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Understory Plant Community Structure in Forests Invaded by Garlic Mustard (*Alliaria petiolata*)

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Understory Plant Community Structure in Forests Invaded by Garlic Mustard (*Alliaria
petiolata*)

A Thesis Presented

by

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ABSTRACT

UNDERSTORY PLANT COMMUNITY STRUCTURE IN FORESTS INVADED BY GARLIC MUSTARD (*ALLIARIA PETIOLATA*)

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Plant invasions represent a significant threat to the structure and function of natural ecosystems. Garlic mustard (*Alliaria petiolata*) has been identified as a threat to native communities mostly through small-scale studies and focused experiments. In this *in situ* observational study I examined the effects of garlic mustard invasion on species composition across multiple sites by comparing plant diversity and composition in invaded and adjacent non-invaded communities. Mean Shannon diversity was higher in invaded compared to non-invaded plots and invasion was associated with greater densities of invasive species such as burning bush (*Euonymus alatus*), and greater celandine (*Chelidonium majus*). In ordination space, the sites grouped more closely by geographic region than by invasion status, suggesting that regional environmental variation is important for community structure. My findings indicate that garlic mustard invasion is associated with other invasive plants, and that the understory plant community varies considerably across the region regardless of invasion status. Overall we show that community structure in garlic mustard invaded forest understories is not consistent across the landscape.

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CHAPTER 1

INTRODUCTION

Garlic Mustard (*Alliaria petiolata*), is a Eurasian biennial invasive plant introduced to North America in the mid 1800s (Nuzzo 1999, Cavers *et al.* 1979). In the last two decades, garlic mustard has increased its presence throughout North America, invading forest-edges, riparian, and interior forest habitats (Nuzzo 2000, Welk *et al.* 2002). It now occupies 35 states and 4 Canadian provinces (USDA NRCS, National Plant Data Center, 2015). Garlic mustard's ability to invade closed canopy intact ecosystems is of special concern when endemic native flora is present (Brothers and Spingarn 1992, DeGasperi and Motzkin 2007, Von Holle and Motzkin 2007, Belote *et al.* 2008); phytochemical exudates of garlic mustard are known to suppress plant-mycorrhizal associations and subsequent growth of native plant species (Stinson *et al.*, 2006). While studies have shown that older populations of garlic mustard may become less toxic (Lankau *et al.* 2009), its long-term presence in forests, even if eradicated, could have long-term legacy effects on native plant diversity and composition.

Much of the research on garlic mustard has either been conducted in a greenhouse setting (Callaway *et al.* 2008, Stinson *et al.* 2007), or as part of a single forest stand or localized geographic area (e.g., Stinson *et al.* 2006, Cipollini 2002, Van Riper *et al.* 2010). More recently there have been studies on the interactive effects of garlic mustard, herbivory, and earthworms (Blossey *et al.* 2013, Davalos *et al.* 2015a, Davalos *et al.* 2015b). A few studies have examined trait variation within garlic mustard populations from different geographic regions (Callaway 2008, Wolfe 2008, Lankau 2011). However little is known about the effects of garlic mustard on native vegetation *in situ* across a

broader geographic range in North America. The purpose of this study was to test for patterns in understory plant communities that have been invaded by garlic mustard, particularly differences in diversity and composition between invaded and non-invaded forest communities.

This study focused on forested sites in the Northern-hardwood and Transitional-hardwood forest types (Westveld *et al.*. 1956) across Massachusetts and southeastern New York. Using plant census data from sites across this region, I examined plant community composition and species diversity in garlic mustard invaded and non-invaded plots for plant species and functional groups. Based on prior research, I predicted that invasion would accompany a homogenization of invaded communities, lower total plant diversity, and reduced tree seedlings (Stinson *et al.* 2006, Callaway *et al.* 2007, Stinson *et al.* 2007, Wolfe *et al.* 2008). Because invasive species often co-occur within a habitat I also predicted a positive relationship between garlic mustard and other invasive plants. The main objective of this work was to characterize landscape level patterns of invaded forest composition and diversity across the study region in order to help inform managers considering eradication and restoration efforts.

