RESEARCH ARTICLE

The role of hemiparasitic plants: influencing tallgrass prairie quality, diversity, and structure

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Wood betony, Orobanchaceae (*Pedicularis canadensis*) and bastard toadflax, Santalaceae (*Comandra umbellata*) are two root-hemiparasitic plant species found in tallgrass prairie communities. Natural resource managers are interested in utilizing these species as "pseudograzers" in grasslands to reduce competitively dominant grasses and thereby increase ecological diversity and quality in prairie restorations and urban plantings. We performed an observational field study at 5 tallgrass prairie sites to investigate the association of hemiparasite abundance with metrics of phylogenetic and ecological diversity, as well as floristic quality. Although no reduction in C_4 grasses was detected, there was a significant association between hemiparasite abundance and increased floristic quality at all 5 sites. Hemiparasite abundance and species richness were positively correlated at one restoration site. In a greenhouse mesocosm experiment, we investigated response to parasitism by *P. canadensis* in 6 species representing different plant functional groups of the tallgrass prairie. The annual legume partridge pea, Fabaceae (*Chamaecrista fasciculata*) had the greatest significant dry biomass reduction among 6 host species, but the C_4 grass big bluestem, Poaceae (*Andropogon gerardii*) had significantly greater aboveground biomass when grown with the hemiparasite. Overall, host species biomass as a total community was significantly reduced in mesocosms, consistent with other investigations that demonstrate influence on community structure by hemiparasitic plant species. Although hemiparasites were not acting as pseudograzers, they have the potential to influence community structure in grassland restorations and remnants.

Key words: *Comandra umbellata*, grassland, mesocosm, *Pedicularis canadensis*, phylogenetic diversity, restoration

Implications for Practice

- Hemiparasitic plants have the potential to affect plant community structure and biomass in grassland restorations and remnants.
- The relationship between hemiparasite cover and plant communities varies among sites, challenging simple assumptions about how including these species in seed mixes will affect restoration outcomes. However, hemiparasite abundance is consistently, positively associated with community floristic quality, as measured by floristic quality index.
- Effects of hemiparasites vary among host plant species and do not necessarily reduce C_4 grass growth in a community setting. Rapidly growing annual forbs may also be susceptible to growth reductions by hemiparasites.

Introduction

Hemiparasitic plants can influence the structure and diversity of plant communities through differential host selection and indirect effects on community interactions (Hedberg et al. 2005; Phoenix & Press 2005; Hatcher et al. 2012; Bao et al. 2015). Studies reveal a general pattern of dominant grass suppression and a concomitant increase in diversity of forbs and legumes (Cameron et al. 2005). Many of these studies have focused on the annual hemiparasite yellow rattle (*Rhinanthus minor*) in dry grasslands (Bardgett et al. 2006; Watson 2009; Fisher et al. 2013). Hemiparasites have been described as ecosystem engineers for influencing community dynamics (Hatcher et al. 2012), and as keystone species for affecting nutrient cycling (Watson 2009). Recently, tallgrass prairie managers have asked whether hemiparasites may act as pseudograzers by reducing biomass of dominant grasses in prairies (Henderson 2003; Campbell 2014).

Late season dominant C_4 grasses can sometimes overtake tallgrass prairie restorations, reducing forb diversity and ecological function (McCain et al. 2010). Grasslands of North America evolved with regular disturbances such as fire and grazing. Fire naturally stabilizes prairie communities, increases

diversity, and favors plant species representing later successional stages (Larkin et al. 2015). Fire has been used as a management tool on restored and remnant prairies for the past several decades. Bison (*Bison bison*) favor grasses, and their grazing increases landscape heterogeneity and diversity (Knapp et al. 1999; Collins & Calabrese 2012). Managers report that patches of hemiparasitic plants in prairies appear to exhibit similar structure to areas grazed by bison, with an apparent reduction of dominant tall grasses and increase in forb diversity (Henderson 2003). Thus, there is potential for hemiparasites to act as pseudograzers in smaller prairie restorations and urban native plant landscapes where native or domestic grazer introduction is not feasible (Campbell 2014).

Two previous studies investigated the effect of wood betony, Orobanchaceae (*Pedicularis canadensis*) on a tallgrass prairie plant community. *Pedicularis canadensis* abundance was significantly correlated with species richness (SR) (Hedberg et al. 2005), and forb biomass was reduced in plots with *P. canadensis* compared to areas where the hemiparasite had been removed three years earlier (Borowicz & Armstrong 2012). The presence of *P. canadensis* also reduced grass biomass by 80% and total biomass by 32%, demonstrating that this hemiparasite can exert a similar pattern on community structure as the annual *R. minor* in European meadows (Cameron et al. 2005). Similarly, the annual or biennial hemiparasite *Pedicularis kansuensis* increased SR and Shannon index in central Asian alpine grasslands (Bao et al. 2015). Combined, these studies suggest that hemiparasites affect community structure through differential host selection, shoot biomass reduction, and perhaps modifying competitive interactions to the advantage of non-dominant species.

