Dominance across montane meadows: patterns and processes structuring plant communities

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Abstract

Background. Understanding the underlying factors that determine the relative abundance of plant species is critical to predict both biodiversity and ecosystem function. Biotic and abiotic factors can shape the distribution and the relative abundance of species across natural communities, greatly influencing local biodiversity.

Methods. Using a combination of an observational study and a five-year plant removal experiment we: (1) documented how plant diversity and composition of montane meadow assemblages vary along a plant dominance gradient using an observational study; (2) tracked above- and belowground functional traits of co-dominant plant species *Potentilla* and *Festuca* along a plant dominance gradient in an observational study; (3) determined whether plant species diversity and composition was directly influenced by commonly occurring species *Potentilla* and *Festuca* with the use of a randomized plot design, 5-year plant removal experiment (no removal control, *Potentilla* removed, *Festuca* removed, n=10) .

Results. We found that subordinate species diversity and compositional dissimilarity were greatest in *Potentilla* and *Festuca* co-dominated sites, where neither *Potentilla* nor *Festuca* dominated, rather than at sites where either species became dominant. Further, while above- and belowground plant functional traits varied along a dominance gradient, they did so in a way that inconsistently predicted plant species relative abundance. Also, neither variation in plant functional traits of *Festuca* and *Potentilla* nor variation in resources and conditions (such as soil nitrogen and temperature) explained our subordinate diversity patterns. Finally, neither *Potentilla* nor *Festuca* influenced subordinate diversity or composition when we directly tested for their impacts in a plant removal experiment.

Discussion. Taken together, patterns of subordinate diversity and composition were likely driven by abiotic factors rather than biotic interactions. As a result, the role of abiotic factors influencing local-level species interactions can be just as important as biotic interactions themselves in structuring plant communities.

Introduction

Linkages between species' relative abundance and ecosystem function are important to predict ecosystem resistance and resilience to global change pressures. Dominant species, with high relative abundance (i.e., primary production), have been shown to strongly impact community dynamics and ecosystem function (Whitaker 1972; Wardle et al. 1999; Grime 1977 2001 2006; Hooper et al. 2005). In fact, according to Grime's (1998) "mass ratio hypothesis" species with greater primary production exert the main controls for the functioning of ecosystems. Based on this hypothesis, dominant species are considered more important in an ecosystem because of the greater aboveground abundance of biomass or leaf area (e.g., foliar cover) that promotes resource uptake. However, an increasing amount of recent studies are showing that the subordinate species potentially have an even greater impact on ecosystem function, despite what their relative abundance suggests. In fact, the importance of subordinate species may be seen during environmental change. For example, the results of a mesocosm experiment (Kardol et al. 2010) and a field experiment in mountain grassland (Mariotte et al. 2013a) demonstrated that subordinate species can produce relatively more biomass in changed environmental conditions, such as a drought, which may increase community stability in a time of disturbance.
Furthermore, Grime (1998) suggests subordinates can also associate with dominant species acting as a sieve that influences regeneration of dominants succeeding major perturbations, such as impact events, human impact, and climate change. This suggests that dominant species can respond strongly to the direct presence of an abiotic factor, while subordinate species can be more resistant to abiotic influences and take advantage of the reduced competition (Mariotte et al. 2013a). This promotes ecosystem stability, as the subordinate species are capable of taking over the biomass production through the reduced competition of the dominant species.
Environmental filters such as abiotic conditions and resources (Wellenstein et al. 2013), can shape dominance patterns in plant communities. The environment may select/dictate the ability of species to acquire resources and/or tolerate conditions and dominate, or not, in local communities. In fact, dominant and subordinate species have been shown to vary in above- and belowground functional trait attributes (e.g., specific leaf area and height) across environmental gradients.

Plant functional traits, above- and belowground, provide a critical link between species relative abundances and the functioning of ecosystems (Lavorel 2013). Dominant and subordinate species have been shown to differ in aboveground functional traits (specific leaf area, leaf C:N) that determine plant performance. For instance, dominant species have fast growing/high resource acquisition strategies while subordinate species are associated with resource conservation/slow growing strategies (Diaz et al. 2004; Wright et al. 2004; Mariotte et al. 2013b, 2014). Moreover, dominant species have larger leaf areas that allow better light capture, which in turn leads to a larger production of biomass. Although subordinate species do not exhibit high aboveground biomass production, they allocate resources towards a higher nutrient retention below ground (Lavorel et al. 2011; Mariotte et al. 2013b, 2014). Through this we can see that dominant species have aboveground functional traits that are more resource acquiring and subordinate species have traits that are more resource conservative (Grime et al. 1997; Diaz et al. 2004; Mariotte et al. 2014). While 'aboveground' functional traits have revealed the greater aboveground primary production of dominant species relative to subordinates, 'belowground' functional traits are underexplored to determine ecosystem functions contributions by subordinate species (Mariotte et al. 2014). Alternatively, dominant species may exhibit high abundance relative to subordinate simply by their ability to tolerate environmental conditions rather than by rapid resource acquisition.

