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Title: Investigating alpine plant community responses to simulated warming and dominant species removal at a low and high elevation in the Colorado Rocky Mountains

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Abstract: Global climate change leads to rising air temperatures and altered precipitation regimes, requiring many organisms to adapt or relocate in order to survive. Terrestrial ecosystems face shifts in diversity, productivity, and composition leading to alterations in ecosystem functioning that depend on the species in question. Elevational gradients can be used as proxies for long-term climate change (cooler at high elevations and warmer at lower elevations) and passive warming structures (open top chambers, OTCs) can simulate rising temperatures. Species loss is another consequence of climate change that has implications for ecosystem biodiversity and functioning. This study examined the impacts of dominant species removal, simulated warming, and their combination on alpine-plant community species composition, diversity, and productivity at a high and low elevation in the Colorado Rocky Mountains. Plot-level biomass responded significantly to all treatments at the low elevation site. The WC (warming control), WR (warming removal), and AR (ambient removal) treatments revealed a 47.7%, 20.1%, and 5.0% decrease in plot-level biomass, respectively, when compared to the AC treatment. At the high elevation site, only species removal had a significant effect on mean plot-level biomass, resulting in a 21% decrease when compared to the control treatment. While biodiversity was not significantly impacted by any of the treatments, different species showed significant increases and decreases to warming and species removal. These findings add to a larger body of knowledge surrounding plant community responses to warming and species composition shifts as well as the efficacy of climate ecology research.

Introduction: Some of the most vulnerable ecosystems on the planet are alpine regions that span environmental gradients leading to variance in abiotic variables that contribute to diversity and ecosystem function (Grabherr et al., 2000; Sundqvist et al., 2013). In fact, natural elevational gradients are frequently used as predictive models for how an ecosystem may react to anthropogenic climate change (Blois et al., 2013; Elmendorf et al., 2015; Sundqvist et al., 2013). In alpine systems, as elevation increases, temperatures tend to drop and snow melt occurs at a later date, creating a colder, wetter, and more ecologically stressful environment and thus impacting the strategies of species present at higher altitudes (Sundqvist et al., 2013). Depending on elevation, plant communities have adapted different biomass and root allocation strategies (Blume-Werry et al., 2018), and displayed decreases in total biomass with increasing altitude (Blume-Werry et al., 2018; Sundqvist et al., 2013). Researchers have also developed a theory that discusses the positive correlation between the frequency of facilitative plant interactions and the stress of increasing elevation (Callaway et al., 2002). Considering both plant interactions and plant physiology are influenced by the abiotic facets of elevation, plant community responses to warming and species removal should be examined at varying altitudes.

Global change is leading to rising air temperatures which have a myriad of impacts on

communities across the globe, including changes in phenological processes and species interactions (Cleland et al., 2006; Suonan et al., 2019; Walther, 2010), and an upward elevational shift of warm acclimated species in montane and alpine communities (Cannone et al., 2007; Elmendorf et al., 2015; Gottfried et al., 2012). Plant communities growing in cold climates have adapted lower optimal temperatures (Kirschbaum, 2004), and their photosynthetic rates, access to nutrients, and overall growth is limited by temperature (Kirschbaum, 2004; Sundqvist et al., 2013). Warmer temperatures favor higher rates of photosynthesis and nitrogen mineralization (Kirschbaum, 2004), therefore, experimental warming should increase photosynthesis and plant biomass production at high elevation sites. Additionally, because plant-plant interactions at higher elevations are more facilitative (Callaway et al., 2002), an increase in the productivity of one individual (via biomass production) may impact other plants, increasing or decreasing diversity via shifts in positive or negative interactions. Plant communities at lower elevations are adapted to warmer climates and have broader thermal niches relative to communities at colder sites (Pellissier et al., 2013). Increasing the air temperature may have a positive impact on these plant communities, but the response may be of a smaller magnitude. Competition tends to be higher at lower elevations (Callaway et al., 2002), so less competitive species may be outcompeted, thereby decreasing diversity.

Ecologists continue to search for answers regarding the consequences of climate warming, leveraging natural altitudinal gradients, experimental warming methods, and observational studies to ascertain how various species and communities will respond to warming (Elmendorf et al., 2015). Open top chambers (OTCs), an experimental method used to passively warm plant communities, have been proven to effectively simulate climate warming (Hollister & Webber, 2000; Marion et al., 1997). OTCs are vital in helping ecologists create predictive models and develop strategies to mitigate the effects of climate change.

Species removal can have varied effects on community composition and ecosystem productivity depending on ecosystem composition and abiotic conditions. Some plant communities appear to compensate for functional group loss (Cross & Harte, 2007) or rare species loss (Smith & Knapp, 2003), while others become more vulnerable to invasion (Lyons & Schwartz, 2001). Other communities display species-level shifts but community-level stability (Marraffini et al., in review). Still others exhibit responses dependent upon the identity of the species removed within the scope of the ecosystem (Wardle & Zackrisson, 2005). Because facilitative relationships between plants increase in frequency along with elevation (Callaway et al., 2002), species removal may decrease community biomass production, as observed by Smith & Knapp (2003). However, species removal may also allow for an increase in the abundance of less common species if they acquire available resources and maintain surviving positive species interactions. This would increase species diversity but would not necessarily increase whole community biomass when compared to biomass before removal. In contrast, competition is more intense at lower elevations, where abiotic strain is less prominent (Callaway et al., 2002). Thus, removing a dominant species may allow remaining species to capitalize on the extra resources and expand their biomass. In a removal experiment by Rewcastle et al. (in review), nitrogen mineralization rates decreased irrespective of the species removed and elevation, meaning plants at lower elevation may face less hospitable soil properties with removal treatments. It is likely that a few species will arise as superior competitors, prevailing over less common species and reducing community biodiversity. The merits of exploring species loss in natural settings has been well documented (Díaz et al., 2003), and I sought to continue to add to the growing body of literature concerning biodiversity loss with climate change.

Ecosystems are governed not only by an assortment of combined abiotic factors (temperature, precipitation, wind, etc.) and combined biotic factors (species interaction, competition, etc.), but by the interactions *among* abiotic and biotic variables (Sundqvist et al., 2013; Walther, 2010). Though species removal alone may have detrimental effects on overall community productivity at the high elevation site, warming may counteract this response to species loss, by relieving temperature stress and possibly enhancing facilitative species interactions. Less stressful abiotic conditions may allow remaining species to compensate for the biomass loss from removal treatments, to the point of stable productivity. An increase in less common life forms would also increase the species diversity in the plots. At lower elevations, dominant species removal may result in remaining plants competing over extra resources, thereby increasing biomass production. Adding warmer air temperatures to the mix would only serve to intensify biomass production of competitive individuals, while less common species suffer, leading to a decline in species diversity. While the first two elements of this study centered on the *individual* effects of simulated warming and species removal, the combined impact of these two variables on alpine-plant communities was also explored. This allowed some insight as to whether one variable has more influence than the other, whether warming and species loss have synergistic or additive effects, or whether their interaction dampens individual variable effects.

I leveraged a 6 year warming and species removal experiment in a low and high elevation montane meadow to test three hypotheses:

1. Warming will increase biomass and biodiversity at the high elevation site and increase plot-level biomass and decrease biodiversity at the low elevation site.
2. Dominant species removal will decrease plot-level biomass and increase biodiversity at the high elevation site, with the opposite prediction for the low site.
3. In terms of warming *and* removal, warming will mitigate the effects of species loss at the high elevation site, leading to stable plot-level biomass and increased diversity. At the low elevation site, the combination of warming and species removal will increase biomass while decreasing diversity.

Methods

Experimental Design

The experiment run was part of the WaRM (Warming and Removal in Mountains) experiment, established in 2014. The low elevation site is located in the Almont Triangle (2740 m a.s.l., 38.71°/-106.82°) and the high elevation site is on Cinnamon Mountain (3460 m a.s.l., 38.99°/-107.06°) (Fig. 1). Both research sites are alpine meadow communities consisting of mainly forb and graminoid functional types (Prager et al., in review; Rewcastle et al., in review).

There are eight replicate blocks at the Almont and Cinnamon research sites. Within each replicate block there are four separate 2m x 2m plots, each with a buffer zone of 2 meters surrounding them. The entire research site encompasses a total of 32 plots and is cordoned off by an electric fence to deter any large herbivores from entering the research plots. The four plots in each row were randomly assigned one of the following treatments: Ambient Control (AC), Ambient Removal (AR), Warming Control (WC), and Warming Removal (WR).

Plots assigned to either Warming Control (WC) or Warming Removal (WR) treatments were warmed via open top chambers (OTCs), hexagonal structures made of fiberglass, that reach a height of roughly 2 feet. The OTCs surround the vegetation, but do not impede plant growth from the top, and are staked into the ground to prevent collapse. Two members of the Classen research team, Dr. Jennie DeMarco and Bailey Sharon, set up the OTCs for each site and labeled each plot with flags to denote

which plot was assigned to which treatment. OTCs were set up on June 7 and July 1, at the Almont and Cinnamon sites, respectively.

When the WaRM project began, the dominant species at each elevational site was determined by abundance; the species with the greatest estimated percent cover was removed in 2014 and subsequent years. The forb species *Wyethia amplexicaulis* dominates the Almont research site, while the graminoid species *Juncus drummondii* dominates the Cinnamon research site. Dominant species were removed by clipping the plants at the base. Vegetation clipping was concurrent with OTC set up for each site.

Response Variable Measurement

Because of the differences in temperature between the low and high elevation sites, the peak of the growing season occurs at different times for each site, usually in late June or early July for the warmer low elevation site and in mid-July for the cooler high elevation site. Response variable measurements for the low elevation site were taken over the span of three days: July 15th, July 17th, and July 18th, 2020 (Table 1). Measurements for the high elevation site were taken over the span of two days, July 23rd and 27th, 2020 (Table 2).

The pin drop method was employed to sample species cover in this study, with separate values for each species in each plot. At the Almont research site, the middle of plot 1 was obscured by a large ant hill that made sampling impossible, therefore, this plot was left untouched. Additionally, plot 7 (the first plot measured on the 15th) was measured incorrectly; instead of 25 pin drops, 72 were performed in this plot as a result of unfamiliarity with the research instruments and protocol. Thus, plot 7 was remeasured on the second day of sampling (July 17th, 2020). Species were categorized by functional type (e.g. forb, graminoid, shrub, etc.) to determine aboveground functional type composition and biomass.

The WaRM network has developed a series of allometric equations, equations approximating species aboveground biomass via species cover, to erase the need for destructive sampling of vegetation in the research plots. To generate an allometric equation for each research site, destructive plots were set up at each elevation and exact plant biomass was determined by clipping and weighing the aboveground plant matter. Species cover was calculated using the pin drop method, which involves placing a PVC quadrat divided into 25 equal squares in each plot and recording the number of times a species touched the metal pin dropped into each square. For each research site, a regression line was produced relating aboveground plant biomass and species hits (Tables 3 and 4). The use of these equations ensures that the WaRM project can continue to run long-term without the need to reestablish treatment plots. Functional type biomass was determined by constructing allometric equations from a previous years' WaRM species hit data for each functional type at each site (Tables 3 and 4).

Statistical Analyses

Plot-level species composition was examined by analyzing species present in the most plots at each site, as well as species that appeared responsive to treatments (Tables 5 and 6). Plot level diversity was calculated using Hurlbert's PIE (probability of interspecific encounter) equation, where p_i is the proportion of each species in each plot and N is the total number of pin drops (25), $PIE = \frac{N}{N-1} \times 1.0 - \sum_{i=1}^S (p_i)^2$ (Hurlbert, 1971).

Plot level biomass was determined using the WaRM network allometric equations. For the Almont site, plots 23, 23, and 32 had very few species hits and thus when using the WaRM network

allometric equation, they returned negative values. These three plots were all given a base value of 1, lower than any of the other biomass values that were positive for the rest of the plots. For Almont graminoid functional type biomass, negative values (Plots 12, 14, 16, 18, 19, 20, 22, 23, 29, 31) were given a base value of 0.5, a value lower than the lowest positive value that could be derived from the allometric equation. The PVC quadrat used while measuring species hit data covers an area of 0.25 m². Thus, all biomass values, both plot-level and functional type, were multiplied by 4, to determine the biomass in terms of g/m².

To determine whether there was any effect of warming and species removal on composition, diversity, and biomass, both among treatments and elevations, I planned on using a two-way factorial ANOVA (Analysis of Variance). However, the assumptions for the ANOVA statistical test (normal distribution of data and equal variances) were not wholly met for any of the response variables. Therefore, a generalized linear model with a Poisson distribution was used to determine whether any of the treatments had significant effects on the response variables.

Results

Plot-Level Biomass

At Almont, the low elevation site, there was a significant warming x removal interaction (Table 5). When species removal and warming interact, the direct effects of warming on plant biomass appear to be reduced. The WC, WR, and AR treatments reduced mean plot-level biomass by 47.7%, 20.1%, and 5.0%, respectively, when compared to the AC treatment (Fig. 2C). There were also significant direct effects of the broader warming and removal treatments on plot-level biomass. Disregarding removal, warming alone decreased plot-level biomass by 33% (Fig. 2A). Factoring out temperature, removal alone increased plot-level biomass by 15.6% (Fig. 2B). At Cinnamon, the high elevation site, only the individual species removal treatment had a significant effect on mean plot-level biomass, resulting in a 21% decrease when compared to the control treatment (Table 6, Fig. 3B).

Forb Biomass

At Almont, the low elevation site, the interaction between warming and removal also significantly decreased forb biomass (Table 5). When warming and species removal interact, the direct effects of warming are reduced, dampening the biomass increase that warming alone created. The WC, WR, and AR treatments increased forb biomass by 37.4%, 23.8%, and 19.4%, respectively, when compared to the AC treatment (Fig. 4C). Warming, regardless of removal, had a significant impact on forb biomass, increasing biomass by 19.5% (Fig. 4A). At the high elevation site, only the individual removal treatment had a significant effect on mean forb biomass, resulting in a 46.4% decrease (Table 6, Fig. 5B).

Graminoid Biomass

The interaction between warming and removal significantly decreased mean graminoid biomass at Almont (Table 5). The impact of warming appeared to be tempered by species removal when the two interacted. The WC, WR, and AR treatments engendered a 96.4%, 59.5%, and 29.1% decrease in mean graminoid biomass, respectively, when compared to the AC treatment (Fig. 6C). There were also significant direct effects of both the individual warming and removal treatments on graminoid biomass (Table 5). Warming alone decreased graminoid biomass by 75.7%, while removal alone increased graminoid biomass 9.5% (Figs. 6A and 6B).

The warming and removal interaction significantly decreased mean graminoid biomass at

Cinnamon (Table 6). The WC, WR, and AR treatments displayed a 2.9%, 18.3%, and 52.7% decrease in mean graminoid biomass, respectively, when compared to the AC treatment (Fig. 7B). Here, warming seems to mitigate the effects of species removal, when the two interact. The individual warming and removal treatments also had direct effects on mean graminoid biomass (Table 6). Warming, disregarding removal, increased graminoid biomass by 21.4% (Fig. 7A). Removal, factoring out temperature, decreased graminoid biomass by 34.6% (Fig. 7B).

Shrub Biomass

At Almont, the warming and removal interaction treatment significantly influenced mean shrub biomass (Table 5). When warming and removal are combined, it appears that species removal reverses the direct effects of warming. The AR and WR treatments increased shrub biomass by 276.8% and 391.9%, respectively, when compared to the AC treatment (Fig. 8C). The WC treatment caused a 100% decrease in mean shrub biomass, in comparison to the AC treatment (Fig. 8C). There were also direct effects of the individual warming and removal treatments on mean shrub biomass (Table 5). Warming, ignoring removal, decreased shrub biomass by 3.7% (Fig. 8A). Removal, neglecting temperature, increased shrub biomass by 761% (Fig. 8B). At Cinnamon, only the individual warming treatment (disregarding removal) had a significant impact on mean shrub biomass, resulting in a 13.2% decrease, in contrast to the ambient treatment (Table 6, Fig. 9B).

Plot-Level Biodiversity

At Almont, none of the treatments had a significant effect on plot-level biodiversity (Table 5, Fig. 10). The interaction between warming and removal appeared to cause an increase in mean biodiversity above the WC, AR, and AC treatments, but this was insignificant.

At Cinnamon, none of the treatments had a significant effect on plot-level biodiversity (Table 6, Fig. 11). The interaction between warming and removal fell between the WC and AR treatments, but this was not significant.

Almont Species Composition

The forb species *Achillea millefolium* responded significantly to the individual removal treatment, disregarding temperature, demonstrating a 1,393.3% increase in mean hits (Table 5, Fig. 12B). The forb species *Erigeron speciosus* revealed a significant response to the interaction treatment (Table 5, Fig. 13C). The AR and WC treatments increased mean *E. speciosus* hits by 185.7% and 85.7%, respectively, when compared to the AC treatment. Meanwhile, the WR treatment generated a 2% decrease in *E. speciosus* mean hits, in juxtaposition to the AC treatment. The forb species *Wyethia amplexicaulis* displayed a significant response to the individual removal treatment, exhibiting an 86% decrease in mean hits, when compared to the control treatment (Table 5, Fig. 14B).

