bio15	-12.97	-2.39	0.02	0.19	1.03	0.31	−6.35	−3.63	>0.01
	bio19	8.50	1.95	0.05	0.26	1.77	0.08	−1.89	−1.34	0.18
	Bulk density	-6484.92	-2.71	0.01	−199.26	−2.45	0.02	424.78	0.55	0.58
	Soil clay	195.24	2.86	0.01	6.32	2.73	0.01	−5.41	−0.25	0.81
	Soil ocd	1061.36	3.18	>0.01	27.92	2.47	0.02	−2.91	−0.03	0.98
	Soil silt	-84.38	-2.78	0.01	−2.86	−2.78	0.01	4.55	0.47	0.64
	Soil pH	1295.97	2.61	0.01	46.62	2.77	0.01	−77.43	−0.48	0.63
Frasera speciosa	(Intercept)	−733.90	−1.23	0.22	−2269.14	−1.86	0.07	455.36	0.91	0.37
	Elevation	0.33	3.34	>0.01	−0.09	−0.42	0.67	−0.11	−1.28	0.20

	Soil moisture	−13.26	−3.16	>0.01	1.46	0.17	0.87	3.33	0.94	0.35
	bio15	21.80	2.89	>0.01	2.28	0.15	0.88	4.09	0.64	0.52
	bio18	−1.83	−2.80	0.01	3.47	2.58	0.01	0.68	1.23	0.22
	bio19	−3.05	−2.38	0.02	0.74	0.28	0.78	−0.47	−0.43	0.67
	Soil clay	2.27	0.55	0.59	7.28	0.86	0.39	2.05	0.59	0.56
	Soil ocd	216.81	2.27	0.03	89.46	0.46	0.65	56.70	0.70	0.48
	Soil pH	−112.40	−2.78	0.01	207.15	2.50	0.01	−50.49	−1.48	0.14
	Soil silt	−4.75	−3.40	>0.01	5.08	1.77	0.08	−2.50	−2.12	0.04
Linum lewisii	(Intercept)	395.17	1.76	0.08	3.81	0.68	0.50	−917.87	−3.17	0.00
	Elevation	0.00	−0.27	0.79	0.00	−0.76	0.45	−0.05	−4.17	0.00
	Soil moisture	−4.71	−1.05	0.30	−0.06	−0.50	0.62	15.04	2.58	0.01
	bio15	−5.89	−3.80	>0.01	−0.02	−0.26	0.80	−4.68	−2.33	0.02
	bio11	6.91	2.07	0.04	0.02	0.20	0.84	4.56	1.05	0.29
	bio18	−0.54	−1.26	0.21	0.00	−0.03	0.98	2.28	4.09	0.00
	Bulk density	−69.25	−0.98	0.33	−1.10	−0.80	0.43	234.75	2.56	0.01
	Soil clay	−4.10	−1.23	0.22	−0.09	−0.64	0.52	16.02	3.72	0.00
	Soil ocd	−38.57	−1.20	0.23	0.18	0.42	0.68	162.94	3.93	0.00
	Soil pH	40.66	2.26	0.03	0.09	0.19	0.85	−76.29	−3.28	0.00

Table 4. Summary of p values and AIC values produced by the 15 ANOVA-like tables for random-effects: Single term deletions were run on each of the species and trait values. The random effect of site was not significant in all species. AIC values for models run with site as a random effect were slightly lower in all cases.

		SLA		**LA**		**H**	
Species	**Variable**	**AIC**	**Pr(◦ Chisq)**	**AIC**	**Pr(◦ Chisq)**	**AIC**	**Pr(◦ Chisq)**
Castilleja septentrionalis	<none>	920.53	NA	245.14	NA	1524.96	NA
	Site.name	918.53	1	243.14	0.99	1522.96	1
Erigeron speciosus	<none>	780.67	NA	198.73	NA	1535.76	NA
	Site.name	778.67	0.99	196.73	0.99	1533.76	0.99
Festuca thurberi	<none>	962.48	NA	285.66	NA	736.17	NA
	Site.name	960.48	1	283.66	0.999998	734.17	1
Frasera speciosa	<none>	846.04	NA	989.74	NA	2224.54	NA
	Site.name	844.04	1	987.74	1	2222.54	0.999999
Linum lewisii	<none>	600.5	NA	−102.05	NA	1831.18	NA
	Site.name	598.5	1	−104.05	1	1829.18	0.999999

Table S1. Pairwise differences between sites of *Castilleja septentrionalis*. Most site pairs were significantly different in plant height, but only select pairs showed significant differences in terms of leaf area and specific leaf area.

