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PLANT SPECIES ASSOCIATED WITH A REGIONALLY RARE HEMIPARASITIC PLANT, *PEDICULARIS LANCEOLATA* (OROBANCHACEAE), THROUGHOUT ITS GEOGRAPHIC RANGE

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ABSTRACT. Typically, non-native invasive plant species are considered a threat to rare native plants, but this generalization may not hold true for rare parasitic plants that depend upon host plants to complete their life cycles. It is essential to know what plant species a particular hemiparasitic species associates with in the field, in order to determine host plant preferences and to make broader inferences about host plants. *Pedicularis lanceolata* is a hemiparasite that is regionally rare in New England and the southeastern margins of its range, but more abundant in the core of its range in the Midwest. I sought to compare the species associated with *P. lanceolata* in the core and margins of its range to determine if marginal populations have different associates from core populations. I hypothesized that *P. lanceolata* may be rare in the eastern United States because it encounters fewer suitable associates, and potentially more competitive invasive species, at the margins of its range than at the center of its range. In each of 22 populations of *P. lanceolata* I recorded abundances of all vascular plants growing near five focal *P. lanceolata* individuals. Different suites of species co-occurred with *P. lanceolata* in different parts of its range, but there were no significant differences across its range in the percent covers of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes. These results suggest that non-native invasive species do not pose greater threats to edge populations of *P. lanceolata* than to core populations. The data suggest that candidates for potential hosts include members of the Asteraceae and Poaceae, *Cirsium discolor*, *Clematis virginiana*, *Cornus amomum*, *Eupatorium maculatum*, *E. perfoliatum*, *Impatiens capensis*, *Lycopus uniflorus*, and *Vernonia gigantea.* These data provide baseline data for future manipulative studies on host-preference of *P. lanceolata*.

Key Words: *Pedicularis lanceolata*, hemiparasitic plants, host plants, non-native plants, regionally rare plants

Approximately 4500 of the world's plants are holoparasites (plants lacking chlorophyll and completely dependent on host plants to survive) or hemiparasites (plants with chlorophyll that rely on host plants for supplemental resources to complete their life cycle; Heide-Jørgensen 2008). The availability of suitable hosts is critical to rare hemiparasites, whether they are specialists utilizing a single host species or generalists capable of parasitizing a suite of hosts (Marvier and Smith 1997).

Rare native hemiparasites co-occurring with non-native, invasive species pose a management conundrum. A review of approximately 2500 imperiled or federally listed plant and animal species in the United States concluded that competition with, or predation by, invasive species is the second greatest threat to imperiled species, affecting 49% of the analyzed species (Wilcove et al. 1998). As such, the management of rare plants usually involves removing or controlling the density of non-native invasive species co-occurring with them. Such management, however, may not be appropriate for rare hemiparasitic plants that have unique interactions with host plants. If invasive plants co-occur with rare, generalist hemiparasites and serve as alternate hosts for the hemiparasites, or if facilitative (parasitic) interactions between hosts and hemiparasites outweigh negative competitive interactions, it may be detrimental to remove or control the co-occurring invasive plants. Whereas a number of studies have investigated interactions between native host plants and native hemiparasites (e.g., Adler 2002; Gibson and Watkinson 1989; Lawrence and Kaye 2008), interactions between non-native invasive host species and native hemiparasites remain relatively understudied. Further, the few studies addressing the effects of non-native invasive hosts on native hemiparasites have yielded conflicting results (Fellows and Zedler 2005; Prider et al. 2009).

Regionally rare species [i.e., Division 2 rare taxa according to Brumback et al. (1996)] that reach the edge of their geographic range in the Northeast, and have fewer than 20 occurrences in New England, are ideal for studies on the effects of native and non-native invasive plants on native hemiparasites. Such conditions allow for comparisons between areas where the target species are common within their ranges and areas in which they are rare. Regionally rare species also enable investigation into correlates of rarity because conditions in which a species is common can provide hints as to limiting factors at the edge of the range where the species may be rare (Kunin and Gaston 1997; Rabinowitz 1981). Finally, data from comparisons between different areas of regionally rare species' geographic ranges can be used to adapt management approaches to the particular needs of core and edge populations. Such adaptive management is important because at the edge of a species' range there is greater potential for evolutionary change (Grant and Antonovics 1978; Lesica and Allendorf 1995). For instance, populations at the periphery of a species' range may exhibit founder effects due to isolation from gene flow compared to more centrally located populations (Lammi et al. 1999).

Pedicularis lanceolata Michx. is a "regionally rare" North American generalist hemiparasite; that is, it is listed as rare in the states at the northeastern and southeastern portions of its range, but is considered secure and has more numerous populations in the geographic heart of its range in the Midwest (NatureServe 2009). Prior studies have provided some data on interactions between *P. lanceolata* and some of its host species. Foster (2003) studied the effects of *P. lanceolata* on three native (*Chelone glabra*, *Juncus effusus*, and *Scirpus cyperinus*) and one non-native invasive (*Phalaris arundinacea*) hosts in a container experiment to see if *P. lanceolata* could be used as a biological control agent on *P. arundinacea*. Seedlings of *P. lanceolata* established haustoria with all four hosts in this study. The biomass of *P. arundinacea* was only decreased when *P. lanceolata* was accompanied by the other native species, suggesting that competition by multiple native species was needed to depress growth of *P. arundinacea* (Foster 2003).

Previous studies also have provided information on potential or known hosts of *Pedicularis lanceolata* (i.e., species with which *P. lanceolata* are known to form haustoria). Macior (1969) and Farnsworth et al. (2007) recorded a total of 73 associated species of *P. lanceolata* in the field in Ohio and Massachusetts, respectively, but could not confirm if *P. lanceolata* formed haustorial connections to these species (Appendix). Other studies documented direct haustorial connections between *P. lanceolata* and 29 host species through root excavations in the field (Piehl 1965), lab experiments (Lackney 1981), and outdoor container experiments (Foster 2003; Appendix). Only two of the 29 species with which *P. lanceolata* was known to form haustoria were invasive species: *Frangula alnus* Mill. and *Phalaris arundinacea* (Appendix). Three quarters of these known hosts came from a study of a single site in Michigan, the geographic center of *P. lanceolata*'s range (Piehl 1965).

The first objective of this study was to document plant species growing with *Pedicularis lanceolata* in populations in the center of its range in the Midwest where the species is common (henceforth, the "core") and at the margins of its range in the Northeast and Southeast where the species is rare (henceforth, the "edge"). While some habitats, such as stream banks, are common to different regions where *P. lanceolata* occurs, other habitats are unique to certain portions of its range, such as prairies in the Midwest or tidal wetlands along the east coast. As such, I hypothesized that marginal populations of *P. lanceolata* in the northeastern and southeastern states would establish associations with different species from those associated with populations of *P. lanceolata* in the Midwest.

The second objective of this study was to determine whether the types and relative abundances of native and invasive species associated with *Pedicularis lanceolata* differed among core and edge geographic areas. I hypothesized that *P. lanceolata* in the edge of its range, where it is considered as rare, occurs more frequently with invasive species that are potentially suboptimal hosts or stronger competitors for resources, than in the Midwest. I predicted that the proportions of invasive species associated with *P. lanceolata* would be higher in eastern populations, if populations along the eastern coast of the United States where *P. lanceolata* is considered rare occur more frequently with less suitable associates (i.e., invasive species) than populations in the Midwest, where the species is considered common. Alternatively, I predicted that the relative abundances of native and invasive species would not differ between midwestern and eastern populations of *P. lanceolata* throughout its geographic range, if those populations are similarly associated with invasive species. To identify finer-scale differences in associated species due to latitudinal variation, I compared edge populations at the regional level (i.e., Northeast, Southeast). I was not able to confirm the hosts utilized by *P. lanceolata* or whether or not interactions with associated species were competitive or beneficial, but the data presented here do help to identify a suite of potential host plant species.