Understanding the relative importance of biotic vs. abiotic processes determining the relative abundances of species (Weiz et al. 2013), and how these processes shape above-and belowground traits, is critical to isolate the processes influencing biodiversity of dominant and subordinate plant genotypes (Read et al. 2014) and species (Koerner et al. 1987). For example, in this study, we investigated how subordinate species diversity and composition varied along a plant dominance gradient and then we directly tested the effects of two co-occurring dominant montane meadow plant species: *Festuca thurberi* (hereafter *Festuca*) and *Potentilla graciilis* (hereafter *Potentilla*) to influence community diversity and composition of subordinate species. We first conducted an observational study that compared subordinate diversity and composition along a plant dominance gradient (from *Potentilla dominance* to *Potentilla* and *Festuca* co-dominance to *Festuca* dominance). We then conducted a four-year plant removal study that directly tested the effects of *Festuca* and *Potentilla* on subordinate species diversity and compositional similarity with the following treatments: control (no plant removal), *Potentilla* removed, *Festuca* removed. Specifically, we asked the following questions: (1) Does diversity and composition of subordinate montane meadow assemblages vary along a plant dominance gradient?; (2) Do above- and belowground functional traits of dominant vs. subordinate species vary along a plant dominance gradient? ; (3) How do co-occurring dominant species alter subordinate diversity and composition?

Materials and Methods

Study Site

Our study sites were located at the Rocky Mountain Biological Laboratory (RMBL), Gothic Colorado (latitude 38º53' N, longitude 107º02' W, elevation 2920 meters above sea level) (Saleska et al. 1999). Annual precipitation averages 750 mm, 80% of which was snow (snowmelt typically ending in May) (Saleska et al. 1999; Harte et al. 1995). Mean daily-average summer air temperature is ~10ºC. Mean snowfall at RMBL is 1,1140 cm with a trend towards lower snowfall overtime (Inouye et al. 2000) with field summer seasons ranging from 0.69 m and 0.47 m (water equivalent), respectively (Harte et al. 1995). Soil texture is a well-drained Cryoboroll, which is a deep rocky outcrop that is non-calcareous and formed on a glacial till (Saleska et al. 1999). Below a sparse litter layer (due to snowpack), the soil is uniform in color and texture down to about 50cm. Organic content averages ~10% at a soil depth of 5 cm below the litter layer and drops to ~6% at 50 cm (Harte et al. 1995). Soils at the experimental and observational sites averaged a pH of 5.7-6.3 (Saleska et al. 1999).

Experimental Design

Observational Study

We selected three montane meadow sites where: (1) *Festuca thurberi* exhibited high abundance (i.e., *Potentilla* low abundance), (2) *Festuca* and *Potentilla* exhibited similar abundances (i.e., co-dominated), and (3) *Potentilla gracilis* exhibited high abundance (i.e., *Festuca* low abundance). In each observational site, we established 9, 1-m^2 plots and tracked the identity and relative abundance of all species (dominant and subordinate) over a growing season from the beginning of July to late June in 2014. The plots were selected by laying down three transects at each observational site, about 3 meters apart. Three 1-m^2 plots were measured out per transect, about 1 meter between each plot along a transect. The transects were randomly selected and the plots were determined along each transect to fulfill one of each of the following: *Potentilla* Dominated, *Festuca* Dominated, and Co-Dominated. Therefore, each of the three transects included 1-m^2 plots of *Festuca* Dominated, a *Potentilla* Dominated, and a Co-Dominated.

Experimental Study

We manipulated the presence of *Festuca* and *Potentilla,* which co-dominate within this existing montane meadow vegetation, across 1.5m × 1.5m plots (N=30). The plots were spaced one meter from each other in a completely randomized plot design with the following three treatments: (1) control (no plant species removed), *Festuca* removed, *Potentilla* removed. In removal treatments, plant species were clipped (to 1cm from the ground) throughout the growing season (June-August), for three growing seasons (2013-2015).

Above and Below Ground Functional Trait Measurements

To determine above- and belowground variability across three sites (ranging in the dominance *Festuca* and *Potentilla*), 2 thirty-meter transects were established at each site (outside of our plant sampling plots). Every 6-meters, a 1m ×1m plot was placed (totaling 5, 1-m^2 sampling plots per transect and N=10 per site). At each plot for *Festuca* and *Potentilla*, percent coverage was recorded and leaves and roots were harvested according to the methods by Cornelissen et al. 2003. Specific leaf area (SLA) was taken by harvesting three relatively young but fully expanded and hardened leaves from each individual. Leaves were then scanned to obtain area (cm^2) using ImageJ. Leaves were then oven dried for approximately 48 hours at 65ºC and weighted. We then divided area by mass to obtain SLA (cm^2 g^{-1}). We sampled absorptive roots from a single individual of each species (*Festuca* and *Potentilla*) per plot in each transect to estimate specific root length (SRL, cm g^{-1}). For *Potentilla* we dug up the entire plant and root systems with a spade and then bagged the entire mass for later analysis. For *Festuca* we used a large soil core to sample roots from the plant species, by angling the soil core into the base of the plant, to ensure only roots of that species were extracted. Ten fine root pieces from each core were separated and used for analysis. Using ImageJ again, we scanned and interpreted the data using a Plugin called 'IJ Rhizo v0beta'. We then oven dried roots for approximately 48 hours at 65ºC and weighted.

Plant Community Measurements

To examine how subordinate diversity varied along a plant dominance gradient (*Observational Study*) and how dominant species directly affected subordinate diversity (*Experimental Study*), we measured species-specific foliar cover, species richness (the number of species), Shannon's diversity and evenness in each observational and experimental plot twice in each growing season (Observational Study= 1 growing season, Experimental Study= 3 growing seasons). To estimate species-specific foliar cover, we used a modified Braun-Blanquet scale that included six categories: <1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-100%. H´was calculated as: H´=-sum(pi*(ln*pi))and evenness was calculated as J'=H'/S.

