

Community effects and plant associations of two sub-alpine *Castilleja* species in the White Mountains, California

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ABSTRACT

Parasitic plants obtain resources from hosts and can greatly influence community dynamics. While this influence has been well studied in grassland systems, community effects of parasitic plants in other environments are less clear. We set out to investigate how the occurrence of two species, *Castilleja applegatei* and *Castilleja linariifolia*, may affect the health and percent cover of plants around them in a harsh subalpine environment. We recorded the occurrence, percent cover, and proportion of living branches of associated species in plots with *Castilleja applegatei*, *Castilleja linariifolia*, and in null plots, and analyzed the differences between these three categories. We found a total of 31 different plant species across our plots, and differences in community structure between plots with *Castilleja applegatei* and *Castilleja linariifolia*. In addition, the presence of each *Castilleja* affected health in select neighbor species differently. Overall, we found that these two *Castilleja* species exhibit different community associations and effects on dominant species in the landscape.

Keywords: parasitic plants, community impacts, Castilleja, subalpine, White Mountains

INTRODUCTION

While the ability of pathogens and herbivores to influence plant community structure is well documented, the impact of parasitic plants has received less attention (Pennings and Callaway 2002). Parasitism in plants is widespread, occurring in over 4,000 species and all major ecosystems across the globe (Musselman and Nickrent 2016). Parasitic plants gain some or all of their water and nutrients from other plants through haustoria, specialized structures which penetrate the xylem and phloem of hosts (Dobbins and Kuijt 1973, Press and

Phoenix 2005). Holoparasitic plants derive all of their nutrients from their hosts, while hemiparasites supplement this nutrient source with photosynthesis (Musselman and Nickrent 2016). Hosts of parasitic plants can be negatively affected and exhibit reduced biomass and fitness (Matthies 1996, 1997, Seel and Press 1996). At an ecosystem scale, this parasitic influence may shift the makeup of plant communities by altering the competitive ability of their hosts. (Davies et al. 1997, Phoenix and Press 2005, Press and Phoenix 2005).

Most parasitic plants are generalists with an ability to parasitize a wide range of hosts

(Press and Phoenix 2005), yet many seem to exhibit “preferences”, i.e. associating with a subset of possible hosts (Werth and Riopel 1979, Gibson and Watkinson 1989). For example, there is evidence that *Cuscuta spp.*, a group of plant parasites, detect the identity and nutritional profile of their neighbors through chemical cues and either approach, reject or attack the source plant based off these signals (Kelly 1990, 1992). The factors that influence these preferences are difficult to discern, but these detections may make more common or nutritionally advantageous hosts easier to parasitize (Cameron et al. 2006).

By suppressing certain species, parasitic plants allow other species to better compete and change the community structure of the ecosystem around them (Press 1998, Fibich et al. 2017). Associations and increases in landscape-level diversity with parasitic plants have been extensively studied in grassland systems (Davies et al. 1997, Joshi et al. 2000, Westbury et al. 2006, Fibich et al. 2017). However, when parasites attack less-common species in other ecosystems, biodiversity is lowered (Gibson and Watkinson 1989). One example of this is the root parasite, *Rhinanthus minor*, which contributes to declines in its own population by suppressing its preferred hosts. However, as preferred host populations recover, *R. minor* populations also recover, and so the cycle continues (Dobbins and Kuijt 1973, Gibson and Watkinson 1992). While parasitic plants can affect community-level diversity patterns, these effects are moderated as diversity increases. Joshi et al. 2000 found that increasingly biodiverse grasslands were less sensitive to community-level impacts of parasitic plants. In harsher, less speciose regions, community effects of parasitic

plants may be heightened without biodiversity as a buffer.

