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The Effects of Hemiparasitism by *Castilleja* Species on Community Structure in Alpine Ecosystems

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There is a long history in ecology of examining how interactions such as competition, predation, and mutualism influence the structure and dynamics of natural communities. However, few studies to date have experimentally assessed the role of hemiparasitic plants as a structuring force. Hemiparasitic plants have the potential to shape plant communities because of their ability to photosynthesize and parasitize and because of their abundance in a variety of natural and managed ecosystems. A study was conducted which focused on the impacts of hemiparasitic species in the genus Castilleja, which are ubiquitous in montane meadows in the Colorado Rockies. This study employed a manipulative experiment in which Castilleja was removed from intact communities and surveys were conducted over an extensive elevational gradient to examine the relationship between the natural density of Castilleja and a suite of community-level properties. The experiment showed that the communities in which Castilleja was removed had lower evenness than plots where Castilleja was present. This suggests that the presence of Castilleja promotes evenness or more equal dominance of plant species in the community. The observational study, in contrast, showed no statistical differences in community-level properties in plots with and without Castilleja species present. Taken together, this research demonstrates that hemiparasites do have the potential to shape plant communities in alpine ecosystems, but more research should be done to determine the extent of their effects in natural and manipulated systems.

Introduction

Plant community ecologists have examined the effects of competition and herbivory on plant community structure and ecosystem processes for decades while generally ignoring whether parasitic or hemiparasitic plants might also have effects. Parasitic plants are comprised of two main groups, holoparasites (plants that are completely parasitic and contain virtually no chlorophyll) and hemiparasites (plants that are both parasitic and photosynthetic), and each has the potential to play major roles in shaping community structure and driving ecosystem functions. Globally, there are over three thousand parasitic flowering plant species, and most plant assemblages contain one or more of these species (Marvier 1996; Bardgett et al. 2006; Quested 2008). Parasitic plants are also represented in every major ecosystem (Adler 2002). Given their ubiquity and diversity, it is surprising that so few studies have examined whether they have had impacts on communities and ecosystems.

Though few studies have examined community-level impacts, several experiments on the impacts of parasitic plants on host performance have been conducted (see Bardgett et al. 2006). Hemiparasitic plants obtain some resources, including water, fixed carbon compounds, nitrogen, etc., from their host plants, but they also compete with their hosts for light, water, and soil nutrients (Pennings and Callaway 2002; Press and Phoenix 2005; Marvier 1996). Hemiparasitic plants have the potential to determine the productivity and structure of the plant communities in which they are present because hemiparasitic plants can decrease the growth of host species. This might indirectly affect other plants by altering the competitive balance between hosts and non-host species in a community (Press and Phoenix 2005). Put another way, when hemiparasitic plants have detrimental effects on their hosts, this allows non-host plants to gain a competitive advantage and become more abundant in the community (Bardgett et al. 2006). Hemiparasitic plants, therefore, have the potential to alter community biomass and the relative abundance of particular species by reducing the competitive advantage and abundance of their hosts even if the hemiparasitic plants represent only a small percentage of the cover or biomass.

Nutrient availability in the system, density of parasitic plants, and parasitic plant host preference can all drive changes in community composition which is why more studies on the community effects of hemiparasitic plants are needed to better understand their potential role in plant communities (Spasojevic and Suding 2010; Quested 2008). Most parasitic plants are thought to be generalists, meaning that they parasitize many different plant species, and *Castilleja* spp. are thought to parasitize over 100 different hosts (Press 1998). It is common, however, for parasitic plants to behave more as specialists because they show various levels of host preference (Press and Phoenix 2005).