MATERIALS AND METHODS

Study species. Laboratory studies show that *Pedicularis lanceolata* is an obligate hemiparasite: seedlings become chlorotic and die when grown without a host (Lackney 1981). In observational field studies and laboratory and outdoor container experiments, *P. lanceolata* acts as a generalist, forming haustorial connections with

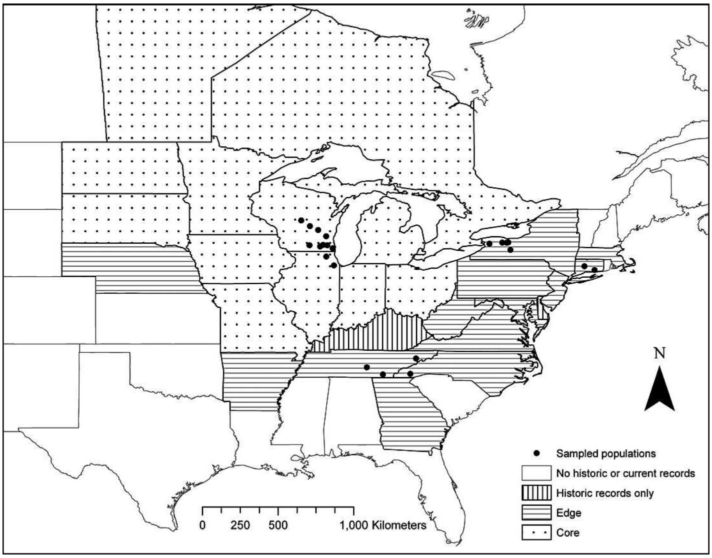

Figure 1. Range map of *Pedicularis lanceolata*'s global distribution showing locations of sample populations. The fill of each state or province reflects whether there are historic records or the state is considered as being in the "core" or "edge" of the species' geographic range. White fill denotes states or provinces with no historic or current records of *P. lanceolata*. Kentucky is the sole state with historic records only and has a fill of vertical lines. States or provinces filled with horizontal lines are considered to be "edge" of range and have state (USA) or provincial (Canada) statuses of critically imperiled (S1), imperiled (S2), or vulnerable (S3; NatureServe 2009). Stippled fill shows areas in the "core" of the range with state or provincial statuses that are apparently secure (S4) or are not ranked.

a number of species to obtain water and mineral nutrients (Foster 2003; Lackney 1981; Piehl 1965; Appendix).

Pedicularis lanceolata grows in habitats that are periodically inundated, such as wet meadows, prairies, swamps, freshwater tidal marshes, and stream sides and other early-successional habitats (Allard 2001). The global conservation status of *P. lanceolata* is secure (G5), but it is listed as historic, endangered, threatened, or a species of concern in 15 of the 25 states in which it occurs in the United States (NatureServe 2009; Figure 1). Most of the states in which *P. lanceolata* is considered rare are along the eastern coast of the United States, with the exception of Kentucky, where the species is possibly extinct and is known only from historic records

(NatureServe 2009). *Pedicularis lanceolata* is most secure (S4) along the northern edge of its range in Manitoba and Ontario (NatureServe 2009).

Field methods. In July and August of 2007, I sampled 11 populations of *Pedicularis lanceolata* in Illinois and Wisconsin where the species was classified by the state as common, and 11 populations in Connecticut, New York, North Carolina, and Tennessee where the species was state-listed as rare. In the states where *P. lanceolata* was considered rare, there were 2–17 extant populations per state, with population sizes varying from three to hundreds of individuals. Populations were defined as groups of co-occurring organisms of the same species that were likely to interbreed. Macior (1969) showed that *P. lanceolata* is an obligate outcrossing species pollinated by bumblebees (*Bombus* spp.), particularly *Bombus vagans* Smith. While the foraging distances of *B. vagans* have not been investigated in detail, there are data on foraging ranges for other species in the genus. Knight et al. (2005) conservatively estimated the maximal foraging range for the genus as 758 m in the United Kingdom, based on studies that used molecular markers. Thus, each site in this study was considered a separate population because all sites were further than 10 km away from one another.

I selected sampling sites based upon the most recently updated state Natural Heritage and Endangered Species Program field forms for states where *Pedicularis lanceolata* was classified as rare, and on herbarium specimens dating back to 1990 for locations where the species was considered common. I did not seek to sample similar types of habitats in each of the three sectors because one objective of this study was to see if *P. lanceolata* occurred with different species at core and edge sites. For this same reason, I sampled along a broader latitudinal gradient in the edge than in the core, in order to capture any differences in associated species and potential hosts due to climatic and other differences between the southeastern and northeastern margins of the range. Despite the greater aggregation of sites in the Midwest, the habitats sampled were variable (e.g., fens, stream sides, prairies, lake shores, city parks), so the closer proximities of sites in the Midwest should not have biased the results in regards to habitat types. Logistical constraints and differences in the numbers of extant populations in different states resulted in an imbalanced design, with seven populations in the Midwest, four in the Southeast, and seven in the Northeast.

At each site, I set up a transect through the center of the population and used random numbers to select plants based on their positions relative to the transect (Haahr 2006). Abundances in six cover classes (< 1%, 2–5%, 6–25%, 26–50%, 51–75%, and 76–100%) of all vascular plant species were recorded within half-meter-radius circular plots centered on five focal *Pedicularis lanceolata* plants per population. The scarcity of *P. lanceolata* in many of the edge, and some of the core, populations limited the number of focal plants sampled in each population to five. I chose the size of the plots based upon my previous root excavations of five plants in the midwestern United States, which revealed that the roots of *P. lanceolata* extended approximately one-half meter from the base of an individual. Thus, I assumed that associated vascular species occurring within one-half meter of the focal *P. lanceolata* plant were available as potential hosts. Also, associated plants within one-half meter of *P. lanceolata* were the most likely to compete with it for light. I did not collect data on the species pool at the sites, beyond the sampling that I did around the focal *P. lanceolata* individuals. Other studies on hemiparasitic species have done this, and analyzed the data with an association analysis to see if the hemiparasite was correlated with certain associated species. However, Gibson and Watkinson (1989) showed that an association analysis of *Rhinanthus minor* L. only revealed two potential hosts, whereas direct examination of the plants' roots showed that the plants were forming haustorial connections with 20 species. Further, at none of the 22 sites was there great variation in species present in areas with or without *P. lanceolata*. As such, I chose to sample more populations, only recording information from plots with *P. lanceolata* present, rather than visiting fewer populations while sampling plots with and without *P. lanceolata.* All vascular plants were identified to species using Gleason and Cronquist (1991), with the exception of some *Carex* species for which positive identification was not possible because perigynia were undeveloped at the time of sampling. Unidentifiable *Carex* species were treated as different un-named taxa based on gross morphology. Nomenclature follows the Integrated Taxonomic Information System (2010). Voucher specimens were housed in the herbaria of the Universities of Massachusetts (MASS), Tennessee (TENN), and Wisconsin (WIS; Appendix).