CHAPTER 2

METHODS

Site Description and Census Methods

To assess relationships between garlic mustard invasions and the diversity and composition of understory plant communities, eight forested sites with invaded and adjacent, non-invaded areas were selected for study in the spring of 2013. The sites are distributed longitudinally from the greater Boston area westward to the Massachusetts Berkshire Mountains, and southward into southeastern New York State (Table 1 and Figure 1). Seven out of eight sites were dominated by an over-story of sugar maple in combination with white ash, red oak, and to a lesser extent black cherry, silver maple, and green ash. The Drumlin Farm Canopy differed, as it was dominated by White pine. All soils had a clay-loam component. Elevation ranged from 131' at the River Road site (RR), to a high of 1327' at the Questing Forest site (QF). Average annual temperatures vary as much as 4⁰C, and nitrogen deposition rates range from between 3.3 – 12.7 kg ha⁻¹ yr⁻¹ (Ollinger *et al* 1995).

Plots were 3×3m (9 m²) with a central sampling area 2×2 m (4 m²). The target density of garlic mustard was 20 plants per square meter covering a large enough area to include three replicate invaded plots. Three non-invaded plots of the same size were located approximately 20 - 250 meters from the invaded plots and were similar in slope, aspect, and tree canopy composition. The total number of plots in the study is 48.

All vascular plants one meter and less in height were counted and identified to the species level. In addition, garlic mustard plants were identified as 1st or 2nd year plants. The plots were selected to represent the native vegetation but other invasive plants besides garlic mustard were encountered and were included in the survey. Plant censuses

were conducted in each plot during July 2013 (summer), early June 2014 (spring) and August 2014 (summer). Species densities were averaged across the three sampling periods by plot and analyzed as a single dataset. This was done because statistics did not change much from sampling to sampling period. Appendix 1 has species NMDS results for each sampling analysis. Species nomenclature follows Haines (2011).

Statistical analysis

Plant Community Structure

To assess the differences in plant species composition by invasion status (invaded vs. non-invaded plots), I used non-metric multidimensional scaling analysis (NMDS), based on a Bray-Curtis dissimilarity matrix. I chose this technique because of its ability to handle zero inflated data sets and because there are no assumptions of normality (McCune and Grace 2002). I did not include garlic mustard as a dependent variable in this analysis because I considered invasion status part of the sampling design. I conducted NMDS analyses at the plot level (to assess variability within the individual sites) based on species density, and functional group composition was also assessed by collapsing species data into the following functional groups; herbs, trees, shrubs, ferns, grass, and non-natives. The non-native category included all non-native plants across all functional groups; this was done because the invasional meltdown hypothesis groups all non-indigenous species together (Simberloff and Von Holle 1999). Both the species space and functional group space NMDS analyses were conducted on census data that had been averaged across the three sampling periods. Species data also had been standardized by species maximum and to reduce the effect of rare species, species with a count of two or less were removed for the multivariate analyses (McCune and Grace 2002).

To test for the relative effects of site and garlic mustard density on the plant community composition, I implemented a per-mutational multivariate analysis of variance (PERMANOVA) model with 1000 permutations using site and garlic mustard abundance as predictor variables and species composition as the response variable. The model used for the PERMANOVA was: species composition = site + garlic mustard abundance + site × garlic mustard abundance.

To reduce the effect of rare species on both multivariate analyses, I removed species with an occurrence of 2 individuals or less (McCune and Grace 2002), which dropped the species count from 90 to 65 species. I then standardized the data using the column maximum in the decostand function from the Vegan package, implemented in R (Oksanen *et al.* 2015, R Core Team 2015), which divides all abundance data for a given species by the maximum abundance value of that species, and scales the data between zero and one.

Plant Diversity and Density

To compare species diversity between invaded and non-invaded communities and among sites, I calculated three diversity indices at the plot level using all plants in the census except garlic mustard. Species richness (S) is the total number of species present in each plot. Shannon diversity (H') was calculated as:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

Where p_i = the number of individuals per species / the total number of individuals in the community. Pielou's evenness (J) was calculated as: $J = H' / \ln S$.

To test whether species diversity differed by invasion status and by site, generalized linear models (GLMs) were applied using the GLIMMIX procedure in SAS (SAS v. 9.4, SAS Institute Inc., Cary, NC, 1998-2013). For these analyses, species richness (discrete counts) followed a Poisson distribution, and the Shannon diversity and Pielou's evenness (continuous values) followed lognormal and normal distributions, respectively. The statistical model for these analyses was: species diversity = site + invasion status + (site \times invasion status).