Pedicularis canadensis and bastard toadflax, Santalaceae (*Comandra umbellata*) are two perennial hemiparasites found in tallgrass prairie communities. *Pedicularis canadensis* is an obligate generalist hemiparasite and has been shown to parasitize 80 species from 35 families (Piehl 1963). *Comandra umbellata,* a facultative generalist, has been reported to have as many as 40 different host species from at least five families (Moss 1926; Zentz & Jacobi 1989). Both species are found in remnant and restored prairie sites in the Chicago region, where this study took place. We investigate whether the abundance of these hemiparasites is associated with increased phylogenetic diversity (PD), ecological diversity, and floristic quality, as well as reduced cover of dominant C_4 grasses in tallgrass prairies. We predict that hemiparasite abundance will be associated with an increase in diversity and floristic quality. If hemiparasite abundance is associated with reduced dominant grass cover and increased diversity metrics, the role of these hemiparasitic species as pseudograzers will be supported.

In previous greenhouse experiments, *P. canadensis* was grown with one or two host species in a pot. Shoots of big bluestem, Poaceae (*Andropogon gerardii*) were marginally reduced by *P. canadensis* when it was the only host species offered (Borowicz & Armstrong 2012), and the hemiparasite did not significantly affect interspecific or intraspecific competition between pairs of host plants (*A. gerardii,* showy

tick-trefoil [*Desmodium canadense*], and/or late goldenrod [*Solidago altissima*]) (Hedberg et al. 2005). In this study, we examined how biomass of host species was affected by *P. canadensis* in a mesocosm composed of potential host plants from different functional groups likely to be encountered in a tallgrass prairie, predicting that biomass effects will differ among host species. Specifically, we predicted the response to parasitism will be greatest in a C_4 grass, based on managers' observations, but forb responses will vary. These approaches will help to determine if managers could use hemiparasitic plants to increase plant diversity and ecological function in prairie restorations where grazing is not feasible.

Methods

Field Study Sites

We selected four tallgrass prairie restoration plots at Fermi National Laboratory in Batavia, IL, and a similar reference remnant site within the West Chicago Prairie (WCP) Forest Preserve in West Chicago, IL, approximately 6 km north of the restorations (Table 1). The remnant site was never cultivated, although it did receive some grazing by livestock from nearby railways prior to 1960 (Jastrow 1987). Cultivation at the Fermilab location began in mid-19th century and ended in 1970 (Betz 1986). Prairie restoration began at Fermilab in 1975 under a four-stage planting strategy called successional restoration. First, a "prairie matrix" seed mix of 25 species with wide ecological tolerances was planted. This early successional stage included tall grasses such as *Andropogon gerardii* and Indiangrass (*Sorghastrum nutans*) as well as early colonizing forbs such as black-eyed susan (*Rudbekia hirta*), golden Alexander (*Zizia aurea*), and *Desmodium canadense*. Five years after planting, the stage one species were established, soil aggregates developed, and fuel load was adequate to sustain a managed burn. Subsequent seed mixes of stages two, three, and four consisted of species with narrower ecological tolerances based on observations of plant species dispersal into local remnant prairies. Stages two and three were interseeded in series within the next 15 years of restoration. Stage four species were added in the third decade of restoration. Three hemiparasitic species were included in the stage two list: *Pedicularis canadensis*, *P. lanceolata*, and *C. umbellata* (Betz et al. 1996), resulting in patchy distribution of *P. canadensis*, similar to the WCP remnant, where *C. umbellata* is ubiquitous.

Table 1. Sites in the field study, with location, year planted, and age during year 1 of the study (2014).

Site	Location	Planted	Age
WCP remnant	DuPage Co. Forest Preserve	—	—
MRNE	Fermilab accelerator ring	1981	33
MRNW	Fermilab accelerator ring	1981	33
MRSW	Fermilab accelerator ring	1979	35
P15	Fermilab public access	1986	28

Field Study Methods

We surveyed plant communities in each site in late summer (August–September) of year 1 and spring (May–June) of year 2 of the study within thirty $1\,m^2$ quadrats. At each site, we established a permanent starting point with a metal stake and five 60 m transects extending in five different directions. Along each transect, six quadrats were located at random distances along and to the right or left of the line. In total, over two seasons at each of the five study sites, we surveyed six quadrats along 10 different transects for a total of 60 samples per site (300 samples total). This sampling method is a modification of that used by Hedberg et al. (2005). We recorded percent cover of bare soil and all plant species within each quadrat.