Data analysis. To visualize differences in the species associated with *Pedicularis lanceolata* throughout its range, I analyzed the abundance data of all species encountered. I used non-metric multidimensional scaling (NMDS), using Bray's distance measure and two dimensions to plot an ordination showing relationships between species and sites (McGarigal et al. 2000). Non-metric multidimensional scaling was employed rather than correspondence analysis (CA) or detrended correspondence analysis (DCA) because, as a non-parametric procedure, NMDS was less sensitive to outliers and made no assumption that the species' distributions along the underlying gradient exhibited unimodal or linear responses (McGarigal et al. 2000). To determine whether population-level differences in associated species were due to the greater latitudinal gradient sampled in the edge, I overlaid ellipses onto the ordination plot showing the standard deviations of the point scores for species within each portion of the range (core or edge) and region (Midwest, Northeast, or Southeast) using the 'ordi.ellipse' function from the Vegan package in R statistical software (R Development Core Team 2005).

All co-occurring plant species were categorized into the following groups: natives, non-native invasives, non-native non-invasives, and non-invasive species having co-occurring native and non-native genotypes (Appendix). Classifications of species by origin and invasiveness in the United States Department of Agriculture PLANTS database (USDA, NRCS 2009) were inconsistent with individual state classifications, so associated non-native species were only considered invasive in a state when they were listed as invasive by the U.S.D.A. and at least one other source. References for individual states were: Connecticut (Mehrhoff et al. 2003), Illinois (Howe et al. 2008), North Carolina (Smith 2008), New York (Invasive Plant Council of New York State 2005; O'Neill 2008), Tennessee (Franklin et al. 2004; Miller 2003), and Wisconsin (Howe et al. 2008; Reinartz 2003). Species with both non-native and native genotypes included: *Achillea millefolium*, *Poa pratensis*, *Ranunculus acris*, *Rubus idaeus*, *Taraxacum officinale*, and *Phalaris arundinacea* (USDA, NRCS 2009). *Phalaris arundinacea* (Gifford et al. 2002) was one of the most abundant co-occurring species at many of the study sites, suggesting that the non-native genotype may have been at the sites studied. Thus, I performed two separate analyses where *P. arundinacea* was either treated as non-native invasive or as a species with native and invasive genotypes. I confirmed that none of the unknown *Carex* species were considered non-native invasive based on comparisons of vegetative characters with known invasive *Carex* species.

To determine whether there were regional or subregional differences in the percent covers of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes associated with *Pedicularis lanceolata*, I performed four nested analyses of variance (ANOVAs). I averaged the relative abundances of all species in a category (i.e., natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes) over the five independently sampled plants in each population to emphasize population-level rather than plot-level differences. Since relative abundances were recorded as percent cover classes, the averages were based on the median value for the range of values in a cover class (e.g., for the cover class ranging from 1% to 5%, I used 3% to calculate the average). The response variables in the four ANOVAs were these population-level averages for the percent covers of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes. Plot-level averages were arcsine square-root transformed to meet the model assumptions of residual normality and homogeneity of variance. I tested the response of either average cover of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes to two predictor variables: part of range (i.e., core, edge), and region nested within part of range (i.e., Northeast and Southeast nested within edge; Midwest nested within core). Region was included to test for any effects due to latitudinal differences in the species pools of associated species in the populations sampled. All statistical analyses were performed using R statistical software version 2.10.1.

RESULTS

Pedicularis lanceolata co-occurred with a total of 265 different species representing 66 families across the 22 sites sampled (Appendix). The families with the most representatives were the Asteraceae and the Poaceae. *Lycopus uniflorus* occurred most frequently in all three regions. Of the 265 species documented, 155 species were found in the Midwest (including 70 species only found in this region), 154 in the Northeast (62 unique to this region), and 81 in the Southeast (32 unique to this region; Appendix). None of

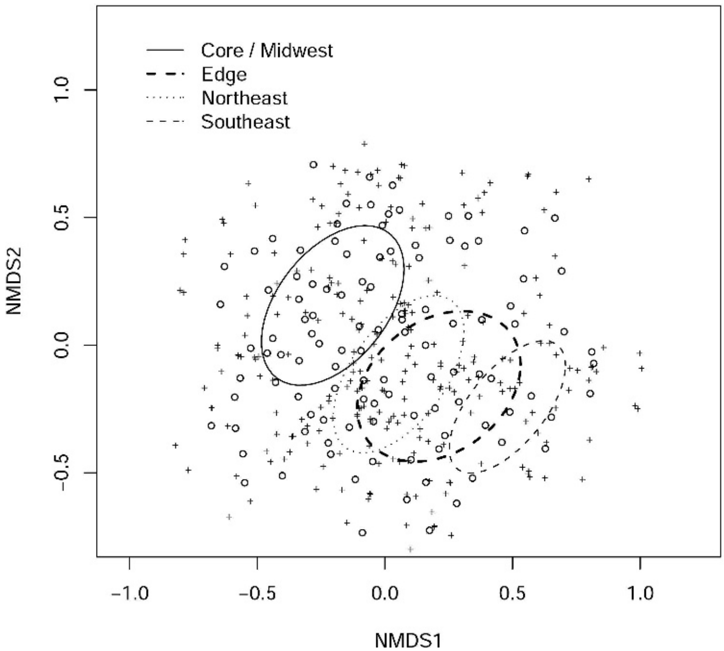

Figure 2. Ordination projection of all associated species encountered with *Pedicularis lanceolata*, generated using Nonmetric Multidimensional Scaling. Species are open circles, and crosses are plots within sites. Ellipses depict the standard deviations of point scores from the covariance matrix for each region: Core/Midwest (solid line), Edge (bold dashed line), Northeast (dotted line), and Southeast (dashed line).

the species occurred at all 22 sites. Nine percent of the plots sampled at the 22 sites did not contain any of the hosts known to form haustoria with *P. lanceolata* (Foster 2003; Lackney 1981; Piehl 1965). The ordination showed that the standard deviations of the species' ordination scores for the core and edge overall did not overlap, although the standard deviations of the Midwest and Northeast regions' species' ordination scores overlapped. The Midwest and Northeast regions shared more co-occurring species than either did with the Southeast region (Figure 2).