To further elucidate the differences of functional groups in the presence/absence of garlic mustard, I compared functional group density and species diversity in invaded and non-invaded plots at the site level using GLMs (as described above). Functional group densities were calculated by dividing the total abundance of each functional group by 4 m², species richness was the total number of species within a given functional group, and Shannon diversity calculations used the proportion of individuals within a given functional group. The statistical model was the same as described above, but density and diversity indices were the response variables. These models followed a Gaussian distribution (except for species richness, for which a Poisson distribution was used).

To test for species-specific differences by garlic mustard invasion status, species totals were averaged across the three sampling periods and were analyzed using a zero-inflated Poisson (ZIP) model using the GENMOD procedure in SAS. The ZIP model did a better job at predicting the distribution than the Poisson model due to the high number of zeros (i.e., a high number of plots without a given species). Model fit (ZIP vs. Poisson) was assessed using the Vuong test (Vuong 1989), implemented using a SAS macro program (<http://support.sas.com/kb/42/514.html>). Since the parameter estimates were at

the same scale as the plot means, the estimates were divided by four to get species density per meter squared.

Except where indicated, P-values less than or equal to 0.05 are deemed significant. P-values for comparing least square means in the GLMs were adjusted for multiple comparisons using Tukey's HSD.

CHAPTER 3

RESULTS

Plant Community Structure

Plant species composition and functional groups of invaded and non-invaded plots overlapped in the ordination and there was no clear distinction between invaded and non-invaded plots. The NMDS (Figure 2) did not show clear separation of invaded and non-invaded plots, indicating there was no consistent community response to garlic mustard invasion. There was also overlap between sites and variable dis-similarity between plots at the same site. Generally, the New York sites clustered together and the Berkshire sites clustered with the Harvard Forest sites. The River Road and Drumlin Farm sites separated out on their own. Within a site dissimilarities varied from being quite close like the West Point site to quite variable like the Pittsfield forest site. The functional group NMDS also showed overlap as well as variation at the site level.

Garlic mustard densities varied considerably from site to site, and a high proportion of the plants were first year stage (Table 2). The density of garlic mustard, site, and the interaction were significant drivers of this pattern (Table 2 perMANOVA). The plant community composition varied significantly with garlic mustard abundance, site, and their interaction, as determined using PERMANOVA (Table 3).

Plant Diversity and Density

Functional group proportional densities (Figure 3) showed a greater proportion of herbs in non-invaded plots, which was associated with high numbers of *Maianthemum canadense* in these plots, compared to the invaded plots. Non-native species and tree density were greater in the invaded plots. The non-native density included high densities

of burning-bush (*Euonymus*). A high density of sugar maple (*Acer saccharum*) seedlings were observed in the invaded plots at West Point and were associated with high native tree density.

Shannon diversity was significantly greater in invaded compared to non-invaded ($F_{1,32}=6.55$, $P=0.0154$) (Figure 4). Richness and evenness showed a similar pattern but were not significant ($F_{1,32}=3.29$ $P=0.079$ and $F_{1,32}=2.13$ $P=0.154$ respectively). When the diversity indices were used as the response variable in the GLM models, Pielou's evenness varied significantly by site and the interaction of site and garlic mustard presence (Table 3). The significant interaction of site and garlic mustard presence for Pielou's evenness indicates that the influence of garlic mustard cannot be predicted without taking the site into consideration. The primary driver for this was the conflicting trend of higher evenness in non-invaded compared to invaded plots at the McLennan, Pittsfield, and the West Points, in contrast to the higher evenness in invaded plots for many of the other sites (Figure 5). Species richness did not vary significantly by invasion status.

The only plant functional group that was strongly influenced by garlic mustard presence was herbs, which had significantly higher Shannon diversity in invaded compared to non-invaded plots (Table 3, Figure 6). Both the herbs and non-native groups were influenced by Site and the interaction between Site and Invasion status. This suggests that predicting the diversity of these two groups is influenced by where in the landscape they occur because the same trend is not found from site to site. Woody species (shrubs and trees) were influenced by site but not invasion status or the interaction between the two, meaning that the diversity of these functional groups are only different

at the site level, suggesting that invasion is not as influential on these two groups compared to herbs or non-native species.

