

Hemiparasitic *Castilleja* presence correlated with increased plant diversity across montane plant communities.

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ABSTRACT:

Root hemiparasites utilize haustoria to connect to host belowground roots and extract nutrients and water from surrounding hosts. Through parasitic symbiosis, parasitic plants disproportionately affect plant communities relative to their abundance by reducing host size, altering nutrient flow, and increasing local biodiversity. Their prevalence and potential as keystone species position hemiparasites as important

drivers of community structure. Here, we explored how the presence of hemiparasitic *Castilleja* is associated with differences in the structure of montane plant communities. Our objectives were to: (1) observe the relationship between three hemiparasitic *Castilleja* species and plant community diversity and composition, and (2) assess the host range and preference for each species in situ using direct and indirect sampling. We established a two-year study beginning in summer 2023 at the Rocky Mountain Biological Laboratory. We selected paired *Castilleja* presence and absence plots for three species across seven study sites. Percent cover of all species was recorded to assess the effect of *Castilleja* presence on plant community diversity and composition. To assess host range and preference, and to support nearest-neighbor and indicator-species analyses, we excavated *Castilleja* individuals to observe haustorial connections. Across sites, species, and years, the presence of *Castilleja* was consistently correlated with increased plant diversity, although not with consistent shifts in community composition. Excavations suggested that *Castilleja* species are generalist hemiparasites with some preference for common, dominant hosts. Our results identify a positive relationship between *Castilleja* presence and local plant community diversity and support the interpretation that these species act as facultative generalist hemiparasites.

KEYWORDS

Castilleja, parasitic plants, biodiversity, hemiparasitism, Orobanchaceae, community ecology, Rocky Mountains

INTRODUCTION:

Parasitic plants form a large and functionally diverse group of partial to full heterotrophs that have the potential to drive key community assembly processes, yet are understudied considering their prevalence across natural systems (Press and Phoenix, 2005; Nickrent, 2020). The parasitic habit has evolved independently across 13 different lineages and is unified by the formation of a unique organ called a haustorium. Parasitic plants utilize haustoria to connect to host branches and stems aboveground (aerial parasites) or to belowground roots (root parasites), extracting carbon, nutrients, and water for their growth and survival (Watson et al., 2022). Through the direct and indirect effects of parasitic symbiosis, parasitic plants disproportionately affect plant communities relative to their abundance by reducing host size, altering nutrient flow, and increasing local community diversity (Griebel et al., 2017; Craven et al., 2018). The prevalence, distinct physiology, and potential as keystone species position parasitic plants as a crucial piece in the puzzle of our understanding of ecological communities (Watson, 2009).

Root hemiparasites, which account for approximately 90% of parasitic plants (Nickrent, 2020), are partial parasites that maintain the ability to photosynthesize, and thus are not wholly reliant on their hosts to supply their nutrient and carbon demands (Terry, 1996; Watson et al., 2022). Recent evidence

suggests that root hemiparasites can drive plant community diversity, richness, and productivity (Press and Phoenix, 2005; DiGiovanni et al., 2017; Heer et al., 2018). While many hemiparasites are generalists with broad host ranges, they often exhibit varying degrees of specificity and show a higher preference for nitrogen-rich hosts (Gibson and Watkinson, 1989; Malcolm C. Press, 1998; Press and Phoenix, 2005). Hemiparasites may alter community structure and competitive dynamics between surrounding plants by preferentially targeting dominant host species and reducing competitive pressures (Gibson and Watkinson, 1989; Phoenix and Press, 2005; Hartley et al., 2015; McKibben and Henning, 2018; Hodžić et al., 2022). Host identity and dominance can determine whether the parasite causes a net increase or decrease in co-occurring plant diversity (Phoenix and Press, 2005; Hodžić et al., 2022). This suggests that our ability to predict the impact of hemiparasites on plant communities hinges on a more detailed understanding of parasite-host interactions (Gibson and Watkinson, 1989; Phoenix and Press, 2005).