The average proportion of native species was much greater than the average proportion of non-native invasive or non-native non-invasive species in each part of the range (core or edge) and region (Figure 3). Sixteen non-native invasive and 23 non-native non-invasive species co-occurred with *Pedicularis lanceolata* in the 22

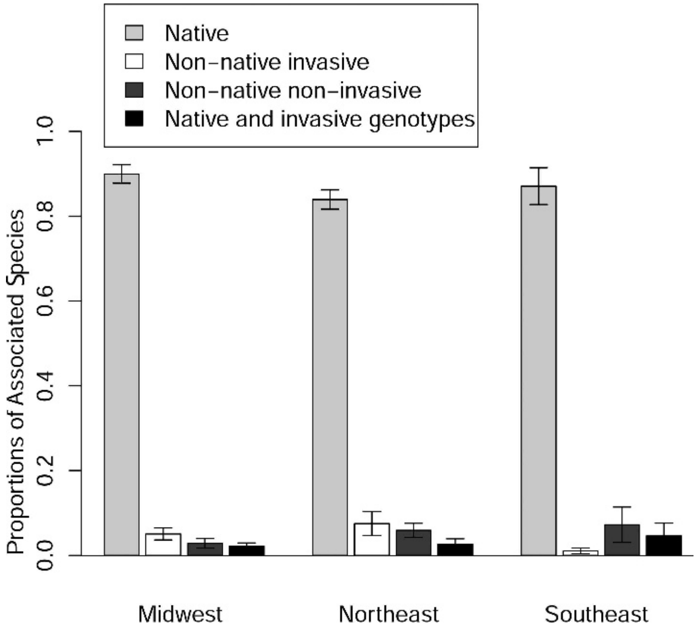

Figure 3. Average proportions of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes of *Pedicularis lanceolata* in the Midwest, Northeast, and Southeast regions based on relative abundances. The Midwest region is equivalent to the core, and the sum of the proportions for the Northeast and Southeast regions is the edge. Error bars show one standard error of the mean.

populations sampled. Two of the 16 non-native invasive species were found in both edge and core populations (*Rhamnus frangula* and *Lonicera morrowii*). *Phalaris arundinacea* and *R. frangula* were the most predominant species, with co-occurring native and non-native genotypes and non-native invasive species, respectively, associated with *P. lanceolata* in the Midwest. In the Northeast, the most common non-native invasive species or species with co-occurring native and non-native genotypes growing with *P. lanceolata* were *Cynanchum louiseae*, *Lythrum salicaria*, and *P. arundinacea*. In the Southeast, *Lonicera japonica* and *Ligustrum vulgare* were the non-native invasives that occurred with *P. lanceolata* at the highest frequencies. The percent covers of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes did not differ between core and

Table 1. A summary of statistical results from the ANOVA models testing for effects of region (Northeast, Southeast, or Midwest) nested within part of range (core or edge) on the percent cover of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes associated with *Pedicularis lanceolata*. In this analysis, *Phalaris arundinacea* was classified as a non-native invasive species rather than as a species with native and non-native genotypes.

Effect	df	M.S.	F	p
Natives				
Core / Edge	1	0.0400	3.3947	0.0819
Region	2	0.0251	2.1269	0.1482
Residuals	18	0.0118		
Non-native invasives				
Core / Edge	1	0.0020	0.0108	0.9183
Region	2	0.0508	2.8129	0.0865
Residuals	18	0.0181		
Non-native non-invasives				
Core / Edge	1	0.0631	3.7076	0.0701
Region	2	0.0132	0.7756	0.4752
Residuals	18	0.0170		
Species with native and non-native genotypes				
Core / Edge	1	0.0010	0.7661	0.3930
Region	2	0.0212	1.6266	0.2242
Residuals	18	0.0130		

edge populations or regions of edge populations (Table 1). The ANOVA results were consistent regardless of whether *P. arundinacea* was classified as a non-native invasive species or as a species with native and non-native genotypes. As such, I presented only the results of the analysis where *P. arundinacea* was treated as a non-native invasive species (Table 1).

DISCUSSION

This study has documented associated species for a regionally rare hemiparasite, *Pedicularis lanceolata*, across a broad geographic extent, and found that there were no significant differences among edge and core populations in the relative abundances of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes. For *P. lanceolata*, greenhouse (Foster 2003; Lackney 1981) and root excavation (Piehl 1965) studies have provided data on hosts with which haustoria were formed, but the majority of the documented species came from a single study in Michigan (Piehl 1965). Hosts with which *P. lanceolata* formed haustoria, documented from these past studies, did not occur in 9% of the plots I sampled, suggesting that there were undocumented hosts of *P. lanceolata* in these plots.

The ordination analysis showed that associated species in the Midwest and Northeast had more overlap with one another than with the Southeast (Figure 2). The Northeast and Midwest regions lie on similar latitudes, so this result was likely due to latitudinal differences in species distributions. In the ordination, there were a number of distinct species that projected far from regional centroids and did not fall within the standard deviations of species' scores for other regions, suggesting that some species were exclusive to a particular region. Data in the Appendix also show that there were a number of species that were unique to each region. These results suggest that *Pedicularis lanceolata* grew with some unique species in different parts of its range.

Based on the data, *Lycopus uniflorus* was a candidate host plant because it occurred most frequently and occasionally at high abundances in all three subregions. In the Midwest, *Pedicularis lanceolata* was most often found growing with *Cirsium discolor*, *Eupatorium maculatum*, and *Equisetum palustre*. Likely candidates for hosts in the Northeast included *Cornus amomum* and *Eupatorium perfoliatum*. In the Southeast, *Clematis virginiana* L., *Impatiens capensis*, and *Vernonia gigantea* subsp. *gigantea* commonly co-occurred with *P. lanceolata*. Also, the families of plants most frequently associated with *P. lanceolata* were the Asteraceae and Poaceae, so members of these families were also candidates for potential hosts.

In the populations sampled, the proportions of non-native invasives, non-native non-invasives, and species with native and non-native genotypes were much smaller than those of native species (Figure 3). This high ratio of native to non-native species could be due to a number of reasons. The sites sampled in this study could have been at early stages in the invasion process. Alternatively, *Pedicularis lanceolata* may not have been able to establish haustoria with many invasives and thus did not occur with them. *Pedicularis lanceolata* could also have been associated with some other variable (e.g., historical land-use practices) that resulted in sites being less invaded. The differences between non-native invasive species' cover among all populations were all less than five percent and there were no significant differences between the percent covers of natives and non-natives. These results imply that at the sites sampled, the edge populations were not more likely to be threatened by non-native species than the core populations. This conclusion should not, however, discount the relevance of future studies investigating the relationships between hemiparasites, native hosts, and non-native hosts because non-native invasives may be locally dominant at particular sites of interest. For instance, the only population of *P. lanceolata* in the entire state of Massachusetts has been heavily invaded by *Phalaris arundinacea* (Farnsworth et al. 2007).

There are some limitations to this study that should be addressed. First, the number of plants sampled per population was low due to the scarcity of individuals in populations along the east coast where *Pedicularis lanceolata* was rare. One potential caveat to such a low sample size is that the associated species might not have been representative of a site. Small sample sizes are an inherent issue when working with rare species that are not locally abundant. Despite this limitation, it is reassuring that in this study, the associated species within different populations were not highly variable, so the sampling scheme presented here is likely a good representation of the associated species at the sites sampled. A second limitation of this study is that haustorial connections between *P. lanceolata* and its associated species were not confirmed, so the data provided suggest potential rather than known hosts. While it was not possible to quantify haustorial connections in the field due to the rarity of *P. lanceolata* in many of the sites sampled, the documentation of associated species in this study is relevant for comparing characteristics of populations that occurred where the species was rare versus where the species was common.

The results of this study are valuable for tailoring the management of core and edge populations of *Pedicularis lanceolata* and for providing data on host plants that can be used to broaden inferences from subsequent field or greenhouse experiments. Given their potential management implications, future studies on the effects of non-native invasive species on hemiparasites, such as *P. lanceolata*, should include a field component and management treatments. Using the rare hemiparasite, *Castilleja levisecta* Greenm. with different native hosts, Lawrence and Kaye (2008) showed that greenhouse experiments alone were poor predictors of how the hemiparasite and hosts interacted in the field because the experiments lacked important indirect effects between host and hemiparasite exerted by vole herbivory. Without a field component, experiments on non-native invasive species and hemiparasites may not accurately portray host-hemiparasite interactions. Further, few experiments on hemiparasites include possible management scenarios (but see Petrů 2005). In combination with the extensive field survey data illustrated here, manipulative studies of *P. lanceolata* and other rare hemiparasites will provide many opportunities to better understand the interactions between hemiparasites and their native and non-native hosts.