The graminoid species *Festuca thurberi* exhibited significant responses to the interaction of warming and species removal (Table 5, Fig. 15). The combination of warming and removal appeared to reduce the effects of warming on mean species hits. The WC, WR, and AR treatments reduced mean *F. thurberi* hits by 100%, 73.9%, and 32.9%, respectively, in comparison to the AC treatment (Fig. 15C). Warming, ignoring removal, had a significant direct effect on *F. thurberi*, decreasing mean hits by 85.4% (Fig. 15A). Removal, neglecting temperature, also had significant direct effect on *F. thurberi*, decreasing mean hits by 4% (Fig. 15B).

Cinnamon Species Composition

The interaction between warming and removal significantly decreased mean hits for the forb species *Castilleja sulphurea* (Table 6, Fig. 16). Again, the interaction between warming and removal seemed to reduce the direct impact of warming, when the two were combined. The WC, WR, and AR treatments showed a respective 93.3%, 80%, and 73.3% decrease in mean *C. sulphurea* hits, in contrast to the AC treatment (Fig. 16C). Warming, regardless of removal, had a significant direct effect on *C. sulphurea*, decreasing mean hits by 78.9% (Fig. 16A).

The individual warming and removal treatments had direct effects on the mean number of hits for the forb species *Senecio crassulus* (Table 6, Fig. 20). Warming, ignoring removal, caused a 112.5% increase in mean *S. crassulus* hits, while removal, neglecting temperature, resulted in a 52.9% decrease in mean *S. crassulus* hits (Figs. 20A and 20B). The forb species *Sibbaldia procumbens* was influenced significantly by the removal treatment (omitting temperature), which decreased mean *S. procumbens* hits by 75.9% (Fig. 21B).

The interaction between warming and removal significantly increased mean number of hits for the graminoid species *Deschampsia caespitosa* (Table 6, Fig. 17). The AR and WR treatments increased mean hits by 55.6% and 377.8%, respectively, while the WC treatment decreased mean hits by 22.2%, when compared to the AC treatment (Fig. 17C). The removal treatment, overlooking temperature, significantly increased mean *D. caespitosa* hits by 256.3% (Fig. 17B).

The interaction of warming and removal significantly decreased mean hits for the graminoid species *Juncus drummondii* (Table 6, Fig. 18). When warming and removal were combined, warming appeared to mitigate some of the direct effects of species removal. The WC, WR, and AR treatments decreased mean hits by 49.4%, 73%, and 76.4%, respectively, in relation to the AC treatment (Fig. 18C). Species removal, excluding temperature, significantly decreased mean *J. drummondii* hits, by 66.4% (Fig. 18B).

The interaction of warming and removal significantly decreased mean hits for the graminoid species *Poa arctica* (Table 6, Fig. 19). The AR and WC treatments resulted in a respective 160% and 960% increase in mean *P. arctica* hits, while the WR treatment caused a 40% decrease in mean *P. arctica* hits, when compared to the AC treatment (Fig. 19C). The combination of warming and removal appeared to reverse the effects of the AR and WC treatments. Species removal, factoring out temperature, significantly decreased mean *P. arctica* hits by 72.4% (Fig. 19B).

The graminoid species *Trisetum spicatum* and the shrub species *Vaccinium caespitosum* did not respond to any of the treatments (Table 6, Figs. 22 and 23).

Discussion

Plot-Level and Functional Type Biomass

At Almont, the low elevation site, plot-level biomass decreased in response to the WC, WR and individual warming (excluding removal) treatments, in contrast to my hypothesis. Both graminoid and shrub biomass decreased under the individual warming treatment, while forb biomass increased. The individual removal treatment (disregarding temperature) resulted in a mean increase in plot-level biomass, though the AR treatment caused a slight decrease. The individual removal treatment increased both graminoid and shrub biomass.

The observed warming induced *decrease* in plot-level biomass at the low site was contrary to my expectations. A higher air temperature may reduce soil moisture which in turn could lead to a narrowing of the species able to withstand the physiological stress and survive under warmer conditions (Fu et al., 2013; Winkler et al., 2016). The mean decrease in graminoids was also surprising, as this functional

group is thought to be less susceptible to dry soil conditions, because they are more drought resistant. However, graminoids and shrubs have shallower roots than forbs (Pohl et al., 2011), thus even with an increased resistance to drier soils, perhaps they could not withstand the low soil moisture level induced by the warming treatment. There was also species-specific variation in the graminoid functional type, which includes grasses (ex. *D. caespitosa* and *P. arctica*), sedges, and rushes (ex. *J. drummondii*) and the number and type of species represented was small. It is possible that these few species-specific responses do not dictate the fate of the graminoid functional type, or even its subsets, as suggested by Klanderud (2008). Further research into these subsets and the overall graminoid and shrub functional types is necessary to confirm larger shifts in response to warming and removal. The mean increase in plot-level biomass due to the removal treatment at the low site was as I hypothesized. This may be due to remaining species profiting off of extra resources and space and seeing as plant relationships are generally more competitive and less facilitative at lower elevations (Callaway et al., 2002), I would expect the removal of a major ecosystem player to benefit surrounding species, an observation also noted by Hobbie et al. (1999). An increase in productivity above the level of the non-manipulated plots suggests that remaining species compensated in the wake of dominant species removal a phenomenon observed by Cross & Harte (2007) and Smith & Knapp (2003).

At Cinnamon, the high elevation site, simulated warming had no significant effect on plot-level biomass. Though plot level biomass at the higher elevation was unaffected, graminoid biomass increased and shrub biomass decreased under warmer temperatures. Therefore, while overall plot biomass was unchanged, functional type biomass fluctuated along with warming and the diverging responses of different life forms seemed to dampen a greater community response to warming. This is a trend also seen by Winkler et al. (2016), where opposing responses to warming between functional types lessened the community response. Species removal resulted in a mean decrease in plot-level biomass. Forb and graminoid mean biomass decreased with removal, likely accounting for the overall decrease in plot-level biomass. Plant relationships are generally more facilitative at higher elevations, in order to cope with environmentally harsh conditions (Callaway et al., 2002). Removal of a dominant species could potentially negatively influence several surrounding species, due the loss of a network of positive species interactions and altered nutrient cycling. Rewcastle et al. (in review) noted that removing a dominant species, regardless of elevation, resulted in less than ideal soil properties. However, the impact of worsened soil characteristics may be greater for plants that are more reliant on each other for survival.

Biodiversity

Plot-level biodiversity was unaffected by any of the treatments at both elevations, contrary to what I hypothesized. However, even though biodiversity showed no reaction to warming or removal, functional type and species composition both fluctuated. The species-specific increases and decreases in abundance cancelled out, and thus the overall diversity value remained stagnant. This observation of species level shifts with greater community stability has been observed in other studies (Marraffini et al., in review; Winkler et al., 2016), emphasizing the importance of species-specific responses to climate warming and variable interaction. The makeup of a plant community is relevant to ecosystem functioning and services regardless of the level of diversity in a community – different species and functional types fill complementary roles within the scope of a system, which allows for balance and longevity.

Composition

At the low elevation site, warming and removal both had significant impacts on species composition. For the forb species *A. millefolium*, species removal (regardless of warming) generated an increase in mean species hits. Plant relationships are generally more competitive at lower, more habitable climates (Callaway et al., 2002), therefore, it is likely that dominant species removal allowed for greater interspecific competition for existing space and nutrients, thereby enhancing the growth of this species. Interestingly, *E. speciosus* increased in response to the AR and WC treatments but decreased when warming and removal were combined. It appears that the interaction of these two variables causes detrimental effects for mean species hits, but the reasoning behind this should be further investigated. In contrast, the other forb species, *W. amplexicaulis*, was negatively impacted by the individual removal treatment. *W. amplexicaulis* is the dominant species at the low elevation site, and it is therefore the species removed during treatments. The graminoid *F. thurberi* was negatively impacted most notably by the WC treatment, possibly because this species is less impervious to dry soils. The effects of warming were lessened with the addition of species removal, likely because *F. thurberi* was given more space to branch out and more access to water below the soil surface.

At the high elevation site, graminoids were more influenced by species removal than warming, with three of four graminoid species displaying varying responses to the removal treatment (excluding temperature) and interaction treatment, but not the individual warming treatment. The two grass species *D. caespitosa* and *P. arctica* both increased under the AR treatment, while the rush *J. drummondii* decreased, likely because it is the dominant species removed. All three species had different responses to the other treatments, suggesting that the response of the greater graminoid functional type is highly dependent on the species comprising it in a specific setting. The three forb species that responded to treatments were much more variable, though *S. crassulus* and *S. procumbens* decreased with species removal, regardless of temperature. Here, species removal had a greater influence on plant abundance (via species hits), likely due to the loss of facilitative plant relationships brought on by species removal. If plant species at the high elevation site are more reliant on each other for growth and survival, removing the widespread dominant species would have detrimental effects on several surrounding species through decreased soil stability and nutrient availability.

Conclusion

Investigating the interaction between warming and dominant species removal revealed the importance of species-specific reactions to climate change. The general trend of removal reducing the direct effects of warming when the two were combined is pertinent to the future of alpine plant communities and is a pattern worth exploring further. Though greater community aspects such as biodiversity and plot-level biomass (Cinnamon) were not significantly changed between treatments, species and functional type level shifts were observed, highlighting greater implications of altered composition on ecosystem functioning. This experiment augments the data and findings already attributed to the WaRM project and suggests further study in several areas. It would be prudent to inspect several elevations along the RMBL gradient, as opposed to just the lowest and highest possible altitudes. Testing other WaRM sites would allow researchers to determine the rate at which different processes change along an elevational gradient (Marraffini et al., in review; Prager et al., in review). Additionally, collecting data on plant physiology would provide evidence for finer scale shifts in species composition. Plant functional traits such as leaf surface area and leaf C:N ratio should be scrutinized in the face of climate change, especially in areas where plants are more susceptible to climate warming. To

determine whether soil drying due to warming negatively impacts different plant species, analyzing the interaction between temperature and soil moisture via warming x precipitation treatments is advised. Furthermore, studying the influence that different types of species (rare, common, dominant) have on community composition and productivity via removal experiments is recommended (Lyons & Schwartz, 2001).

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Sampling Notes

There are 52 species present at the low elevation site and 47 species present at the high elevation site. Any species that were not identifiable in the field were sampled and sent to the RMBL herbarium; Dr. Rick Williams identified and confirmed species names, and most unknowns were replaced by their species code. On the first day of sampling at Almont, species hit values were mistakenly assigned to the false dandelion genus *Agoseris*. These values were later reassigned to the true dandelion species *Taraxacum officinale*, and species identity was confirmed via sampling. One Almont species labeled UNKN4, was in fact two distinct forb species (*Polygonum douglasii* and *Collomia linearis*), and the species hits for the first sampling day (July 15) were denoted under the UNKN4 species code. Additionally, the Almont *Carex* species (labeled CARSP) was not sampled; a sample was not collected on the day it was observed (July 17) and upon return to the research site the following day, the *Carex* species was indiscernible from *Festuca thurberi*.

At the Cinnamon research site, it was difficult to determine the difference between an unknown *Carex* species and *Deschampsia caespitosa*, another graminoid. Therefore, all hits for this unknown graminoid species were ascribed to the species code GRAMSP, except in plot 17, where species hits were verified as *Deschampsia* via a photograph. There were three remaining unknown forb species that were unidentifiable, and these were labeled under the species codes FORB1, FORB5, and FORB6.

Table Appendix

Table 1-Almont Measurement Dates

Dates and plots measured at the low elevation site, Almont, CO.

Date	Plots Measured
July 15, 2020	2, 3, 6, 7*, 11, 15
July 17, 2020	1, 4, 5, 7-10, 12-14, 16-24, 27-31
July 18, 2020	25, 26, 28, 30, 32

*Plot 7 was redone on July 17, 2020 with only 25 pin drop points

Table 2-Cinnamon Measurement Dates

Date	Plots Measured
July 23, 2020	2, 3, 6, 7, 10, 11, 14, 15, 18, 19, 22, 23, 26, 27, 30, 31
July 27, 2020	1, 4, 5, 8, 9, 12, 13, 16, 17, 20, 21, 24, 25, 28, 29, 32

Dates and plots measured at the high elevation site, Cinnamon Mountain, CO.

Table 3-Almont Allometric Equations-Functional Type Biomass

Category	Equation	R ² Value
Whole Site	$y = 1.0755x - 3.2817$	0.6415
Forb	$y = 0.7682x + 5.0416$	0.658
Graminoid	$y = 0.8309x - 3.498$	0.8069
Shrub	$y = 1.5887x + 0.4797$	0.7048

Table 4-Cinnamon Allometric Equations-Functional Type Biomass

Category	Equation	R ² Value
Whole Site	$y = 0.5251x + 6.1482$	0.7192

Forb	$y = 0.6042x + 0.0066$	0.5561
Graminoid	$y = 0.5938x - 0.6374$	0.5714
Shrub	$y = 0.5103x + 4.0179$	0.6422

Table 5-Almont P-Values and Chi Squared Values

Response Variable	Treatment	P Value	Chi Squared Value
Plot-Level Biomass	Warming	<0.0001	44.014612
Plot-Level Biomass	Removal	0.0028	8.9122195
Plot-Level Biomass	Warming*Removal	0.0001	14.475338
Forb Biomass	Warming	0.0034	8.5812927
Forb Biomass	Removal	0.5498	0.3576325
Forb Biomass	Warming*Removal	0.0198	5.4291392
Graminoid Biomass	Warming	<0.0001	165.3394
Graminoid Biomass	Removal	<0.0001	33.8879
Graminoid Biomass	Warming*Removal	<0.0001	66.62858
Shrub Biomass	Warming	0.0032	8.7160093
Shrub Biomass	Removal	<0.0001	65.403154
Shrub Biomass	Warming*Removal	0.0004	12.649284
Plot-Level PIE	Warming	0.9391	0.0058452
Plot-Level PIE	Removal	0.7325	0.116849
Plot-Level PIE	Warming*Removal	0.9055	0.0140894
Achillea millefolium	Warming	0.1855	1.7528346
Achillea millefolium	Removal	<0.0001	15.319286
Achillea millefolium	Warming*Removal	0.3257	0.966059
Erigeron speciosus	Warming	0.4933	0.4693474
Erigeron speciosus	Removal	0.5358	0.3833175
Erigeron speciosus	Warming*Removal	0.0074	7.165916
Festuca thurberi	Warming	<0.0001	94.901864
Festuca thurberi	Removal	<0.0001	16.693666
Festuca thurberi	Warming*Removal	<0.0001	28.674441
Wyethia amplexicaulis	Warming	0.3783	0.7762305
Wyethia amplexicaulis	Removal	<0.0001	19.020808
Wyethia amplexicaulis	Warming*Removal	0.1405	2.1723221

Table 6-Cinnamon P-Values and Chi Squared Values

Response Variable	Treatment	P Value	Chi Squared Value
Plot-Level Biomass	Warming	0.4571	0.5530953
Plot-Level Biomass	Removal	0.0034	8.5968257
Plot-Level Biomass	Warming*Removal	0.0709	3.2620287
Forb Biomass	Warming	0.0501	3.8369132
Forb Biomass	Removal	<0.0001	27.606863
Forb Biomass	Warming*Removal	0.2206	1.5005054
Graminoid Biomass	Warming	<0.0001	16.423968

Graminoid Biomass	Removal	<0.0001	53.075121
Graminoid Biomass	Warming*Removal	<0.0001	20.456117
Shrub Biomass	Warming	0.0472	3.9376522
Shrub Biomass	Removal	0.5001	0.4546431
Shrub Biomass	Warming*Removal	0.5901	0.2901516
Plot-Level PIE	Warming	0.7359	0.1137235
Plot-Level PIE	Removal	0.9038	0.0146066
Plot-Level PIE	Warming*Removal	0.9819	0.0005169
Castilleja sulphurea	Warming	0.0080	7.042925
Castilleja sulphurea	Removal	0.8637	0.0294701
Castilleja sulphurea	Warming*Removal	0.0401	4.2116513
Deschampsia caespitosa	Warming	0.1448	2.1267053
Deschampsia caespitosa	Removal	<0.0001	16.322354
Deschampsia caespitosa	Warming*Removal	0.0191	5.4909599
Juncus drummondii	Warming	0.1188	2.4327792
Juncus drummondii	Removal	<0.0001	39.241092
Juncus drummondii	Warming*Removal	0.0196	5.444474
Poa arctica	Warming	0.2758	1.1875938
Poa arctica	Removal	0.0141	6.0290495
Poa arctica	Warming*Removal	<0.0001	32.600312
Senecio crassulus	Warming	0.0222	5.2333577
Senecio crassulus	Removal	0.0222	5.2333577
Senecio crassulus	Warming*Removal	0.1310	2.2803405
Sibbaldia procumbens	Warming	0.1076	2.5893804
Sibbaldia procumbens	Removal	0.0002	14.213863
Sibbaldia procumbens	Warming*Removal	0.6390	0.2200932
Trisetum spicatum	Warming	0.2997	1.0753224
Trisetum spicatum	Removal	0.7418	0.1085574
Trisetum spicatum	Warming*Removal	0.5123	0.4294157
Vaccinium caespitosum	Warming	0.7640	0.0901498
Vaccinium caespitosum	Removal	0.8991	0.0160663
Vaccinium caespitosum	Warming*Removal	0.2096	1.5742005



Fig. 1 Left-Almont research site, the low elevation site. Right-Cinnamon research site, the high elevation site (photo courtesy of Bailey Sharon).