The Orobanchaceae is the largest family of parasitic plants with a global distribution of over 2000 species (McNeal et al., 2013). Root parasitism is ubiquitous in the family, occurring in all but one genus (Schneeweiss, 2013). Most field ecological research on the family has been concentrated within the genera *Pedicularis* and *Rhinanthus* in Europe, which has shown root hemiparasites to positively or negatively impact species diversity (Gibson and Watkinson, 1989; Fibich et al., 2017; Scheidel and Borowicz, 2024), have variable effects on productivity (Davies et al., 1997; Hellström et al., 2011; Heer et al., 2018), and locally increase decomposition and nutrient availability (Malcolm C. Press, 1998; Bardgett et al., 2006; Watson, 2009; Demey et al., 2013). *Castilleja* is a widespread genus in the Orobanchaceae, comprising approximately 200 species that occur across North America, South America, and Asia. However, the highest number of species within the genus occurs in western North America (Tank et al., 2009). The diversity of *Castilleja* and its prevalence across North America position the genus as an ideal group for comparison with our understanding of European Orobanchaceae, where root hemiparasites have been more rigorously studied.

Whether *Castilleja* plays a keystone role in promoting diversity of co-occurring North American plant communities remains poorly understood. In a study on the impacts of parasitic plants in restoration, the presence of *Castilleja sessiliflora* Pursh was associated with increased species richness and soil phosphorus within an Illinois tallgrass prairie (Scheidel and Borowicz, 2024). A field-based survey assessing the impact of *Castilleja occidentalis* Torr. on diversity and productivity in the alpine tundra found *C. occidentalis* to be associated with increased biomass with minor changes in community diversity (Spasojevic and Suding, 2011). Two short-term studies conducted at the Rocky Mountain Biological Laboratory found neutral to positive associations between *Castilleja* and plant diversity. An experimental removal of *Castilleja* found no effect on plant community diversity (Reed, 2012), while an observational study found positive associations between of *Castilleja* species presence and plant diversity, across an

elevation gradient (McKibben and Henning, 2018). Altogether, these studies suggest that North American hemiparasites may share functional similarities with European species. While these results suggest similar ecological impacts between North American and European hemiparasites, the inconsistent results and limited number of species surveyed highlight a need for more comprehensive studies and evidence in the North American context.

While generalist hemiparasites have the potential to connect to a wide range of species within a community, those that exhibit a strong host preference may have impacts that are resource-, habitat-, or community-dependent (Atsatt and Strong, 1970; Gibson and Watkinson, 1989). As a result, parasites with host preference have the potential to drive and contribute to community dynamics and species interactions across different temporal and spatial scales. However, our understanding of host-parasite biology is limited by the restrictive methods available to quantify belowground parasitism in situ. For example, host range can be gleaned directly by extracting the host and parasite via digging (Musselman and Mann, 1977; Gibson and Watkinson, 1989), which risks the loss of haustorial connections during extraction. An alternative, indirect method to understand both host range and preference is via aboveground observation to detect the frequency with which a given potential host is more closely associated with the parasite than would be expected by chance alone (Gibson and Watkinson, 1989; Lymbery, 1989). While this method is non-destructive, it is limited due to the lack of confirmation of active haustoria on closely associated plants. Ex situ methods, such as greenhouse experiments, can provide vital information about how host species influence parasite growth rates (Matthies, 2017a), carbon acquisition (Press et al., 1987; Tennakoon and Pate, 1996; Světlíková et al., 2016), and resource allocation (Matthies, 2017b), but are limited in their ability to predict host species in situ. Despite these difficulties, a few studies have attempted to characterize the host range of parasitic *Castilleja* in North America, both in situ (Musselman and Mann, 1977; Montes-Hernández et al., 2015) and ex situ (Malcolm, 1966; Montes-Hernández et al., 2019), finding support for a generalist habit. However, no study has cross-validated the direct and indirect methods for assessing hemiparasitic plant hosts in situ. Connecting host preference to impacts on plant community diversity in situ will allow for more accurate predictions of the ecological impacts of hemiparasitic plants in natural communities.