Microclimate measurements

To determine how resources and conditions varied along a dominance gradient (*Observational study*), as well as being impacted by dominant species (*Experimental study*), we tracked light and soil nutrient availability (resources) as well as soil temperature (conditions). We measured photosynthetic active radiation (PAR, hereafter light availability) during the peak of the growing season (July) in each of the experimental and observational plots, as well as soil temperature and soil nitrogen availability. To estimate light availability, we used a line-integrating ceptometer (Decagon Accupar; Decagon Devices, Pullman, WA) with all light availability measurements made on clear days between 11 am and 2 pm. To determine soil temperature, we used ibuttons (MAXIM) that recorded surface soil temperature every minute. To assess the availability of NO3-N and NH4-N in the soil solution, we placed mixed-bed ion-exchange resin bags in nylon stockings (H-OH form, #R231-500; Fisher Scientific International Inc., Pittsburgh, PA) at 5-cm soil depth at two locations in each of the experimental and observational plots (Hart et al. 1994). Resins were then air-dried, and 2 g of resins from each plot were extracted with 2 M KCl. Pool sizes of NO3_ and NH4 + were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000; Hach Corporation, Loveland, OH). All values expressed in this article are based on air-dried resins.

Statistical Analyses

To determine how subordinate species diversity, as well as above- (SLA) and below-ground (SRL) plant functional traits, varied along a plant dominance gradient (*Observational study*), we ran a series of one-way analyses of variance (ANOVAs) with 'site' as our main fixed effect (e.g., *Potentilla* dominated, *Festuca* dominated, Co-dominated). To determine the direct role of dominant species on subordinate species diversity we performed one-way ANOVAs with 'plant removal' (control, *Potentilla* removed, *Festuca* removed) as our main fixed effect (*Experimental study*). All the ANOVA analyses were conducted using Jump 11 (JMP).

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To determine (1) how compositional similarity of subordinate species varied along a plant dominance gradient and (2) how dominant species affected compositional similarity of subordinate species, we generated a Bray-Curtis similarity matrix from the log transformed plant composition (log x+1). We then performed a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on the Bray Curtis similarity matrix. A pseudo F-ratio is calculated within the PERMANOVA framework comparing the variability in species composition both *within* treatments and *among* treatments based on the observed variability in species composition vs. the variability in species composition using a generated null distribution (Anderson et al. 2006). PERMDISP (permutational multivariate analysis of dispersion) analysis, on the other hand, is a measure of 'dispersion' of community composition in multivariate space (Anderson et al. 2006). We used PRIMER version 1.0.3 (Plymouth Marine Laboratory, UK) for these analyses. We performed a series of principal coordinate analyses (PCO) to illustrate species compositional similarity and dissimilarity in a two-dimensional multivariate space,. Finally, we used a a similarity percentage analysis (SIMPER) to determine the relative contribution of plant species driving compositional dissimilarities both in the observational as in the experimental study.

Results

Community structure and compositional similarity across a dominance gradient (*Observational Study*)

Plant community structure differed across a dominance gradient. Co-dominated sites, generally, had greater total cover, richness, evenness and diversity than *Potentilla* or *Festuca* dominated sites (Table 1, Figure 1). For example, total cover was 26% greater while evenness, richness, and diversity were 6%, 24%, and 15% greater respectively when both *Festuca* and *Potentilla* co-dominated than when either species became dominant. Plant species composition, similarly to community diversity, differed across a dominance gradient (Table 2, Figure 2). While all sites differed from one another in compositional similarity, co-dominated sites differed the most in compositional similarity to either *Potentilla* or *Festuca* dominated sites. Co-dominated communities had a greater proportion of perennial forb species that differed in identity from perennial forbs in dominated sites by either *Potentilla* or *Festuca*. For example, co-dominated communities had a greater abundance of *Erigeron speciosa*, *Artemesia ludiciviana,* and *Fragaria virginiana* than *Potentilla* or *Festuca* dominated sites (which had greater proportion of perennial forbs such as *Helianthella quinquenervis* and *Thalictrum fendleri*) which is a clear shift in composition.

Shifts in above-and belowground functional traits across a dominance gradient (*Observational Study*)

Both above- and belowground plant functional traits varied along a plant dominance gradient, but plant identity dictated such variation. For example, the average area of *Festuca* leaves (F=9.24, P=0.001), but not SLA (P>0.05), was 40% greater in *Festuca* dominated (9.79 ± 0.54) and co-dominated sites (11.15 ± 0.75) compared to *Potentilla* dominated sites (6.86 ± 0.84) where *Festuca* is subordinate. On the other hand, *Festuca* SRL was 38% greater when it became subordinate (e.g., *Festuca* 2712.88 ± 351.58 in *Potentilla* dominated site) than when it dominated local communities (1990.39 ± 214.44 in *Festuca* dominated site) (F=9.37, P=0.001). Similarly, *Potentilla* differed marginally in aboveground functional traits, while differing strongly in belowground functional traits across a plant dominance gradient. For the aboveground functional traits, the average area of *Potentilla* leaves was greater in *Festuca* dominated than co-dominated or *Potentilla* dominated sites (F=2.83, P=0.07). *Potentilla* dominated site leaf area was on average 143.95 cm^2 ± 19.74 while in co-dominated site and *Festuca* dominated site leaf area was 171.26 cm^2 ± 6.99 and 170.16 cm^2 ± 20.35 respectively. Specific leaf area, on the other hand, did not differ (F=0.84, P=0.44) across dominance gradient for *Potentilla* (*Potentilla* dominated site: 103.37 cm^2 ± 10.82; Co-dominated site: 102.52 cm^2 ± 10.21; *Festuca* dominated site: 131.72 cm^2 ± 8.42). Belowground functional trait (SRL) for *Potentilla* was 30% greater when (F=3.77, P=0.35) *Potentilla* was a co-dominant than when it was a dominant (*Potentilla* dominated site) or subordinate (*Festuca* dominated site).