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APPENDIX

SPECIES FOUND GROWING WITH *PEDICULARIS LANCEOLATA*

This appendix contains a list of all species that were found growing with *Pedicularis lanceolata* in this study and in previous studies. Cit. = Citations reference the following studies by the first author's initials shown here in parentheses: Farnsworth et al. 2007 (EF), Foster 2003 (RF), Lackney 1981 (VL), Macior 1969 (LM), and Piehl 1965 (MP). An asterisk (*) indicates species for which direct haustorial attachments between *P. lanceolata* and the species have been documented in the indicated studies. The numbers listed for each species by region (Midwest, Northeast, or Southeast) are the occurrence (proportion of sites where the species occurred within the region) and the % cover (mean and variance of the percent cover of that species in the region). 'N/A' for 'not applicable' = species not found in a particular region in this study, but previously documented as an associated species in other studies. Voucher specimens are housed in the herbaria of the University of Massachusetts Amherst (MASS), the University of Tennessee Knoxville (TENN), and the University of Wisconsin Madison (WIS). The herbarium acronym where the specimen is stored and the accession number, where available, appear below the taxon's name.

		Occurrence and % Cover ± Variance		
Taxon (Voucher)	Cit.	Midwest	Northeast	Southeast
ACERACEAE				
Acer rubrum L.	EF	0.09 0.02±0.02	0.71 2±46	0.25 6±193
ALISMATACEAE				
Sagittaria latifolia Willd.		0.18 0.3±4	0.14 1±41	0
AMARANTHACEAE				
Gomphrena globosa L.		0	0.14 2±47	0
ANACARDIACEAE				
Toxicodendron radicans (L.) Kuntze		0.09 0.8±12	0.29 2±47	0.25 4±137
APIACEAE				
Angelica atropurpurea L.		0.18 2±55	0	0
Cicuta bulbifera L.		0.27 0.1±0.09	0.14 0.03±0.03	0
Cicuta maculata L.	EF	0.09 0.7±26	0.29 2±80	0
**Daucus carota* L.	EF; MP	0.18 0.06±0.06	0.57 3±84	0.25 0.05±0.05
Hydrocotyle americana L.		0	0.14 0.03±0.03	0
Oxypolis rigidior (L.) Raf.		0.27 3±121	0	0.25 0.8±11
Sanicula odorata (Raf.) K.M. Pryer & L.R. Phillippe (WIS: #0260350) (TENN: #not available)		0.09 1±30	0	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
APOCYNACEAE				
**Apocynum cannabinum* L.	MP	N/A	N/A	N/A
ARACEAE				
**Peltandra virginica* (L.) Schott	MP	N/A	N/A	N/A
Symplocarpus foetidus (L.) Salisb. *ex* Nutt.		0	0.14 0.03±0.03	0
ASCLEPIADACEAE				
Asclepias incarnata L.	EF	0.27 0.8±26	0.29 1±41	0
Asclepias syriaca L.	EF	N/A	N/A	N/A
Cynanchum louiseae Kartesz & Gandhi	EF	0	0.29 4±123	0
ASTERACEAE				
Achillea millefolium L.		0.18 0.05±0.05	0.14 1±41	0.25 6±194
Ambrosia artemisiifolia L.	EF	0.09 0.7±26	0.14 0.03±0.03	0.25 0.05±0.05
Ambrosia trifida L.		0.09 0.7±26	0	0
Antennaria neglecta Greene		0.09 0.3±4	0	0
Arnoglossum plantagineum Raf.		0.09 0.02±0.02	0	0
Bidens cernua L.		0	0	0.25 0.8±11
Bidens connata Muhl. *ex* Willd.		0.09 0.02±0.02	0	0
Bidens frondosa L. (WIS: #0260354)	EF	0	0.14 0.03±0.03	0
Carduus arvensis (L.) Robson		0.09 0.3±4	0	0
Cirsium altissimum (L.) Hill	LM	N/A	N/A	N/A
Cirsium discolor (Muhl. *ex* Willd.) Spreng.		0.55 4±121	0.14 1±41	0
Doellingeria (Mill.) Nees *umbellata* var. *umbellata*		0	0.29 2±47	0
Eupatorium fistulosum Barratt		0	0	0.50 2±72

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
**Eupatorium maculatum* L.	EF; MP	0.63 10±228	1 8±185	0
Eupatorium perfoliatum L.	EF	0.36 4±108	0.71 4±95	0.50 3±87
Euthamia graminifolia (L.) Nutt.	EF	0.36 6±208	0.43 9±261	0
Euthamia tenuifolia (Pursh) Nutt. var. *tenuifolia*		0.09 0.9±12	0	0
Helenium autumnale L.		0.18 1±30	0	0.25 0.8±11
Helianthus decapetalus L.	LM	N/A	N/A	N/A
Helianthus giganteus L.		0.36 5±171	0	0
Helianthus grosseserratus M. Martens (WIS: #0260360)		0.09 2±58	0	0
Hieracium caespitosum Dumort.		0.09 1±30	0.43 3±84	0
Lactuca sp.	EF	N/A	N/A	N/A
Leucanthemum vulgare Lam.		0.09 0.02±0.02	0.43 1±41	0.25 0.05±0.05
Liatris scariosa (L.) Willd. var. *novae-angliae* Lunell		0	0.14 0.4±6	0
Machaeranthera parviflora A. Gray		0	0	0.25 2±72
Oligoneuron ohioensis (Frank *ex* Riddell) G.N. Jones		0.27 5±146	0	0
Oligoneuron riddellii (Frank *ex* Riddell) Rydb. (WIS: #0260364)		0.09 0.7±26	0	0
Packera schweinitziana (Nutt.) W.A. Weber & Á. Löve		0.09 0.04±0.04	0	0
Rudbeckia fulgida Aiton var. *speciosa* (Wender.) Perdue		0	0	0.25 0.8±11
Rudbeckia laciniata L.		0	0	0.25 0.8±11
Solidago canadensis L.		0.36 7±202	0.14 0.4±6	0

Appendix. Continued.