Here, we address critical knowledge gaps for North American root hemiparasitic plants in the Rocky Mountain region. First, we established the relationships between three hemiparasitic *Castilleja* species and the diversity and composition of plant communities. Second, we assessed the host range and preference of each species in situ using both direct and indirect sampling methods. We posed three questions: (1) Is the presence of *Castilleja* species associated with more diverse plant communities? (2) Is the presence of *Castilleja* species associated with plant community compositional differences? (3) Do the *Castilleja* species of the Colorado Rockies exhibit host preference? We hypothesized that plant diversity

would be higher in the presence of *Castilleja*, and community composition to differ between presence and absence plots, potentially interacting with site and species-specific effects. We expected *Castilleja* of the Colorado Rockies to have broad host ranges, but we anticipated evidence for species-specific host preferences for locally dominant species.

METHODS:

Study Sites

We conducted a two-year study in the summers of 2023-24 at the Rocky Mountain Biological Laboratory (RMBL), located in the East River valley of the West Elk mountains, approximately 10 km North of Crested Butte, Colorado (38.9592° N, 106.9898° W, elevation 2,895 m). Field sites spanned an elevation gradient of 2,637 m to 3,191 m, with ecosystems ranging from sagebrush steppe to montane and subalpine meadows. The region receives significant annual snowfall from November to May, with accumulations of 246 cm in 2023 and 164 cm in 2024 (Barr, 2025). Average summer temperature and precipitation (May – August) were 20.1 °C, 0.80 in for 2023 and 18.1 °C, 2.24 in for 2024 (Barr, 2025). We studied three species of *Castilleja* across seven study sites. All sites were surveyed in both summers of 2023 and 2024, except for Johnson Hill, Copper Creek, and Almont, which we established and surveyed in the summer of 2024 (Table I).

We studied communities with *Castilleja chromosa* A. Nelson at one site, “Almont,” located roughly 11 km east of CO-135 along Jacks Cabin Cutoff (Table I), south of RMBL. *C. chromosa* grows in sagebrush communities, where it receives direct sunlight and is situated on dry, rocky sediment. It occurs at lower elevations than the other species studied and flowers from late April to early July. Dominant members of this plant community included *Chrysothamnus depresus* Nutt., *Artemisia arbuscula* Nutt., *Chrysothamnus vaseyi* (A.Gray) Greene, and *Phlox multiflora* A. Nelson.

We studied communities with *Castilleja linariifolia* Benth. at three sites. Two of the sites, “Deer Creek 1 & 2”, are roughly 1.5 km from RMBL on a subalpine meadow hillslope above the Deer Creek Trail (Table I). Dominant members of the Deer Creek plant community included *Artemisia tridentata* Nutt., *Symphoricarpos rotundifolius* A. Gray, *Eriogonum umbellatum* Torr. var. *majus* Hook., and *Festuca thurberi* Vasey. The third site, “Johnson Hill”, is located on a small hill near the RMBL townsite (Table I). Dominant members of the plant community included *Populus tremuloides* Michx., *Berberis repens* Lindl., *Heliomeris multiflora* Nutt., *Lathyrus lanszwertii* Kellogg, and *Bromus frondosus* (Shear) Wooton & Standl. *C. linariifolia* grows in both sagebrush communities and subalpine meadows dominated by perennial wildflowers and grasses. It grows at higher elevations than *C. chromosa* and flowers throughout the growing season.