The three most widespread, abundant native species that were significantly impacted by garlic mustard invasion status are trout lily (*Erythronium americanum*), Canadian mayflower (*Maianthemum canadense*), and sugar maple. Trout lily and Canadian mayflower had greater densities in the non-invaded compared to invaded plots ($Z=-5.35$, $P<.0001$ and $Z=-30.81$, $P<.0001$, respectively; Figure 7). Sugar maple, however, was denser in invaded compared to non-invaded plots ($Z=6.19$ $P<.0001$). Non-native species that were abundant and widespread were greater celandine (*Chelidonium majus*) and burning bush (*Euonymus alatus*); both of these species were positively associated with garlic mustard invaded plots ($Z=6.84$, $P<.0001$ and $Z=7.76$, $P<.0001$, respectively; Figure 7). The most common species in the shrub category were the Virginia creeper and *Rubus. sp.* The densest non-native species regardless of invasion status (aside from garlic mustard) was the burning bush. See Table 4 for a full species list and their density estimates.

CHAPTER 4

DISCUSSION

This study provides much-needed data on geographic variation in plant communities invaded by garlic mustard in Northeastern North America. Forest plant communities invaded by garlic mustard differed in plant community structure, species diversity, and individual species abundances from their proximate, uninvaded sites. In general the results demonstrate that while there are some patterns that are broadly maintained across the study region, site-specificity is also important.

Plant Community Structure

The results of NMDS and PerMANOVA suggest that garlic mustard, site, and the interaction were significant drivers of community composition. This is interesting, because I had predicted a difference in community composition between the invaded and non-native plots. Previous experimental work showed reductions in native plant growth (Stinson *et al.* 2006, Callaway *et al.* 2007, Stinson *et al.* 2007, Wolfe *et al.* 2008) and I expected this to translate to reductions in the abundances of species in this *in situ* observational study. This suggests that there are other interactive forces such as variations in herbivory, earthworms and other invasives (Blossey *et al.* 2013, Davalos *et al.* 2015a, Davalos *et al.* 2015b) working to structure the community. All of these interactive factors may have site level variability, and may be the reason for the lack of consistent differences between invaded versus non-invaded communities.

While these results do not indicate how plant community composition varied with garlic mustard density and site, they indicate that these factors (or factors that are associated with garlic mustard presence and site) highly influence species composition.

Higher densities of tree seedlings in the invaded plots, but the same number of species in both invaded and non-invaded plots as shown in Figure 3 were contrary to the prediction that tree seedling density would decline in invaded plots (Barto *et al.* 2011, Calloway *et al.* 2008, Stinson *et al.* 2007). This pattern was driven by large numbers of sugar maple seedlings in the invaded plots especially at West Point. The forbs demonstrated an expected pattern of reduced density in the invaded plots even though the number of species remained the same between invaded and non-invaded plots (Morris *et al.* 2012, Shartell *et al.* 2012, Stinson *et al.* 2007). The most interesting difference between the invaded and non-invaded plots was an increase in the density and richness of invasive species in the invaded plots. This could be because of facilitation between invasives, or the beginnings of invasional meltdown (Simberloff 1999). Since the disturbance history is not well known at this time past resource availability and propagule pressure (Lockwood *et al.* 2005) may have paved the way for multiple invasive plants.

Plant and Functional Group Diversity

My initial prediction of lower plant diversity in the invaded communities was not supported, in fact I had overall significantly greater Shannon Diversity in invaded plots ($F_{1,32}=6.55$, $P=0.0154$). Higher species diversity has also been seen in other studies that have investigated invaded communities ((Levine and D'Antonio 1999, Shea and Chesson 2002, and Fridley *et al.* 2007). Typically, studies that have seen this pattern in diversity are at larger spatial scales than this work, and these larger scale studies suggest support for invasive species being passengers of ecological changes as opposed to drivers (MacDougal and Turkington 2005, Fridley *et al.* 2007). This study was not set up to test garlic mustard's role in the invasion paradox debate. Specifically, I observed greater