Fig. 2 Mean plot-level biomass values (g/m^2) at the low elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 2

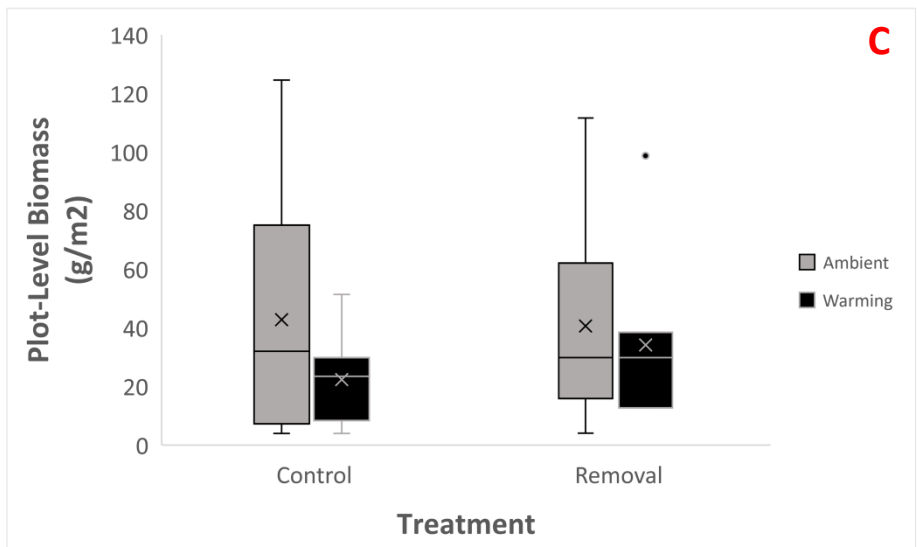
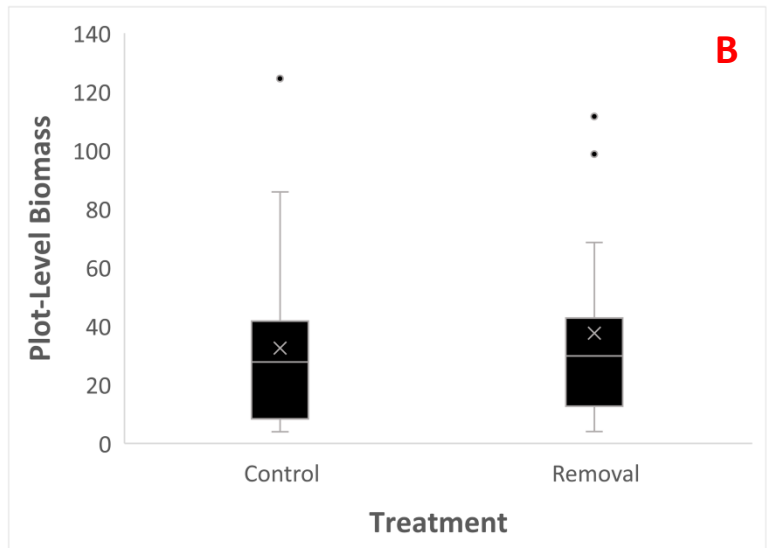
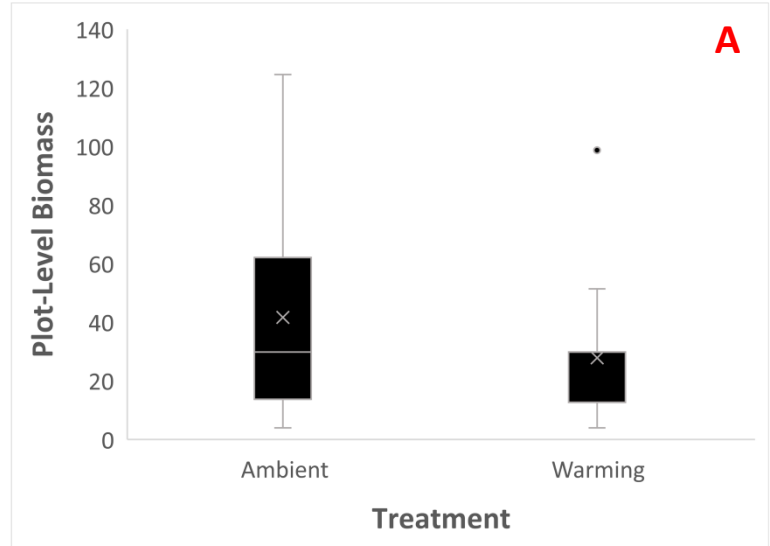


Fig. 3 Mean plot-level biomass values (g/m^2) at the high elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 3

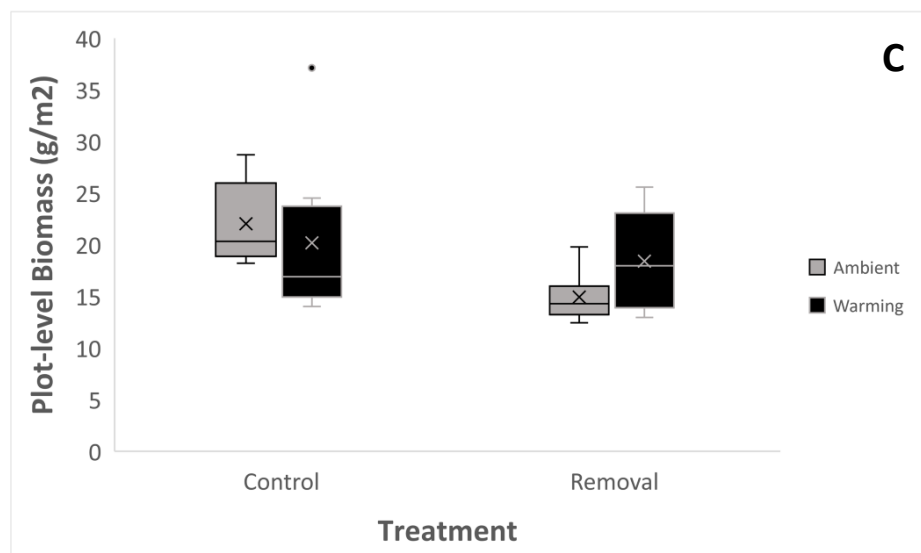
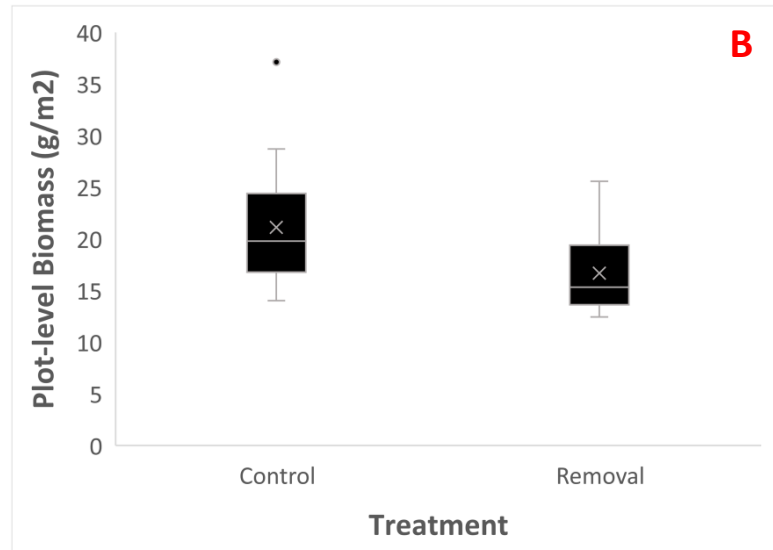
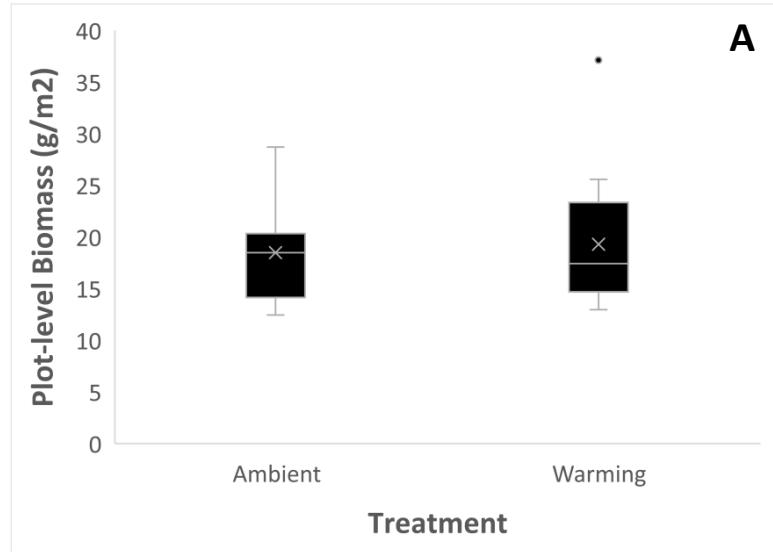


Fig. 4 Mean plot-level forb biomass at the low elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 4

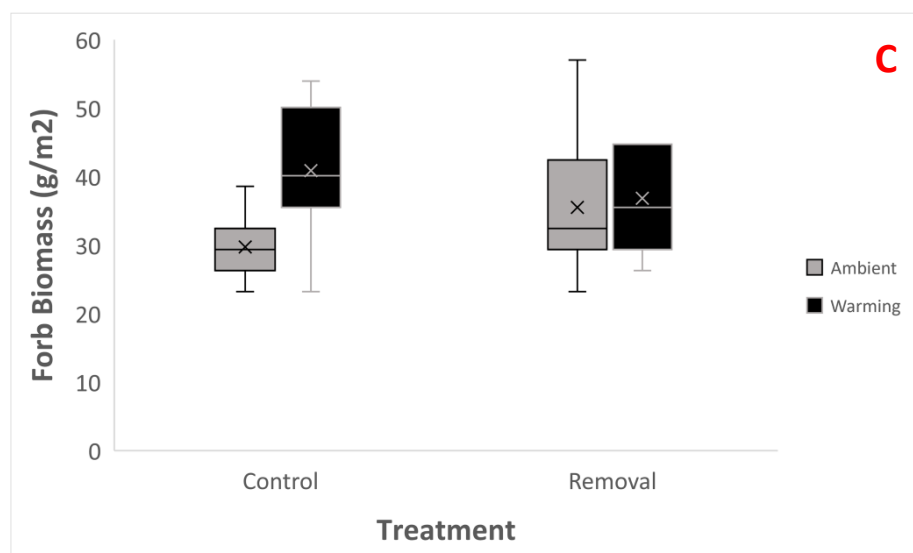
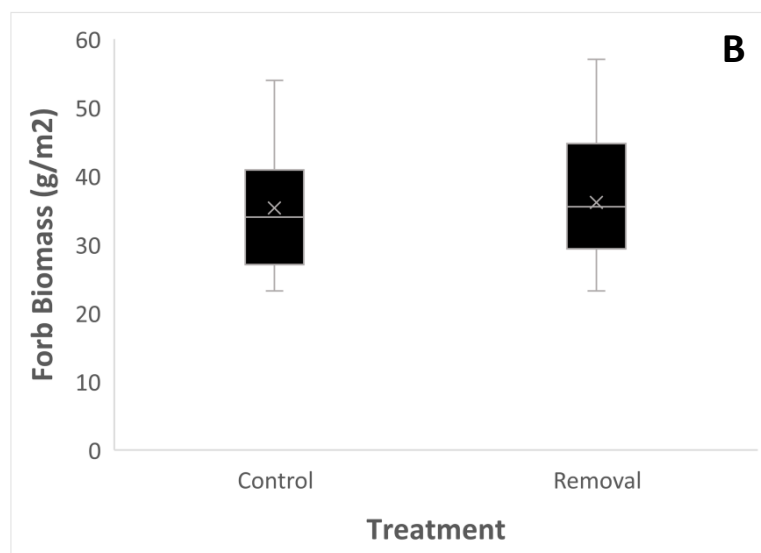
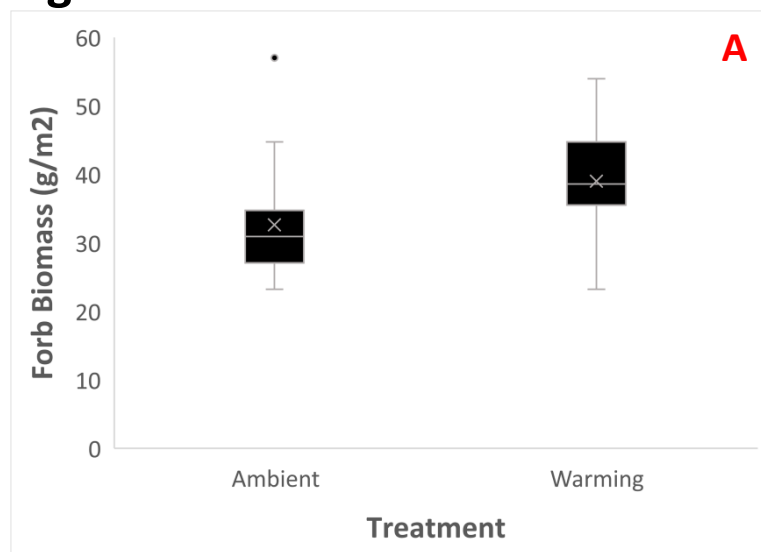


Fig. 5 Mean plot-level forb biomass at the high elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 5

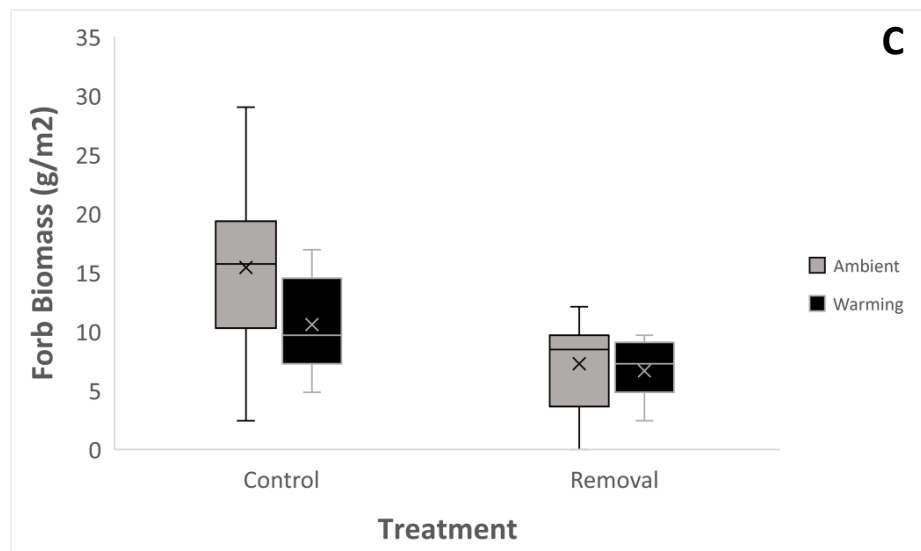
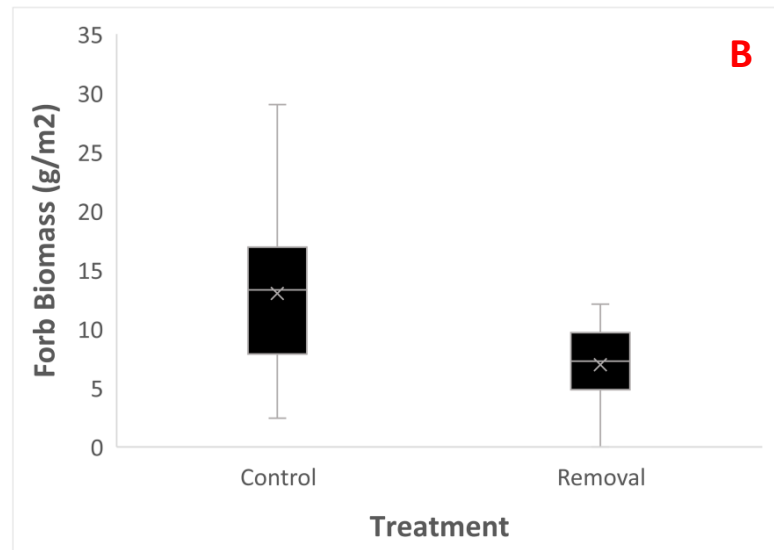
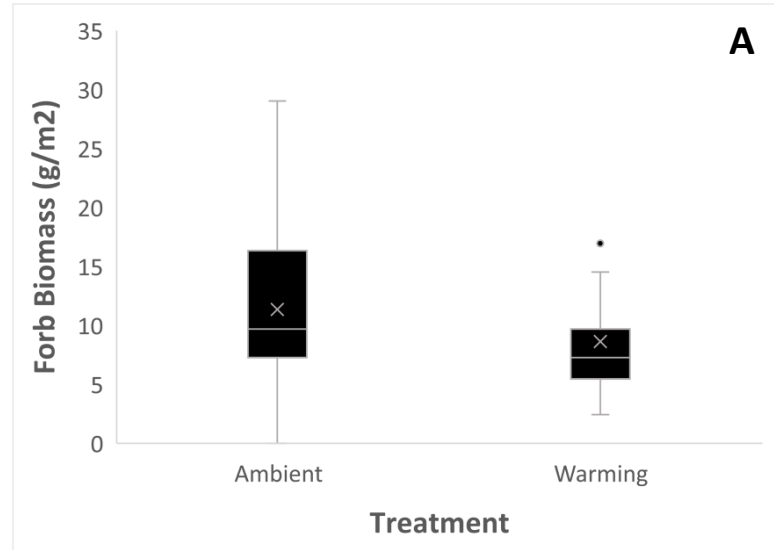