Castilleja septentrionalis	SLA				LA				Height			
Site pairs	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**
COPCK-401	−13.19	−45.93	19.55	0.95	−1.31	−2.43	−0.19	0.01	−4.98	−9.47	−0.49	0.02
DTOP-401	19.02	−13.72	51.76	0.68	−0.72	−1.84	0.39	0.53	−9.40	−13.89	−4.91	0.00
EMLK-401	18.85	−13.89	51.59	0.69	−1.05	−2.17	0.07	0.08	0.68	−3.81	5.17	1.00
END-401	7.72	−25.03	40.46	1.00	−1.96	−3.07	−0.84	0.00	−5.01	−9.50	−0.52	0.02
LL-401	4.58	−28.16	37.32	1.00	−0.36	−1.48	0.76	0.99	−0.14	−4.63	4.35	1.00
OBJ-401	12.00	−20.74	44.74	0.97	−0.27	−1.39	0.85	1.00	3.80	−0.69	8.29	0.18
RD378-401	9.86	−22.88	42.60	0.99	0.31	−0.80	1.43	1.00	−5.21	−9.70	−0.72	0.01
RGUL-401	17.19	−15.55	49.93	0.79	−0.30	−1.41	0.82	1.00	−5.21	−9.70	−0.72	0.01
WW-401	−6.28	−39.02	26.46	1.00	−0.79	−1.91	0.33	0.41	3.24	−1.25	7.73	0.39
DTOP-COPCK	32.21	−0.53	64.95	0.06	0.58	−0.53	1.70	0.80	−4.42	−8.91	0.07	0.06
EMLK-COPCK	32.05	−0.69	64.79	0.06	0.26	−0.86	1.37	1.00	5.66	1.17	10.15	0.00
END-COPCK	20.91	−11.83	53.65	0.55	−0.65	−1.77	0.47	0.68	−0.02	−4.51	4.47	1.00
LL-COPCK	17.77	−14.97	50.51	0.76	0.95	−0.17	2.07	0.17	4.84	0.35	9.33	0.02
OBJ-COPCK	25.19	−7.55	57.94	0.28	1.04	−0.08	2.15	0.09	8.79	4.30	13.28	0.00
RD378-COPCK	23.06	−9.68	55.80	0.41	1.62	0.50	2.74	0.00	−0.22	−4.71	4.27	1.00
RGUL-COPCK	30.38	−2.36	63.12	0.09	1.01	−0.11	2.13	0.11	−0.23	−4.72	4.26	1.00
WW-COPCK	6.91	−25.83	39.65	1.00	0.52	−0.60	1.64	0.89	8.22	3.73	12.71	0.00
EMLK-DTOP	−0.17	−32.91	32.57	1.00	−0.33	−1.44	0.79	0.99	10.08	5.59	14.57	0.00
END-DTOP	−11.31	−44.05	21.44	0.98	−1.23	−2.35	−0.11	0.02	4.40	−0.09	8.89	0.06
LL-DTOP	−14.44	−47.18	18.30	0.91	0.37	−0.75	1.48	0.99	9.26	4.77	13.75	0.00
OBJ-DTOP	−7.02	−39.76	25.72	1.00	0.45	−0.67	1.57	0.95	13.21	8.72	17.70	0.00
RD378-DTOP	−9.16	−41.90	23.58	1.00	1.04	−0.08	2.16	0.09	4.20	−0.29	8.69	0.09
RGUL-DTOP	−1.83	−34.57	30.91	1.00	0.43	−0.69	1.55	0.96	4.19	−0.30	8.68	0.09
WW-DTOP	−25.30	−58.05	7.44	0.28	−0.06	−1.18	1.05	1.00	12.64	8.15	17.13	0.00
END-EMLK	−11.14	−43.88	21.60	0.98	−0.91	−2.02	0.21	0.22	−5.68	−10.17	−1.19	0.00
LL-EMLK	−14.28	−47.02	18.47	0.92	0.69	−0.43	1.81	0.60	−0.82	−5.31	3.67	1.00

OBJ-EMLK	−6.85	−39.59	25.89	1.00	0.78	−0.34	1.90	0.42	3.13	−1.36	7.62	0.44
RD378-EMLK	−8.99	−41.73	23.75	1.00	1.37	0.25	2.48	0.01	−5.88	−10.37	−1.39	0.00
RGUL-EMLK	−1.66	−34.40	31.08	1.00	0.76	−0.36	1.87	0.47	−5.89	−10.38	−1.40	0.00
WW-EMLK	−25.14	−57.88	7.60	0.29	0.26	−0.86	1.38	1.00	2.56	−1.93	7.05	0.72
LL-END	−3.14	−35.88	29.60	1.00	1.60	0.48	2.71	0.00	4.86	0.37	9.35	0.02
OBJ-END	4.29	−28.45	37.03	1.00	1.68	0.57	2.80	0.00	8.81	4.32	13.30	0.00
RD378-END	2.15	−30.59	34.89	1.00	2.27	1.15	3.39	0.00	−0.20	−4.69	4.29	1.00
RGUL-END	9.47	−23.27	42.21	0.99	1.66	0.54	2.78	0.00	−0.20	−4.69	4.29	1.00
WW-END	−14.00	−46.74	18.74	0.93	1.17	0.05	2.29	0.03	8.24	3.75	12.73	0.00
OBJ-LL	7.42	−25.32	40.17	1.00	0.09	−1.03	1.21	1.00	3.95	−0.54	8.44	0.14
RD378-LL	5.29	−27.45	38.03	1.00	0.67	−0.44	1.79	0.63	−5.06	−9.55	−0.57	0.01
RGUL-LL	12.61	−20.13	45.35	0.96	0.06	−1.05	1.18	1.00	−5.07	−9.56	−0.58	0.01
WW-LL	−10.86	−43.60	21.88	0.99	−0.43	−1.55	0.69	0.96	3.38	−1.11	7.87	0.33
RD378-OBJ	−2.14	−34.88	30.60	1.00	0.59	−0.53	1.70	0.79	−9.01	−13.50	−4.52	0.00
RGUL-OBJ	5.19	−27.55	37.93	1.00	−0.02	−1.14	1.09	1.00	−9.02	−13.51	−4.53	0.00
WW-OBJ	−18.29	−51.03	14.46	0.73	−0.52	−1.64	0.60	0.89	−0.57	−5.06	3.92	1.00
RGUL-RD378	7.33	−25.42	40.07	1.00	−0.61	−1.73	0.51	0.75	0.00	−4.49	4.49	1.00
WW-RD378	−16.15	−48.89	16.59	0.84	−1.10	−2.22	0.02	0.06	8.44	3.95	12.93	0.00
WW-RGUL	−23.47	−56.21	9.27	0.38	−0.49	−1.61	0.62	0.91	8.45	3.96	12.94	0.00