We studied communities with *Castilleja septentrionalis* Lindl. at three sites. The first site, “Avery Picnic”, is roughly 2.3 km north of RMBL in a meadow by the Avery Picnic parking area (Table I). At Avery, dominant species included *Taraxacum officinale* F.H. Wigg, *Potentilla pulcherrima* Lehm., *Poa pratensis* L., *Erigeron subtrinervis* Rydb. Ex Porter & Britton, and *Ipomopsis aggregata* (Pursh) V.E. Grant. The second site, “Copper Creek”, was located roughly 1.5 km east of RMBL along the Copper Creek trail (Table I). Dominant species at Copper Creek included *Eremogone congesta* (Nutt.) Ikonn., *Taraxacum officinale*, *Poa pratensis*, *Thalictrum fendleri* Engelm. ex A Gray, and *Maianthemum stellatum* (L.) Link. The third site, “Emerald Lake”, roughly 7.2 km north of RMBL, was located in a meadow 50 m southeast of Emerald Lake (Table I). Dominant members of the plant community included *Potentilla pulcherrima*, *Fragaria virginiana* Mill., *Senecio crassulus* A. Gray, *Deschampsia cespitosa* (L.) P.Beauv., and *Anemone multifida* Poir. In general, *C. septentrionalis* grows in moist subalpine meadows dominated by perennial wildflowers at moderate to higher elevations and flowers all summer.

Although we did not conduct community diversity or composition analysis for *Castilleja miniata* Douglas ex Hook. var. *miniata* is a common and abundant species that occurs across a wide range of habitats throughout the study area, and we were able to conduct host assessments for the species.

Community Diversity Sampling

We estimated community composition and species abundance at each study site from 20 50 x 50 cm (0.25 m²) paired plots with *Castilleja* (treatment) or without *Castilleja* (control) (40 plots total/site/year). At each study site, we selected 20 random sampling points along a 50 m transect to place a 0.25 m² quadrat centered around the closest *Castilleja*. We then selected a paired plot within 2 m, which was absent of *Castilleja* or any other hemiparasite. In each plot, we recorded the number of plant species, the number of individuals of each species, and the percent cover of each species, including bare ground. In *Castilleja* present plots, species growing within a 10 cm radius of *Castilleja* were identified and documented as nearest neighbors (NN) (Gibson and Watkinson, 1989). In each year, 20 plot pairs were sampled within each study site. All 2023 sites were resampled in 2024, in addition to those established in the second year (total $n = 220$ paired-plots) (Table I). Samples of all plant community members were vouchered at the RMBL Herbarium to ensure the accuracy of species identifications. As population density and habitat varied between sites and species, we occasionally modified the specific data collection methods to ensure accurate surveys of all sites (see below).

We sampled *C. chromosa* without modifications to the methods above (total $n = 20$ paired plots). *C. linariifolia* populations required several modifications. Given their lower density relative to other *Castilleja* species, we found it more effective to sample every *Castilleja* that we encountered along the transect at both Deer Creek Sites. In denser clumps of *Castilleja* (<1 m apart), the focal *Castilleja*

plant was selected via a random number generator. At Johnson Hill, the population was too sparse for transect sampling. Instead, every *Castilleja* individual in the population was sampled.

Host identity and haustoria analysis

We collected *Castilleja* nearby but not within our study plots (Table SI). To identify hosts, we excavated soil and roots to a depth of ~15 cm within a 10 cm radius of a focal *Castilleja* plant. Excavated plants were then transported to the RMBL Herbarium and soaked in water. Typically, soils with a higher clay content were soaked for longer, usually over 12 hours. We then agitated the root mix to release adhered soil particles and prepared collections for observation. Root mats were examined under a dissecting microscope to identify haustoria. If haustoria were found, we recorded the host species as a confirmed host. When attached haustoria could not be traced back to a host plant, either due to severed root connections or high root density, haustoria segments with unidentified host roots were collected and preserved with the specimen. The *Castilleja*, host, and haustoria were then vouchered as an extended specimen for the RMBL Herbarium (Teixeira-Costa et al., 2023). In total, we made 29 collections of *C. chromosa*, *C. linariifolia*, *C. miniata*, and *C. septentrionalis* from 2023 to 2025 (Table SI).