Fig. 6 Mean plot-level graminoid biomass at the low elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 6

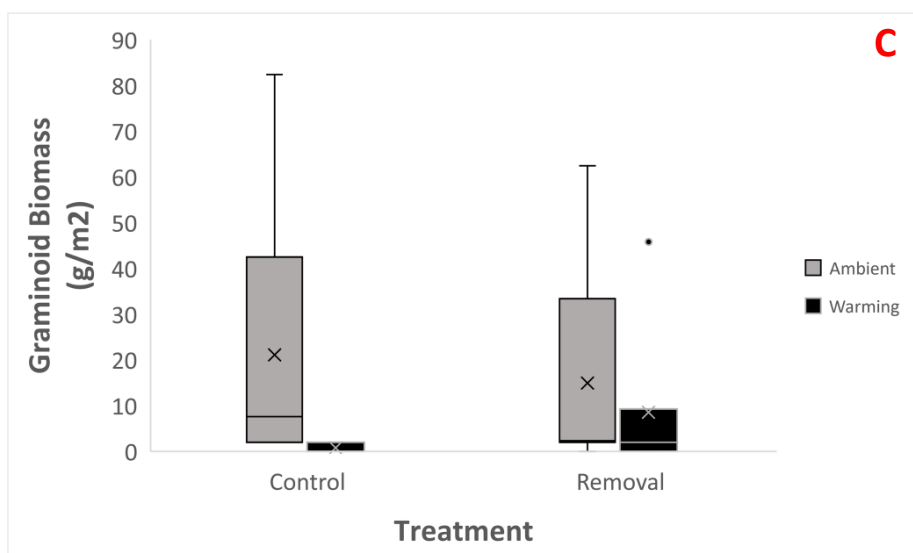
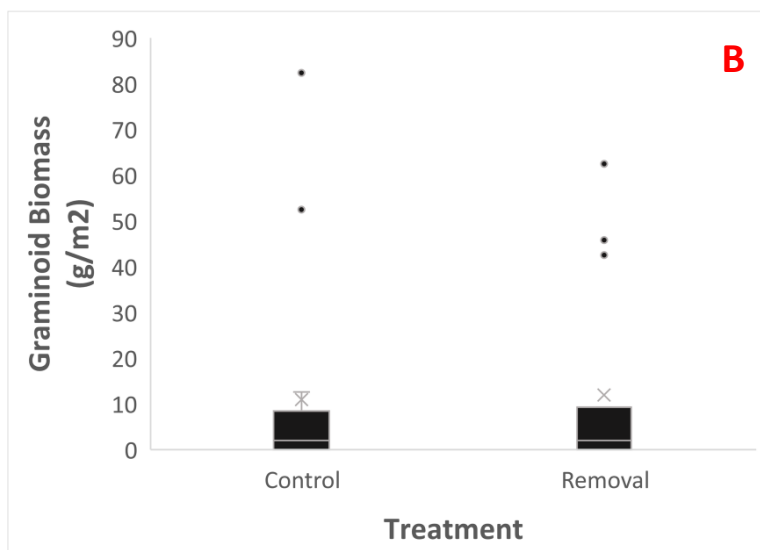
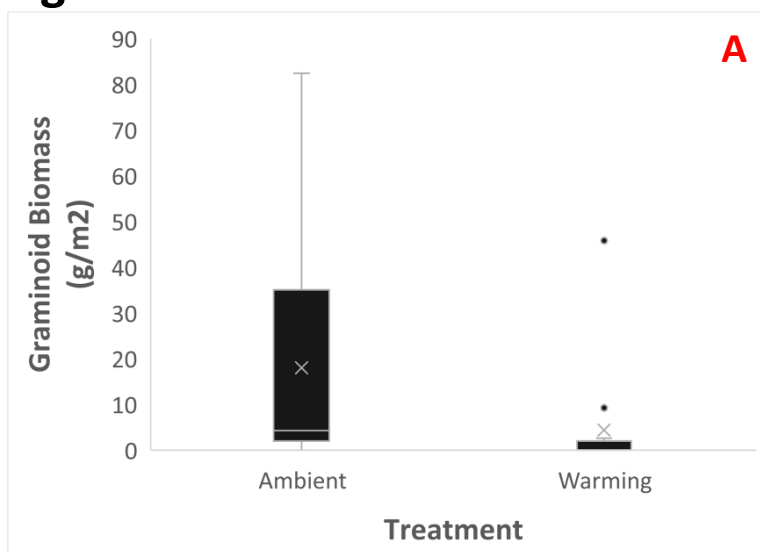


Fig. 7 Mean plot-level graminoid biomass at the high elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 7

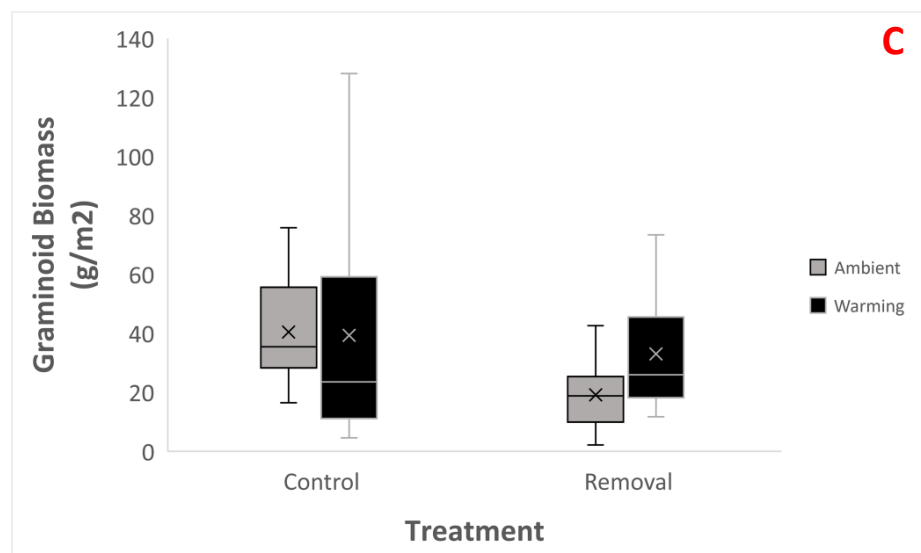
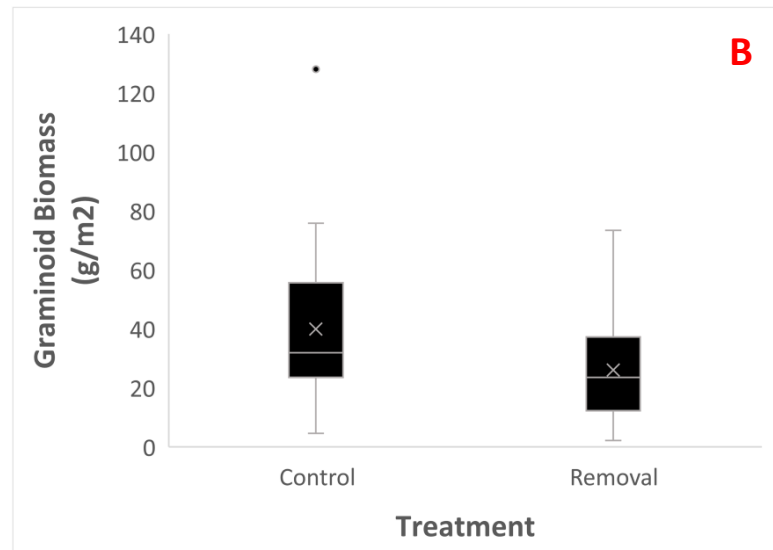
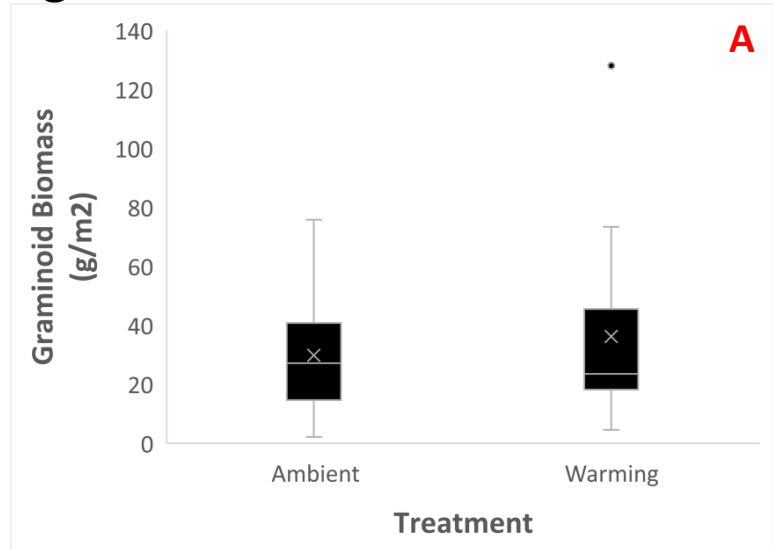


Fig. 8 Mean plot-level shrub biomass at the low elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 8

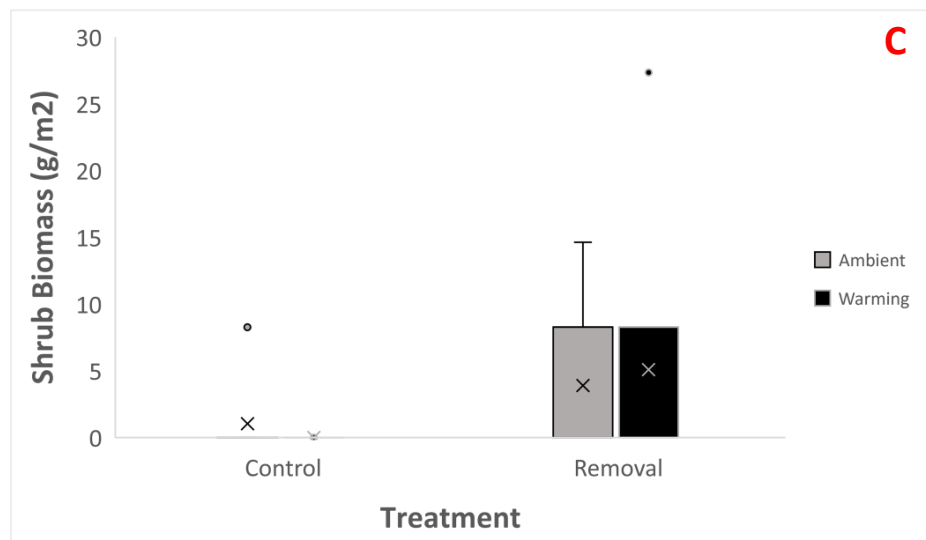
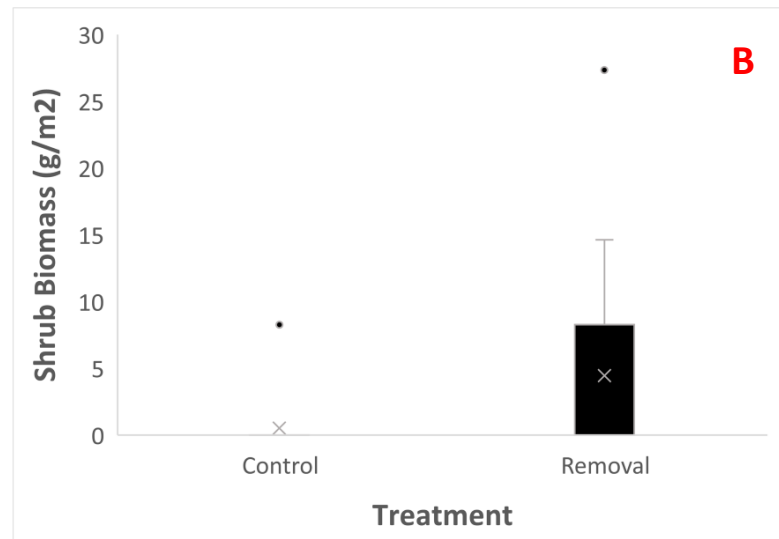
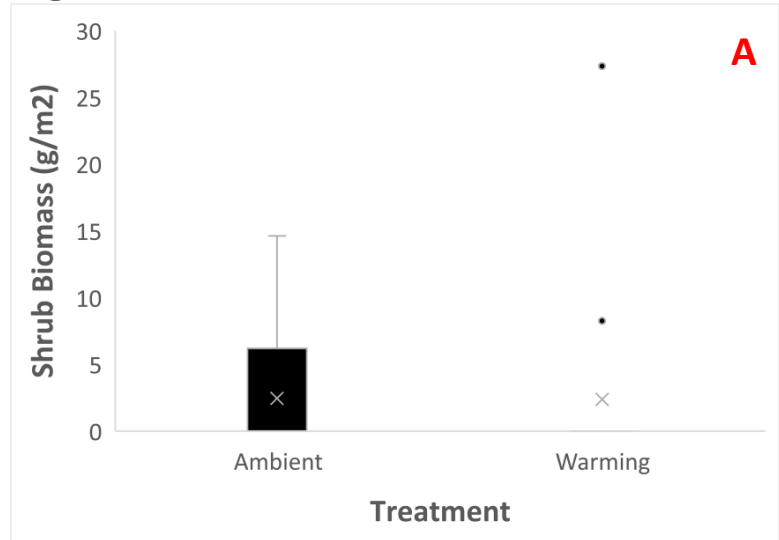


Fig. 9 Mean plot-level shrub biomass at the high elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 9

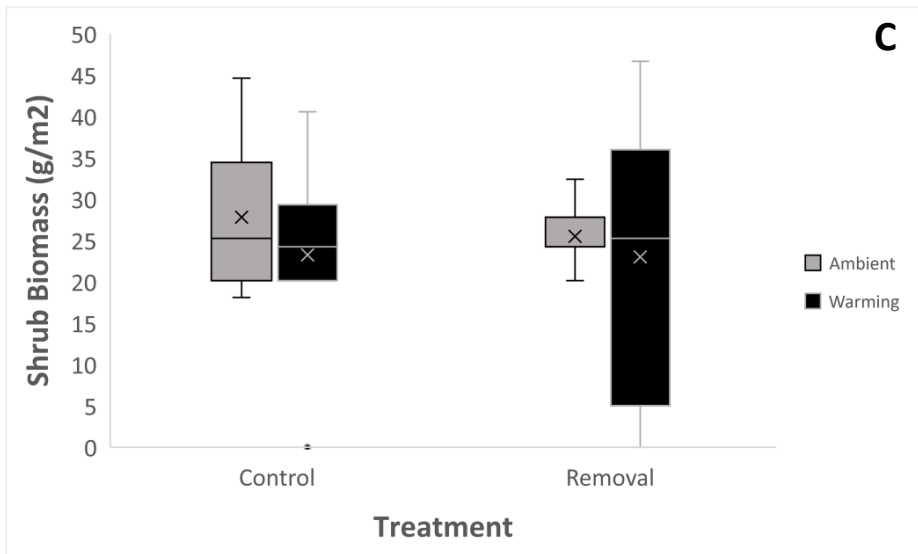
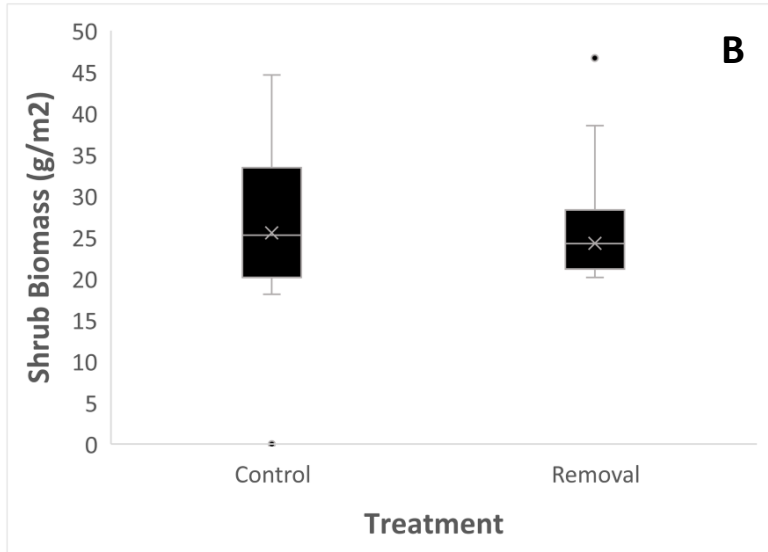
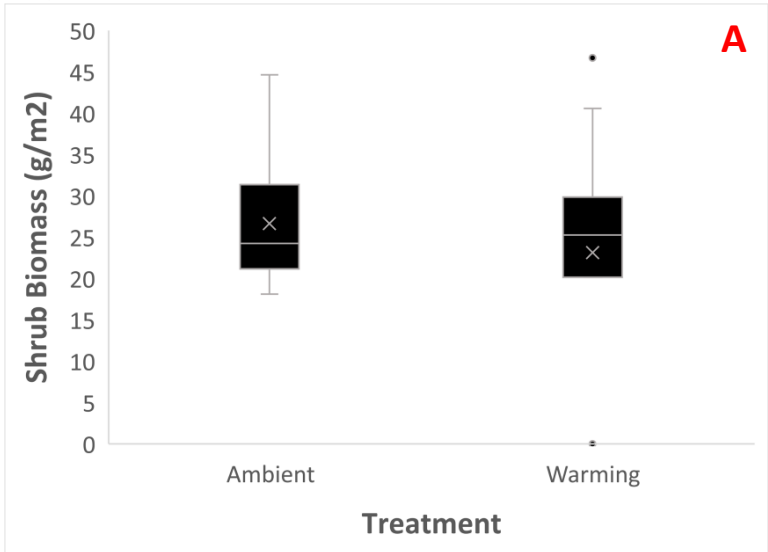