Table S2. Pairwise differences between sites of *Erigeron speciosus* Most site pairs were significantly different in plant height, but only select pairs showed significant differences in terms of leaf area and specific leaf area.

Erigeron speciosus	**SLA**				**LA**				**Height**			
Site pairs	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**
COPCK-401	−3.21	−19.48	13.06	1.00	0.74	−0.14	1.63	0.18	−0.65	−5.24	3.94	1.00
D317-401	8.95	−7.32	25.22	0.74	1.56	0.68	2.45	0.00	3.32	−1.27	7.91	0.39
DEERCK-401	10.20	−6.07	26.47	0.58	1.61	0.73	2.50	0.00	8.27	3.68	12.86	0.00
DTOP-401	−0.31	−16.58	15.96	1.00	1.20	0.31	2.09	0.00	−5.78	−10.37	−1.19	0.00
ELKBS-401	−9.37	−25.64	6.90	0.69	1.13	0.24	2.01	0.00	−4.46	−9.05	0.13	0.06
EMLK-401	−5.72	−21.99	10.55	0.98	1.63	0.74	2.51	0.00	8.01	3.42	12.60	0.00

PNTLK-401	−8.63	−24.90	7.64	0.78	0.71	−0.18	1.60	0.23	−7.67	−12.26	−3.08	0.00
STFALL-401	15.85	−0.42	32.12	0.06	1.79	0.90	2.68	0.00	6.28	1.70	10.87	0.00
WW-401	0.51	−15.76	16.78	1.00	1.78	0.90	2.67	0.00	4.11	−0.48	8.70	0.12
D317-COPCK	12.16	−4.11	28.43	0.32	0.82	−0.07	1.71	0.10	3.97	−0.62	8.56	0.16
DEERCK-COPCK	13.41	−2.86	29.68	0.20	0.87	−0.02	1.76	0.06	8.92	4.33	13.51	0.00
DTOP-COPCK	2.90	−13.37	19.17	1.00	0.45	−0.43	1.34	0.81	−5.13	−9.72	−0.54	0.02
ELKBS-COPCK	−6.16	−22.44	10.11	0.97	0.38	−0.51	1.27	0.93	−3.81	−8.40	0.78	0.20
EMLK-COPCK	−2.52	−18.79	13.75	1.00	0.88	−0.01	1.77	0.05	8.66	4.07	13.25	0.00
PNTLK-COPCK	−5.42	−21.69	10.85	0.99	−0.03	−0.92	0.85	1.00	−7.02	−11.61	−2.43	0.00
STFALL-COPCK	19.06	2.79	35.33	0.01	1.05	0.16	1.93	0.01	6.93	2.34	11.52	0.00
WW-COPCK	3.72	−12.55	19.99	1.00	1.04	0.15	1.93	0.01	4.76	0.17	9.35	0.03
DEERCK-D317	1.25	−15.02	17.52	1.00	0.05	−0.84	0.94	1.00	4.95	0.36	9.54	0.02
DTOP-D317	−9.26	−25.53	7.01	0.70	−0.37	−1.25	0.52	0.94	−9.10	−13.69	−4.51	0.00
ELKBS-D317	−18.32	−34.59	−2.05	0.01	−0.44	−1.32	0.45	0.84	−7.78	−12.37	−3.19	0.00
EMLK-D317	−14.68	−30.95	1.59	0.11	0.06	−0.83	0.95	1.00	4.69	0.10	9.28	0.04
PNTLK-D317	−17.58	−33.85	−1.31	0.02	−0.85	−1.74	0.03	0.07	−10.99	−15.58	−6.40	0.00
STFALL-D317	6.90	−9.37	23.17	0.93	0.23	−0.66	1.11	1.00	2.96	−1.62	7.55	0.56
WW-D317	−8.44	−24.71	7.83	0.80	0.22	−0.67	1.11	1.00	0.79	−3.80	5.38	1.00
DTOP-DEERCK	−10.51	−26.78	5.76	0.54	−0.42	−1.30	0.47	0.88	−14.05	−18.64	−9.46	0.00
ELKBS-DEERCK	−19.57	−35.84	−3.30	0.01	−0.49	−1.38	0.40	0.74	−12.73	−17.32	−8.14	0.00
EMLK-DEERCK	−15.92	−32.19	0.35	0.06	0.01	−0.88	0.90	1.00	−0.26	−4.85	4.33	1.00
PNTLK-DEERCK	−18.83	−35.10	−2.56	0.01	−0.90	−1.79	−0.02	0.04	−15.94	−20.53	−11.35	0.00
STFALL-DEERCK	5.65	−10.62	21.92	0.98	0.18	−0.71	1.06	1.00	−1.99	−6.58	2.60	0.93
WW-DEERCK	−9.69	−25.96	6.58	0.65	0.17	−0.72	1.06	1.00	−4.16	−8.75	0.43	0.11
ELKBS-DTOP	−9.06	−25.33	7.21	0.73	−0.07	−0.96	0.81	1.00	1.32	−3.27	5.91	1.00
EMLK-DTOP	−5.42	−21.69	10.85	0.99	0.43	−0.46	1.31	0.86	13.79	9.20	18.38	0.00
PNTLK-DTOP	−8.32	−24.59	7.95	0.81	−0.49	−1.38	0.40	0.74	−1.89	−6.48	2.70	0.95
STFALL-DTOP	16.16	−0.11	32.43	0.05	0.59	−0.30	1.48	0.49	12.06	7.48	16.65	0.00
WW-DTOP	0.82	−15.45	17.09	1.00	0.58	−0.30	1.47	0.50	9.89	5.30	14.48	0.00
EMLK-ELKBS	3.65	−12.62	19.92	1.00	0.50	−0.39	1.39	0.72	12.47	7.88	17.06	0.00
PNTLK-ELKBS	0.74	−15.53	17.01	1.00	−0.42	−1.30	0.47	0.88	−3.21	−7.80	1.38	0.44
STFALL-ELKBS	25.23	8.96	41.50	0.00	0.66	−0.22	1.55	0.32	10.74	6.16	15.33	0.00