Castilleja species are facultative root hemiparasites. Their roots grow until they touch roots of other plants, and then they penetrate the roots of the host plant with haustoria and obtain a portion of its nutrients (Bardgett et al. 2006; Press and Phoenix 2005; Cameron et al. 2009; Quested 2008). Hemiparasitic plants like *Castilleja* species can "forage" by selectively growing in a specific direction (toward or away from host plants) or by selectively penetrating a host's roots upon contact (Pennings and Callaway 2002). It is difficult to determine the host for most *Castilleja* individuals, but it is understood that *Castilleja* species can live on a wide range of plant species in montane and alpine communities (Spasojevic and Suding 2010), including deeply rooted sagebrush, fast-growing grasses, lupines, and other plants (Darrow 2006). Adler conducted a study using *Castilleja indivisa* in Texas and found that lupines benefit the *Castilleja* host more than grass hosts, contributing to the idea that though *Castilleja* can parasitize a wide range of species, some hosts have stronger positive effects on the hemiparasite's productivity than others (Adler 2003).

Although *Castilleja* species are common in alpine systems in Colorado and the Rocky Mountains, their community and ecosystem effects have not been widely studied. One exception is the work of Spasojevic and Suding (2010). They conducted an experiment in the Front Range of the Rocky Mountains focusing on the effects of *Castilleja* *occidentalis,* and this confirmed that litter effects of long-lived hemiparasitic plants in nutrient poor systems may increase the availability of nitrogen in the system (Spasojevic and Suding 2010). This positive nutrient effect would compensate for the negative effects of parasitism on the host by significantly increasing productivity and slightly increasing diversity. This is one study that shows the importance of hemiparasitism in shaping community structure and driving ecosystem processes in Rocky Mountain ecosystems.

Importantly, Spasojevic and Suding (2010) and most other studies of the effects of parasitism and hemiparasitism in plant communities have focused on single sites while it is clear that the effects of interspecific interactions in plant communities can vary with elevation (Callaway et al. 2002). Distributions and abundances of plant species may vary depending on their interactions with other plant species and the elevation (Callaway et al. 2002). In general, competition is more important for interactions within plant communities at lower elevations while interactions among plants at high elevations are more often mutually beneficial (Callaway et al. 2002). According to Pennings and Callaway (2002), parasitic and hemiparasitic plants could have varying types of effects at different elevations depending on their differences in virulence, host-preference, and community interactions.

This study employed a manipulative experiment and conducted surveys over an extensive elevational gradient to examine the relationship between the density of *Castilleja* spp. and a suite of community-level properties. In particular, the following questions were addressed:

1. Is there a relationship between the abundance (both percent cover and biomass) of *Castilleja* and species diversity and community composition? If there are clear relationships, are they positive, negative, or neutral? It is predicted that if *Castilleja* species have an effect on plant communities, then there would be a visible relationship between *Castilleja* abundance and species diversity and community composition. If there was a high abundance of *Castilleja* species, then the richness and evenness of the rest of the plant community would be higher.
2. Are these relationships between Castilleja abundance and richness and evenness represented across an elevational gradient? It is predicted that the relationships will remain relatively the same because all elevational gradient sites are similar in plant communities, but all plots, regardless of presence of *Castilleja*, will decrease in richness and evenness with increasing elevation, as abiotic stress is higher. This will cause certain competitive species, like *Artemisia tridentata*, to become more abundant while other species cannot thrive under such abiotic stress.

Overall, this research leads to a better understanding of the roles of parasitic plants in shaping community structure and ecological processes in alpine systems.

Methods

Manipulative Removal Study

This research was conducted in Gothic, Colorado, near Judd Falls. The study site was located at approximately 3000 meters in elevation in a dry montane meadow near Judd Falls. Common plant species at the site included *Populus tremuloides, Artemisia* spp., *Potentilla hippiana, Mahonia repens,* and *Lomatium dissectum*.

To determine if *Castilleja* influences the structure of plant communities and ecosystem processes, 18 1-m^2 plots were established in six blocks with a 0.5 × 0.5 m buffer zone surrounding each of the plots. Each plot within a block was approximately one to two meters away from adjacent plots, but the exact distance was not measured as it depended on the topography and vegetation of the area. Within each block, three treatments were implemented: a control plot in which nothing was manipulated; a *Castilleja* removal plot, in which *Castilleja* was removed by clipping to ground level each week during the growing season (primarily July 2011); and a random biomass removal plot, in which a comparable amount of biomass (compared to the *Castilleja* removal plot within the block) was removed. A random biomass removal plot was included in each block to account for the removal of *Castilleja* biomass and the impacts that removing biomass in general could have on plant community structure. The biomass removed from the *Castilleja* removal plots and random biomass removal plots were air dried in paper bags and then dried for 72 hours at 70°C in a static air oven. The biomass was then weighed to the nearest 0.01 gram.