Parasitic plants are common in stressful and nutrient-poor environments (Press 1998), and their effects on the surrounding community may be explained by abiotic factors. Extreme temperatures and aridity represent challenges for plants, and evolutionary pressure favors adaptations to overcome these challenges (Bray 2007). Cold, arid, and nutrient-poor environments are generally less speciose (Szabados et al. 2011). In nutrient-poor environments, parasitism is evolutionarily incentivized because it allows plants to decouple reproductive success from environmental stressors and limitations (Hansen 1979, Těšitel et al. 2010). For instance, hemiparasitic mistletoe display higher host specificity in environments with lower diversity than in those with higher diversity (Norton and Carpenter 1998, Musselman and Nickrent 2016). As reviewed in Press 1998, while parasitic plants may generally suppress productivity in their communities, they may play an important role in nutrient-constrained ecosystems by unlocking long-held nutrients, such as nitrogen and phosphorous, from perennial dominants and concentrating them in leaves that decompose as leaf litter. Understanding the net effects of parasitic plants under harsh conditions is important, as it is unclear how the interaction between these varied effects shapes the community as a whole (Press 1998). Further, because parasitic plants represent a larger proportion in plant diversity in species-poor environments, they may exert a greater effect on the community.

One plant that uses parasitism to survive in nutrient-poor environments is the genus *Castilleja*, a widespread group of

hemiparasitic plants commonly known as paintbrush (L. R. Heckard 1962, Press 1998, Tank and Olmstead 2009, Wenzell et al. 2021). *Castilleja* are generalists, and are known to parasitize over 100 different species across a variety of families (Musselman and Nickrent 2016). However, the specific hosts of each *Castilleja* species have not been extensively documented.

Castilleja species can be found in the particularly stressful environment of the White Mountains of Eastern California (Wright and Mooney 1965, LaMarche 1973). High-elevation habitats in the White Mountains are susceptible to strong winds, UV radiation, and nutrient-poor soil (Tabler 1964). In addition, the short growing season does not coincide with the rain season. Despite these challenges, the White Mountains represent the range of multiple *Castilleja* species. Two such species are *Castilleja applegatei* (hereafter referred to as *C. applegatei*), which is found mainly in California, and *Castilleja linariifolia* (hereafter referred to as *C. linariifolia*), a predominantly Great Basin species. These *Castilleja* species coexist in a clumped distribution in the White Mountains' subalpine sagebrush steppe. The intersection of these similar, closely related species may be explained by some form of niche partitioning (Chesson 2000, Villanueva-Bonilla et al. 2019). While *Castilleja* are generalist hemiparasites (Musselman and Nickrent 2016), they may have different preferences for particular hosts between different species.

Specific host preferences of *Castilleja* are not well documented, nor is their effect on community structure. Understanding how these two species affect their communities and how these impacts differ may provide important insights into the role of parasitic

plants in maintaining plant community diversity. We set out to investigate how two co-occurring species of *Castilleja* may affect the health and composition of communities around them. Specifically, we investigated the following questions: (1) What are the plant community associations of these two co-occurring species and how do they differ? (2) Are *Castilleja* associated with greater species diversity compared to the surrounding environment? (3) Does the presence of *Castilleja* alter the abundance of associated species when compared to the surrounding environment? (4) Do frequently associated plant species show indications of lower health in the presence of *Castilleja*?

METHODS

2.1 Study Site

This study was conducted at the University of California Natural Reserve System's Crooked Creek Research Station in the White Mountains of California. The habitat type of our study area is subalpine sagebrush steppe dominated by big sagebrush (*Artemisia tridentata*) and timberline sagebrush (*Artemisia rothrockii*) (hereafter referred to as *Artemisia spp.*) and various grass species (hereafter referred to as *Poaecae spp.*). We surveyed five study sites that were around 100 m long and chosen for their clustered populations of *Castilleja* plants. Our study sites were all at similar elevations (~3090 m) and slopes, with the predominant soil at each site consisting of granite or quartzite. Each *Castilleja* species was found on both soil types.

2.2 *Castilleja* Surveys

From August 2–6, 2021, we surveyed a total of 148 plots. To sample *C. applegatei*

and *C. linariifolia* plants, we visually identified a dense area of *Castilleja* in each site and laid out a 100-meter transect between the two most distant plants in the cluster. The *Castilleja* plant that was the closest to zero on the transect was sampled first. At each plot, a quadrat (1 m²) was centered on the *Castilleja* plant. Each *Castilleja* plot had a minimum five-meter distance from plots of the same species, and a three-meter minimum distance from members of the other species.