Statistical Analysis

Data curation, analysis, and visualizations were conducted using R Statistical Software version 4.5.1 (R Core Team, 2024) in RStudio (Posit team, 2025). *Castilleja* species were removed from the dataset for all diversity and compositional analyses to determine differences between the co-occurring plant community (Wickham, 2016). To assess differences in Shannon diversity, plant richness, and Pielou's evenness between *Castilleja* presence and absence plots, we used a linear mixed-effect model in the lme4 package (Bates et al., 2003) with *Castilleja* presence, species, and year as fixed effects, and pair-plot ID and site as random intercepts [lme4 package (Bates et al., 2003)]. Model assumptions were assessed using the performance package (Lüdtke et al., 2019). Post-hoc analyses were then conducted using the emmeans package (Lenth, 2017) to investigate pairwise differences between sites, presence-absence plots, and their interactions. We used the Anova function from the car package (Fox et al., 2001) to conduct null hypothesis tests for all fixed effects in the mixed models. To determine differences in species composition, we first conducted an indicator species analysis (De Cáceres et al., 2010) for each site to assess which species were associated with *Castilleja* presence or absence communities. We then performed a Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray-Curtis dissimilarities and the adonis() function in the vegan package (Oksanen et al., 2001) with *Castilleja* presence, species, year, and site, and their interactions as predictor variables. Data were visualized using ggplot2 (Wickham et al., 2007), and ggpubr (Kassambara, 2016) packages.

To analyze nearest neighbor data, we conducted a linear regression of relative NN frequency (the number of observations of a species as a NN divided by the total number of NN observations) on the relative total frequency of all species. This way, the total expected frequency is 100% for both NN and total. We then calculated 95% prediction intervals alongside 95% Confidence intervals. Species that fell outside the 95% prediction interval were significantly more (or less) abundant as a NN than expected by chance alone.

RESULTS:

Community diversity is higher in association with *Castilleja*

Across sites, species, and years, we found that the presence of *Castilleja* was positively associated with plant community Shannon diversity ($\chi^2 = 13.57, p < 0.001$) (Fig. 1a), which was driven by increased species richness ($\chi^2 = 18.32, p < 0.001$) (Fig. 1b), but not evenness ($\chi^2 = 2.06, p = 0.151$) (Fig. 1c). For species richness averaged across hemiparasite species, our post-hoc analysis showed higher species richness in *Castilleja* presence plots by about half a species (estimate = 0.590) ($p = 0.08$) in 2023 and by 0.844 species ($p < 0.001$) in 2024. These results support our hypothesis that plant diversity is higher in the presence of *Castilleja*. Contrary to our expectations, we found no significant differences among *Castilleja* species in their impact on co-occurring plant Shannon diversity, species richness, or species evenness. These results suggest that the presence or absence of *Castilleja* is a stronger predictor of plant community diversity than the potential variation among species within the genus. Sampling year, most likely driven by interannual changes in snowpack, temperature, and precipitation, was significantly correlated with changes in Shannon diversity ($\chi^2 = 35.36, p < 0.001$), species richness ($\chi^2 = 141.69, p < 0.001$), and species evenness ($\chi^2 = 6.07, p < 0.05$) (Fig. 1).

Plant community composition is robust against *Castilleja*'s effect on species diversity

Despite differences in diversity, we found that *Castilleja* presence was not associated with differences in plant community composition (PERMANOVA $F_{1,424} = 0.77, p = 0.72$), contrary to our expectations (Fig. 2). However, community composition was significantly predicted by species (PERMANOVA $F_{2,424} = 91.90, p = 0.0001$), site (PERMANOVA $F_{4,424} = 40.97, p = 0.0001$), and year (PERMANOVA $F_{4,424} = 21.85, p = 0.0001$). Our indicator species analysis revealed several significant associations between co-occurring plant species and *Castilleja* species at the site level (Table II). This suggests that while differences in plant community diversity and site-level compositional changes exist, they were either insufficient in magnitude or consistency to alter community composition between hemiparasite presence and absence plots across Rocky Mountain plant communities.