Community Structure, Compositional Similarity (*Experimental Study*)

We found that neither dominant species, *Potentilla* or *Festuca*, affected plant richness, evenness and diversity (Table 3, Figure 3, Appendix Figure 1). Similarly, compositional similarity was not impacted by dominant species (Table 4, Figure 4, Appendix Figure 2).

Microclimate across a plant dominance gradient (*Observational & Experimental Study*)

We found light availability and temperature, but not soil N availability, to vary along a plant dominance gradient. Light availability was 25% greater in *Festuca* dominated sites than co-dominated or *Potentilla* dominated communities. Further, co-Dominated sites and *Festuca* dominated sites had the largest minimum and maximum temperature difference (60.20ºC and 60.11ºC, respectively). *Potentilla* dominated sites had a lower temperature difference of 53.28ºC, which coincides with having the lowest light availability measurements within these plots. Finally, we found no effects of dominant species on resources (light availability and soil N) or conditions (soil temperature) (Tables 5 & 6).

Discussion

Subordinate species diversity and composition varied along a dominance gradient with highest diversity, yet lowest compositional similarity, in plant communities co-dominated by both *Festuca* and *Potentilla*, rather than communities dominated by either species. In other words, in co-dominated sites, where *Potentilla* and *Festuca* were equally abundant, subordinate diversity and compositional dissimilarity were the greatest. While above- and belowground plant functional traits varied along a dominance gradient, neither above- nor belowground plant functional trait of *Festuca* and *Potentilla* consistently predicted relative abundance. Further, variation in resources and conditions did not explain our subordinate diversity patterns. Finally, neither *Potentilla* nor *Festuca* influenced subordinate diversity or composition when we directly tested for their impacts in a plant removal experiment. Taken together, patterns of subordinate diversity and composition were likely driven by unaccounted abiotic factors rather than biotic interactions. Alternatively, subordinate species could have rapidly compensated for the loss of dominance and therefore we did not record the changes as our measurements were taken a month after the manipulation of the plots.

Community diversity and compositional similarity across a dominance gradient: Observation vs. Experiment

Co-dominance by *Potentilla* and *Festuca* was associated with greater subordinate species' abundance and overall diversity than when either *Potentilla* or *Festuca* was manipulated to become dominant in a plot, along a dominance gradient. Dominant species have been shown to strongly impact subordinate species' abundance and biodiversity by disproportionately utilizing resources or conditions that would otherwise be available for subordinate species, especially in favorable (Wardle et al. 1999; Wilsey & Polley 2002; Diaz et al 2003) rather than unfavorable environments (Smith et al. 2004). Under favorable conditions, dominant species can have antagonistic effects on subordinate counterparts given their higher competitive abilities with higher resource availability. Over–yielding, dominant individuals may modify resources and conditions for subordinates drastically. Similar to our documented patterns, Suding et al. (2001), found dominant species to reduce subordinate biodiversity by monopolizing resources and therefore exhibiting greater resource uptake rates, reducing subordinate species' abundance. Plant dominance may not only lower biodiversity at the plot level, but overall diversity among subordinate assemblages. Lower among assemblage diversity or spatial-temporal homogenization of subordinate species, can lead to a potentially long-term biodiversity deficit due to a lower regional species-pool which won't be resupplying local subordinate assemblages with more plant species propagules. In other words, co-dominance patterns could promote short- (richness, evenness, diversity) and long-term (compositional similarity) biodiversity patterns in montane meadows.

However, when we directly tested for the effects of co-dominant species to influence subordinate biodiversity we found that removing either *Festuca* or *Potentilla* did not affect subordinate diversity. Similar to our findings, Smith and Knapp (2003) also found that dominant species did not affect subordinate species diversity. Smith and Knapp found that after removing dominant C_4 grasses the subordinate assemblage in the grassland ecosystem did not compensate for the loss of dominant species. Instead, they found that subordinate productivity was unaffected by even a 50% reduction in density. In a field experiment conducted by Souza et al. (2011), diversity of the subordinate community was found to be on average 20% greater in plots with the removal of a dominant forb species, *Solidago altissima*. Similarly, in *Verbesina* removal plots, diversity on average was 30% greater than in plots where *Verbesina* was present. Even though the removal of dominant species affected diversity and evenness, there were no effects on composition of these plots, because richness did not change (Souza et al. 2011). On the other hand, dominant species may attain high abundance by being good ‘stress-tolerators’ rather than a great competitor relative to other species (Read et al. 2017) that have low abundance and classified as subordinate or transient.

Whittaker (1965) suggests that a closer look should be taken to differentiate between subordinate and transient species, as there is a keen distinction that separates them. Where subordinates consistently co-occur with specific dominants in larger abundance than the dominants, though smaller in build, transient species lack consistency of association with dominants and infrequent occurrence temporally and spatially. Transient species have been found to make a small contribution to biomass, though most are species that occur as dominants or subordinates in other communities, often nearby. Though through our observations and experiments, we found that dominant species did not affect subordinate diversity as expected, as the majority of the plant species in our montane meadows were transient and very few were actually subordinate species (see Appendix Table 1).