Fig. 10 Mean plot-level diversity at the low elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 10

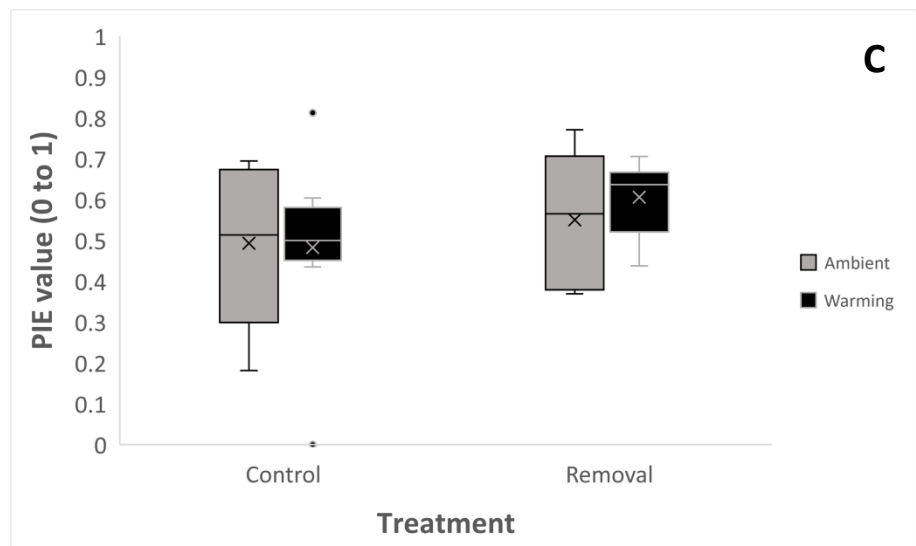
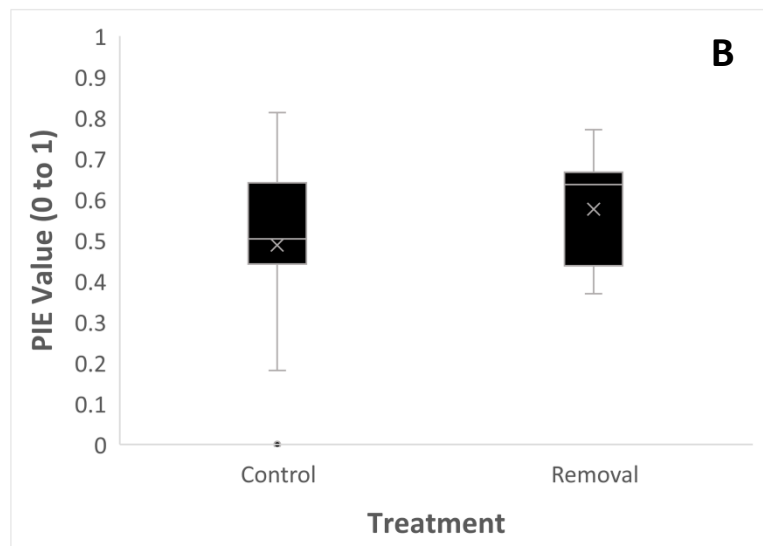
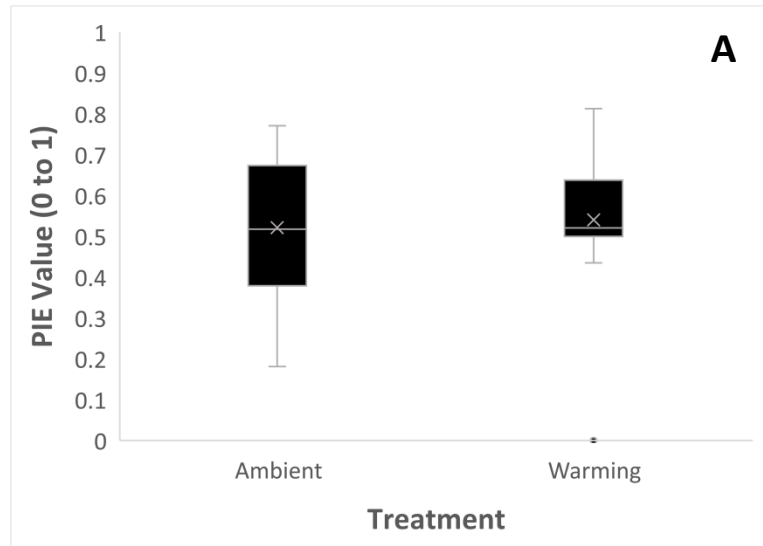


Fig. 11 Mean plot-level diversity at the high elevation site for A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 11

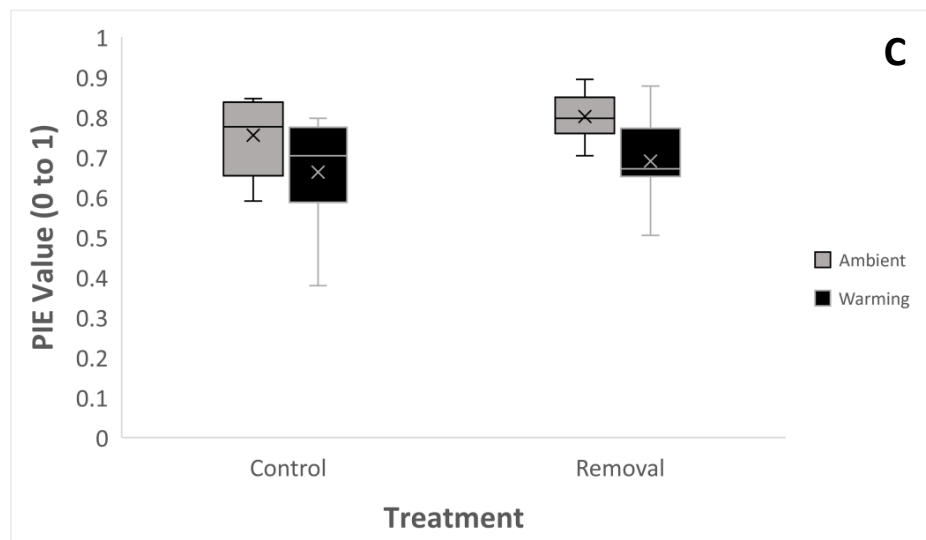
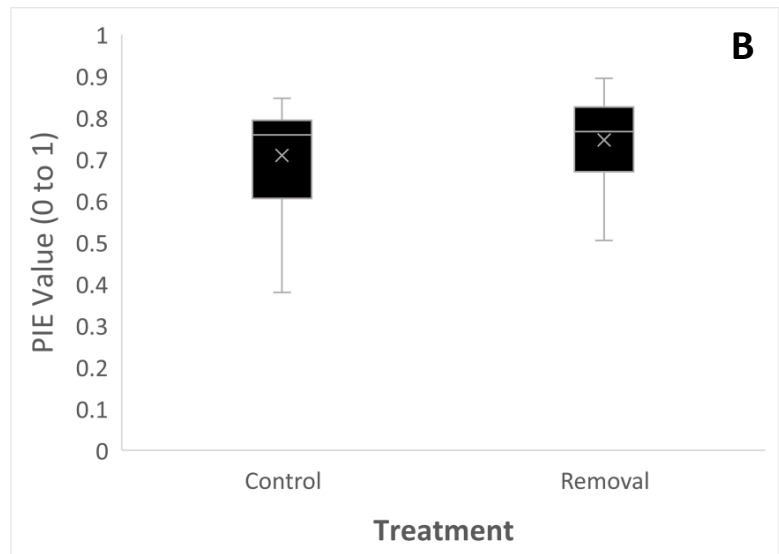
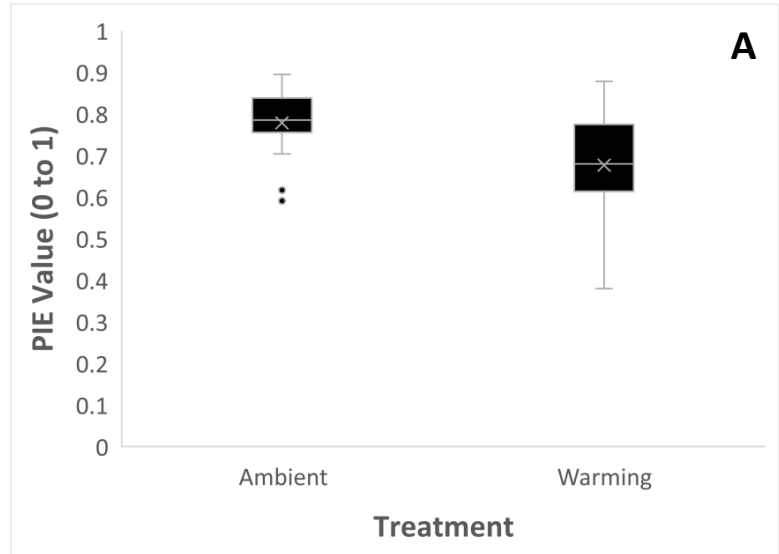


Figure 12

Fig. 12 Mean number of hits for the Almont forb species *Achillea millefolium* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

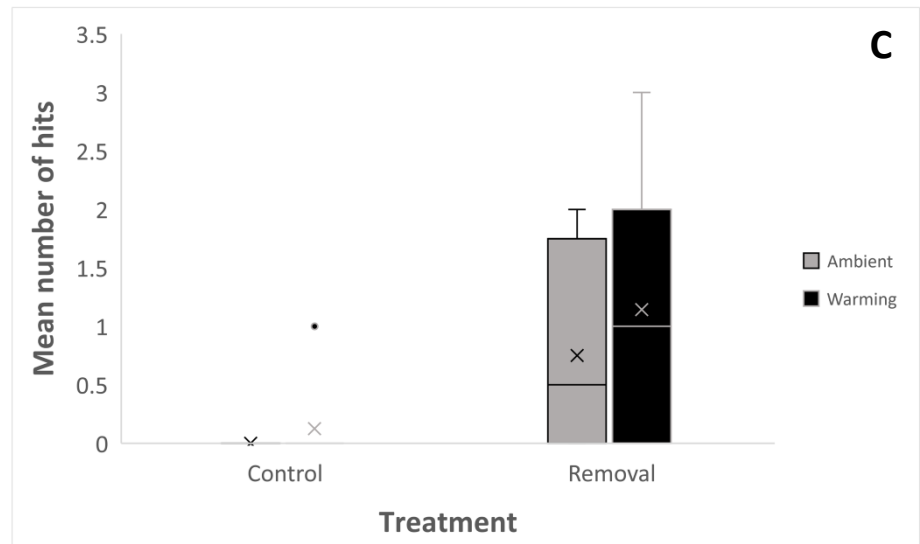
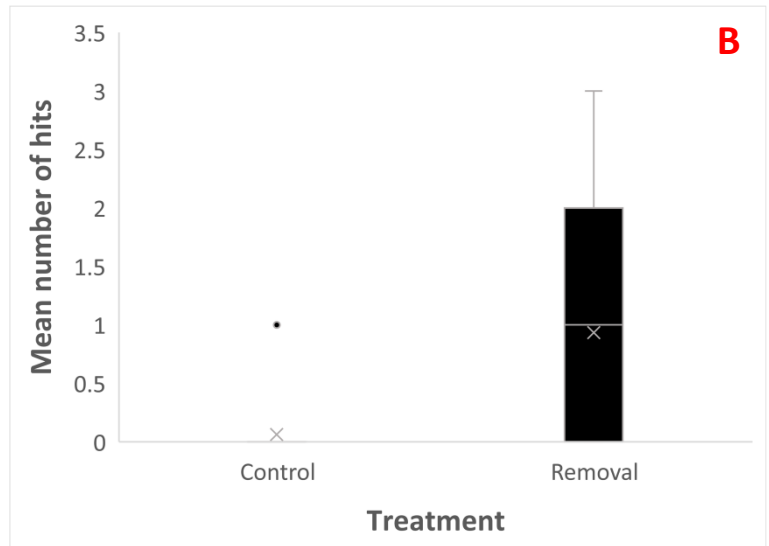
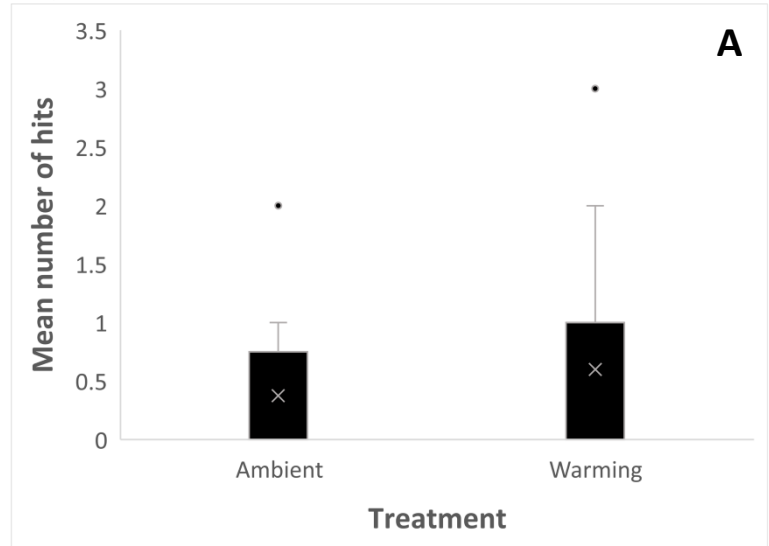


Figure 13

Fig. 13 Mean number of hits for the Almont forb species *Erigeron speciosus* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

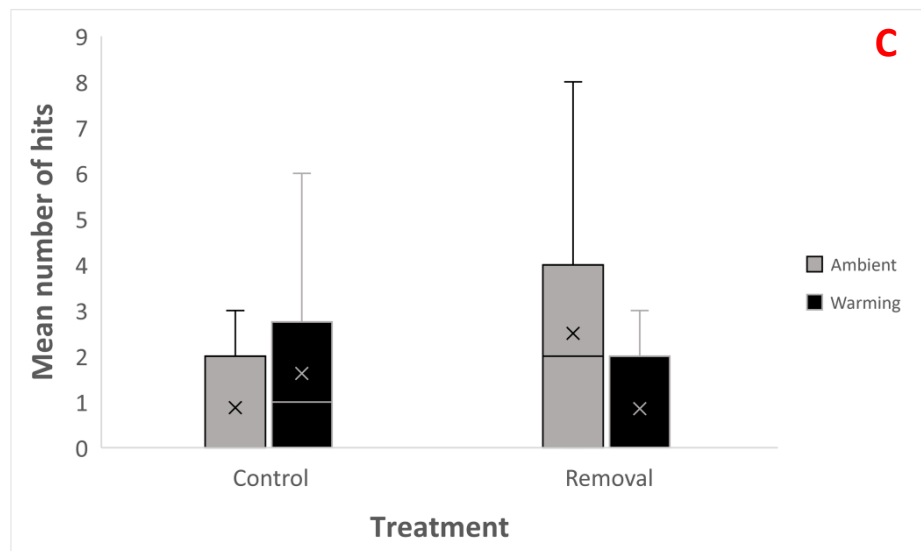
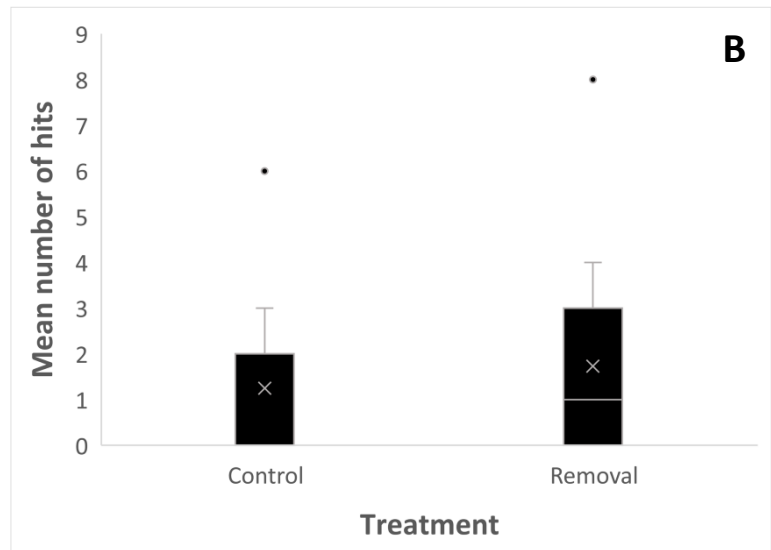
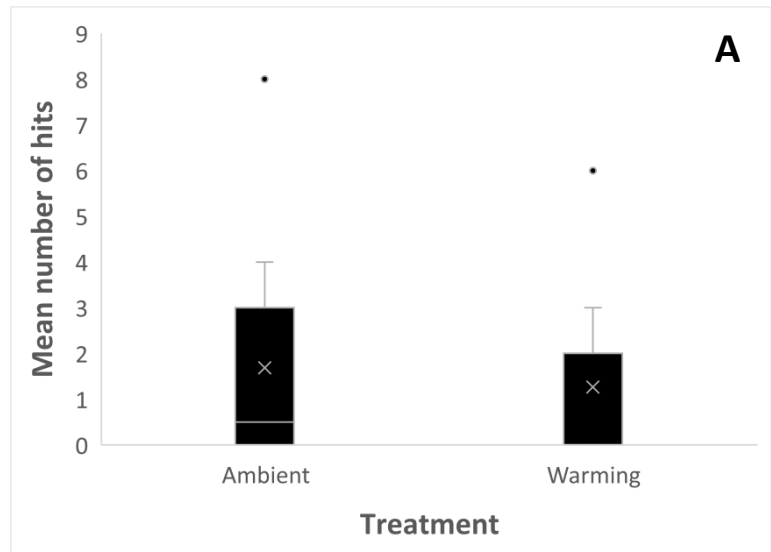