We calculated community metrics for ecological diversity, floristic quality, and PD. Shannon index and SR measured ecological biodiversity per quadrat. The floristic quality index (FQI) is based on coefficients of conservatism that are provided for each native species in Swink and Wilhelm (1994). Coefficients of conservatism ("C-values") are integers ranging from 0 to 10 based on ecological tolerance for disturbance. Taxa with high C-values (7–10) are the first to be lost when a natural area is degraded, so high floristic quality indices indicate sites have experienced minimal degradation. Those taxa with values lower than 3 are species that inhabit areas that have experienced extreme degradation such as toxic pollution, vehicular traffic, or overgrazing (Freyman et al. 2015). Floristic quality tends to increase in prairie restorations with age and proper management (Spyreas et al. 2012) and is useful in evaluating restoration progress (Matthews et al. 2015). Furthermore, a new website increases accessibility of floristic quality assessment worldwide (Freyman et al. 2015; http://universalFQA.org). One PD metric, mean pair-wise distance (mpd), has been used in similar studies (Whitfeld et al. 2013) and measures mean phylogenetic distance between all pairs of species in each quadrat (Webb et al. 2002). Phylogenetic methods and calculation of mpd are explained in Appendix S1, Supporting Information including the species analyzed (Table S3) and the resulting phylogram (Fig. S1).

We analyzed SR, Shannon index, FQI, and mpd with multivariate analysis of covariance (MANCOVA), treating site as an independent factor and total percent cover of hemiparasitic plant species as a covariate. Percent cover of *P. canadensis* and *C. umbellata* were combined because both species could exert similar effects on prairie host species and subsequently on the metrics used in the analysis. Percent cover for the hemiparasites was removed from metric calculations to avoid collinearity. A separate analysis of covariance (ANCOVA) compared percent cover of C_4 grass species with hemiparasite cover per site to test the hypothesis that hemiparasitism reduces C_4 cover in particular.

Mesocosm Experiment Methods

To determine how the hemiparasite *P. canadensis* affects growth of potential host plants in different functional groups, we assembled prairie mesocosms with and without *P. canadensis*. Each mesocosm consisted of a C_3 grass, a C_4 grass, an annual

Table 2. Plant species in each mesocosm, coefficient of conservatism in Illinois, and functional group.

Species	Family	Coefficient	Functional Group
Andropogon gerardii	Poaceae	5	Perennial C_4 grass
Koeleria macrantha	Poaceae	7	Perennial C_3 grass
Dalea candida	Fabaceae	10	Perennial legume
Chamaecrista fasciculata	Fabaceae	1	Annual legume
Penstemon hirsutus	Plantaginaceae	8	Perennial summer-blooming forb
Symphyotrichum oolentangiensis	Asteraceae	8	Perennial autumn-blooming forb
Pedicularis canadensis	Orobanchaceae	7	Hemiparasite

legume, a perennial legume, and two perennial non-leguminous forbs (Table 2). Seeds of the annual *Chamaecrista fasciculata* were germinated prior to transplanting into mesocosms in April 2015. Junegrass (*Koeleria macrantha*) seeds were germinated the preceding September, given winter dormancy in February in an environmental chamber at 4.4°C/ −2.2°C and 10 hours light/14 hours dark for four weeks, and then transplanted. Seeds of the C_4 grass *A. gerardii* were germinated in December but did not receive a winter dormancy period because the seedlings were judged to be too young for extreme cold temperatures. Second-year plugs of the perennial species white prairie clover (*Dalea candida*), sky blue aster (*Symphyotrichum oolentangiensis*), and hairy beardtongue (*Pentstemon hirsutus*) were obtained (Pizzo Native Plant Nursery, Leland, IL, U.S.A.) and transplanted into mesocosms. *Pedicularis canadensis* plants were transplanted from the Fermilab prairie in early October and overwintered in a cold frame until mesocosm assembly in April.