numbers of other invasive plants in the invaded sites. Invasives commonly associated with garlic mustard invasion are Burning bush (*Euonymus alatus*) and greater Celandine (*Chelidonium majus*). With regard to the native community diversity, there are several possible explanations for higher species diversity at the invaded locations. First, these communities are relatively new to garlic mustard invasion and have not yet experienced richness reduction, alternatively the garlic mustard that is invading is from older source populations have reduced allocation to chemical defenses (Lankau 2009), reducing its pressure on the native community. Second, the environmental conditions that promote high levels of diversity also facilitate garlic mustard invasion. This observation follows a “rich get richer” pattern in invaded communities (Stohlgren 2003, Levine 2000), and could be further explained by the “biotic acceptance” hypothesis (Stohlgren *et al.* 2006). This hypothesis explains that early in the invasion process, native species outnumber the invaders, but this resistance becomes overwhelmed and co-existence is a stronger force than exclusion, and leads to increased plant turnover (Stohlgren *et al.* 2006). There is probably no cause and effect relationship between native and non-native richness (Stohlgren 2003), but instead is likely the result of spatial heterogeneity, including factors such as slope, elevation, and distance to rivers, where the configuration of the landscape influences both native and non-native species richness (Kumar *et al.* 2006).

When the diversity metrics were tested as a function of Garlic mustard invasion, site and the interaction of garlic mustard and site (Table 3 diversity GLM, functional group GLM), was a strong predictor of both Shannon diversity and Pielou’s Evenness. Site was also a significant predictor for the Shannon diversity of the functional groups. The interaction of site and garlic mustard presence was also significant for Pielou’s

evenness and non-native Shannon diversity. As shown in Figure 5, not all of the sites show the same trends in evenness, and this is what is influencing this interaction. This suggests that garlic mustard has different effects on overall diversity and diversity of the functional groups from site to site. This makes generalizations about the region hard to predict.

Species Level Response

Of the six tree species whose densities were different between garlic mustard invaded and non-invaded plots, red maple (*Acer rubrum*), white ash (*Fraxinus americana*), and white pine (*Pinus strobus*) were negatively associated with garlic mustard. This was not surprising based on the work done by Stinson *et al.* (2006), which linked anti-fungal phytochemistry of garlic mustard to the disruption of arbuscular mycorrhizae that lead to the suppression of seedling growth of red maple and white ash. Sugar maple (*Acer saccharum*), butternut (*Juglans cinerea*), and black cherry (*Prunus serotina*) were positively associated with garlic mustard invasion. Butternut is a small tree and does not typically do well under a closed canopy (Burns *et al.* 1990). It was only found at the Drumlin farm site, which had the most open canopy of our sites. Black cherry was more widely distributed across our sites, and typically does not survive for long under closed canopy scenarios, but is known to put down seed every year and replace seedlings under a closed canopy (Burns *et al.* 1990). This suggests that garlic mustard and these species show similar preferences for high light habitats.

Trout lily and Canadian mayflower densities were reduced in the invaded plots. These species were often found in dense monocultures in the non-invaded areas; this contributed to reduced diversity indices in non-invaded areas. Both of these species may

have experienced population decline following events that lead to the establishment of greater native and non-native species diversity. Meekins and McCarthy (1999) in a garlic mustard competition experiment suggested that the garlic mustard was more competitive with plants of a similar height, presumably for light resources. The interspecific species competition for light could be a possible explanation for the reduction in trout lily and Canadian mayflower densities. Both of these native, low-growing, perennial herbs resprout each spring and would have to compete for light especially with over wintered garlic mustard rosettes. This could further be influenced by competition with other species and garlic mustards phytochemistry.

Sugar maple was present at greater densities in the garlic mustard invaded plots than non-invaded. I expected to see high numbers of sugar maple in the non-invaded plots because it is part of the rich mesic forest found in the Berkshire plateau (Bellemare *et al.* 2005) and the Hudson Highland region (Schuster *et al.* 2008). However, I did not expect to find equally dense sugar maple seedlings in invaded plots due to the reliance of sugar maples on mycorrhizae and the reductions in mycorrhizal infection found on their roots in areas occupied by garlic mustard (Stinson *et al.*, 2006, Barto *et al.* 2011). These contrasting results may be partially explained by the fact that sugar maple is shade tolerant (Kobe *et al.* 1995), produces large numbers of seeds (masting years have been reported to produce 4-8 million samaras per acre), and has a germination rate of approximately 95% during optimum conditions (Godman, Yawney, and Tubbs 1990). Sugar maple seedling mortality is 50% during the first year (Godman, Yawney, and Tubbs 1990), and 96.6% over seven years (Cleavitt *et al.* 2014), but its abundant seed production may easily offset these losses. Sugar maple and garlic mustard both have early

germination times (Godman, Yawney, and Tubbs 1990, and Carvers 1979), so garlic mustard may not have a strong advantage through priority effects, as has been seen with other invasive species (Dickson *et al.* 2012). The competition with an allelopathic, aggressive colonizer may negatively impact sugar maple establishment and survival in some settings, but I have not observed this in the current study. This unexpected pattern maybe the result of soil preferences or microhabitat that supports high densities of garlic mustard and sugar maple, and is further confounded by episodic high levels of sugar maple seed production and germination rates at a subset of our plots. Negative impacts of garlic mustard on sugar maple establishment require additional study.