For each of the 18 1-m^2 plots richness and evenness were measured on three occasions (June 28th, July 14th and July 28th) during the 2011 growing season. Richness was measured in all plots by identifying and recording each plant species present in the plots, and evenness (Evenness=$(1/\Sigma p_i^2)(1/S)$; where p_i is the proportion of each species and S is the total number of species) was measured by estimating the relative abundance of each species based on percent cover in five percent intervals. Note that in all cases the response variable does not include *Castilleja*; instead, the focus is on the rest of the plant community.

Soil moisture was also measured for all plots periodically using a soil moisture probe to determine if all plots were similar in their abiotic pressures and properties. Two measurements were taken in each plot throughout the peak growing time for *Castilleja*, and the probe measured volumetric water content as a percent. The moisture of the experimental plots was the same across all treatments (Fig. 2)

To determine the relationship between abundance of *Castilleja* species and a suite of community-level variables such as species composition and diversity, several statistical analyses were performed with the data. The effects of the presence of *Castilleja* on these diversity measures were analyzed using Analysis of Variance and Analysis of Covariance statistical tests. A one-way analysis on evenness and richness by treatment and date was performed and the values were compared to the control using Dunnett's method. The significance threshold for all statistical tests was $\alpha = 0.05$.

Observational Elevational Gradient Study

For the elevational gradient portion of this study, plant communities were surveyed along an elevational gradient at 2450 m, 2700 m 2750 m, 3000 m, and 3260 m (Tab. 1). To determine if there is a relationship between *Castilleja* abundance and species richness and evenness along an elevational gradient, an observational study was conducted related to the experimental study explained above. Specifically, sites that were dry montane meadows and thus similar in plant composition were chosen. Twelve 1 × 1 m quadrats at each site were randomly placed, with two conditions: six of the twelve plots at each site contained *Castilleja*, and six did not. Richness and evenness were measured within each 1m^2 plot. This correlational study was conducted to draw parallels between the results of the experimental study and the results of a natural, observational study. This study also helped to identify any trends related to *Castilleja* abundance and community structure among elevations.

To determine if there is a relationship between *Castilleja* abundance and species richness and evenness along an elevational gradient, Analysis of Variance and Analysis of Covariance statistical tests were used. A fit model was used to see if *Castilleja*, elevation, or both *Castilleja* and elevation had an effect on the richness and evenness of plots. All elevation evenness and richness data were compared using Tukey-Kramer HSD. The significance threshold for all statistical tests was $\alpha = 0.05$. All data met the assumptions of normality.

Results

There is a positive relationship between the abundance (both percent cover and biomass) of Castilleja and community composition or evenness.

Before plant removals, richness and evenness did not differ among treatments (Fig. 1a and 1d). Similarly, volumetric soil moisture content was consistent across all treatments (Fig. 2).

Richness in the experimental plots did not vary among treatments or over time (Fig. 1d, 1e, 1f), but evenness in the *Castilleja* removal plots was significantly different than in the control plots after plants were removed (Fig. 1b and 1c). Using Dunnett's method for comparing treatments to a control, it was found that evenness was lower in Castilleja removal plots by 34% (Fig. 1b) and 25% (Fig.1c) when compared to the control plots.

There are no significant relationships between *Castilleja* abundance and richness and evenness across an elevational gradient.