We established 70 mesocosms in early April 2015, each containing the six potential host species with positions randomized to provide equal opportunity of parasitism among host species, and 35 containing a *P. canadensis* individual. Each mesocosm consisted of a plastic cache pot (27.94 cm diameter, 10.29 L) filled two-thirds full with a 50/50 mixture of live screened prairie soil and Fafard 3B (Sun Gro Horticulture, Agawam, Massachusetts, USA) growing medium to aid drainage. Field soil was collected and pooled from each of the four restorations in the field study, including soil from patches both with and without *P. canadensis*, to control for potential soil microbes that may be specific to *P. canadensis* patches. At planting, spaces between plants were filled with growing medium. We monitored plant growth, survival, and development for 18 weeks of growth in a research greenhouse where natural light was supplemented with high pressure sodium vapor lights, with daylengths and temperature adjusted weekly to mimic natural outdoor conditions. Water was provided as needed to maintain a relatively dry soil environment. No fertilizers were given throughout the growing period to maintain a low-nutrient environment. Plants
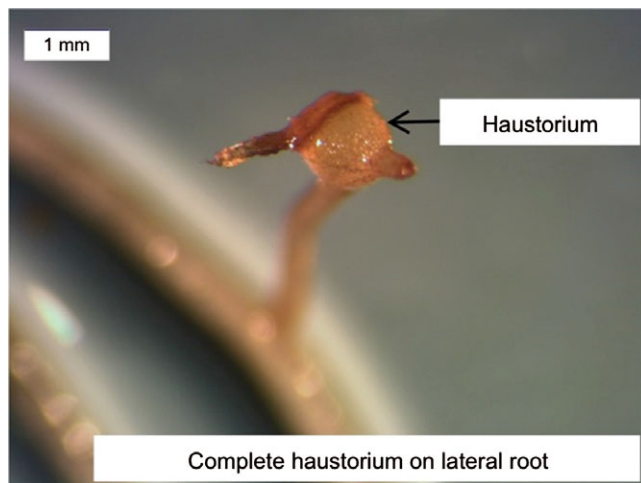
Figure 1. *Pedicularis canadensis* haustorium, the site of nutrient absorption for the hemiparasite. Scale bar = 1 mm.

were staked as needed to remain upright, and no cutting or artificial herbivory was applied. Pot positions were randomized on the benches monthly.

After 18 weeks, shoots of each plant in all mesocosms were cut, dried for 72 hours at 60°C, and weighed. Parasitism was confirmed in treatment replicates by locating haustoria on *P. canadensis* roots under a stereomicroscope (Fig. 1). Haustoria were found on small lateral roots as well as on primary roots, indicating that they did develop and colonize host plants during the mesocosm growth period. We analyzed shoot biomass of host species using MANOVA followed by univariate (protected) ANOVAs for each species, treating *P. canadensis* presence as an independent variable.

Results

Field Study

Hemiparasite percent cover (Wilkes $\Lambda = 0.917$, $p < 0.001$), site (Wilkes $\Lambda = 0.372$, $p < 0.001$), and site × hemiparasite cover interaction (Wilkes $\Lambda = 0.907$, $p = 0.027$) were all significant factors in the MANCOVA. We present results from univariate analyses of each metric. There was a significant site × hemiparasite interaction for SR, indicating that the effect of hemiparasite differed among sites (Table S1; Fig. 2A). Site-specific regression revealed that at only one site (MRSW) did the slope differ significantly from zero ($F_{[1,58]} = 7.81$, $p = 0.007$, $R = 0.34$). Shannon index was unaffected by hemiparasites but did differ among sites (Table S1). Floristic quality was significantly associated with hemiparasite cover, with greater FQI in quadrats that also had higher cover (Fig. 2B). The site × cover interaction for FQI was marginally significant. Although mpd varied among sites, it was unrelated to hemiparasite cover (Table S1). Percent cover by C_4 grasses was unaffected by site ($F_{[4,293]} = 2.12$, $p = 0.078$), hemiparasite cover ($F_{[1,293]} = 1.03$, $p = 0.310$), and their interaction ($F_{[4,293]} = 1.62$, $p = 0.170$).
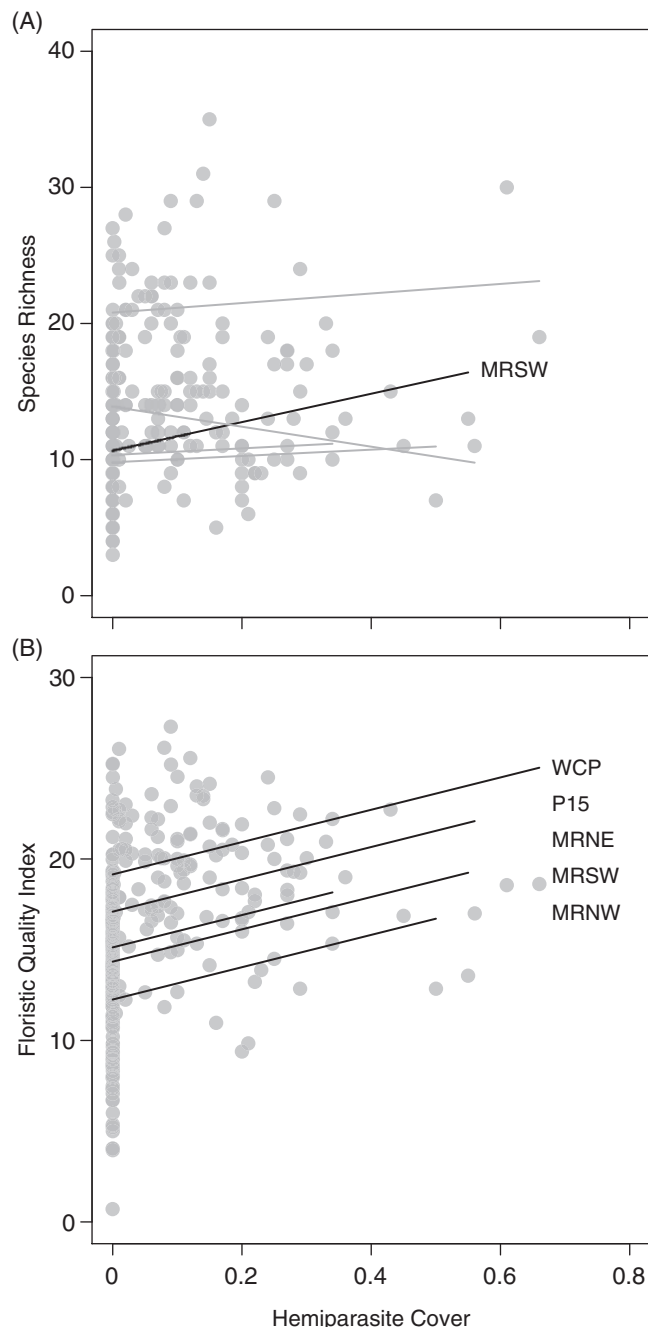