WW-ELKBS	9.88	−6.39	26.15	0.62	0.66	−0.23	1.54	0.33	8.57	3.98	13.16	0.00
PNTLK-EMLK	−2.90	−19.17	13.37	1.00	−0.92	−1.80	−0.03	0.04	−15.68	−20.27	−11.09	0.00
STFALL-EMLK	21.58	5.31	37.85	0.00	0.16	−0.72	1.05	1.00	−1.73	−6.32	2.86	0.97
WW-EMLK	6.23	−10.04	22.50	0.96	0.16	−0.73	1.05	1.00	−3.90	−8.49	0.69	0.17
STFALL-PNTLK	24.48	8.21	40.75	0.00	1.08	0.19	1.97	0.01	13.95	9.36	18.54	0.00
WW-PNTLK	9.14	−7.13	25.41	0.72	1.07	0.19	1.96	0.01	11.78	7.19	16.37	0.00
WW-STFALL	−15.34	−31.61	0.93	0.08	−0.01	−0.89	0.88	1.00	−2.17	−6.76	2.42	0.89

Table S3. Pairwise differences between sites of *Festuca thurberi*. Several site pairs were significantly different in leaf area, but only select pairs showed significant differences in terms of plant height and specific leaf area.

Festuca thurberi	**SLA**				**LA**				**Height**			
Site pairs	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**
BCK2-BCK	25.79	−14.59	66.17	0.55	−0.30	−1.67	1.07	1.00	8.57	−4.45	21.59	0.51
COPCK-BCK	16.23	−24.15	56.61	0.95	1.30	−0.07	2.67	0.08	9.42	−3.60	22.44	0.37
DEERCK-BCK	6.65	−33.73	47.03	1.00	0.46	−0.91	1.83	0.98	8.71	−4.31	21.73	0.48
DTOP-BCK	34.72	−5.66	75.11	0.16	2.13	0.76	3.50	0.00	−8.53	−21.55	4.49	0.52
EMLK-BCK	34.44	−5.94	74.82	0.16	−0.81	−2.18	0.56	0.65	10.12	−2.90	23.14	0.27
STFALL-BCK	40.77	0.39	81.15	0.05	1.43	0.06	2.80	0.03	8.62	−4.40	21.64	0.50
TEOC-BCK	24.73	−15.65	65.11	0.61	1.06	−0.31	2.43	0.28	0.67	−12.35	13.69	1.00
WGUL-BCK	29.55	−10.84	69.93	0.35	0.97	−0.40	2.34	0.40	7.07	−5.95	20.09	0.76
WW-BCK	14.58	−25.80	54.96	0.97	−0.18	−1.55	1.19	1.00	−5.28	−18.30	7.74	0.95
COPCK-BCK2	−9.56	−49.94	30.82	1.00	1.60	0.23	2.97	0.01	0.85	−12.17	13.87	1.00
DEERCK-BCK2	−19.14	−59.53	21.24	0.87	0.76	−0.61	2.13	0.73	0.14	−12.88	13.16	1.00
DTOP-BCK2	8.93	−31.45	49.31	1.00	2.43	1.06	3.80	0.00	−17.10	−30.12	−4.08	0.00
EMLK-BCK2	8.65	−31.74	49.03	1.00	−0.51	−1.88	0.86	0.97	1.55	−11.47	14.57	1.00
STFALL-BCK2	14.98	−25.40	55.36	0.97	1.73	0.36	3.10	0.00	0.05	−12.97	13.07	1.00
TEOC-BCK2	−1.06	−41.44	39.32	1.00	1.36	−0.01	2.73	0.05	−7.90	−20.92	5.12	0.62
WGUL-BCK2	3.75	−36.63	44.14	1.00	1.27	−0.10	2.64	0.09	−1.50	−14.52	11.52	1.00
WW-BCK2	−11.21	−51.59	29.17	1.00	0.12	−1.25	1.49	1.00	−13.85	−26.87	−0.83	0.03
DEERCK-COPCK	−9.59	−49.97	30.79	1.00	−0.84	−2.21	0.53	0.61	−0.71	−13.73	12.31	1.00
DTOP-COPCK	18.49	−21.89	58.87	0.89	0.83	−0.54	2.20	0.62	−17.95	−30.97	−4.93	0.00