At the community level, no significant difference was found in richness within the *Castilleja* present plots (F=0.7041, P=0.5966) or richness within the *Castilleja* absent plots (F=0.2137, P=0.9283) across the elevational gradient (Fig. 3). Neither elevation nor the presence or absence of *Castilleja* had an effect on the richness of the plant communities. It was found that elevation did have an effect on overall evenness (F=3.46, P=0.014) (Tab. 2), but it did not have an effect on evenness within the *Castilleja* present plots (F=1.9667, P=0.1306) or within the *Castilleja* absent plots (F=1.9753, P=0.1292) over the elevational gradient (Fig. 4). There is no trend in the percent cover or estimated biomass of *Castilleja* and richness or evenness.

Discussion

The purpose of this study was to investigate whether or not there is a relationship between *Castilleja* spp. abundance and species diversity and composition in a community. Richness was not affected by the presence of *Castilleja* in the experimental plots or associated with the presence of *Castilleja* across the elevational gradient, but evenness was affected in some cases. Evenness in plots where *Castilleja* was removed was significantly reduced, and this decrease in evenness compared to the control plots persisted throughout the 2011 growing season (Fig. 1b. and 1c.). In other words, the presence of *Castilleja* matters for evenness. This result supports the hypothesis that there is a positive relationship between *Castilleja* abundance and community composition because *Castilleja* presence increases the evenness of the rest of the plant community in the manipulated plots. The elevational gradient correlational study did not support this conclusion, however, because there was no significant difference in richness or evenness in plots that contained *Castilleja* at all elevations.

Seeing only shifts in evenness was somewhat expected because the removal of *Castilleja* simply decreased the evenness or percent cover of plant species rather than making new species appear or others become extinct in removal plots over one growing season. Studies that have seen larger effects of hemiparasitism on community structure were longer experiments that extended over several growing seasons (See Bardgett et al. 2006 and Marvier 1998), so it may be beneficial to extend this study over more growing seasons to see if any richness or evenness measurements change over more time. Effects also may be limited depending on how selective *Castilleja* is for its host and how virulent it is in montane meadows and alpine ecosystems in general (Pennings and Callaway 2002). If *Castilleja* is largely a generalist, then it would parasitize multiple plant species and have little effect on plant structure. If *Castilleja* is primarily a specialist, then it would have more effect on the abundance of a few species, causing a shift in the evenness and possibly richness of the community over time. In general, plots that had *Castilleja* present increased species evenness while leaving species richness unchanged, so this study suggests that *Castilleja* may be more of a specialist hemiparasite than a generalist in alpine ecosystems. Considering Castilleja a specialist when referring to its host preference accounts for the significant increase in evenness and relatively no change in richness.

Parasitic and hemiparasitic plants are a largely ubiquitous group of plants that have been largely excluded from community-level studies. Hemiparasites have the potential to influence community structure and composition, so it is important that plant community ecologists consider their roles in various ecosystems in order to obtain a better understanding of their potential impacts. Through several studies, it is understood that hemiparasites have varying effects on their plant communities depending on factors such as abundance, host preference, and soil fertility of the system. According to this study, *Castilleja* spp generally increase the evenness or diversity (according to the inverse Simpson's index) of the rest of the plant community, which is similar to the finding that *Rhinanthus minor,* also a hemiparasite, in grassland ecosystems increases plant diversity (Bardgett et al. 2006). *R. minor* is a facultative root hemiparasite that, like Castilleja, affects the community composition (Bardgett et al. 2006). This study, however, was conducted in low-to-moderately productive grassland, so it is interesting to see how similar effects of hemiparasites can extend across different ecosystems. In a Spasojevic and Suding study, *Castilleja occidentalis* was associated with slight changes in plant diversity in the alpine tundra, similar to Castilleja spp. in montane meadows.

The results of this study indicated that the hemiparasite *Castilleja* does significantly increase evenness in alpine ecosystems, enforcing the idea that hemiparasites can have large effects on community structure. Hemiparasites have largely been excluded from community-level studies, yet several studies show their importance in shaping and changing communities (Bardgett et al. 2006; Press and Phoenix 2005; Spasojevic and Suding 2010). The findings of this study suggest that hemiparasitic plants act as driving forces in shaping plant communities in alpine ecosystems, and, given these findings and the fact that almost all terrestrial ecosystems support hemiparisites and parasites, they are likely to have additional unknown effects on plant communities and ecosystems. It is also possible that with a changing world and changing ecosystems due to climate change and human modification, hemiparasitic and parasitic plants could have increasingly stronger effects on community composition and structure as abiotic stress intensifies and resources become more limited. Because of the possible influences on plant communities, hemiparasitic plants should not be excluded from community theory and should be more widely studied.