CHAPTER 5

CONCLUSION

Garlic mustard invasion has a strong impact on understory structure, but this impact varies between sites. Thus, forests of Massachusetts and the Hudson Highlands of Southeastern New York have site-to-site variation in species composition and the attributes of the individual site should be taken into consideration when predicting effects of garlic mustard invasion. Moreover, a higher Shannon diversity in invaded than non-invaded sites was indicative of increased abundances of invasive shrubs rather than higher diversity of native species, indicating the need for management to consider impacts of multiple invasive plants. As indicated by species-specific responses, garlic mustard invasion is negatively associated with abundance of trout lily (*Erythronium americanum*), and Canadian mayflower (*Maianthemum canadense*). A positive association between garlic mustard and sugar maple appears to be site-driven and requires further study.

Table 1. Physical descriptions of the eight study sites containing garlic mustard invasions. Sites are listed from northeast to southwest.

Site	Northing	Westing	Soil	Eleva meters	Slope %	Aspect Deg.	Dominant Forest Canopy Species
Drumlin Farm (DF)	42° 24' 33.79" N	71° 19' 37.23" W	Clay Loam (Entisol)	74.3	13.3	80.11	White pine
Harvard Forest (HF)	42°31'45. 82" N	72°11'25. 49" W	Clay Loam (Inceptisol)	315.7	17.2	253.2	Sugar Maple- White Ash- Black Cherry
River Road, Deerfield (RR)	42°32'11. 25" N	72°34'08. 67" W	Clay Loam (Inceptisol)	40	12.16	109.4	Sugar Maple- White Ash- Silver Maple
Pittsfield State Forest (PF)	42°29'12. 47" N	73°17'59. 33" W	Silt Clay Loam (Spodosol)	360.5	4.6	102.2	Sugar Maple- Black Cherry- American Beech
McLennan Forest (MC)	42°13'17. 44" N	73°10'23. 49" W	Clay Loam (Spodosol)	340.7	28.5	218.9	Sugar Maple
Questing Forest (QF)	42°07'15. 82" N	73°15'14. 97" W	Sand Clay Loam (Spodosol)	404.4	18.72	297	Sugar Maple- White Ash
Black Rock (BR)	41°25'16. 54" N	74°00'34. 44"W	Sand Clay Loam (Inceptisol)	212.7	24.75	321.5	Sugar Maple- Red Oak- Green Ash
West Point (WP)	41°22'45. 45" N	74°01'09. 16" W	Clay Loam (Inceptisol)	343.2	20.5	116.5	Sugar Maple- Red Oak

Table 2. Mean garlic mustard densities in meters squared of both life cycles combined (total) and for 1st year plants and 2nd year plants separately. Site abbreviations follow names in Table 1. Species Richness, Shannon Diversity and Pielou's Evenness are reported as the site means, by invasion status.

Site	Total gm Density m ²	1 st Year gm Density m ²	2 nd Year gm Density m ²	Species Richness	Shannon Diversity	Pielou's Evenness
DF invaded	129.16	104.8	24.36	11.6	1.45	0.59
DF non-invaded	X	X	X	11	0.59	0.24
QF Invaded	102.54	95.13	7.38	8	1.64	0.80
QF non-invaded	X	X	X	7.3	1.17	0.58
WP Invaded	69.3	67.13	2.16	9	0.73	0.32
WP non-invaded	X	X	X	7.3	0.89	0.47
RR invaded	62.72	54.83	7.88	10.6	1.86	0.78
RR non-invaded	X	X	X	6.6	1.45	0.76
PF invaded	54.83	49.0	5.83	10.3	1.18	0.49
PF non-invaded	X	X	X	12.6	1.42	0.55
MC invaded	47.58	39.33	8.25	8.3	1.34	0.62
MC non-invaded	X	X	X	4.3	0.95	0.67
HF invaded	34.33	32.02	2.30	8.6	1.76	0.81
HF non-invaded	X	X	X	9	1.78	0.81
BR invaded	19.91	18.66	1.25	10.6	1.53	0.66
BR non-invaded	X	X	X	8.6	1.28	0.60