Figure 14

Fig. 14 Mean number of hits for the Almont graminoid species *Festuca thurberi* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

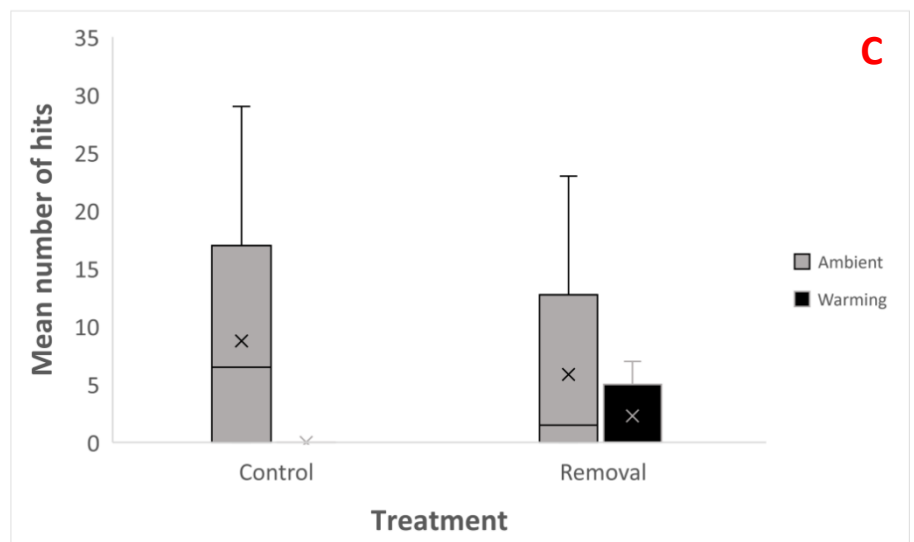
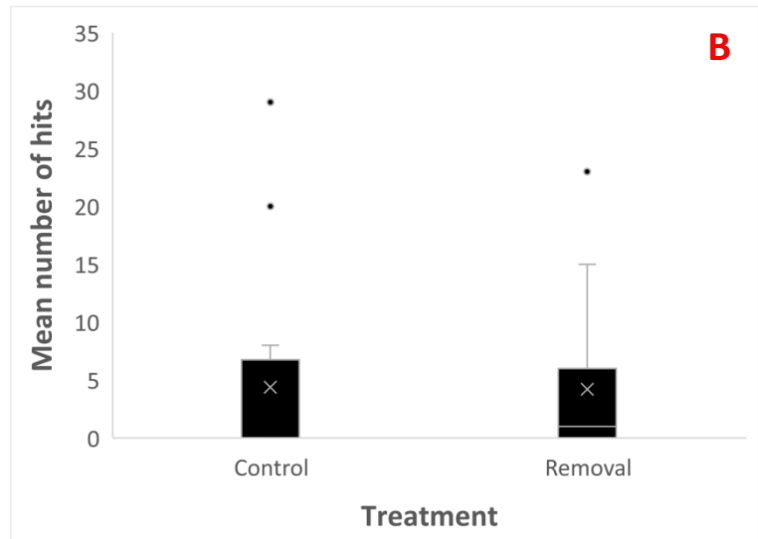
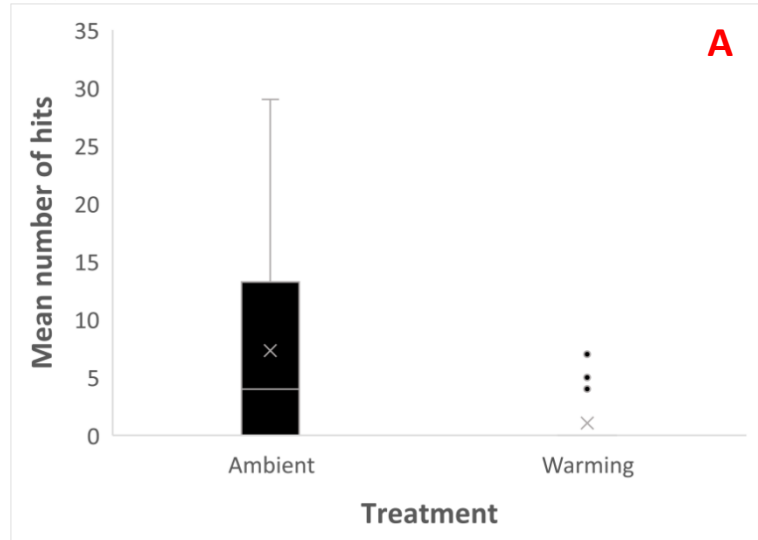


Fig. 15 Mean number of hits for the Almont forb species *Wyethia amplexicaulis* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 15

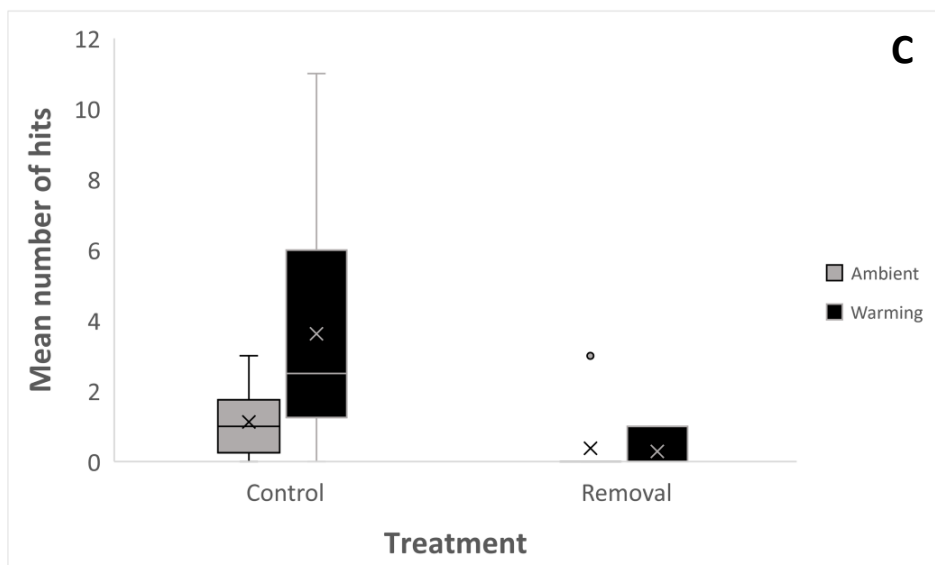
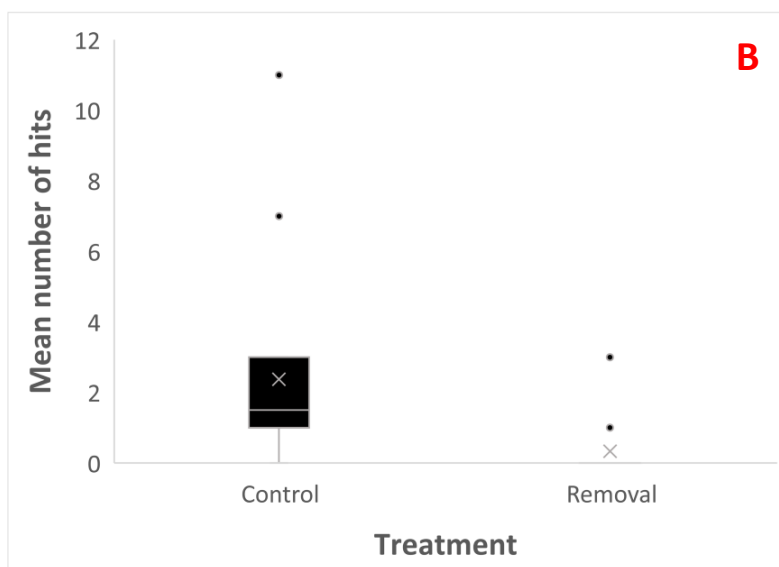
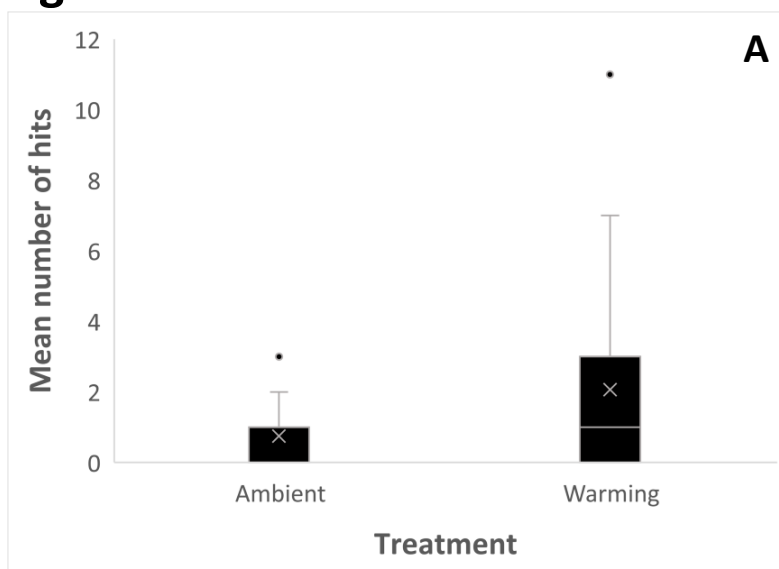


Fig. 16 Mean number of hits for the Cinnamon forb species *Castilleja sulphurea* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

Figure 16

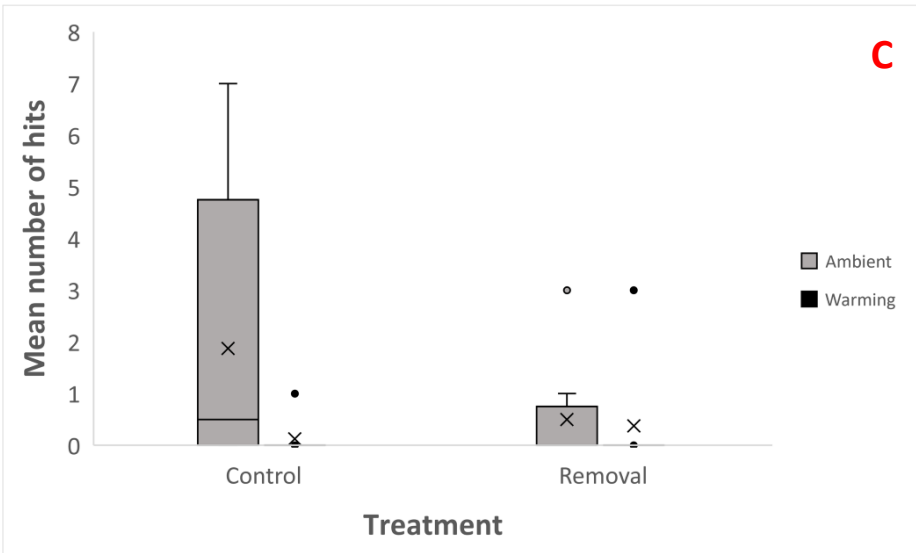
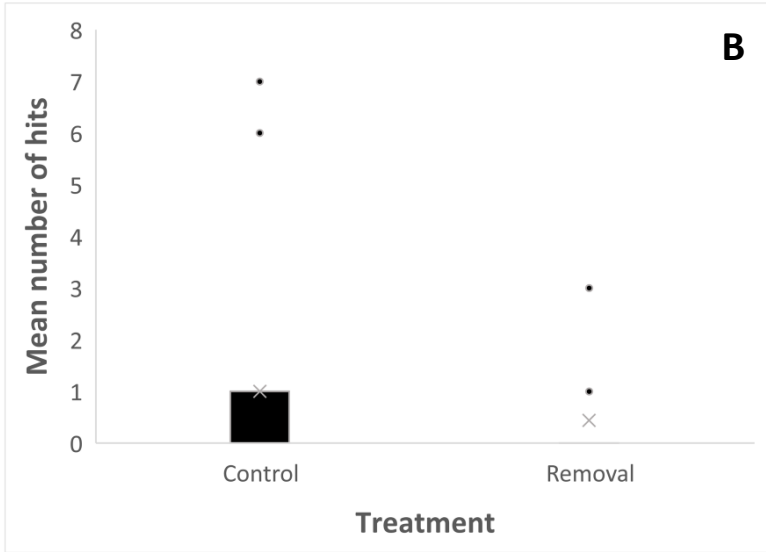
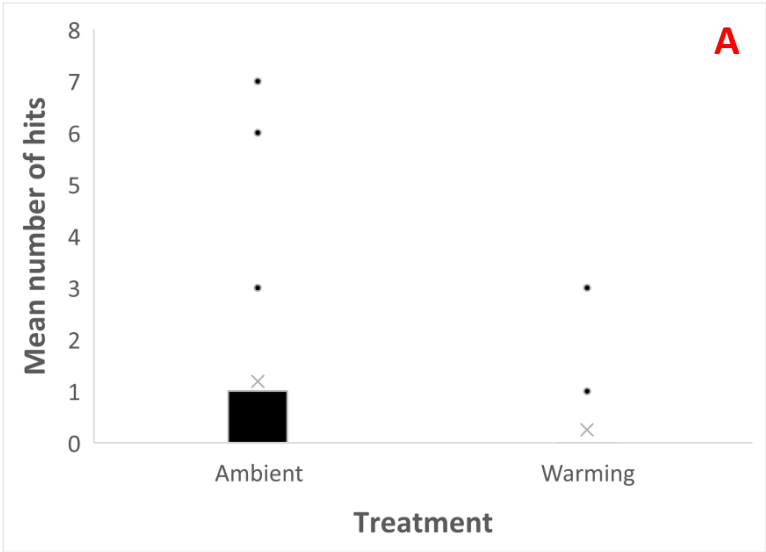


Figure 17

Fig. 17 Mean number of hits for the Cinnamon graminoid species *Deschampsia caespitosa* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