		Occurrence and % Cover ± Variance		
Taxon (Voucher)	Cit.	Midwest	Northeast	Southeast
Solidago canadensis var. *scabra* Torr. & A. Gray	LM	0	0.14 2±80	0
Solidago gigantea Aiton	EF	0.55 10±213	0.43 2±80	0.50 3±80
Solidago nemoralis Aiton		0.09 0.04±0.04	0	0
**Solidago patula* Muhl. *ex* Willd.	MP; EF	0	0.43 7±185	0.5 2±30
Solidago rugosa Mill.	EF	0	0.57 7±185	0
Solidago uliginosa Nutt.		0.18 4±106	0.43 6±195	0.25 0.8±11
Solidago sp.	EF	N/A	N/A	N/A
Sonchus arvensis L.		0.27 1±33	0	0
Symphyotrichum boreale (Torr. & A. Gray) Á & D. Löve		0.09 0.04±0.04	0	0
Symphyotrichum laeve (L.) Á & D. Löve var. *laeve*		0.09 1±30	0	0
**Symphyotrichum lateriflorum* (L.) Á & D. Löve var. *lateriflorum*	MP	0	0.14 2±80	0.25 2±72
**Symphyotrichum novae-angliae* (L.) G.L. Nesom	LM; MP	0.45 6±185	0.57 7±184	0
Symphyotrichum pilosum (Willd.) G.L. Nesom var. *pilosum*	LM	N/A	N/A	N/A
Symphyotrichum praealtum (Poir.) G.L. Nesom var. *praealtum*		0.09 0.3±4	0	0
Symphyotrichum prenanthoides (Muhl. *ex* Willd.) G.L. Nesom		0.09 1±34	0	0
Symphyotrichum puniceum (L.) Á & D. Löve var. *puniceum* (WIS: #0260352)	EF	0.36 4±127	0.29 3±84	0.50 5±145

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Symphyotrichum sp.	EF	N/A	N/A	N/A
Taraxacum officinale F.H.Wigg.		0.45 0.1±0.1	0.57 2±46	0.50 2±72
Vernonia gigantea (Walter) Trel. subsp. *gigantea*		0.09 1±30	0	0.75 6±196
Vernonia noveboracensis (L.) Michx.		0	0.14 2±47	0.25 4±93
BALSAMINACEAE				
**Impatiens capensis* Meerb.	EF; MP	0.55 3±78	0.43 3±84	0.75 10±235
BERBERIDACEAE				
Berberis thunbergii DC. var. *atropurpurea* Chenault		0	0.14 1±41	0
BETULACEAE				
Alnus incana (L.) Moench subsp. *rugosa* (Du Roi) R.T. Clausen	EF	0	0.29 8±338	0.25 3±80
BIGNONIACEAE				
Campsis radicans (L.) Seem. *ex* Bureau		0	0	0.25 0.8±11
BORAGINACEAE				
Myosotis scorpioides L.	EF	0.09 0.7±26	0	0
BRASSICACEAE				
Alliaria petiolata (Bieb.) Cavara & Grande		0	0.14 1±41	0
CAMPANULACEAE				
Campanula aparinoides Pursh		0.55 2±75	0	0.25 0.1±0.1
Lobelia kalmia L.		0.18 0.7±26	0.14 0.03±0.03	0
Lobelia siphilitica L.		0	0.14 0.03±0.03	0
CAPRIFOLIACEAE				
Lonicera japonica Thunb.		0	0	0.25 2±30

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance: Midwest	Northeast	Southeast
Lonicera morrowii A. Gray	EF	0.09 1±30	0.43 2±80	0.25 0.05±0.05
Lonicera tatarica L.		0.09 0.5±8	0	0
Viburnum acerifolium L.		0	0.14 0.03±0.03	0
Viburnum dentatum L.		0.09 3±124	0.14 0.06±0.06	0
Viburnum dentatum L. var. *lucidum* Aiton		0	0.43 3±116	0
Viburnum lentago L.		0.09 0.7±26	0.29 1±41	0
Viburnum nudum L.		0	0	0.25 0.05±0.05
Viburnum opulus L. var. *americanum* Aiton		0	0.14 0.03±0.03	0
CARYOPHYLLACEAE				
Cerastium fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet		0.09 0.02±0.02	0.14 0.03±0.03	0
CELASTRACEAE				
Celastrus orbiculata Thunb.	EF	0	0.14 2±113	0
Celastrus scandens L.		0	0	0.25 12±494
CLUSIACEAE				
Hypericum mutilum L.		0	0	0.25 0.8±11
Hypericum perforatum L.		0.09 0.04±0.04	0.29 1±41	0.25 0.05±0.05
CONVOLVULACEAE				
Calystegia sepium (L.) R. Br. subsp. *sepium*		0.09 2±58	0	0
CORNACEAE				
Cornus amomum Mill. (WIS: #0260351)	EF	0.55 5±129	0.86 5±153	0
**Cornus foemina* Mill.	MP	0	0.29 3±116	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance: Midwest	Northeast	Southeast
Cornus rugosa Lam.		0	0.14 0.4±6	0
**Cornus sericea* L.	MP	0	0.14 1±41	0
CUSCUTACEAE				
Cuscuta gronovii Willd. *ex* Schult.		0.09 0.02±0.02	0	0
CYPERACEAE				
Carex aquatilis Wahlenb. (WIS: #0260347)		0.09 4±165	0.29 2±47	0
Carex buxbaumii Wahlenb. (WIS: #0260356)		0.09 3±167	0	0
Carex communis Bailey		0.09 1±72	0	0
Carex crinita Lam.	EF	0	0	0.75 5±98
Carex hystericina Muhl. *ex* Willd. (WIS: #0260363) (MASS: #313340)		0.09 1±72	0.14 3±151	0
Carex lacustris Willd.		0	0.14 0.9±12	0
Carex lasiocarpa Mack. *ex* Bright		0	0.14 3±116	0
Carex lurida Wahlenb. (MASS: #313333) (TENN: # not available)	EF	0	0.29 2±80	0.25 5±285
Carex sartwellii Dewey		0.09 0.7±26	0	0
Carex vulpinoidea Michx.	EF	0	0.29 4±120	0
Carex sp.	EF	N/A	N/A	N/A
Cyperus sp.	EF	N/A	N/A	N/A
Dulichium arundinaceum (L.) Britton		0	0.29 2±80	0
Eleocharis acicularis (L.) Roem. & Schult.		0.09 0.02±0.02	0	0
Eleocharis rostellata (Torr.) Torr.		0.09 0.7±26	0.14 1±41	0
Rhynchospora capitellata (Michx.) Vahl	EF	N/A	N/A	N/A