Changes in biodiversity, along the plant dominance gradient, translated into divergence in subordinate species’ compositional similarity. Co-dominated subordinate communities exhibited greater equitability of subordinate forbs than either *Festuca* or *Potentilla* dominated communities that exhibited two main subdominant forbs making up subordinate species assemblages. Similar to our documented patterns, dominant species have been found to alter compositional similarity of subordinate assemblages (Grime 1998). However, when we directly tested for the effects of co-dominant species to influence subordinate species composition we found that removing either *Festuca* or *Potentilla* did not affect subordinate compositional similarity. Similar to our findings, Souza et al. 2011) also found that dominant species did not affect subordinate species composition in an old-field ecosystem. For instance, when Souza et al. (2011) removed either C_3 perennial forb: *Solidago* or *Verbesina* species, compositional similarity of subordinate species did not converge or diverge relative to dominant species removal treatments.

Shifts in above-and belowground functional traits across a dominance gradient

Plant functional traits varied along the plant dominance gradient, but the documented patterns did not support our original prediction that functional traits would be associated with dominance patterns. Specific root length, plant allocation towards greater investment on root area than mass increasing surface area to volume ratio that promotes greater resource uptake, increased for both *Festuca* and *Potentilla* when they became more subdominant than dominant. Such shift in belowground traits for both *Festuca* and *Potentilla* likely resulted from greater resource competition when they are subdominant than dominant. Such belowground strategy differs from other studies that have found subdominant species to generally have root traits associated with resource conservation rather than rapid acquisition (Mariotte 2013a, 2014). Perhaps montane plant communities with narrower growing season windows relative to other systems, foster greater plasticity in belowground traits that promote persistence of subdominant species.

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Surprisingly aboveground functional traits, such as SLA did not shift when *Festuca* and *Potentilla* became subdominant. Greater total leaf area production (e.g., greater foliar cover) in dominated sites promoted dominance regardless of changes in leaf function. There are many different factors that can contribute to a lack of correlation in diversity and above- and belowground functional traits, such as abiotic constraints (Hooper et al. 2000): species or groups of plants could be responding to different abiotic constraints, such as soil nutrients and water availability (Hooper et al. 2000). Though above- and belowground functional traits do not directly associate with species relative abundance, functional traits of dominant plant species influence ecosystem resilience and resistance. Generally, communities dominated by slow growth plants tend to have low resilience and low resistance, while the opposite is true for communities dominated by fast growing plants (Aerts 1995; Leps et al. 1982; MacGillivray et al. 1995). However, a recent study performed in a montane meadow nearby (with greater dominance of *Festuca* than our plant removal plots) found fast compensatory responses of functional traits in subordinate species in removal relative to control plots (Read et al. 2017).

Biotic and Abiotic filters determining species' relative abundances

Biotic and abiotic filters can determine the distribution and relative abundances of species across space and time. Abiotic filters, such as environmental factors like climate, can dictate the distribution and relative abundance of species across biomes (Whittaker 1975; Grime 1979; Huston 1999; Pavoine et al. 2011). Biotic filters, such as species interactions as in the form of predation or competition, can influence the relative abundance of species in local assemblages (Mouquet & Loreau 2003). Subordinate diversity and composition in our system are likely shaped by differences in environmental factors. Similarly, sedge dominated plots varied in relative abundance due to soil nutrient as an abiotic factor in montane meadows studied by Theodose and Bowman (1997). In these montane dry meadow and wet meadow sites, Theodose and Bowman observed changes in community composition and diversity following additions of nitrogen and phosphorous fertilizers over a five-year study. In the dry meadow, Theodose and Bowman found species diversity increased significantly with fertilization, in the form of Nitrogen and Phosphorus, over the course of the study. This increase of diversity seems to have been due to an increase in the relative abundance of rare species, while the dominant species declined. In juxtaposition, the wet-meadow species diversity decreased in response to fertilization over the course of the study. This comparison allows for the comparison of the effects of fertilization on diversity between communities that differ in resource availability (Theodose & Bowman 1997).

Conclusions

Our study asked: (1) Does diversity and composition of subordinate montane meadow assemblages vary along a plant dominance gradient? (2) Do above- and belowground functional traits of dominant vs. subordinate species vary along a plant dominance gradient? ; (3) How do co-occurring dominant species alter subordinate diversity and composition? We found that subordinate species diversity varies along a plant dominance gradient, peaking when both dominant species co-dominated. We also found that above- and belowground functional traits varied along a plant dominance gradient, but not in always in a predictable way of species' relative abundances. In other words, above- and belowground plant functional traits of dominant species did not consistently exhibit highest values at high relative abundance and low at lower abundance. Finally, co-occurring dominant species did not influence the diversity or compositional similarity demonstrated in our 3-year plant removal experiment. Abiotic factors, rather than biotic interactions, likely shape dominance patterns and subordinate diversity and composition in across *Festuca* and *Potentilla* dominated montane meadow communities. Overall, biotic factors do not seem to drive subordinate dynamics. Therefore, as climate change occurs, it will be extremely important to examine abiotic factors when trying to determine the future structure of plant communities.

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Table 1(on next page)

Plant community metrics across a dominance gradient

Dominant species effects, across sites, influenced total plant community cover and plant community structure (α diversity, shannon's evenness, and shannon's diversity) across montane meadows. Results from one-way analysis of variance (ANOVA) including F-ratio (F) and P-values (P) across time (June and July).

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TOTAL COVER				
	JUNE		JULY	
SOURCE	F	P	F	P
Dominance	9.9815	**0.0006**	6.9543	**0.0037**
α DIVERSITY				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominance	1.1713	0.3252	5.2	**0.0123**
SHANNON'S EVENNESS				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominance	2.2157	0.1284	7.31	**0.0029**
SHANNON'S DIVERSITY				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominance	7.8929	**0.002**	11.845	**0.0002**

Table 2 (on next page)

Species composition across a plant dominance gradient

PERMANOVA analysis results testing for the effect of ‘site’ (plant dominance gradient- *Potentilla* dominated, *Potentilla* and *Festuca* co-dominated, *Festuca* dominated) on subordinate species composition in June and July of 2014.