Rocky Mountain *Castilleja* are generalist hemiparasites

Plants within the *Castilleja* genus appeared to have a broad host range with some host preference for common and dominant members within montane plant communities (Fig. 3). Direct excavation of host-parasite complexes revealed 10 confirmed host species with which *Castilleja* species formed haustoria (Fig. 3). Our nearest neighbor analysis identified 13 plant taxa more likely to occur within a 10 cm radius of *Castilleja* than by chance alone (Fig. 4). By functional group, forbs (11 taxa) and grasses (7 taxa) represent the most common potentially preferred host species (Fig. 3). In total, our analysis shows that only 21 of the 249 plant taxa found in our dataset appear to be potential preferred hosts. Direct observations of haustoria were confirmed on only three of the 13 species that appeared in our Nearest Neighbor analysis, and two of the three species that emerged as indicator species in *Castilleja* presence plots. These results suggest *Castilleja* species are generalist hemiparasites capable of connecting to a broad range of host species.

DISCUSSION:

We found a consistent and positive relationship between *Castilleja* presence and co-occurring plant community diversity. Importantly, this was a general pattern across three *Castilleja* species, seven sites, and two years that differed strongly in abiotic conditions and overall plant diversity. These results expand on and confirm the findings of McKibben and Henning (2018), which similarly found higher plant community diversity across an alpine gradient in the presence of *Castilleja* species at RMBL. However, our results contrast with two other studies on North American *Castilleja*, which found no correlation between parasite presence and community diversity (Spasojevic and Suding, 2011; Reed, 2012). One possible explanation for these differences is the observational nature of our study, which contrasts with the experimental removal (Reed, 2012), as that approach may require a longer duration to develop an effect.

Our results support the theory that the presence of hemiparasitic plants leads to increases in co-occurring plant diversity, and suggest potential similarities between the functioning of European and North American root-hemiparasites (Phoenix and Press, 2005; Fibich et al., 2017; Heer et al., 2018). In addition, our results lay the groundwork for future experimental studies to confirm the mechanisms by which root-hemiparasites facilitate increases in plant community diversity.

Plant community composition is robust against *Castilleja*'s effect on species diversity

Our results suggest that the consistent, albeit small, changes in diversity did not translate into consistent differences in community composition between *Castilleja* presence and absence plots, contrary to our hypothesis. These results contrast with the significant and small effect of *Castilleja* presence on

underlying plant community composition found by McKibben and Henning (2018). Interestingly, our indicator species analysis revealed several species that increased in relative abundance in association with the presence of *Castilleja* (Table II). These differences suggest small-scale compositional changes are likely specific to host-parasite relationships within a given site (Cameron and Phoenix, 2013). Across our study, we observed over 230 species, characterized by high turnover in species among sites. As plant communities were heterogeneous at the plot level, within the landscape, one would expect inconsistent changes in species composition, which could explain the lack of an overall effect of *Castilleja* presence on plant community composition.

Rocky Mountain *Castilleja* are generalist hemiparasites

Our findings provide the first list of putative and confirmed host species for Rocky Mountain *Castilleja* (Fig. 3). We found that Rocky Mountain *Castilleja* species parasitize a broad range of hosts, with no consistent preference for functional groups or species. Our findings suggest that *C. septentrionalis*, *C. linariifolia*, and *C. chromosa* behave as facultative generalist hemiparasites, consistent with hemiparasitic plants of the Orobanchaceae and in support of our hypothesis (Matthies, 2017c). Our work provides support for using both direct and indirect methods to assess host-parasite relations, as putative host species suggested by each method minimally overlapped (Fig. 3). Of particular interest are species, such as *C. septentrionalis*, which we found to parasitize *Fragaria virginiana*, and *C. linariifolia*, which we found to parasitize *Viola praemorsa* and *Eremogone congesta*. These were the only hosts identified through both direct haustoria observation and indirect analysis, which suggests these species may serve as preferential or higher-quality hosts and could be helpful in predicting the ecological impacts of *Castilleja*.