Figure 2. Relationship between hemiparasite cover and (A) species richness and (B) floristic quality index in quadrats for all sites. In both panels, lines represent each study site, with lines significantly differing from zero in black and lines not differing from zero in gray. Abbreviations for each site (listed in Table 1) indicate identity of each significant line.

Mesocosm Experiment

After transplanting, *Pedicularis canadensis* plants established in all 35 experimental mesocosms, and 63% flowered in the first third (6 weeks) of the experiment. By week 13, *P. canadensis* had died in five pots; these were removed from analyses because parasitism effects presumably ended while mesocosm
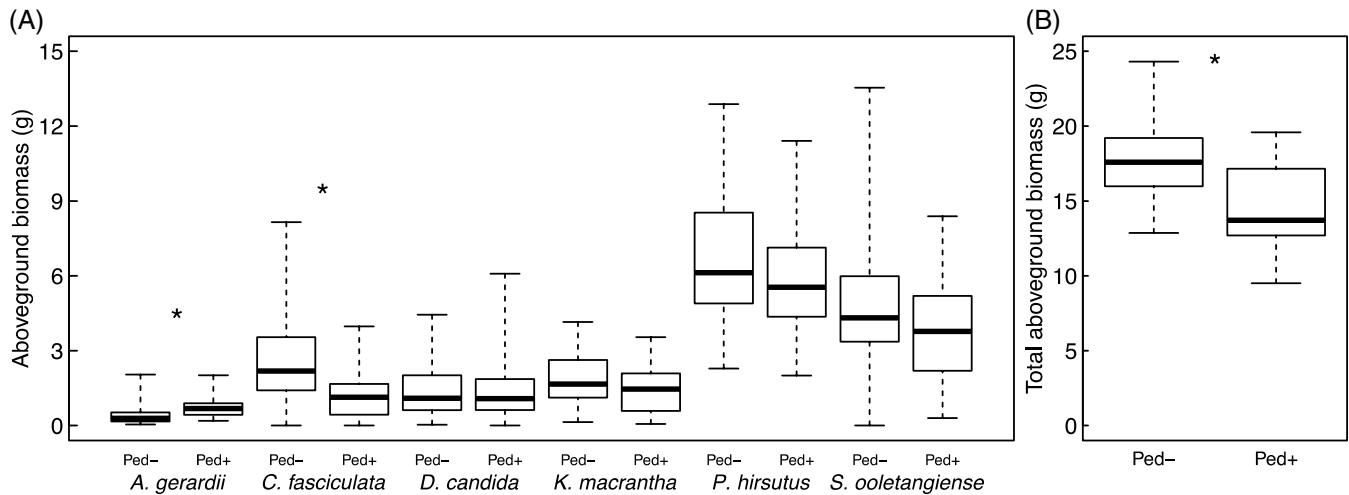
Figure 3. (A) Mean aboveground biomass (±1 SE) of host plant species without (Ped−) and with (Ped+) *Pedicularis canadensis* in mesocosm experiment. (B) Mean total aboveground biomass of all host plant species combined without and with *P. Canadensis*. In both panels, stars indicate a significant effect of hemiparasite presence. Boxes indicate first and third quartiles, the bold line within each box is the median, and whiskers indicate maximum and minimum values.

host plants were still growing vigorously. In five other pots, aboveground tissues of *P. canadensis* died at the end of the experiment, but these were retained in analyses because the hemiparasite was present during the most rapid periods of host plant growth. A similar pattern of senescence was observed simultaneously at field sites in mid-July. Aboveground *P. canadensis* foliage was still present at harvest (week 18) in 25 pots.