EMLK-COPCK	18.20	−22.18	58.58	0.90	−2.11	−3.48	−0.74	0.00	0.70	−12.32	13.72	1.00
STFALL-COPCK	24.53	−15.85	64.92	0.62	0.13	−1.24	1.50	1.00	−0.80	−13.82	12.22	1.00
TEOC-COPCK	8.50	−31.88	48.88	1.00	−0.24	−1.60	1.13	1.00	−8.75	−21.77	4.27	0.48
WGUL-COPCK	13.31	−27.07	53.69	0.99	−0.32	−1.69	1.05	1.00	−2.35	−15.37	10.67	1.00
WW-COPCK	−1.65	−42.03	38.73	1.00	−1.47	−2.84	−0.11	0.02	−14.70	−27.72	−1.68	0.01
DTOP-DEERCK	28.08	−12.30	68.46	0.43	1.67	0.30	3.04	0.01	−17.24	−30.26	−4.22	0.00
EMLK-DEERCK	27.79	−12.59	68.17	0.44	−1.27	−2.64	0.10	0.09	1.41	−11.61	14.43	1.00
STFALL-DEERCK	34.12	−6.26	74.50	0.17	0.97	−0.40	2.34	0.40	−0.09	−13.11	12.93	1.00
TEOC-DEERCK	18.09	−22.29	58.47	0.91	0.60	−0.77	1.97	0.92	−8.04	−21.06	4.98	0.60
WGUL-DEERCK	22.90	−17.48	63.28	0.71	0.51	−0.86	1.88	0.97	−1.64	−14.66	11.38	1.00
WW-DEERCK	7.93	−32.45	48.32	1.00	−0.64	−2.01	0.73	0.88	−13.99	−27.01	−0.97	0.03
EMLK-DTOP	−0.29	−40.67	40.09	1.00	−2.94	−4.31	−1.57	0.00	18.65	5.63	31.67	0.00
STFALL-DTOP	6.04	−34.34	46.42	1.00	−0.70	−2.07	0.67	0.81	17.15	4.13	30.17	0.00
TEOC-DTOP	−9.99	−50.37	30.39	1.00	−1.07	−2.44	0.30	0.26	9.20	−3.82	22.22	0.40
WGUL-DTOP	−5.18	−45.56	35.20	1.00	−1.16	−2.53	0.21	0.17	15.60	2.58	28.62	0.01
WW-DTOP	−20.14	−60.52	20.24	0.84	−2.31	−3.68	−0.94	0.00	3.25	−9.77	16.27	1.00
STFALL-EMLK	6.33	−34.05	46.71	1.00	2.24	0.87	3.61	0.00	−1.50	−14.52	11.52	1.00
TEOC-EMLK	−9.70	−50.08	30.68	1.00	1.87	0.50	3.24	0.00	−9.45	−22.47	3.57	0.37
WGUL-EMLK	−4.89	−45.27	35.49	1.00	1.79	0.42	3.16	0.00	−3.05	−16.07	9.97	1.00
WW-EMLK	−19.86	−60.24	20.53	0.85	0.63	−0.73	2.00	0.89	−15.40	−28.42	−2.38	0.01
TEOC-STFALL	−16.03	−56.42	24.35	0.95	−0.37	−1.74	1.00	1.00	−7.95	−20.97	5.07	0.61
WGUL-STFALL	−11.22	−51.60	29.16	1.00	−0.46	−1.83	0.91	0.99	−1.55	−14.57	11.47	1.00
WW-STFALL	−26.19	−66.57	14.19	0.53	−1.61	−2.98	−0.24	0.01	−13.90	−26.92	−0.88	0.03
WGUL-TEOC	4.81	−35.57	45.19	1.00	−0.09	−1.46	1.28	1.00	6.40	−6.62	19.42	0.85
WW-TEOC	−10.15	−50.53	30.23	1.00	−1.24	−2.61	0.13	0.11	−5.95	−18.97	7.07	0.90
WW-WGUL	−14.96	−55.35	25.42	0.97	−1.15	−2.52	0.22	0.18	−12.35	−25.37	0.67	0.08

Table S4. Pairwise differences between sites of *Frasera speciosa*. Most site pairs were significantly different in plant height, and several pairs showed significant differences in terms of leaf area and specific leaf area.