June- Across Site					
Source	df	SS	MS	Pseudo-F	P(perm)
Site	2	20491	10245	14.838	0.0001
Res	45	31071	690.47		
Total	47	51562			

July- Across Site					
Source	df	SS	MS	Pseudo-F	P(perm)
Site	2	16977	8488.5	12.383	0.0001
Res	45	30848	685.51		
Total	47	47825			

Table 3(on next page)

Community metrics across plant removal treatments

ANOVA analysis results testing for the effect of plant removal (*Potentilla* removal, *Festuca* removal, no removal control) on subordinate plant cover, alpha diversity, shannon's evenness, shannon's diversity for June and July 2014.

CO-DOMINATED SITE

TOTAL COVER				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominant Removal	0.01	0.98	4.16	**0.03**
α DIVERSITY				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominant Removal	0.06	0.94	0.83	0.44
SHANNON'S EVENNESS				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominant Removal	1.07	0.36	0.16	0.85
SHANNON'S DIVERSITY				
	JUNE		**JULY**	
SOURCE	F	P	F	P
Dominant Removal	0.21	0.81	0.61	0.54

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Table 4(on next page)

Species compositional similarity across plant removal treatments

PERMANOVA analysis results testing for the effect of plant removal treatments (*Potentilla* removal, *Festuca* removal, no removal control) for June and July of 2014.

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CO-DOMINATED SITE JUNE					
Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	2	1733.1	866.57	1.3565	0.1682
Residual	27	17249	638.84		
Total	29	18982			

CO-DOMINATED SITE JULY					
Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	2	1022.1	511.06	0.70289	0.8319
Residual	27	19631	727.09		
Total	29	20654			

Table 5 (on next page)

Soil nitrogen and plant dominance

ANOVA table indicating the mean and (SE) of soil ammonium, soil nitrate, and total soil nitrogen, along with model F-ratio and P-value for observational and experimental studies.

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Observational Study

	Ammonium				Nitrate				Total Nitrogen			
	Mean	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**
Potentilla Dominated	2.19	2.41	1.62	0.22	0.28	0.01	0.33	0.72	2.47	2.4	1.62	0.22
Co-Dominated	2.58	6.37			0.3	0.03			2.88	6.39		
Festuca Dominated	2.42	0.84			0.29	0.01			4.77	6.56		

Plant Removal Experiment

	Ammonium				Nitrate				Total Nitrogen			
	Mean	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**
Control	0.98	0.22	0.72	0.49	0.29	0.01	1.19	0.31	1.27	0.74	0.72	0.49
Potentilla removal	1.67	0.77			0.29	0			5.59	11.06		
Festuca removal	1.75	0.57			0.3	0.01			2.04	1.64		

Table 6 (on next page)

Light and soil temperature and plant dominance

ANOVA table indicating the mean and (SE) of light availability (PAR), minimum and maximum temperature, along with model F-ratio and P-value for observational and experimental studies.

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Observational Study

	PAR (umol photons $m^{-2}s^{-1}$)				Min Temperature (°C)				Maximum Temperature (°C)			
	Mean	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**
Potentilla Dominated	970.1	83.6	6.37	0.01	3.78	0.26	3.25	0.06	57.06	2.89	1.26	0.31
Co-Dominated	976.7	47.6			3	0.52			63.2	4.11		
Festuca Dominated	1310.6	99.3			2.44	0.44			62.56	2.64		

Experimental Study

	PAR (umol photons $m^{-2}s^{-1}$)				Min Temperature (°C)				Maximum Temperature (°C)			
	Mean	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**	**Mean**	**SE**	**F**	**P**
Festuca removal	1089.2	261.50	2.36	0.11	3.17	0.17	0.61	0.56	56.83	7.91	1.38	0.29
Control removal	976.7	47.60			3.00	0.52			63.20	4.11		
Potentilla removal	1086.6	47.20			2.30	0.34			68.10	2.50		

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Figure 1(on next page)

Community metrics across a plant dominance gradient

Mean (± standard error) subordinate species' cover, richness, evenness and diversity across a plant dominance gradient (*Potentilla* dominated, *Potentilla* and *Festuca* co-dominated, *Festuca* dominated) for June and July of 2014.