Our study highlights four considerations for reducing bias and maximizing inference when identifying hosts of hemiparasites. First, excavation of root systems can be particularly challenging for larger or woody host species. However, the avoidance of large plants can bias host species lists towards herbaceous and grassy species. In future studies, sampling efforts should prioritize sampling from the observed range of functional groups and growth forms to limit potential bias. Second, as haustoria connections can be delicate, excavation can often separate host and parasite root segments, thereby limiting the ability to trace roots back to aboveground tissue and identify hosts without the use of molecular methods. For our project, whenever possible, we collected and preserved host-parasite root segments, cataloging them alongside herbarium specimens for future molecular identification. Third, direct excavation can be limited by the persistence and potential inactivity of haustoria. To date, we are unaware of any study that has demonstrated how long haustoria persist and remain active on an individual host in the field, which would significantly increase our understanding of host dependency and

340 persistence. Fourth and finally, in our study, we often observed *Castilleja* parasitizing multiple species
341 within a given excavation effort (Table SI), which makes host identity via attached or severed root
342 segments more challenging to confirm. The most rigorous approach, therefore, would be to use a
343 combination of molecular and tracing techniques (Svĕtlíková et al., 2016).

344 Nearest neighbor analysis, especially when paired with additional analyses such as indicator
345 species, provides an ecologically informed estimate of potential hosts. This is because parasitic
346 Orobanchaceae are known to have limited root growth (Van Hovel et al., 2011), so species detected as
347 nearest neighbors are likely to be hosts, particularly for herbaceous hosts. However, this statistical method
348 is less likely to detect host species with deep or sprawling root systems, such as woody species that occur
349 outside the 10 cm radius. Nevertheless, our host species list provides useful information for future studies
350 interested in assessing host-parasite relationships in the field. This enables us to better understand how
351 host identity influences parasite fitness, the ecological impacts of parasitism, and ultimately, to increase
352 our ability to predict the fate of natural communities.

354 **CONCLUSIONS:**

355 Our study reveals a positive correlation between the presence of *Castilleja* and the diversity of
356 Rocky Mountain plant communities. The results of this study provide evidence for the ubiquitous nature
357 of hemiparasitic plants as potential keystone species. Future work should incorporate assessments of
358 productivity alongside diversity, composition, and host identity within plots to better connect host and
359 diversity studies. Additionally, there is a great need for experimental manipulations to identify the
360 underlying mechanisms between the presence of hemiparasitic plants and increased plant community
361 diversity. This would provide a more complete investigation into the effect of hemiparasites on
362 community composition.

365 **CRedit Statement:**

366 **Jordan Argrett:** Conceptualization, Methodology, Validation, Formal analysis, Investigation,
367 Supervision, Project administration, Funding acquisition, Resources, Data Curation, Writing - Original
368 Draft, Visualization. **Makena Lang:** Methodology, Investigation, Data Curation, Funding Acquisition,
369 Visualization, Writing - Original Draft. **Anders Hastings:** Investigation, Data Curation, Writing -
370 Original Draft. **Anny Chung:** Formal analysis, Writing - Review & Editing. **Nina Wurzbarger:** Formal
371 analysis, Writing - Review & Editing. **Charles F. Williams:** Conceptualization, Methodology, Formal
372 analysis, Investigation, Supervision, Project administration, Resources, Writing - Review & Editing

Acknowledgments:

The authors thank the staff of the RMBL Education Program. The RMBL Jean H. Langenheimer Endowed Graduate Fellowship, RMBL Graduate Student Fellowship, RMBL Returning Student Fellowship, and the Lewis and Clark Fund for Exploration and Field Research provided funding for this project. Thank you to Makena Lang for the use of her botanical illustrations and to Katherine Marie Schroder for contributions regarding data presentation and layout.

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