Frasera speciosa	**SLA**	**LA**	**Height**

Site pairs	diff	lwr	upr	p.adj	diff	lwr	upr	p.adj	diff	lwr	upr	p.adj
COPCK-BCK	6.35	−16.21	28.91	1	−2.24	−48.52	44.04	1	−5.12	−23.31	13.07	1
D317-BCK	10.3	−12.25	32.86	0.9	16.05	−30.23	62.33	0.98	5.92	−12.27	24.11	0.99
EMLK-BCK	22.12	−0.44	44.68	0.06	−23.93	−70.21	22.34	0.8	−36.98	−55.17	−18.79	0
PNTLK-BCK	−9.5	−32.06	13.06	0.93	21.66	−24.62	67.94	0.88	8.84	−9.35	27.03	0.87
RGUL-BCK	29.98	7.42	52.54	0	−47.7	−93.98	−1.42	0.04	−43.06	−61.25	−24.87	0
STFALL-BCK	26.71	4.15	49.27	0.01	17.54	−28.74	63.81	0.97	−9.5	−27.69	8.69	0.81
TEOC-BCK	−8.48	−31.04	14.08	0.97	2.05	−44.23	48.33	1	−28.64	−46.83	−10.45	0
VBAS-BCK	17.55	−5.01	40.11	0.27	−30.81	−77.09	15.47	0.49	−51.66	−69.85	−33.47	0
WW-BCK	12.32	−10.24	34.88	0.75	17.98	−28.3	64.26	0.96	2.74	−15.45	20.93	1
D317-COPCK	3.95	−18.61	26.51	1	18.29	−27.99	64.57	0.96	11.04	−7.15	29.23	0.64
EMLK-COPCK	15.76	−6.79	38.32	0.42	−21.69	−67.97	24.59	0.88	−31.86	−50.05	−13.67	0
PNTLK-COPCK	−15.85	−38.41	6.71	0.41	23.9	−22.38	70.18	0.81	13.96	−4.23	32.15	0.3
RGUL-COPCK	23.62	1.06	46.18	0.03	−45.46	−91.74	0.82	0.06	−37.94	−56.13	−19.75	0
STFALL-COPCK	20.36	−2.2	42.92	0.11	19.78	−26.5	66.06	0.93	−4.38	−22.57	13.81	1
TEOC-COPCK	−14.83	−37.39	7.73	0.51	4.29	−41.99	50.57	1	−23.52	−41.71	−5.33	0
VBAS-COPCK	11.2	−11.36	33.76	0.84	−28.57	−74.85	17.71	0.6	−46.54	−64.73	−28.35	0
WW-COPCK	5.96	−16.6	28.52	1	20.22	−26.06	66.5	0.92	7.86	−10.33	26.05	0.93
EMLK-D317	11.81	−10.75	34.37	0.79	−39.99	−86.26	6.29	0.15	−42.9	−61.09	−24.71	0
PNTLK-D317	−19.8	−42.36	2.76	0.14	5.61	−40.67	51.89	1	2.92	−15.27	21.11	1
RGUL-D317	19.67	−2.89	42.23	0.14	−63.75	−110.03	−17.47	0	−48.98	−67.17	−30.79	0
STFALL-D317	16.41	−6.15	38.97	0.36	1.48	−44.79	47.76	1	−15.42	−33.61	2.77	0.18
TEOC-D317	−18.78	−41.34	3.78	0.19	−14	−60.28	32.28	0.99	−34.56	−52.75	−16.37	0
VBAS-D317	7.25	−15.31	29.8	0.99	−46.87	−93.14	−0.59	0.04	−57.58	−75.77	−39.39	0
WW-D317	2.01	−20.55	24.57	1	1.93	−44.35	48.21	1	−3.18	−21.37	15.01	1
PNTLK-EMLK	−31.62	−54.18	−9.06	0	45.59	−0.68	91.87	0.06	45.82	27.63	64.01	0
RGUL-EMLK	7.86	−14.7	30.42	0.98	−23.76	−70.04	22.51	0.81	−6.08	−24.27	12.11	0.99
STFALL-EMLK	4.6	−17.96	27.15	1	41.47	−4.81	87.75	0.12	27.48	9.29	45.67	0
TEOC-EMLK	−30.6	−53.16	−8.04	0	25.98	−20.3	72.26	0.72	8.34	−9.85	26.53	0.9
VBAS-EMLK	−4.57	−27.13	17.99	1	−6.88	−53.16	39.4	1	−14.68	−32.87	3.51	0.23
WW-EMLK	−9.8	−32.36	12.76	0.92	41.92	−4.36	88.19	0.11	39.72	21.53	57.91	0
RGUL-PNTLK	39.47	16.91	62.03	0	−69.36	−115.64	−23.08	0	−51.9	−70.09	−33.71	0