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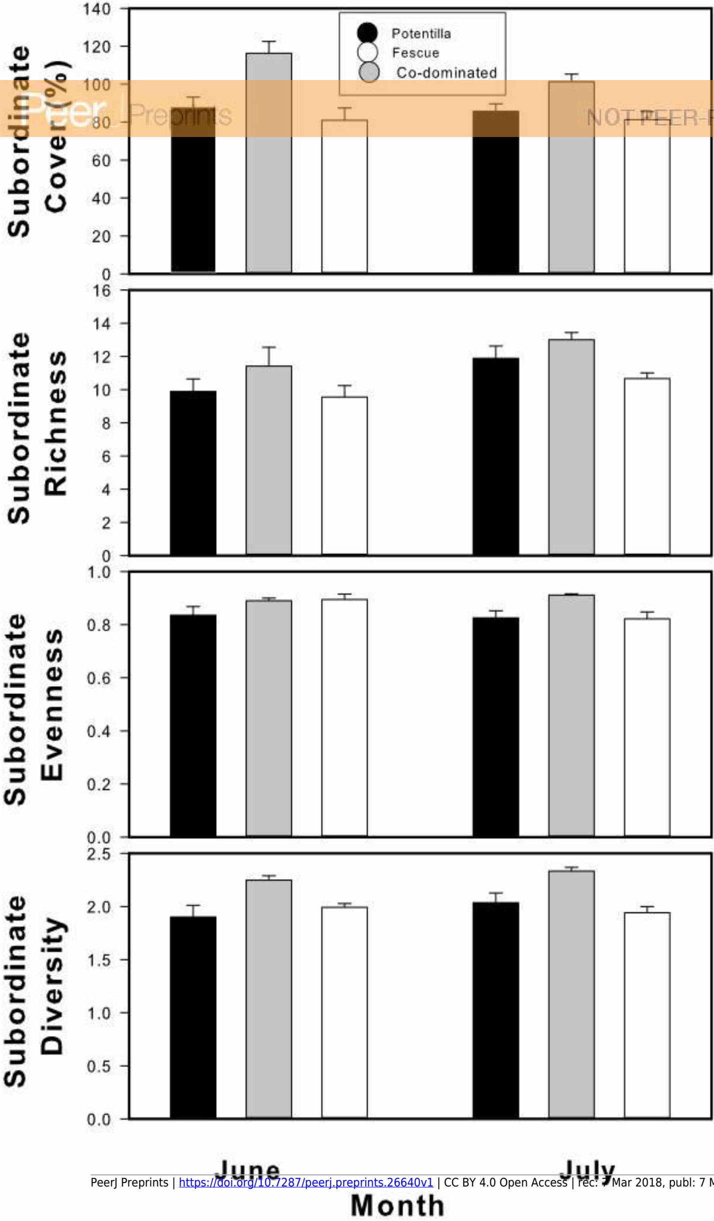
Potentilla
Fescue
Co-dominated
Subordinate Cover (%)
Subordinate Richness
Subordinate Evenness
Subordinate Diversity
June
July
Month

Figure 2(on next page)

Community metrics across a plant dominance gradient

Mean (± standard error) subordinate species' cover, richness, evenness and diversity across plant removal treatments (*Potentilla* removal, *Festuca* removal, no removal control) for June and July of 2014.

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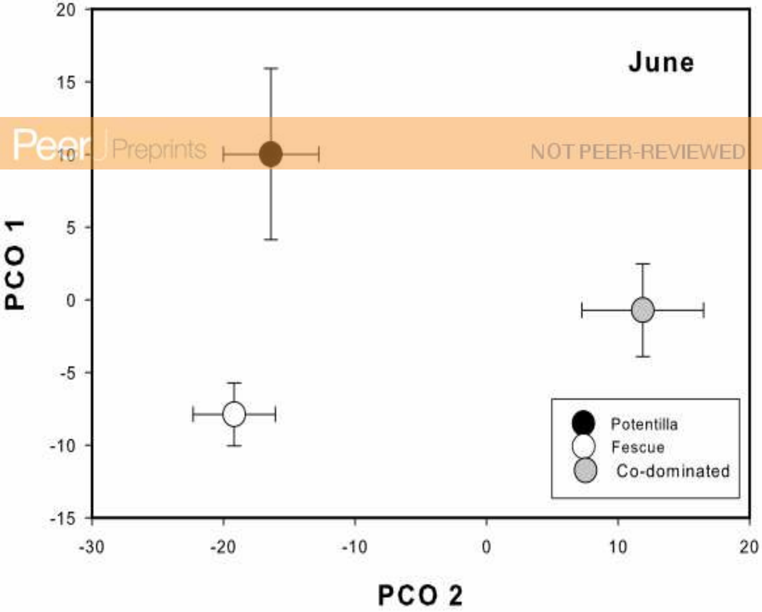
June
PCO 1
PCO 2
Potentilla
Fescue
Co-dominated
20
15
10
5
0
-5
-10
-15
-30
-20
-10
0
10
20

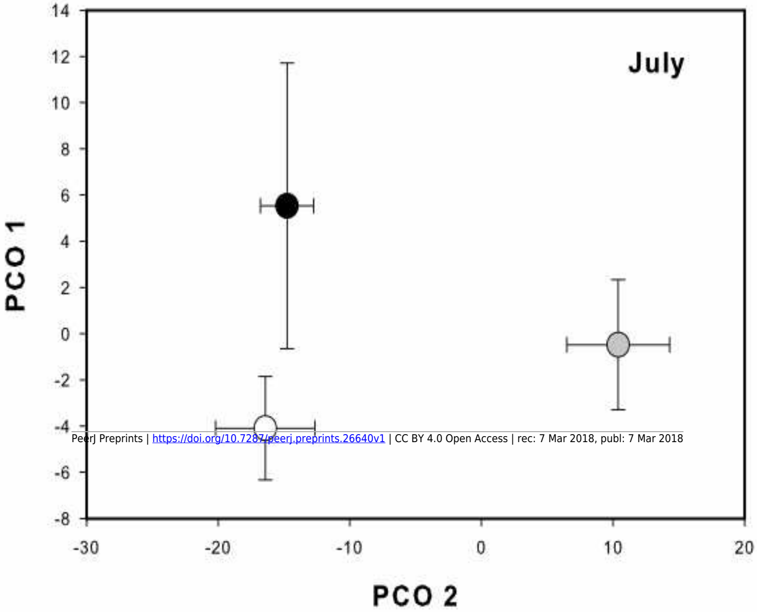
July
PCO 1
PCO 2
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-30
-20
-10
0
10
20

Figure 3(on next page)

Community metrics across plant removal treatments

Mean (± standard error) subordinate species' cover, richness, evenness and diversity across a plant removal treatment (*Potentilla = Potentilla* removed, *Festuca= Festuca* removed, Co-dominated=control or no removal) for June and July of 2014.