We chose null plots without *Castilleja* for each plant by moving three meters east of the *Castilleja* plot and continuing along that line until we found a null plot that was two meters away from any surrounding paintbrush. This distance was chosen because the maximum root spread of *Artemisia tridentata* is 0.9 to 1.5 m around the plant (Tabler 1964). For each plot, we recorded the visual estimate of percent cover and health of associated species. Species were considered healthy if over 60 percent of their branches had leaves, and unhealthy if less than 60 percent of their branches had leaves.

2.3 Statistical Analysis

All statistical analyses were conducted using JMP Statistical Software v16. We calculated the species diversity for each plot using the Shannon-Weiner index, $(H) = -\sum[(p_i) \times \ln(p_i)]$, where H is maximum possible diversity and p_i is proportion of the sample represented by a particular species. We conducted a discriminant analysis to compare plot species composition of *C. applegatei* plots and *C. linariifolia* plots. For species which occurred in at least 45 percent of the plots surveyed, we ran paired t-tests to analyze the effect of the plot type on

associated species percent cover and diversity. A Chi-squared analysis was used to look at *C. applegatei* and *C. linariifolia* effects on associated species health. Across plot types, we examined the proportion of healthy plants out of total plants for each of our most frequently occurring species.

RESULTS

Overall, associated species of *C. applegatei* had slightly different compositions and health than those associated with *C. linariifolia*. We found a total of 31 associated species across plots of *C. applegatei*, *C. linariifolia*, and null plots. The neighboring plants were found in slightly different frequencies between the different types of plots, with some occurring in a much higher percentage of plots containing *C. applegatei* than *C. linariifolia* and null plots. For example, *Packera multilobata* was found in 17.1 percent of *C. applegatei* plots, yet only found in 5.5 percent *C. linariifolia* of null plots, and only 2.6 percent of *C. linariifolia* plots (Table 1). The most commonly occurring associated taxa across all plots were *Poaceae spp.*, *Artemisia spp.*, *Leptisiphon nutallii*, and *Linanthus pungens*. A discriminant analysis correctly predicted plot-level species composition surrounding *C. applegatei* 87.1 percent of the time and correctly predicted plot-level species composition surrounding *C. linariifolia* 70.0 percent of the time, exemplifying how the two *Castilleja* species have differing associated species. Neither *C. applegatei* ($N = 35$, $t = 0.59$, $p = 0.558$) nor *C. linariifolia* ($N = 39$, $t = 0.32$, $p = 0.751$) had an effect on diversity of surrounding plants compared to null plots.

Table 1: Summary of most frequently associated species of *Castilleja*. 31 different associated plants were identified in plots containing *C. applegatei*, plots containing *C. linariifolia*, and plots containing no *Castilleja*. For each of the three plot types, we calculated the frequency of how often each associated plant species occurred. The four most frequent neighboring species appear in boldface type.

| Associated species | Percent occurrence in <i>C. applegatei</i> plots | Percent occurrence in <i>C. linariifolia</i> plots | Percent occurrence in null plots |
|------------------------------------|---|---|-------------------------------------|
| <i>Poaceae spp.</i> | 94.3 | 94.9 | 93.2 |
| <i>Artemisia spp.</i> | 91.4 | 97.4 | 91.8 |
| <i>Leptisiphon nutallii</i> | 65.7 | 51.3 | 47.9 |
| <i>Linanthus pungens</i> | 48.6 | 46.1 | 54.8 |
| <i>Erigeron clokeyi</i> | 42.9 | 53.8 | 42.5 |
| <i>Eremogone kingii</i> | 40.0 | 64.1 | 50.7 |
| <i>Monardella odoratissima</i> | 25.7 | 2.6 | 2.7 |
| <i>Packera multilobata</i> | 17.1 | 2.6 | 5.5 |
| <i>Ericameria suffruticosa</i> | 17.1 | 20.5 | 13.7 |
| <i>Cryptantha flavoculata</i> | 14.3 | 38.5 | 26.0 |
| <i>Eriogonum umbellatum</i> | 14.3 | 25.6 | 21.9 |
| <i>Senecio spartioides</i> | 11.4 | 5.1 | 4.1 |
| <i>Astragalus lentiginosus</i> | 11.4 | 5.1 | 9.6 |
| <i>Eriogonum ovalifolium</i> | 11.5 | 0 | 2.7 |
| <i>Lupinus argenteus</i> | 8.6 | 7.7 | 5.5 |
| <i>Penstemon sp.</i> | 8.6 | 5.1 | 6.8 |
| <i>Dieteria canescens</i> | 8.6 | 0 | 0 |
| <i>Astragalus oophorus</i> | 5.7 | 2.6 | 1.4 |
| <i>Phacelia hastata</i> | 5.7 | 0 | 2.7 |
| <i>Tetradymia canescens</i> | 2.9 | 0 | 2.7 |
| <i>Chrysothamnus viscidiflorus</i> | 2.9 | 7.7 | 1.4 |
| <i>Horkelia hispidula</i> | 2.9 | 0 | 1.4 |
| <i>Astragalus calycosus</i> | 2.9 | 10.3 | 8.2 |
| <i>Stenotus acaulis</i> | 2.9 | 0 | 0 |
| <i>Castilleja nana</i> | 2.9 | 2.6 | 5.5 |
| <i>Boraginaceae sp.</i> | 0 | 0 | 1.4 |
| <i>Horkelia hispidula</i> | 0 | 0 | 1.4 |
| <i>Penstemon speciosus</i> | 0 | 0 | 1.4 |
| <i>Linum lewesii</i> | 0 | 5.1 | 0 |
| <i>Ribes cereum</i> | 0 | 2.6 | 0 |
| <i>Hymenopappus filifolius</i> | 0 | 2.6 | 4.1 |