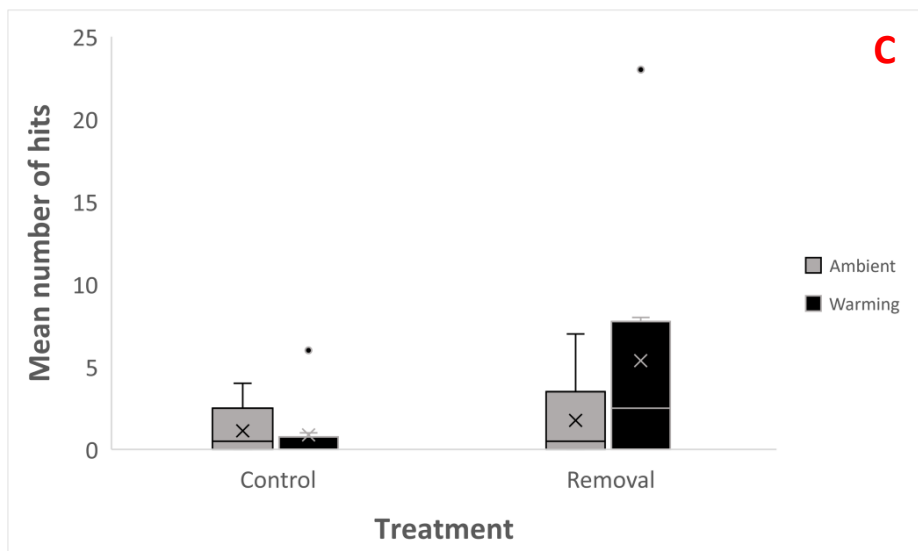
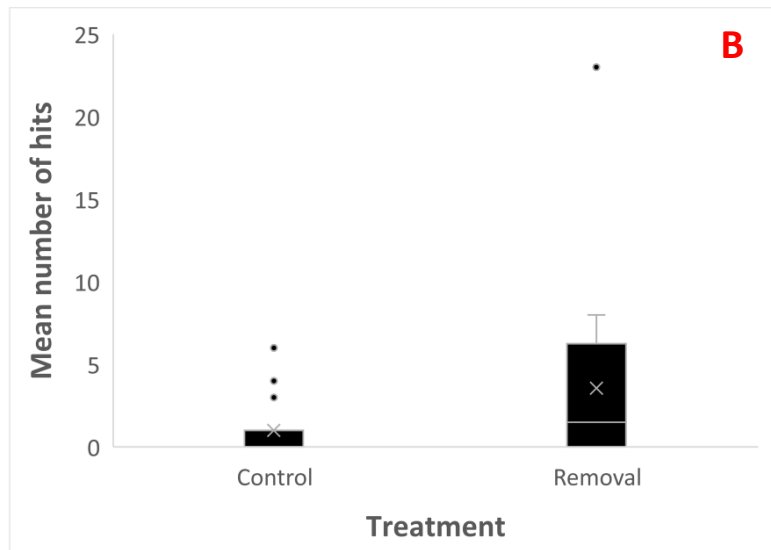
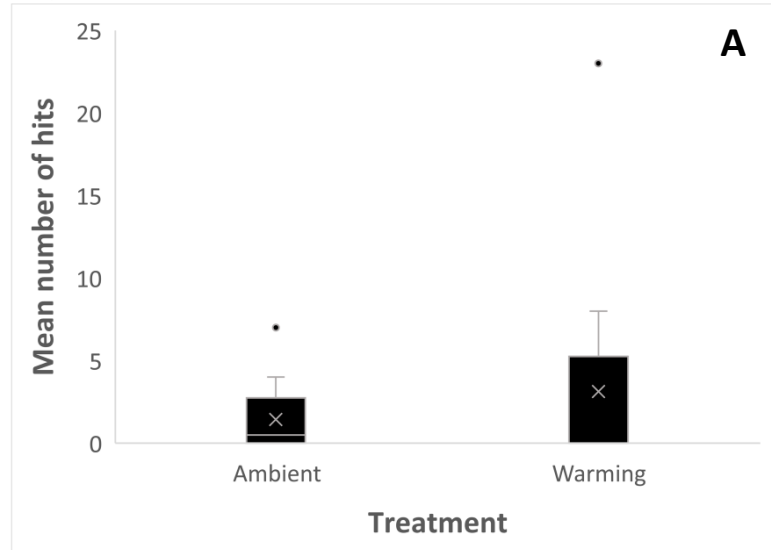


Figure 18

Fig. 18 Mean number of hits for the Cinnamon graminoid species *Juncus drummondii* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

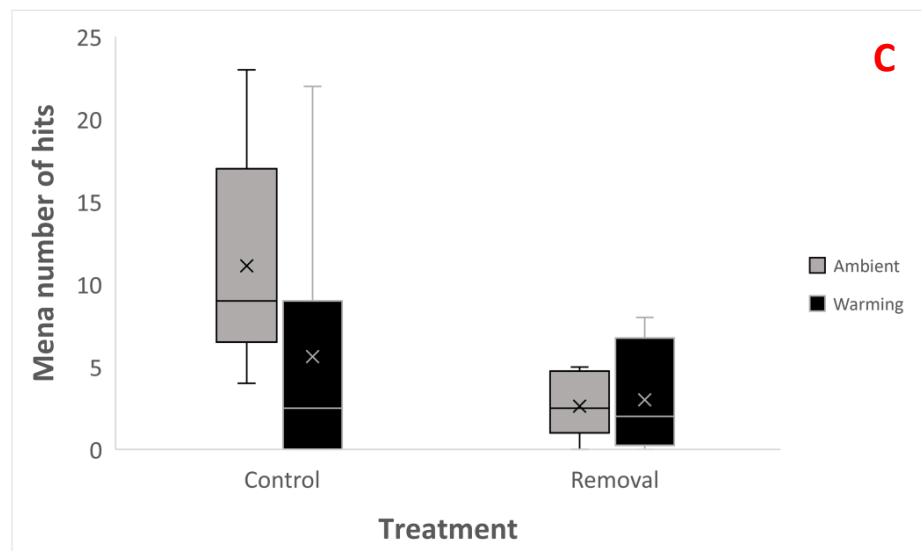
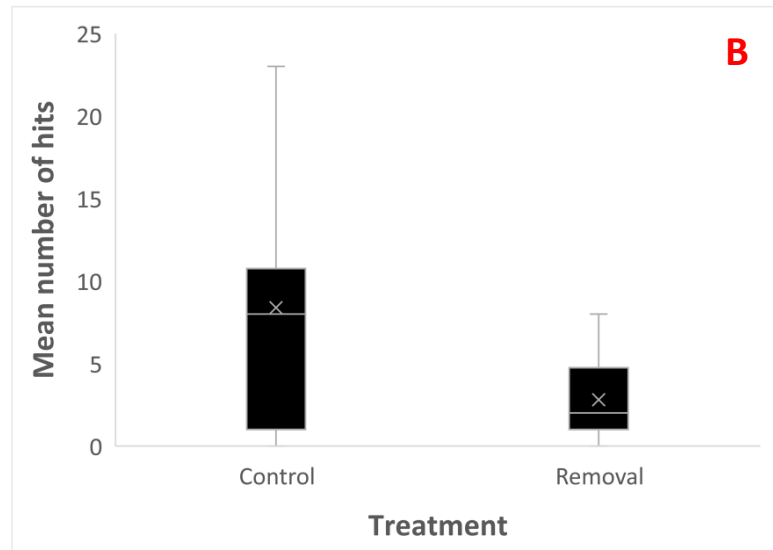
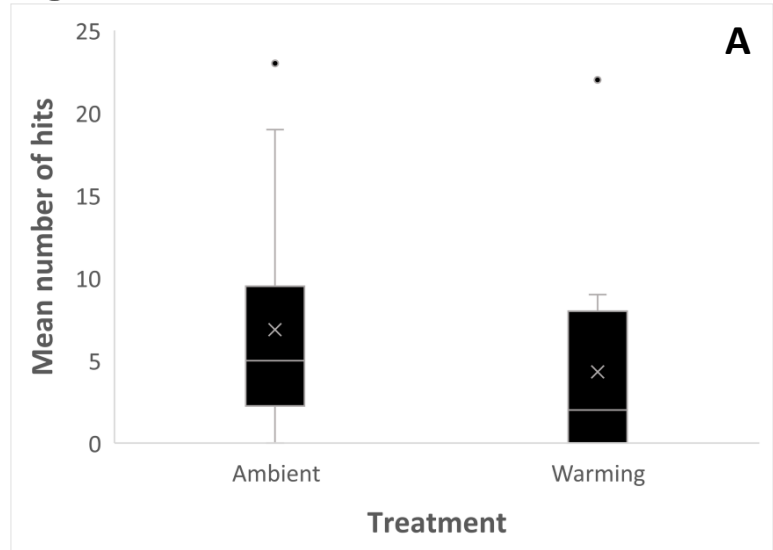


Figure 19

Fig. 19 Mean number of hits for the Cinnamon graminoid species *Poa arctica* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

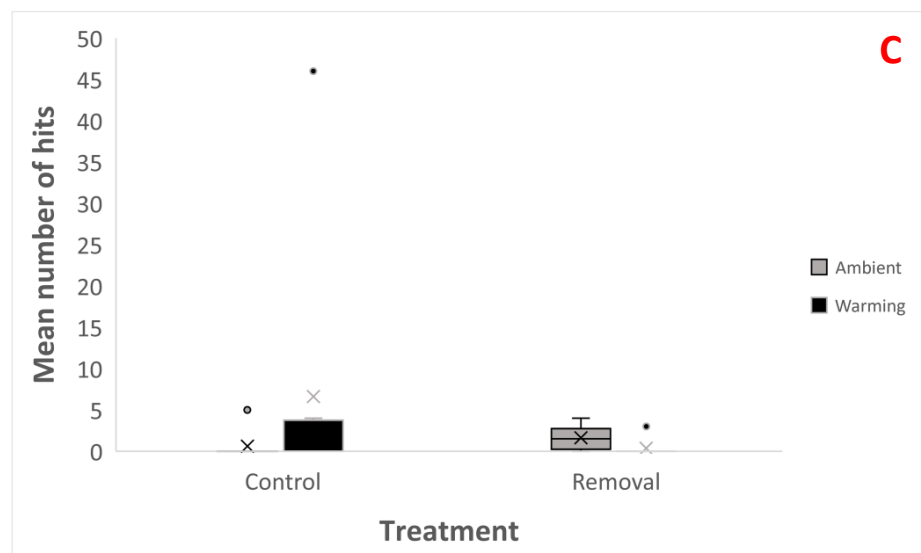
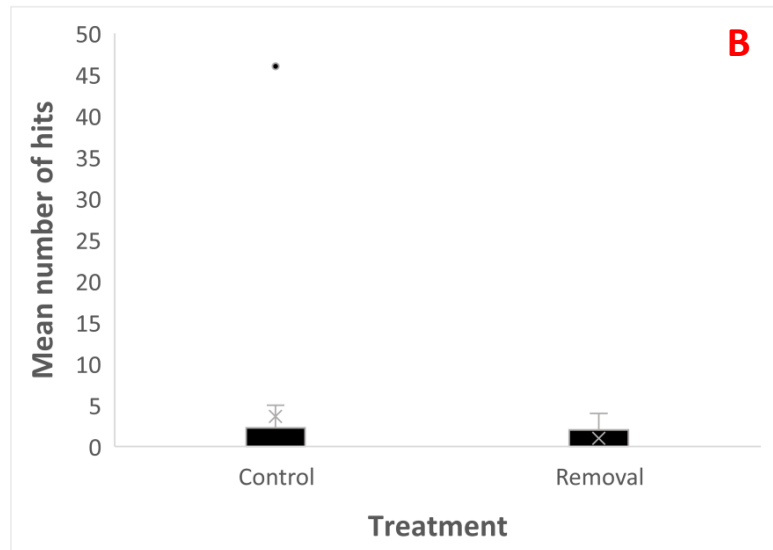
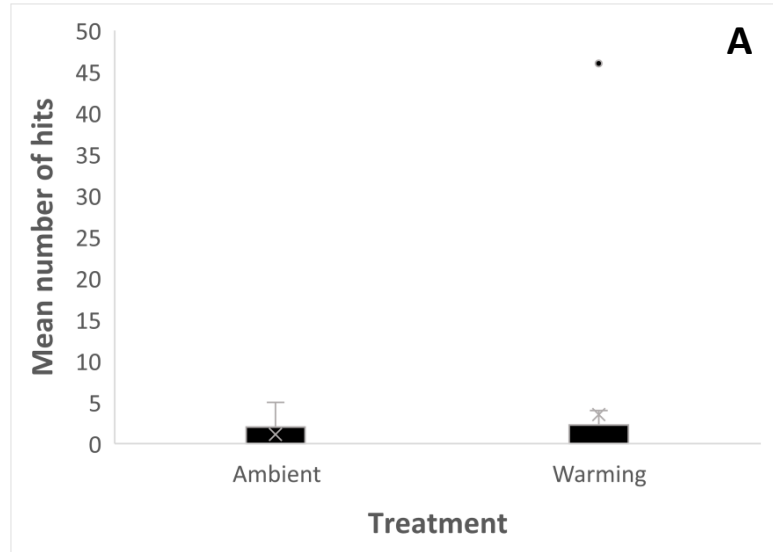


Figure 20

Fig. 20 Mean number of hits for the Cinnamon forb species *Senecio crassulus* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

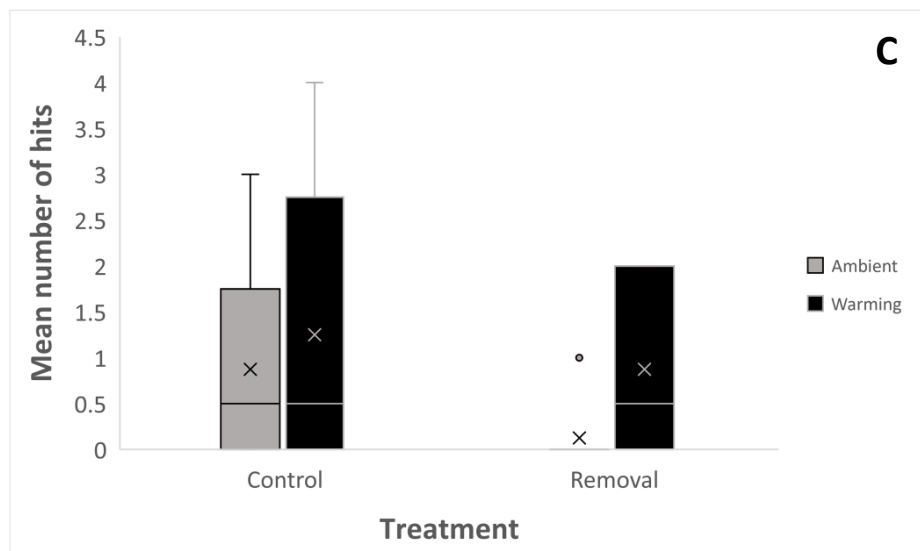
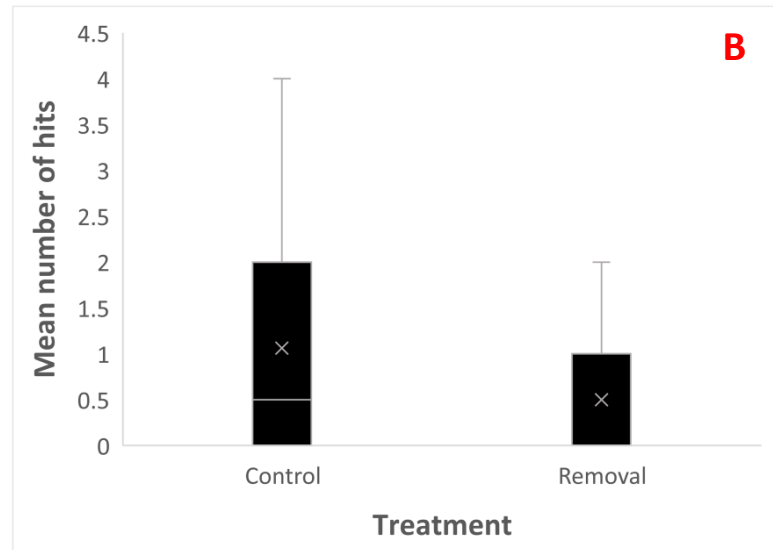
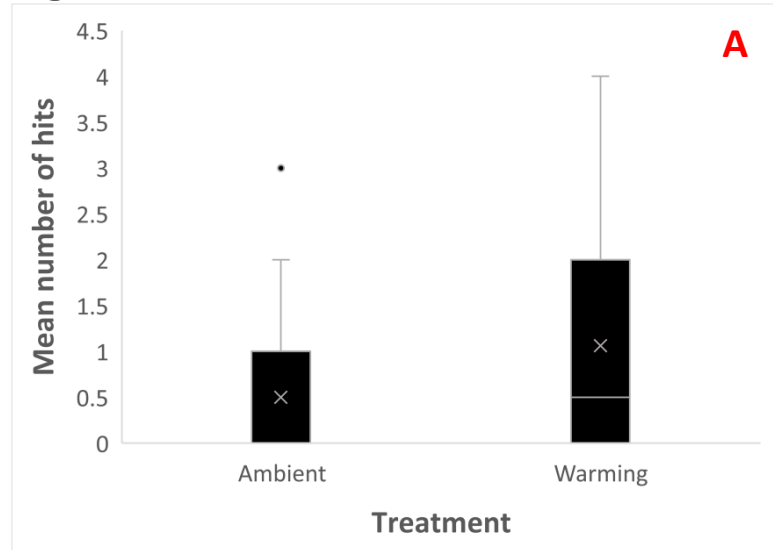


Figure 21

Fig. 21 Mean number of hits for the Cinnamon forb species *Sibbaldia procumbens* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