STFALL-PNTLK	36.21	13.65	58.77	0	−4.12	−50.4	42.15	1	−18.34	−36.53	−0.15	0.05
TEOC-PNTLK	1.02	−21.54	23.58	1	−19.61	−65.89	26.67	0.93	−37.48	−55.67	−19.29	0
VBAS-PNTLK	27.05	4.49	49.61	0.01	−52.47	−98.75	−6.19	0.01	−60.5	−78.69	−42.31	0
WW-PNTLK	21.81	−0.75	44.37	0.07	−3.68	−49.96	42.6	1	−6.1	−24.29	12.09	0.99
STFALL-RGUL	−3.26	−25.82	19.3	1	65.23	18.96	111.51	0	33.56	15.37	51.75	0
TEOC-RGUL	−38.45	−61.01	−15.9	0	49.75	3.47	96.03	0.02	14.42	−3.77	32.61	0.26
VBAS-RGUL	−12.43	−34.99	10.13	0.74	16.88	−29.39	63.16	0.97	−8.6	−26.79	9.59	0.89
WW-RGUL	−17.66	−40.22	4.9	0.26	65.68	19.4	111.96	0	45.8	27.61	63.99	0
TEOC-STFALL	−35.19	−57.75	−12.63	0	−15.49	−61.77	30.79	0.98	−19.14	−37.33	−0.95	0.03
VBAS-STFALL	−9.16	−31.72	13.4	0.95	−48.35	−94.63	−2.07	0.03	−42.16	−60.35	−23.97	0
WW-STFALL	−14.4	−36.96	8.16	0.55	0.45	−45.83	46.72	1	12.24	−5.95	30.43	0.49
VBAS-TEOC	26.03	3.47	48.59	0.01	−32.86	−79.14	13.42	0.4	−23.02	−41.21	−4.83	0
WW-TEOC	20.8	−1.76	43.35	0.1	15.93	−30.35	62.21	0.98	31.38	13.19	49.57	0
WW-VBAS	−5.23	−27.79	17.33	1	48.8	2.52	95.07	0.03	54.4	36.21	72.59	0

Table S5. Pairwise differences between sites of *Linum lewisii*. Several site pairs were significantly different in plant height and specific leaf area, but only one site pair showed significant differences in terms of leaf area.

Linum lewisii	**SLA**				**LA**				**Height**			
Site pairs	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**	**diff**	**lwr**	**upr**	**p.adj**
BCK-401	−14.63	−21.24	−8.02	0.00	−0.01	−0.21	0.18	1.00	7.63	−0.45	15.72	0.08
BCK2-401	−16.56	−23.17	−9.95	0.00	0.09	−0.11	0.29	0.89	14.33	6.25	22.42	0.00
COPCK-401	−6.50	−13.11	0.11	0.06	0.07	−0.13	0.27	0.97	4.11	−3.97	12.20	0.83
DTOP-401	−11.00	−17.61	−4.39	0.00	0.08	−0.12	0.27	0.96	−3.89	−11.97	4.20	0.88
OBJ-401	−13.73	−20.34	−7.12	0.00	0.12	−0.08	0.31	0.67	10.21	2.13	18.30	0.00
RGUL-401	−11.65	−18.26	−5.04	0.00	0.18	−0.01	0.38	0.09	−0.14	−8.22	7.95	1.00
VBAS-401	−10.21	−16.81	−3.60	0.00	−0.01	−0.21	0.18	1.00	−12.94	−21.03	−4.86	0.00
VBAS2-401	−7.63	−14.24	−1.02	0.01	0.04	−0.16	0.24	1.00	8.87	0.79	16.96	0.02
WW-401	−16.25	−22.86	−9.64	0.00	−0.04	−0.24	0.16	1.00	1.10	−6.98	9.19	1.00
BCK2-BCK	−1.93	−8.54	4.68	0.99	0.11	−0.09	0.30	0.77	6.70	−1.46	14.86	0.21
COPCK-BCK	8.14	1.53	14.74	0.00	0.09	−0.11	0.28	0.92	−3.52	−11.68	4.64	0.93