Presence of *P. canadensis* had a significant effect on biomass of mesocosm host plants overall (Wilks' $\Lambda = 0.522$, $p < 0.001$). The total mean host biomass was reduced significantly by 18% overall when grown with *P. canadensis* ($F_{[1,63]} = 22.50$, $p < 0.001$, $\eta^2 = 0.263$). Protected univariate ANOVAs showed that this effect was greatest in the annual legume *C. fasciculata*, which had biomass reduced by 50% compared to those grown without *P. canadensis* (Table S2; Fig. 3). Of the other five host plants, only *A. gerardii* was also affected by *P. canadensis*, surprisingly showing 59% greater biomass in mesocosms with the hemiparasite.

Discussion

Field Study

We investigated the interactions of hemiparasitic plants with other members of prairie communities to test the hypothesis that hemiparasites influence community diversity and quality. In surveys of restored and remnant prairie quadrats, we found that floristic quality varied among sites. Yet, of the four metrics analyzed, only FQI had a significant positive association with hemiparasite cover among all five sites. As expected, the remnant site had highest floristic quality. The P15 restoration site has a FQI intermediate between the remnant and the other restoration sites. Floristic quality takes diversity and degradation tolerance into account, and because native species with higher C-values tend

to co-occur more frequently than by chance alone (Matthews et al. 2015), the hemiparasites *Pedicularis canadensis* (C-value 9) and *Comandra umbellata* (C-value 7) are likely to co-occur with other prairie species that have low degradation tolerance. If high FQI is considered a goal of a prairie restoration project, establishing hemiparasites may contribute to accomplishing that outcome. Because we did not manipulate hemiparasite presence, the association with FQI could also just indicate that *P. canadensis* and *C. umbellata* are more likely to grow in sites that also have higher FQI. Field experiments that manipulate hemiparasites in a restoration setting may clarify the causation of the pattern we document here.

SR also varied across the five study sites, with the remnant prairie having the highest SR. The MRSW site had the strongest positive association between richness and hemiparasite cover. This is the oldest restoration site included, 36 years old at the time of this study. Although MRSW and the remnant have identical soil, Drummer silty clay loam (Soil Survey Staff Natural Resources Conservation Service, United States Department of Agriculture 2008), hemiparasite frequency is considerably lower in MRSW than WCP (30 vs. 92%), and hemiparasites have a more patchy distribution. This may allow better detection of differences along a hemiparasite abundance gradient, consistent with previous studies (Hedberg et al. 2005; Borowicz & Armstrong 2012; Bao et al. 2015), than in the remnant where hemiparasites are almost ubiquitous and effects may be more homogenous. That is, hemiparasites could have increased richness uniformly across the remnant, making it difficult to detect a hemiparasite effect in the absence of a frequency gradient. That this significant association was not found at the three other restoration sites and the remnant emphasizes the importance of site characteristics for this relationship. Community successional stage, management history, soil, topography, and unknown interactions may also influence SR and trump any hemiparasitic plant effects on this metric.

Shannon index and mpd also varied by site, but there were no significant associations between these metrics and hemiparasite cover. PD has recently garnered attention as a potentially valuable metric of the evolutionary diversity contained within a restored community that explains dimensions of biodiversity beyond traditional ecological measures (Hipp et al. 2015; Larkin et al. 2015; Barber et al. 2016) and may help reveal plant community assembly mechanisms (Gerhold et al. 2015). If hemiparasite effects are host specific, as suggested by our mesocosm experiment below, they might increase mpd by eliminating particularly vulnerable species across the community phylogeny. However, the hemiparasite effects we documented were changes in host biomass. Although hemiparasites can clearly affect the growth of neighboring plants, these impacts may not be strong enough to drive phylogenetic community patterns based on species presence/absence as we measured them here.

In contrast, Shannon index incorporates relative abundance of species and here varies significantly by site but not with hemiparasite cover. The wide range of Shannon indices suggests that, while richness may be driven in part by hemiparasitism at some sites, the effects on relative coverage of these neighbor species are not consistent enough to result in a detectable signal. This conflicts with the hypothesized management role of hemiparasites in reducing cover of C_4 grasses, which also was not supported. There was no relationship between combined cover of the four C_4 species present (*Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Sporobolus heterolepis*) and hemiparasite cover at our sites, and no relationship at another site in the region (Hedberg et al. 2005). Grass responses to parasitism might be better determined from dry biomass data rather than by percent cover (Borowicz & Armstrong 2012), so future field studies should determine shoot biomass responses of grasses rather than cover data alone, especially given the unexpected positive growth response of *A. gerardii* in the mesocosm study described here.