Further, both *C. applegatei* and *C. linariifolia* marginally affect percent cover of some top associated species. *C. applegatei* plots had marginally lower percent cover of *Leptisiphon nutallii* and did not change the percent cover of *Poaecaeae spp.*, *Artemisia spp.*, and *Linanthus pungens* compared to null plots (N = 15, t = 2.02, p = 0.063, Table 2). *C. linariifolia* plots had marginally lower percent cover of *Linanthus pungens* and there was no change in percent cover of *Poaecaeae spp.*, *Artemisia spp.*, and *Leptisiphon nutallii* compared to null plots (N = 11, t = 2.11, p = 0.061, Table 3). Additionally, the health of some of these

most frequently occurring associated species marginally correlated to *C. applegatei* and *C. linariifolia* presence. There were fewer healthy *Artemisia spp.* plants in the presence of *C. applegatei* than in null plots, and no change in the number of healthy *Poaecaeae spp.*, *Leptisiphon nutallii*, and *Linanthus pungens* (N = 65, $\chi^2 = 11.20$, p = 0.004, Fig. 1, Table 4). Also, there were fewer healthy *Poaecaeae spp.* in the presence of *C. linariifolia* than in null plots, and no change in the number of healthy *Artemisia spp.*, *Leptisiphon nutallii*, and *Linanthus pungens* (N = 75, $\chi^2 = 5.26$, p = 0.072, Fig. 2, Table 5).

Table 2: *C. applegatei* effect on percent cover of most frequently associated species. *Leptisiphon nutallii* exhibited a marginally lower percent cover in the presence of *C. applegatei* than in null plots. *Poaecaeae spp.*, *Artemisia spp.*, and *Linanthus pungens* exhibited no change in percent cover whether or not *C. applegatei* was present.

| Associated species | t-ratio | p-value | N |
|-----------------------------|---------|---------|----|
| <i>Poaecaeae spp.</i> | 0.39 | 0.700 | 30 |
| <i>Artemisia spp.</i> | 1.06 | 0.300 | 30 |
| <i>Leptisiphon nutallii</i> | 2.02 | 0.063 | 15 |
| <i>Linanthus pungens</i> | 1.23 | 0.244 | 13 |

Table 3: *C. linariifolia* effect on percent cover of most frequently associated species. *Linanthus pungens* exhibited a marginally lower percent cover in the presence of *C. linariifolia* than in null plots. *Poaecaeae spp.*, *Artemisia spp.*, and *Leptisiphon nutallii* exhibited no change in percent cover whether or not *C. linariifolia* was present.