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Scirpus atrovirens Willd. (WIS: #0260355)		0	0.43 4±150	0
**Scirpus cyperinus* (L.) Kunth	EF; RF	N/A	N/A	N/A
Scirpus hattorianus Makino (MASS: #313338)		0.27 3±101	0	0
Scirpus tabernaemontani (C.C. Gmel.) Palla		0	0.14 1±41	0
DROSERACEAE				
Drosera rotundifolia L.		0.09 0.05±0.05	0	0
DRYOPTERIDACEAE				
Onoclea sensibilis L.	EF	0.09 1±30	0.57 6±157	0
EQUISETACEAE				
**Equisetum arvense* L.	MP	0	0.43 5±152	0
Equisetum hyemale L.		0.09 0.7±26	0.14 0.03±0.03	0
Equisetum laevigatum A. Braun		0.27 3±101	0	0
Equisetum palustre L.		0.72 12±352	0.29 6±294	0
Equisetum variegatum Schleich. *ex* F. Weber & D.M.H. Mohr		0	0.29 0.4±6	0
ERICACEAE				
Andromeda polifolia L. var. *glaucophylla* (Link) DC.		0	0	0.25 4±136
FABACEAE				
Amphicarpaea bracteata (L.) Fernald	EF	0.09 0.02±0.02	0.71 0.5±6	0.50 9±241
Apios americana Medik.	EF	0	0.14 0.9±12	0.75 9±241
Baptisia tinctoria (L.) R. Br. *ex* Aiton f.		0	0.14 0.4±6	0
Desmodium cuspidatum (Muhl. *ex* Willd.) DC. *ex* Loudon		0.09 1±34	0.14 1±41	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Lathyrus palustris L.		0.27 1±51	0	0
Lespedeza procumbens Michx.		0	0	0.25 0.05±0.05
Lotus corniculatus L.		0	0.14 0.4±6	0
Medicago lupulina L.		0	0.14 0.03±0.03	0
Melilotus alba Medik.		0.09 0.02±0.02	0	0
Melilotus officinalis (L.) Lam.		0	0.14 0.06±0.06	0
Trifolium campestre Schreb.		0.09 0.02±0.02	0	0
Trifolium dubium Sibth.		0	0	0.25 0.05±0.05
**Trifolium incarnatum* L.	VL	N/A	N/A	N/A
Trifolium pratense L.		0.09 0.7±26	0	0.25 3±80
Trifolium repens L.		0.09 0.02±0.02	0.14 0.03±0.03	0
FAGACEAE				
Quercus macrocarpa Michx.		0.09 0.02±0.02	0.14 0.03±0.03	0
Quercus rubra L.		0.09 0.3±4	0	0
GENTIANACEAE				
Gentiana andrewsii Griseb.	LM	N/A	N/A	N/A
Gentiana clausa Raf.		0.09 0.7±26	0.14 2±46	0
Gentiana puberulenta J.S. Pringle		0.09 0.02±0.02	0	0
Gentianopsis crinita (Froel.) Ma		0	0.14 1±41	0
Gentianopsis virgata (Raf.) Holub		0.09 0.02±0.02	0	0
GROSSULARIACEAE				
Ribes hirtellum Michx. (WIS: #0260346)		0.18 0.3±4	0.14 1±41	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
HAMAMELIDACEAE				
Liquidambar styraciflua L.		0	0	0.25 0.05±0.05
HYDROPHYLLACEAE				
Hydrophyllum appendiculatum Michx.		0	0.14 1±41	0
IRIDACEAE				
Iris pseudacorus L.	EF	N/A	N/A	N/A
Iris versicolor L.		0.18 3±101	0	0
**Iris virginica* L.	MP	N/A	N/A	N/A
JUNCACEAE				
Juncus brevicaudatus (Engelm.) Fernald		0	0.14 0.4±6	0
Juncus canadensis J. Gay *ex* Laharpe		0.09 0.7±26	0	0
**Juncus effusus* L.	EF; RF	0.09 0.7±26	0.14 1±41	0.75 6±196
Juncus nodosus L.		0.36 2±55	0.71 12±297	0
Juncus tenuis Willd.	EF	0.09 0.3±4	0.14 3±116	0
JUNCAGINACEAE				
Triglochin maritima L.		0.09 0.02±0.02	0	0
LAMIACEAE				
Clinopodium vulgare L.		0	0.14 0.03±0.03	0.25 2±72
Glechoma hederacea L.		0	0.14 0.03±0.03	0
Lycopus americanus Muhl. *ex* W.P.C. Barton		0.64 3±99	0.29 0.06±0.06	0
Lycopus uniflorus Michx. (WIS: #0260358)	EF	0.91 10±258	0.86 11±271	0.75 6±196
Mentha aquatica L.		0.09 0.02±0.02	0	0
Mentha arvensis L.	EF	0.09 0.04±0.04	0	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Monarda media Willd.		0.09 0.5±8	0	0
Prunella vulgaris L.	LM	0.45 4±127	0.86 12±244	0.50 0.2±0.2
Pycnanthemum tenuifolium Schrad.		0.18 0.7±26	0	0
**Pycnanthemum virginianum* (L.) T. Durand & B.D. Jacks. *ex* B.L. Rob. & Fernald	MP	0.27 3±103	0.29 3±85	0.25 0.1±0.1
Scutellaria galericulata L.		0.09 1±52	0	0
Scutellaria lateriflora L.	EF	0.18 0.07±0.07	0.14 0.03±0.03	0
LILIACEAE				
Maianthemum canadense Desf.		0.09 0.7±26	0	0
Maianthemum racemosum (L.) Link subsp. *racemosum*		0.09 1±52	0	0
LYTHRACEAE				
Decodon verticillatus (L.) Elliott		0	0.14 1±41	0
Lythrum alatum Pursh		0.18 0.7±26	0	0
Lythrum salicaria L.		0	0.28 4±260	0
MALVACEAE				
Hibiscus moscheutos L. subsp. *moscheutos*		0	0	0.25 2±72
MYRICACEAE				
Myrica gale L.		0	0.14 0.4±6	0
OLEACEAE				
Fraxinus pennsylvanica Marshall		0	0.43 3±116	0.25 3±80
Ligustrum vulgare L.		0	0	0.25 0.8±11

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
ONAGRACEAE				
Circaea lutetiana L. subsp. *canadensis* (L.) Asch. & Magnus		0.09 0.04±0.04	0	0
Epilobium coloratum Biehler	EF	0	0	0.25 0.8±11
Epilobium leptophyllum Raf.		0.09 0.02±0.02	0	0
Epilobium strictum Muhl. *ex* Spreng. (MASS: #313334)		0	0.29 0.1±0.1	0
Ludwigia alternifolia L.		0	0	0.25 2±21
OXALIDACEAE				
Oxalis corniculata L.		0	0.14 1±41	0
Oxalis stricta L.		0.09 0.02±0.02	0.14 3±89	0.50 4±136
PINACEAE				
Larix laricina (Du Roi) K. Koch		0	0.14 1±41	0
Pinus strobus L.	EF	0.09 0.3±4	0	0
PLANTAGINACEAE				
Plantago lanceolata L.		0	0.43 2±52	0
Plantago major L.		0	0.43 2±80	0
Plantago rugelii Dcne.		0.27 1±30	0.14 1±41	0
POACEAE				
Agrostis capillaris L.		0	0.29 5±181	0.25 2±72
Agrostis gigantea Roth		0.55 5±129	0.29 2±80	0.25 4±137
Agrostis stolonifera L. (MASS: #313339) (TENN: # not available)		0	0.14 2±52	0.25 4±137
Alopecurus carolinianus Walter		0	0	0.25 2±21
Bromus inermis Leyss.	EF	N/A	N/A	N/A

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Cinna arundinacea L.	EF	N/A	N/A	N/A
Danthonia spicata (L.) P. Beauv. *ex* Roem. & Schult.		0.09 0.7±26	0	0
Deschampsia cespitosa (L.) P. Beauv.		0.09 2±58	0.14 1±41	0
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark (WIS: #0260353) (MASS: #313337)		0.09 0.3±4	0.43 4±122	0
Dichanthelium clandestinum (L.) Gould		0	0.29 2±80	0.50 4±94
Dichanthelium leucothrix (Nash) Freckmann		0	0	0.25 6±194
Echinochloa muricata (P. Beauv.) Fernald	EF	N/A	N/A	N/A
Elymus riparius Wiegand (WIS: #0260357)		0.09 0.7±26	0.14 3±85	0
Elymus trachycaulus (Link) Gould *ex* Shinners		0.09 0.02±0.02	0	0
Glyceria canadensis (Michx.) Trin.		0.09 0.7±26	0	0
Glyceria grandis S. Watson	EF	N/A	N/A	N/A
Glyceria septentrionalis A.S. Hitchc. (TENN: # not available)		0	0	0.25 2±21
Glyceria striata (Lam.) A.S. Hitchc.		0	0.14 1±41	0
Leersia oryzoides (L.) Sw.	EF	0	0	0.25 3±80
Microstegium vimineum (Trin.) A. Camus		0	0.14 7±461	0
Muhlenbergia asperifolia (Nees & Meyen *ex* Trin.) Parodi		0.09 1±52	0.14 0.03±0.03	0
Panicum flexile (Gatt.) Scribn.		0	0	0.75 9±241
Paspalum dilatatum Poir. (TENN: # not available)		0	0	0.50 8±243