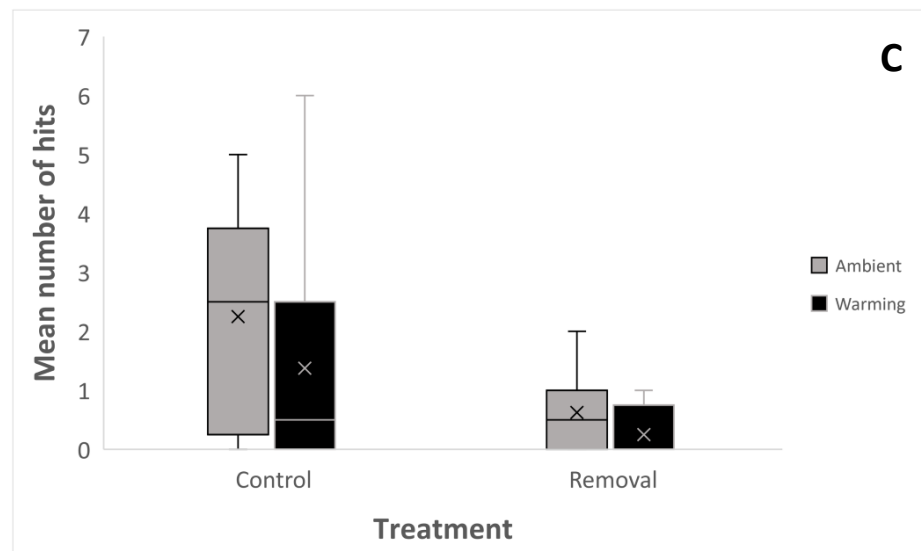
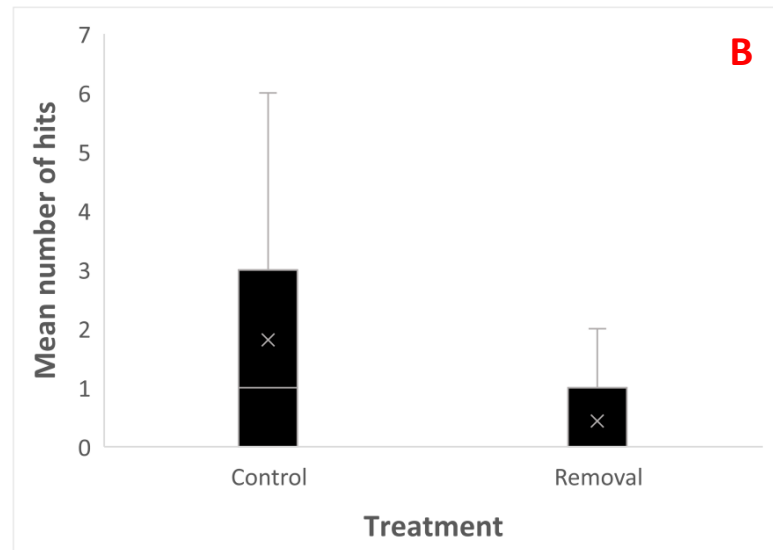
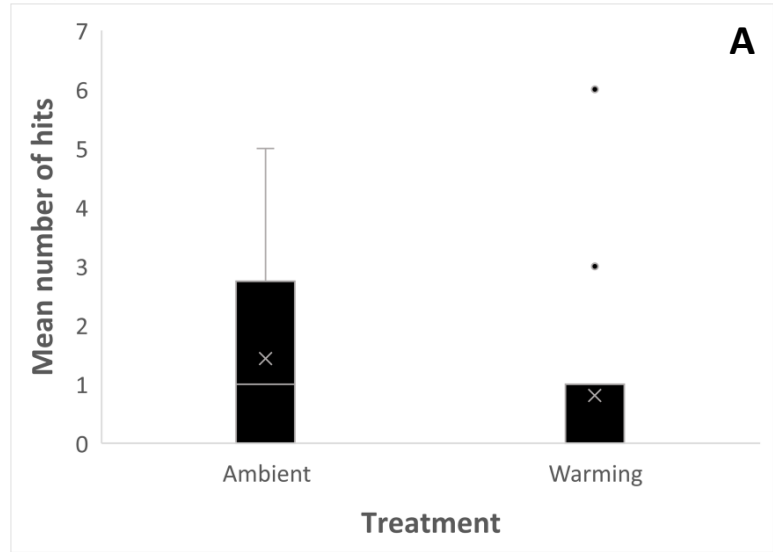


Figure 22

Fig. 22 Mean number of hits for the Cinnamon graminoid species *Trisetum spicatum* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

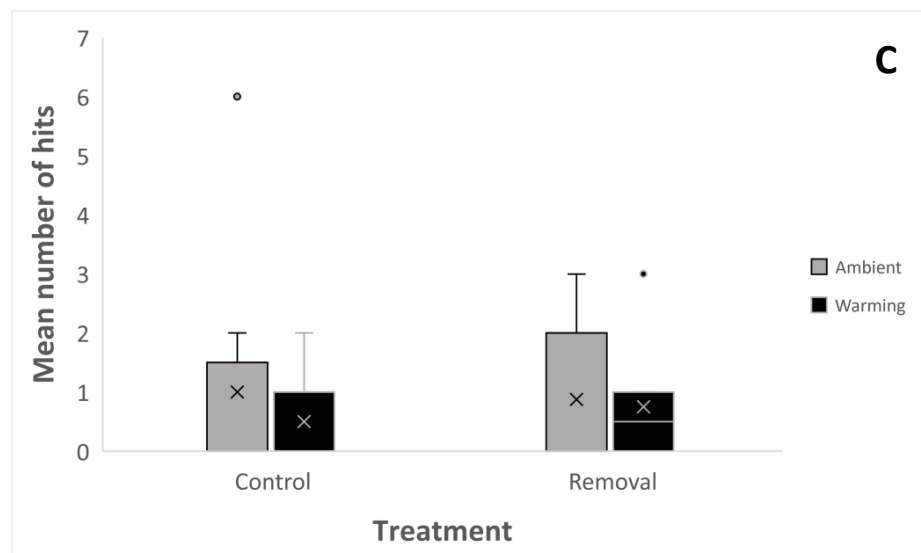
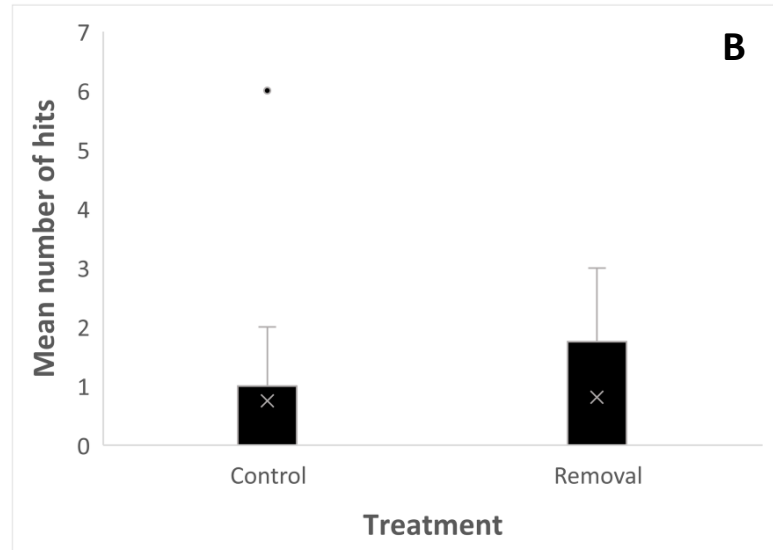
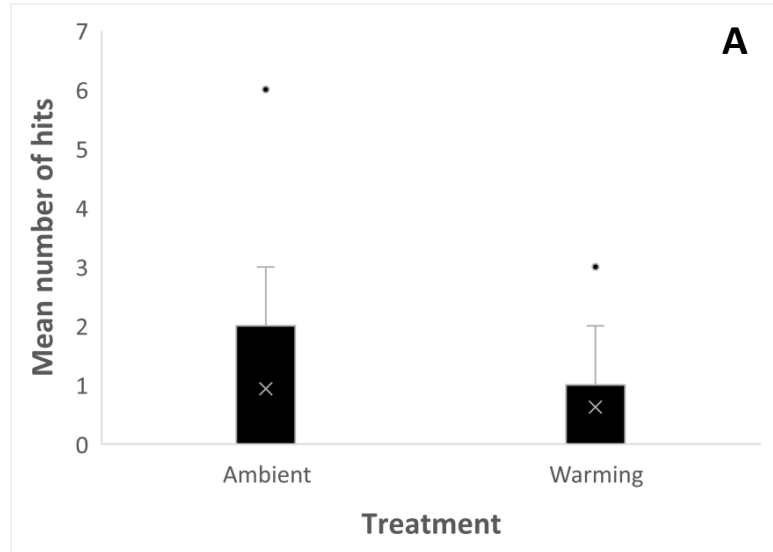


Figure 23

Fig. 23 Mean number of hits for the Cinnamon shrub species *Vaccinium caespitosum* for the A) ambient vs. warming treatments (regardless of removal), B) control vs. removal treatments (regardless of temperature), and C) all unique treatments. Significant responses have a red letter.

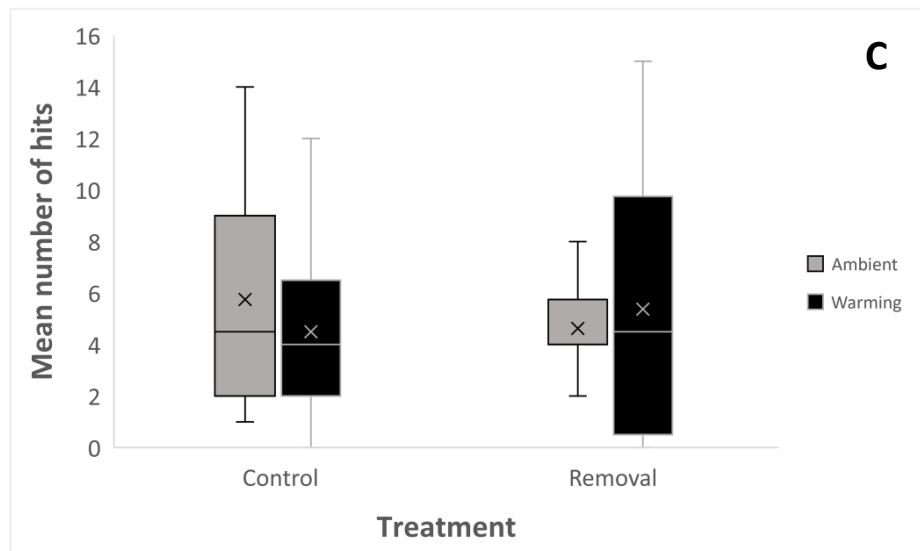
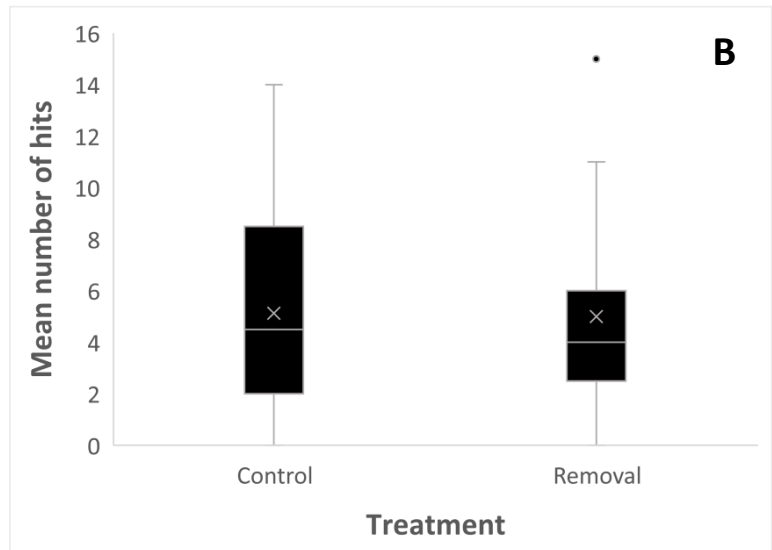
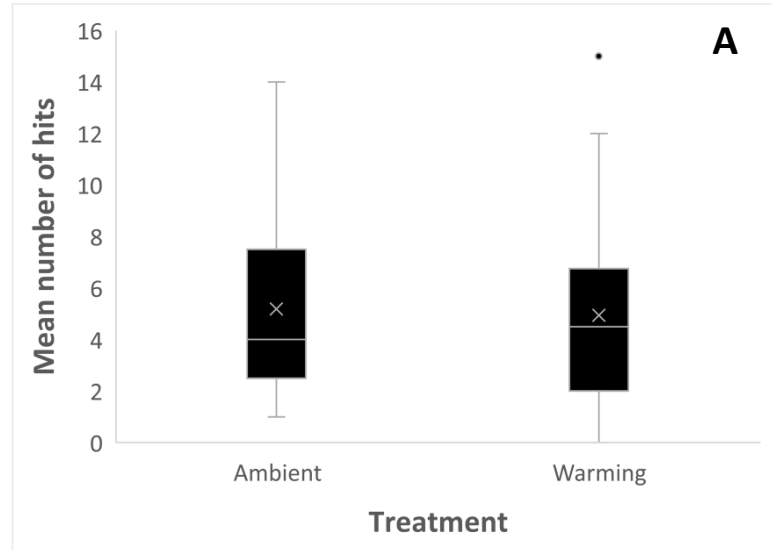
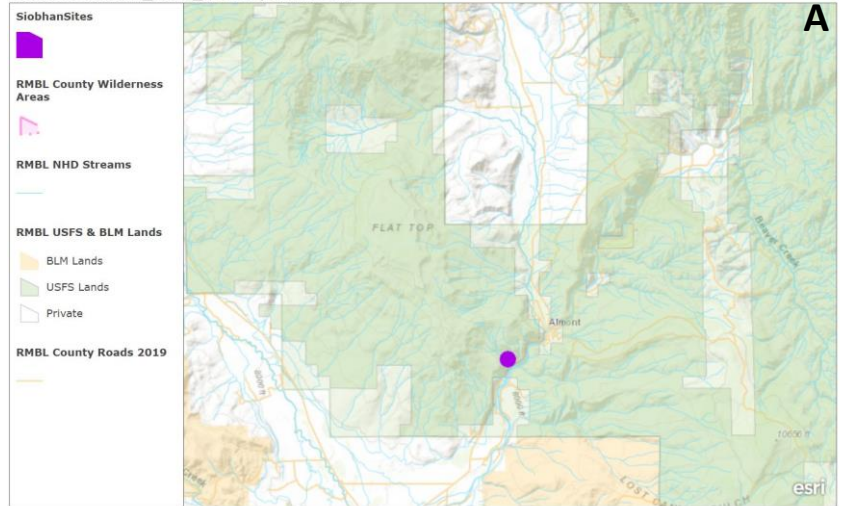


Fig. 24 GIS Maps depicting A) Almont research site, B) Cinnamon research site and C) both research sites.

Figure 24

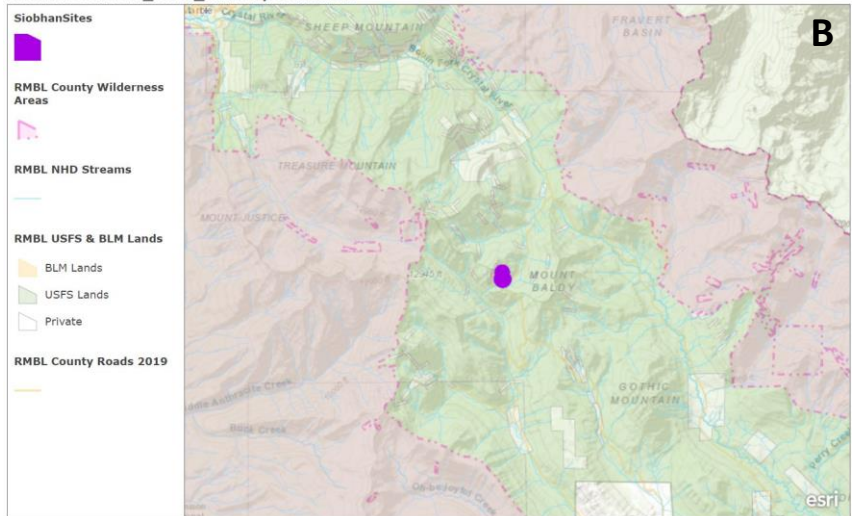
Siobhan Calhoun_2020_Almont/Cinnamon



This map depicts the coordinates of a low elevation research site in the Almont Triangle and a high elevation research site on Cinnamon Mountain. Also included are wilderness areas, streams, forestry lands, and county roads.

Bureau of Land Management, Esri, HERE, Garmin, USGS, NGA, EPA, USDA, NPS

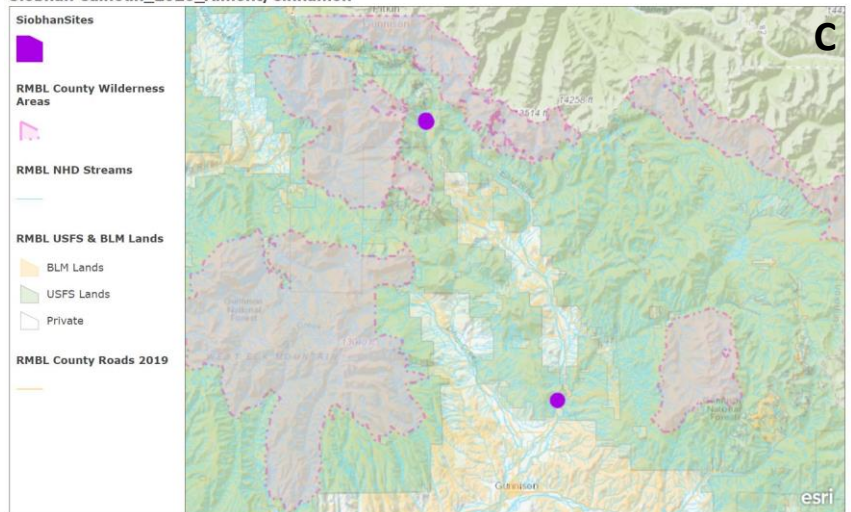
Siobhan Calhoun_2020_Almont/Cinnamon



This map depicts the coordinates of a low elevation research site in the Almont Triangle and a high elevation research site on Cinnamon Mountain. Also included are wilderness areas, streams, forestry lands, and county roads.

County of Pitkin & City of Aspen, Bureau of Land Management, Esri, HERE, Garmin, USGS, NGA, EPA, USDA, NPS

Siobhan Calhoun_2020_Almont/Cinnamon



This map depicts the coordinates of a low elevation research site in the Almont Triangle and a high elevation research site on Cinnamon Mountain. Also included are wilderness areas, streams, forestry lands, and county roads.

Esri, HERE, Garmin, USGS, NGA, EPA, USDA, NPS