| Associated species | t-ratio | p-value | N |
|-----------------------------|---------|---------|----|
| <i>Poaecaeae spp.</i> | 0.39 | 0.700 | 30 |
| <i>Artemisia spp.</i> | 1.06 | 0.300 | 30 |
| <i>Leptisiphon nutallii</i> | 2.02 | 0.063 | 15 |
| <i>Linanthus pungens</i> | 1.23 | 0.244 | 13 |

Table 4: Effect of *C. applegatei* on health of frequently associated species. The health of *Artemisia spp.* was found to be diminished in the presence of *C. applegatei* compared to null plots. *Poaecae spp.*, *Linanthus pungens*, and *Leptisiphon nutallii* exhibited no change in health whether or not *C. applegatei* was present.

| Associated species | t-ratio | p-value | N |
|-----------------------------|---------|---------|----|
| <i>Poaecae spp.</i> | 0.39 | 0.700 | 30 |
| <i>Artemisia spp.</i> | 1.06 | 0.300 | 30 |
| <i>Leptisiphon nutallii</i> | 2.02 | 0.063 | 15 |
| <i>Linanthus pungens</i> | 1.23 | 0.244 | 13 |

Table 5: Effect of *C. linariifolia* health on frequently associated species. The health of *Poaecae spp.* was found to be marginally diminished in the presence of *C. linariifolia* compared to null plots. *Artemisia spp.*, *Linanthus pungens*, and *Leptisiphon nutallii* exhibited no change in health whether or not *C. linariifolia* was present.

| Associated species | t-ratio | p-value | N |
|-----------------------------|---------|---------|----|
| <i>Poaecae spp.</i> | 0.39 | 0.700 | 30 |
| <i>Artemisia spp.</i> | 1.06 | 0.300 | 30 |
| <i>Leptisiphon nutallii</i> | 2.02 | 0.063 | 15 |
| <i>Linanthus pungens</i> | 1.23 | 0.244 | 13 |

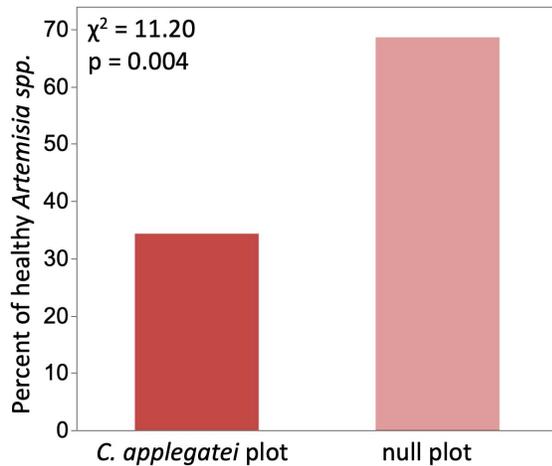


Figure 1: Effect of *C. applegatei* on *Artemisia spp.* health. The health of *Artemisia spp.* was found to be diminished in the presence of *C. applegatei* compared to null plots. The percentage of alive *Artemisia spp.* plants was taken across all plots with *C. applegatei* compared to null plots.

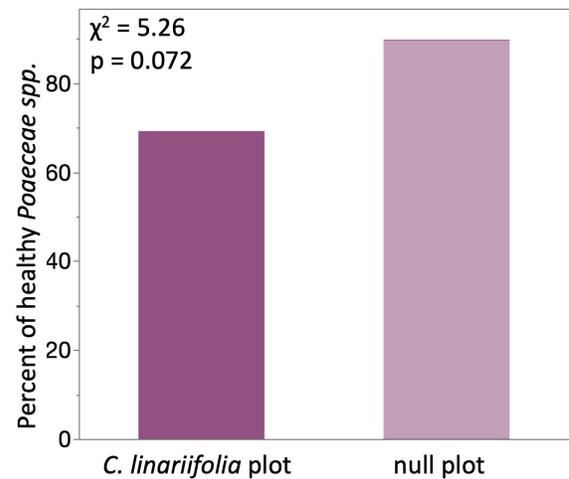


Figure 2: Effect of *C. linariifolia* on *Poaecae spp.* health. The health of *Poaecae spp.* was found to be diminished in the presence of *C. linariifolia* compared to null plots. The percentage of alive *Poaecae spp.* plants was taken across all plots with *C. linariifolia* compared to null plots.