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
**Phalaris arundinacea* L. (WIS: #0260359) (TENN: # not available)	EF; RF	0.45 7±272	0.29 3±92	0
Phleum pratense L.		0	0.57 5±153	0
Poa palustris L. (MASS: #313336)		0	1 0.03±0.03	0
Poa pratensis L.		0.55 5±165	0.29 2±52	0.25 3±80
Schizachyrium scoparium (Michx.) Nash		0.09 0.7±26	0	0
Spartina pectinata Bosc *ex* Link		0.09 1±52	0	0
**Triticum aestivum* L.	VL	N/A	N/A	N/A
POLYGONACEAE				
**Polygonum amphibium* L. (WIS: #0260348)	MP	0.27 3±121	0	0
Polygonum cespitosum Blume		0	0	0.25 6±261
Polygonum sagittatum L.	EF	0.09 2±76	0.29 4±150	0.25 3±80
Polygonum virginianum L.		0	0	0.25 0.05±0.05
Rumex crispus L.		0.09 0.5±8	0	0
PRIMULACEAE				
Lysimachia ciliata L.	EF	0.09 0.7±26	0.14 3±92	0
Lysimachia terrestris (L.) Britton, Sterns & Poggenb.	EF	N/A	N/A	N/A
**Lysimachia quadrifolia* L.	MP	N/A	N/A	N/A
RANUNCULACEAE				
Caltha palustris L.		0.18 1±33	0.43 9±297	0.25 2±30
**Clematis virginiana* L.	EF; RF	0	0.14 1±41	0.75 9±241
Ranunculus acris L.		0	0.71 6±181	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
**Ranunculus hispidus* Michx.	MP	N/A	N/A	N/A
Ranunculus sp.	EF	N/A	N/A	N/A
**Thalictrum dasycarpum* Fisch. & Avé-Lall.	MP	N/A	N/A	N/A
Thalictrum dioicum L.		0.18 0.7±26	0.14 1±41	0
Thalictrum pubescens Pursh	EF	0.27 4±151	0.57 3±88	0
RHAMNACEAE				
**Rhamnus frangula* L.	EF; MP	0.45 7±209	0.29 0.06±0.06	0
ROSACEAE				
Agrimonia parviflora Aiton		0	0.14 1±41	0.50 2±21
Argentina anserine (L.) Rydb.		0.09 3±120	0	0
Dasiphora floribunda (Pursh) Raf. *comb. nov. ined.*		0.27 5±129	0.14 4±120	0
Filipendula rubra (Hill) B.L. Robins.		0.09 0.02±0.02	0	0
Fragaria vesca L.		0.09 0.7±26	0.14 1±41	0
Fragaria virginiana Duchesne		0.18 1±33	0	0
Geum canadense Jacq. (WIS: #0260345)		0.09 0.02±0.02	0.14 0.03±0.03	0.25 0.05±0.05
Geum rivale L.		0.18 1±51	0.14 0.03±0.03	0
Geum sp.	EF	N/A	N/A	N/A
Potentilla recta L. (MASS: #313335)		0	0.29 1±41	0
Potentilla simplex Michx. (WIS: #0260349)	EF	0.09 1±30	0.29 4±120	0.50 3±80
Prunus serotina Ehrh.		0.09 0.3±4	0	0
Rosa carolina L.		0.09 1±30	0	0
Rosa multiflora Thunb. *ex* Murray	EF	0	0.29 1±41	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
Rosa virginiana Mill.		0.09 0.7±26	0	0.50 6±149
Rubus allegheniensis Porter		0.09 1±52	0	0.50 9±241
Rubus idaeus L.		0.09 0.7±26	0.14 1±41	0
Rubus hispidus L.		0	0.14 2±80	0
Rubus pubescens Raf.		0	0.14 0.4±6	0
Rubus sp.	EF	N/A	N/A	N/A
Spiraea alba Du Roi		0	0.14 1±41	0
Spiraea tomentosa L.	EF	0	0.14 0.4±6	0
RUBIACEAE				
Diodia teres Walter		0	0	0.25 2±72
Galium aparine L.		0	0.57 2±79	0.25 0.1±0.1
Galium palustre L.		0.09 0.04±0.04	0.14 1±41	0
Galium tinctorium L.		0	0	0.25 0.05±0.05
Galium trifidum L.		0.09 0.02±0.02	0	0
Galium sp.	EF	N/A	N/A	N/A
SALICACEAE				
Populus deltoides Bartram *ex* Marshall		0	0.14 1±41	0
Populus grandidentata Michx.		0.09 0.02±0.02	0	0
Populus tremuloides Michx.		0.09 0.7±26	0.14 0.03±0.03	0
Salix bebbiana Sarg. (WIS: #0260362)		0.18 0.8±12	0.57 6±157	0
Salix bicolor Fries		0.09 0.3±4	0	0
Salix sericea Marshall		0.09 0.7±26	0	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
SAXIFRAGACEAE				
Parnassia glauca Raf.		0.27 3±81	0.29 4±123	0
Saxifraga pensylvanica L.		0.09 0.04±0.04	0	0
SCROPHULARIACEAE				
Agalinis paupercula (A. Gray) Britton var. *paupercula*		0.09 0.02±0.02	0	0
**Chelone glabra* L.	EF; RF; MP	0	0	0.25 2±72
Chelone lyonii Pursh		0	0.14 0.03±0.03	0
Gratiola aurea Pursh		0.09 2±55	0	0
Mimulus ringens L.	EF	N/A	N/A	N/A
SMILACACEAE				
Smilax herbacea L.		0	0.14 2±80	0
SOLANACEAE				
Solanum carolinense L.		0	0	0.75 3±80
Solanum dulcamara L.	EF	0	0.14 0.03±0.03	0
SPARGANIACEAE				
Sparganium androcladum (Engelm.) Morong		0	0	0.25 2±21
THELYPTERIDACEAE				
**Thelypteris palustris* Schott	MP	0	0.71 8±185	0
TYPHACEAE				
Typha angustifolia L.		0	0.14 1±18	0
**Typha latifolia* L.	MP	0.09 0.7±26	0.14 0.03±0.03	0
ULMACEAE				
Ulmus rubra Muhl.		0.09 0.7±26	0	0

Appendix. Continued.

Taxon (Voucher)	Cit.	Occurrence and % Cover ± Variance		
		Midwest	Northeast	Southeast
URTICACEAE				
Boehmeria cylindrica (L.) Sw.	EF	0.09 0.7±26	0	0.50 8±242
Pilea pumila (L.) A. Gray		0.09 0.6±8	0.14 0.03±0.03	0
VERBENACEAE				
**Verbena hastata* L.	EF; MP	N/A	N/A	N/A
Verbena urticifolia L.		0	0.14 0.5±6	0
VITACEAE				
Parthenocissus quinquefolia (L.) Planch.		0	0.29 0.5±6	0
Vitis labrusca L.		0	0.14 2±47	0.25 5±142
Vitis riparia Michx.		0.18 0.7±26	0.29 0.06±0.06	0