Mesocosm Experiment

Pedicularis canadensis reduced total shoot biomass of all hosts by 18%, although this was largely influenced by the most-affected host species, *Chamaecrista fasciculata*, which experienced a 50% biomass reduction. We had predicted that the C_4 grass *A. gerardii* would be most strongly reduced, by parasitism, yet *A. gerardii* biomass increased by 59% when grown with the hemiparasite. Although the effect of parasitism on different host species varied, reduced mean total biomass may relate to the additive effect of hemiparasites on community members in prairies. For example, even though the significant 50% reduction in *C fasciculata* was offset some by the significant 59% gain in the diminutive *A. gerardii*, the reductions in biomass, albeit insignificant, of *Pentstemon hirsutus, Symphyotrichum oolentangiensis*, and *Koeleria macrantha* together contributed to the overall total mean biomass reduction of 18% which was significant. *P. canadensis* is a generalist hemiparasite, so any plant species encountered by its roots could potentially serve as a host. The impact of this small hemiparasite on community structure therefore may be additive and driven by

chance root encounters between parasite and its multiple hosts. Our host measurements were limited to shoot biomass. In a previous study, however, host root mass and competitive relationships of three species (*A. gerardii*, *Solidago canadensis*, and *Desmodium canadense*) were unaffected by *P. canadensis* parasitism (Hedberg et al. 2005). Thus, we are confident that shoot biomass changes reflect impacts of hemiparasitism.

Chamaecrista fasciculata exhibited rapid and pronounced growth within days of planting, was the tallest host species, and had the third largest biomass at harvest time. This rapid growth likely occurred belowground as well, so *C. fasciculata* roots may have been more likely to encounter *P. canadensis* roots, leading to earlier haustorial formation and a stronger effect of hemiparasitism. While *P. hirsutus* and *Dalea candida* were the first host species to reach full shoot biomass and flower (see discussion below), *C. fasciculata* flowered later from week 12 to the end of the experiment. Its flowering period corresponds to a time when many *P. canadensis* plants were showing signs of vegetative regeneration, suggesting that the hemiparasite had begun to benefit from its haustorial connections with host species. Established *P. canadensis* in a field setting might have more consistent effects on host plants across a growing season. However, this interpretation rests on the assumption that observed aboveground growth of *P. canadensis* in our mesocosms is reflective of the extent of belowground associations, which we were unable to assess. Alternatively, this annual legume may be a preferred host of *P. canadensis* among the six potential host species in the experiment.

Effects of hemiparasites on legumes have varied in previous studies. Some report parasites benefit from the higher nitrogen content obtained from legumes. For example, the hemiparasite *Odontites verna* when grown with barley and clover obtained more nitrogenous compounds from clover and more saccharide compounds from barley, suggesting that hemiparasites benefit from the mixed diet provided from host plants in natural communities (Govier et al. 1967). The legume *Trifolium repens* was more affected by parasitism by *R. minor* than was the grass host *Lolium perenne* (Gibson & Watkinson 1991). Also, *Rhinanthus* grew taller when attached to *Trifolium pretense* than when attached to 10 other hosts or grown unattached (Seel et al. 1993). Other legume species have not been influenced by parasitism (Marvier 1996; Hedberg et al. 2005). The response to parasitism of the two legumes in mesocosms of this study is a striking contrast. Unlike *C. fasciculata*, perennial *D. candida* was unaffected. Hemiparasite host selection may be influenced by physical and physiological resistance to parasitism as well (Piehl 1963; Kujit 1969; Phoenix & Press 2005). The roots of the annual legume were younger and most likely less lignified than the perennial *D. candida*, perhaps making penetration by *P. canadensis* easier (Pérez-de-Luque et al. 2005).

In addition to *D. candida,* the remaining forb host species were not strongly affected by hemiparasite presence. The C_3 grass *K. macrantha* did not increase in the presence of *P. canadensis* like *A. gerardii*. *Penstemon hirsutus* grew rapidly after mesocosm establishment, flowered, and declined in vigor before other species. This rapid shoot growth may have occurred prior to maximal *P. canadensis* parasitism. In contrast, there was

a marginally significant trend (22%) of decreased shoot biomass of the other non-legume forb, *S. oolentangiense*. This late season species had not yet flowered at the end of the experiment, and continuing the experiment to include *S. oolentangiense*'s flowering phase might have resulted in a greater effect size.