Bibliography

Adler, L. S. 2002. Host Effects on Herbivory and Pollination in a Hemiparasitic Plant. Ecology **83**: 2700-2710.

Adler, L. S. 2003. Host Species Affects Herbivory, Pollination, and Reproduction in experiments with Parasitic Castilleja. Ecology **84**: 2083-2091.

Bardgett, R. D., R. S. Smith, R. S. Shiel, S. Peacock, J. M. Simkin, H. Quirk, and P. J. Hobbs. 2006. Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. Nature **439**.

Callaway, R. M., R.W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortle, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature **417**.

Cameron, D. D., A. White and J. Antonovics. 2009. Parasite-grass-forb interactions and rock-paper-scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities. Ecology **97**: 1311-1319.

Cross, M. S. and J. Harte. 2007. Compensatory responses to loss of warming-sensitive plant species. Ecology **88**: 740-748.

Darrow, K. 2006. Wild About Wildflowers: Extreme Botanizing in Crested Butte, Wildflower Capital of Colorado. 2nd Ed. Heel and Toe Publisher, Fort Collins, CO.

Marvier, M. A. 1996. Parasitic plant-host interactions: plant performance and indirect effects on parasite feeding herbivores. Ecology **77**: 1398-1409.

Pennings, S. C. and R. M. Callaway. 2002. Parasitic plants: parallels and contrasts with herbivores. Oceologia **131**: 479-489.

Press, M. C. 1998. Dracula or Robin Hood? A functional role for root hemiparasites in nutrient poor ecosystems. Oikos **82**: 609–611.

Press, M. C. and G. K. Phoenix. 2005. Impacts of parasitic plants on natural communities. New Phytologist **166**: 737-751.

Quested, H. M. 2008. Parasitic plants- impacts on nutrient cycling. Plant Soil **311**:269-272.

Spasojevic, M. J. and K. N. Suding. 2010. Contrasting effects of hemiparasites on ecosystem processes: can positive litter effects offset the negative effects of parasitism? Oecologia **165**: 193-200.

Tables

Table 1: Locations, elevations, and dominant plant species of the elevational gradient sites.

Location	**Elevation (m)**	**Dominant Plant Species**
Almont	2470	Artemisia tridentata, Achillea millefolium, Wyethia amplexicaulis
Cement Creek	2700	*Artemisia tridentata*, *Antennaria rosea*, *Ipomopsis aggregata*
Nordic Center	2750	*Artemisia tridentata*, *Eriogonum umbellatum*, *Lupinus argenteus*
Judd Falls	3000	Paxistima myrsinites, Heterotheca villosa, Lomatium dissectum
Schofield Pass	3260	Chamerion angustifolium, Aquilegia coerulea, Lupinus argenteus

Table 2: Analysis of the effect of *Castilleja* and elevation on evenness in plots.

Source	Sum of Squares	F Ratio	P-value
Castilleja	0.00110697	0.06936057	0.79335239
Elevation	0.22072545	3.45754929	0.01431903*
Castilleja*Elevation	0.03099767	0.48556231	0.74622545

This shows that the only significant variable acting on evenness in the elevational study is elevation itself. *Castilleja* presence does not affect the evenness of the community, but elevation does. *Castilleja* presence and elevation are not interacting.

Figures

Figure 1: Evenness of species (a), (b) and (c) and species richness measured as the number of species m^{-2} (d), (e) and (f) for *Castilleja* removal plots, control plots, and random biomass removal plots. Each bar represents the mean (+ SE) of six plots. Bars marked with * are significantly different at p=0.05 from the control.