DISCUSSION

Overall, we found some preliminary support that the two species associate with different plant communities, and that their effects on those communities differ as well. The two *Castilleja* species, *C. applegatei* and *C. linariifolia*, differ slightly in their plant associations and their effect on these associated species. Our *Castilleja* species did not exhibit association with plots of higher diversity, nor did their presence influence the percent cover of most associates. Notably, the negative impacts of the presence of each *Castilleja* species on the health of dominant associates differed between the two *Castilleja* species.

While the most common species in plots by occurrence were roughly the same overall, the relative frequency of occurrence of these associates was different between our two *Castilleja* species. Plots also differed in both assemblages of species and in percent cover of those species. Our study sites were near one another, and many sites contained clumped populations of both species. Considering this, our results provide evidence that similarly related *Castilleja* may display preferences in community associations even at a highly localized scale. Different microcommunity association may allow these two closely related species to coexist in the same environment (Chesson 2000, Peterson et al. 2013). However, while *Castilleja chromosa* in the White Mountains has been found to be less sensitive to many abiotic microclimate variations (Hansen 1979), these factors may still have an effect on the distribution of our *Castilleja* species and their hosts.

There were few differences in percent cover of various associate species between our *Castilleja* and null plots. The only

differences observed were marginal, with *Leptisiphon nutallii* having marginally higher percent cover in plots with *C. applegatei* compared to null, and *Linanthus pungens* having marginally lower percent cover in plots with *C. linariifolia* compared to null. The marginally higher percent cover of *L. nutallii* in *C. applegatei* plots may be due to a variety of factors. *L. nutallii* may be better able to compete in plots where other species are suppressed by parasitism, but this association could simply reflect that *C. applegatei* and *L. nutallii* prefer similar microhabitats. Conversely, *L. nutallii* may be a preferred host for *C. applegatei*. The opposite trend of these factors may explain the marginally less percent cover of *L. pungens* in *C. linariifolia* plots. Specifically, *L. pungens* may not prefer the same microhabitats as *C. linariifolia*. However, it is difficult to draw definite conclusions from these results because no analysis of haustorial connections was made. Additionally, an analysis of long-term community dynamics may reveal if the colonization of an area by *Castilleja* leads to change in the percent covers of these species over time.

Artemisia spp. exhibited a decline in health in the presence of *C. applegatei*. These results are in line with previous studies of parasitic plants and their effects on host health (Adler 2003, Těšitel et al. 2010). Deep-rooted perennials have been identified as preferred hosts for parasitic plants in the past (Press and Phoenix 2005), a category into which our prominent *Artemisia spp.* falls (Tabler 1964). *Artemisia spp.* had far more dead branches in the presence of *C. applegatei*, suggesting that the effects of parasitism may be leading to adverse health effects in sagebrush. Many of the *C. applegatei* present at our sites had

dead stems from past growth seasons intermixed with younger foliage, suggesting that their effects on these hosts were long term.

The negative effects of *C. linariifolia* presence on *Poaceae* spp. health were marginal, but *Poaceae* spp. has been documented as a host of other *Castilleja* in the past (Adler 2003). *Poaceae* spp were, along with *Artemisia* spp., the most common species in our plots. As a result of greater relative abundance, dominant plants with extensive root systems may find themselves disproportionately under attack by root parasites (Marvier 1998). To combat the seasonality of already limited resources in the environment, parasitic plants may prefer to feed upon relatively resource-rich perennial plants with deep roots.

Notably, *C. applegatei* and *C. linariifolia* had health effects on different plants. *C. linariifolia* presence had no effects on *Artemisia* spp. health, and *C. applegatei* had no effects on the health of *Poaceae* spp. This suggests that these two species may prefer different host species, and that this preference allows these two similar species to coexist in close proximity. While we did not examine root connections to establish clear evidence of parasitism, additional studies could investigate causality in this system by looking at confirmed parasitic links between these species and host health over time.

Castilleja are considered to be generalists (Musselman and Nickrent 2016), but our results support the idea that these two species may be exhibiting different preferences and effects on dominant species in the landscape. Our results provide insights into the effects of parasitic plants on species composition in the surrounding community and suggest that the positive association

between parasitic plants and plant diversity is not universal.

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