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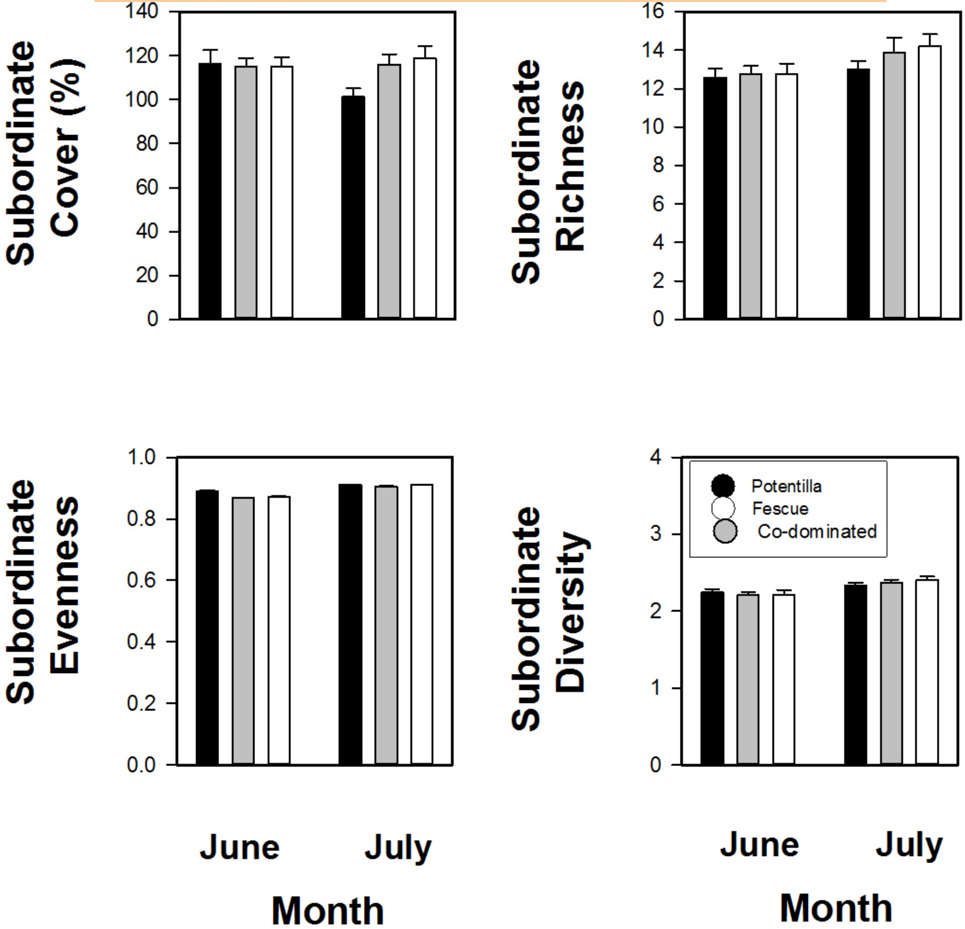
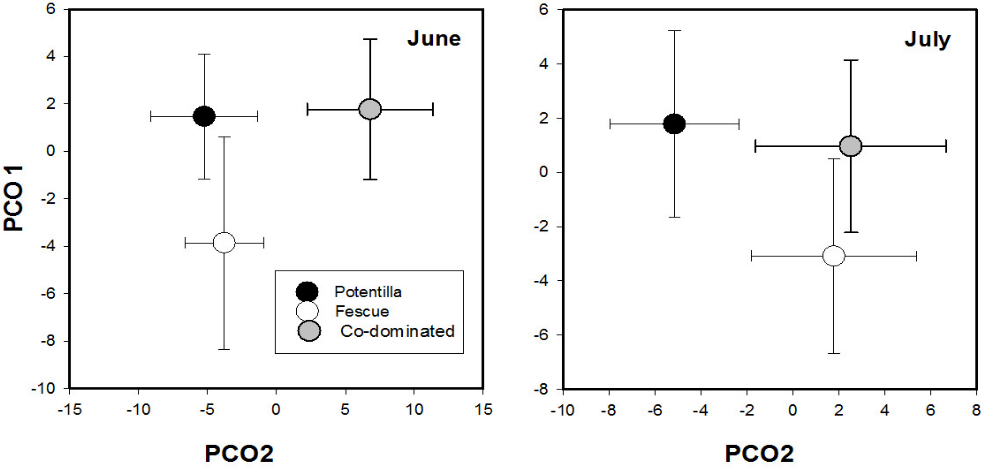

Subordinate Cover (%)
140
120
100
80
60
40
20
0
Subordinate Richness
16
14
12
10
8
6
4
2
0
Subordinate Evenness
1.0
0.8
0.6
0.4
0.2
0.0
Subordinate Diversity
4
3
2
1
0
Potentilla
Fescue
Co-dominated
June
July
Month
June
July
Month

Figure 4(on next page)

Plant composition across plant removal treatments

Principal Coordinate Ordination (PCO) illustrating in a two-dimensional scale (PCO Axis 1 and PCO Axis 2) subordinate species composition across a plant removal treatments (Potentilla= Potentilla removal, Festuca= Festuca removal, Co-dominated= no removal control) for June and July of 2014.



June
July
PCO1
PCO2
PCO2
Potentilla
Fescue
Co-dominated
6
4
2
0
-2
-4
-6
-8
-10
-15
-10
-5
0
5
10
15
-10
-8
-6
-4
-2
0
2
4
6
8