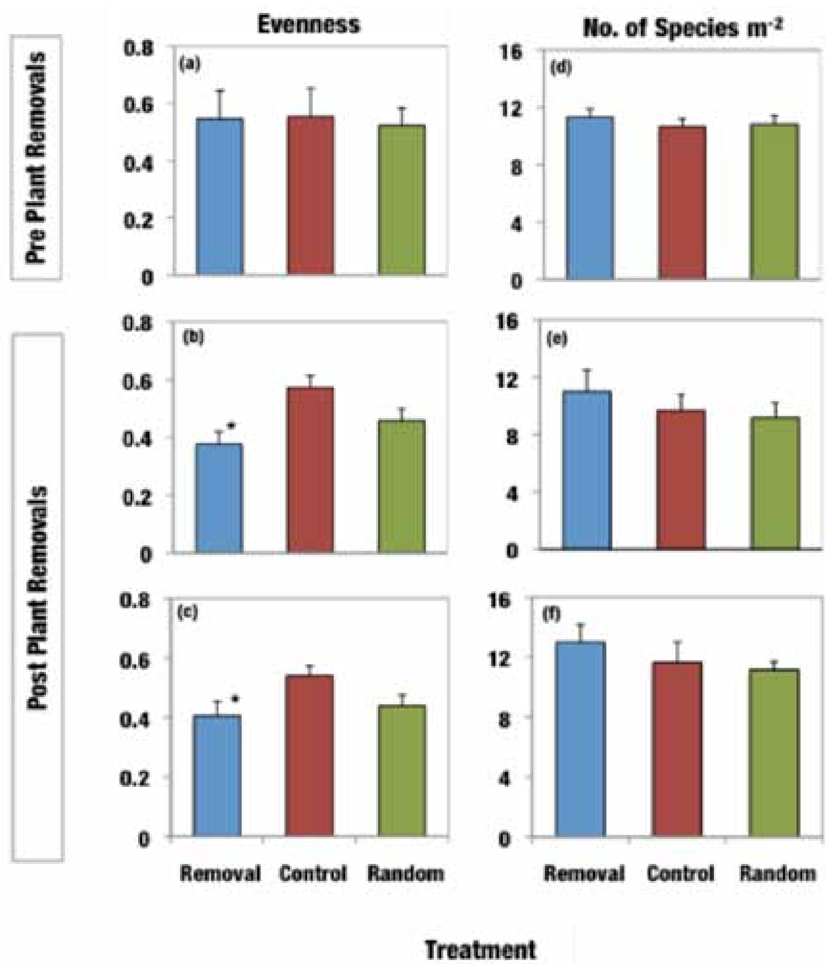


Figure 2: Average Volumetric Water Content (VWC) at 12cm depth for the three treatment plots over time.