Neither *A. gerardii* nor *K. macrantha* flowered during the experiment. The shoot biomass of *A. gerardii* was 59% greater when grown with the hemiparasite, contrary to the pseudo-grazer hypothesis. In contrast, the C_3 grass *K. macrantha* did not increase in the presence of *P. canadensis*. One possible explanation is that root structure differences could lead to fewer chance encounters between hemiparasite roots and the few roots of *A. gerardii*, but more frequent contact with the denser, fine-bunch-type *K. macrantha* roots (Craine et al. 2002). Additionally, *A. gerardii* had the smallest shoot biomass overall among host species in the experiment, suggesting it may have had the slowest growth rate. This could be attributed to a lack of winter dormancy for *A. gerardii* prior to planting, as vernalization increases development rate until the flowering stage (Streck et al. 2003). Also, all host species grew vigorously following winter dormancy in the Hedberg et al. (2005) study. Slow root growth may have further limited the likelihood of hemiparasite contact, and an experiment maintaining consistent developmental stage of host plants may produce different results.

Previous greenhouse experiments demonstrated only a marginal reduction in *A. gerardii* shoot growth by *P. canadensis* (Hedberg et al. 2005; Borowicz & Armstrong 2012). These studies used mesocosms containing only two or three plants, while this experiment replicated a larger, more diverse community. Furthermore, our study utilized live, screened prairie soil as a growing medium thus including established microbial communities (see discussion below). Our results suggest that *P. canadensis* was obtaining significant nutrients from the annual *C. fasciculata*, and possibly other species, which may have allowed *A. gerardii* plants to escape parasitism and gain a growth advantage in the pot. This is the opposite result from observations of *A. gerardii* in situ when it grows in areas with high *P. canadensis* abundance (Borowicz & Armstrong 2012). But there, the established, perennial roots of dominant tall grasses with large root systems may encounter hemiparasitic roots more frequently (Sperry 1935; Craine et al. 2002) and thus exhibit reduced shoot biomass due to parasitism. Furthermore, hemiparasitism has been shown to reduce mycorrhizal colonization in host plants (Davies & Graves 1998). If *A. gerardii* avoided parasitism, it may have maintained mycorrhizal associations that facilitated greater nutrient extraction from the soil and enabled enhanced shoot biomass. Given the strong mycorrhizal dependency of *A. gerardii* (Hartnett & Wilson 1999; Smith et al. 1999) and the finding that some members of *Pedicularis* have mycorrizal associations (Li & Guan 2007), the importance of hemiparasite–host–mycorrhizal associations merits further study.

In greenhouse experiments with *P. canadensis*, Hedberg et al. (2005) had 25% *P. canadensis* mortality, and Borowicz and Armstrong (2012) also reported high mortality. It was suggested that the greenhouse environment favored host species growth

over *P. canadensis* growth (Hedberg et al. 2005). In both previous studies, *P. canadensis* plantlets were field dug in June, while we obtained plants in early October. The transplant timing, along with the use of live, screened prairie soil in the mesocosms, was an attempt to enhance hemiparasite survival in greenhouse conditions and was successful. Using larger pots to minimize root crowding and multiple species also helped mimic a prairie community. Furthermore, to maximize potential for hemiparasitism, a dry, low-nutrient soil environment was maintained (Quested et al. 2003, 2005). These methods may have helped reduce *P. canadensis* mortality (20% here) and could be useful for propagating this species, which is difficult to grow from seed (Sorensen & Holden 1974). *Pedicularis canadensis* size and survival status were monitored throughout the greenhouse experiment.

Prairie managers strive to manage restorations so they will mimic high-quality reference remnant sites, and floristic assessment is useful for evaluating the quality of a natural area and indicating whether management protocols are maximizing synecological potential (Taft et al. 1997). Our results suggest that promotion of hemiparasite populations could help increase success of managed prairie remnants and restorations, as measured by floristic quality, and this could apply in other restored grasslands where a management role of hemiparasites has been proposed (Bullock & Pywell 2005). Although neither the field study nor the mesocosm experiment generated support for the pseudo-grazer hypothesis, the ability of *P. canadensis* to reduce total community biomass may contribute to general changes in community structure of the tallgrass prairie. Furthermore, the differential responses of host species to parasitism by hemiparasites, including *C. umbellata*, merits further investigation. Future field studies along gradients of hemiparasite abundance, examining aboveground and, when possible, belowground biomass responses of late season grasses and other functional groups, could further clarify the role of these plants in prairie communities.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Phylogenetic methods and calculation of mpd.
Table S1. Results of univariate ANCOVAs of ecological, floristic quality, and phylogenetic metrics from the field study.

Table S2. Results of univariate ANOVAs examining effects of *Pedicularis canadensis* on biomass of host plants in mesocosms.
Table S3. List of 169 species included in phylogeny, with family.
Figure S1. A phylogram based on *rbcL* and *matK* sequences for the species or congeners found at the field sites.