DTOP-BCK	3.63	−2.98	10.24	0.75	0.09	−0.11	0.29	0.90	−11.52	−19.68	−3.36	0.00
OBJ-BCK	0.90	−5.71	7.51	1.00	0.13	−0.07	0.33	0.51	2.58	−5.58	10.74	0.99
RGUL-BCK	2.98	−3.63	9.59	0.90	0.20	0.00	0.39	0.05	−7.77	−15.94	0.39	0.08
VBAS-BCK	4.43	−2.18	11.04	0.48	0.00	−0.20	0.20	1.00	−20.58	−28.74	−12.41	0.00
VBAS2-BCK	7.00	0.39	13.61	0.03	0.06	−0.14	0.25	1.00	1.24	−6.92	9.40	1.00
WW-BCK	−1.62	−8.23	4.99	1.00	−0.03	−0.22	0.17	1.00	−6.53	−14.70	1.63	0.25
COPCK-BCK2	10.06	3.45	16.67	0.00	−0.02	−0.22	0.18	1.00	−10.22	−18.38	−2.06	0.00
DTOP-BCK2	5.56	−1.05	12.17	0.18	−0.02	−0.21	0.18	1.00	−18.22	−26.38	−10.06	0.00
OBJ-BCK2	2.83	−3.78	9.44	0.93	0.02	−0.17	0.22	1.00	−4.12	−12.28	4.04	0.84
RGUL-BCK2	4.91	−1.70	11.52	0.33	0.09	−0.11	0.29	0.89	−14.47	−22.64	−6.31	0.00
VBAS-BCK2	6.35	−0.25	12.96	0.07	−0.11	−0.30	0.09	0.76	−27.28	−35.44	−19.11	0.00
VBAS2-BCK2	8.93	2.32	15.54	0.00	−0.05	−0.25	0.15	1.00	−5.46	−13.62	2.70	0.50
WW-BCK2	0.31	−6.30	6.92	1.00	−0.13	−0.33	0.06	0.46	−13.23	−21.40	−5.07	0.00
DTOP-COPCK	−4.51	−11.12	2.10	0.46	0.00	−0.19	0.20	1.00	−8.00	−16.16	0.16	0.06
OBJ-COPCK	−7.23	−13.84	−0.62	0.02	0.04	−0.15	0.24	1.00	6.10	−2.06	14.26	0.34
RGUL-COPCK	−5.16	−11.77	1.45	0.27	0.11	−0.09	0.31	0.72	−4.25	−12.42	3.91	0.81
VBAS-COPCK	−3.71	−10.32	2.90	0.72	−0.09	−0.28	0.11	0.92	−17.06	−25.22	−8.89	0.00
VBAS2-COPCK	−1.13	−7.74	5.48	1.00	−0.03	−0.23	0.17	1.00	4.76	−3.40	12.92	0.69
WW-COPCK	−9.75	−16.36	−3.15	0.00	−0.11	−0.31	0.08	0.69	−3.01	−11.18	5.15	0.98
OBJ-DTOP	−2.73	−9.33	3.88	0.94	0.04	−0.16	0.24	1.00	14.10	5.94	22.26	0.00
RGUL-DTOP	−0.65	−7.26	5.96	1.00	0.11	−0.09	0.30	0.76	3.75	−4.42	11.91	0.90
VBAS-DTOP	0.80	−5.81	7.41	1.00	−0.09	−0.29	0.11	0.89	−9.06	−17.22	−0.89	0.02
VBAS2-DTOP	3.37	−3.23	9.98	0.82	−0.03	−0.23	0.16	1.00	12.76	4.60	20.92	0.00
WW-DTOP	−5.25	−11.86	1.36	0.24	−0.12	−0.31	0.08	0.64	4.99	−3.18	13.15	0.63
RGUL-OBJ	2.08	−4.53	8.69	0.99	0.07	−0.13	0.26	0.98	−10.35	−18.52	−2.19	0.00
VBAS-OBJ	3.52	−3.09	10.13	0.78	−0.13	−0.33	0.07	0.51	−23.16	−31.32	−14.99	0.00
VBAS2-OBJ	6.10	−0.51	12.71	0.10	−0.07	−0.27	0.12	0.97	−1.34	−9.50	6.82	1.00
WW-OBJ	−2.52	−9.13	4.09	0.96	−0.16	−0.35	0.04	0.24	−9.11	−17.28	−0.95	0.02
VBAS-RGUL	1.45	−5.16	8.06	1.00	−0.20	−0.39	0.00	0.05	−12.80	−20.97	−4.64	0.00
VBAS2-RGUL	4.02	−2.58	10.63	0.62	−0.14	−0.34	0.06	0.38	9.01	0.85	17.18	0.02
WW-RGUL	−4.60	−11.21	2.01	0.43	−0.22	−0.42	−0.03	0.01	1.24	−6.92	9.40	1.00
VBAS2-VBAS	2.58	−4.03	9.19	0.96	0.06	−0.14	0.25	1.00	21.82	13.65	29.98	0.00

WW-VBAS	−6.04	−12.65	0.56	0.10	−0.03	−0.22	0.17	1.00	14.04	5.88	22.21	0.00
WW-VBAS2	−8.62	−15.23	−2.01	0.00	−0.08	−0.28	0.11	0.93	−7.77	−15.94	0.39	0.08

Table S6. Analysis of variance results looking at the variation in coefficient of variance for each trait between sites of each species. All sites were significantly different in terms of variance.

Trait	Species	df	F value	Pr(>F)
SLA	*C. septentrionalis*	9	4.99E+29	<2e-16
	E. speciosus	9	1.52E+30	<2e-16
	F. thurberi	9	2.53E+29	<2e-16
	F. speciosa	9	6.23E+29	<2e-16
	L. lewisii	9	4.39E+29	<2e-16
LA	*C. septentrionalis*	9	5.93E+29	<2e-16
	E. speciosus	9	3.03E+29	<2e-16
	F. thurberi	9	3.31E+29	<2e-16
	F. speciosa	9	8.79E+28	<2e-16
	L. lewisii	9	1.53E+30	<2e-16
Height	*C. septentrionalis*	9	6.19E+28	<2e-16
	E. speciosus	9	1.19E+30	<2e-16
	F. thurberi	9	1.01E+29	<2e-16
	F. speciosa	9	2.35E+29	<2e-16
	L. lewisii	9	1.66E+29	<2e-16

Table S7. AIC and p values for the random effects of site and species in our second set of generalized linear mixed models. These were run comparing the coefficient of variance at each site. Both site and species had significant explanatory power.

	Specific leaf area			Leaf area			Plant height		
Variable	AIC	Df	p	AIC	Df	p	AIC	Df	p
<none>	-5253.33	NA	NA	-4336.50	NA	NA	-5306.59	NA	NA
Site	-4061.18	1.00	0.00	-3785.26	1.00	0.00	-4650.31	1.00	0.00
Species	-4880.06	1.00	0.00	-4035.20	1.00	0.00	-4500.03	1.00	0.00