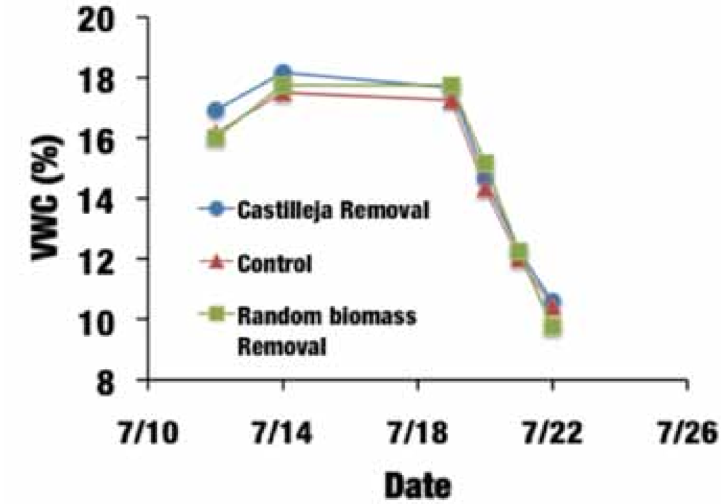
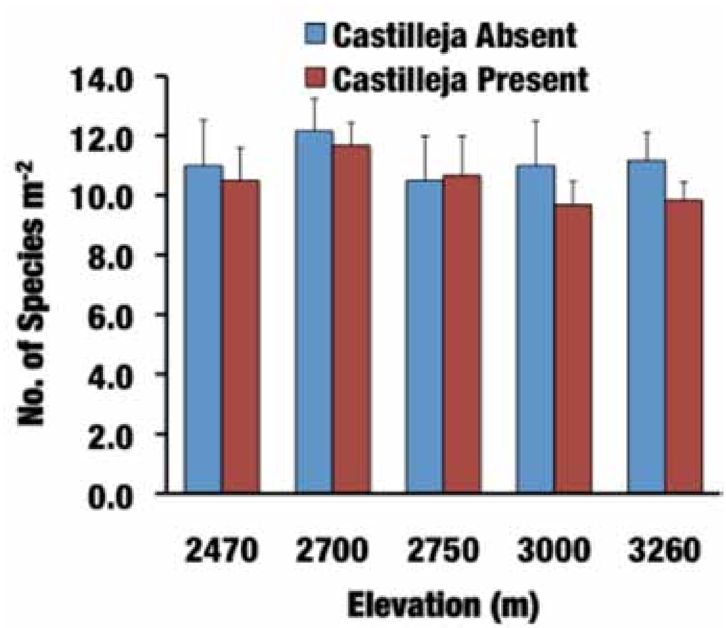
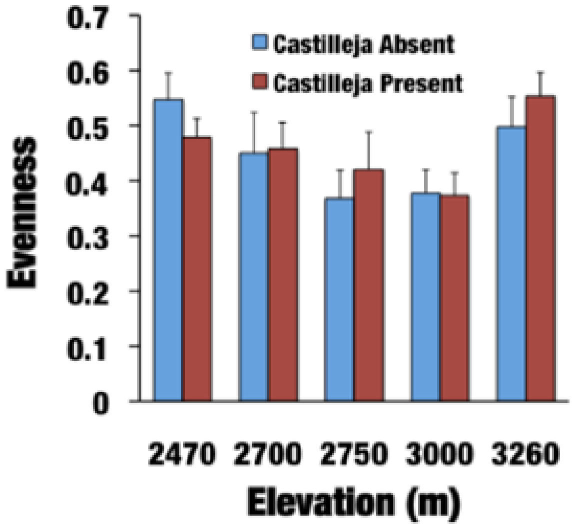


Figure 3: Richness of *Castilleja* present and *Castilleja* absent plots.



This shows the richness data for plots with and without *Castilleja* at each elevational site represented in the observational study. There are no statistical differences (p =0.05) in plots with or without *Castilleja*.

Figure 4: Evenness of *Castilleja* present and *Castilleja* absent plots.



This shows the evenness data for plots with and without *Castilleja* at each elevational site represented in the observational study. There are no statistical differences ($p > 0.05$) in plots with or without *Castilleja*.

About the Author

Johannah Reed will graduate *summa cum laude* from the University of Tennessee in May 2012 with a B.A. in Environmental Studies and minors in Biology and Geology. With the help of the Chancellor's Honors Program and her advisor, Nate Sanders, she was able to spend the summer of 2011 in the Colorado Rockies doing research for this article and her senior thesis. Johannah's love for the environment has been fueled by some unique experiences, including volunteering in the Tortuguero National Park of Costa Rica, conducting research in the Rocky Mountains, taking courses from many different fields, and receiving an interdisciplinary education while at UT. Because of these experiences she wants to continue doing research in Ecology or Conservation Biology and go to graduate school in one of these fields.

About the Advisor

Dr. Nate Sanders received his B.A. from the University of Colorado in 1995 and his Ph.D. from Stanford University in 2000. He is an Associate Professor in the Department of Ecology and Evolutionary Biology at the University of Tennessee, where he has taught since 2004. His research interests include biodiversity and the links between communities and ecosystems. He was a Visiting Associate Professor at the University of Copenhagen from December of 2009 to July of 2010.