Table 3. Effects of garlic mustard and site on native plant communities. GM = garlic mustard

Analysis	Response variable	Effect	DF	F	P
Permanova	Species composition	GM Abundance	1,32	0.02	0.0009
		Site	7,32	0.45	0.0009
		GM Abundance× Site	7,32	0.12	0.0009
GLM	Richness	GM presence	1,32	3.29	0.079
		Site	7,32	2.17	0.0635
		GM presence × Site	7,32	0.9	0.5191
	Shannon diversity	GM presence	1,32	6.55	0.0154
		Site	7,32	5.5	0.0003
		GM presence × Site	7,32	1.86	0.1101
	Pielou's evenness	GM presence	1,32	2.13	0.154
		Site	7,32	10.3	<0.0001
		GM presence × Site	7,32	2.85	0.0198
Functional Group GLM	Herbs Shannon Diversity	GM presence	1,30	18.1	0.0002
		Site	7,30	12.54	<0.0001
		GM presence × Site	7,30	3.07	0.0146
	Non-natives Shannon Diversity	GM presence	1,22	2.13	0.1582
		Site	7,22	8.84	<0.0001
		GM presence × Site	7,22	3.13	0.0188
	Shrubs Shannon Diversity	GM presence	1,21	0.29	0.59
		Site	7,21	2.99	0.024
		GM presence × Site	5,21	1.1	0.3918
	Trees Shannon Diversity	GM presence	1,32	1.31	0.2608
		Site	7,32	12.22	<0.0001
		GM presence × Site	7,32	1.73	0.1366

Table 4. Species density estimates by invasion status and separated by functional group. The statistics reported here are the estimates of density produced from the ZIP analysis. Lowercase x's indicate species that were removed from the multivariate analysis. Density estimates were compared using Tukey's test.

Functional group and species	Density (#/m ²)		Functional group and species	Density (#/m ²)	
	Invaded	Non-invaded		Invaded	Non-invaded
Herbs			Non-natives		
x <i>Actaea pachypoda</i>	0	0.028	<i>Acer platanoides</i>	0.069	0.163
x <i>Actaea rubra</i>	0	0.028	<i>Berberis thunbergii</i>	0.337	0.144
<i>Ageratina altissima</i>	0.281	0.061	<i>Celastrus orbiculatus</i>	0.435	0.565
x <i>Allium stellatum</i>	0.028	0	<i>Chelidonium majus****</i>	9	0.137
<i>Arisaema triphyllum</i>	2.589	3.032	<i>Convallaria majalis</i>	42.168	0
<i>Erythronium americanum****</i>	12.85	19.472	<i>Euonymus alatus****</i>	4.661	1.71
<i>Eurybia divaricata</i>	1.378	0.933	x <i>Lonicera</i> sp.	0.167	0
<i>Galium aparine**</i>	0.695	0.095	<i>Microstegium vimineum*</i>	1.025	2.291
x <i>Galium</i> sp.	0.042	0.014	x <i>Plantago major</i>	0	0.398
x <i>Galium triflorum</i>	0.019	0.009	x <i>Robinia pseudoacacia</i>	0.028	0
x <i>Geranium maculatum</i>	0.007	0	x <i>Rosa multiflora</i>	0.056	0
<i>Geum fragarioides*</i>	0.608	0	<i>Tussilago farfara**</i>	0.026	0.926
<i>Impatiens capensis****</i>	4.208	0.008	Trees		
<i>Lactuca canadensis*</i>	0.705	0	<i>Acer pensylvanicum</i>	0.057	0.04
<i>Maianthemum canadense****</i>	13.274	75.13	<i>Acer rubrum***</i>	0.121	1.184
<i>Maianthemum racemosum</i>	0.355	0.335	<i>Acer saccharum****</i>	9.015	6.442
<i>Mitchella repens</i>	0	7.25	x <i>Betula allegheniensis</i>	0.056	0
x <i>Monotropa uniflora</i>	0	0.056	x <i>Betula lenta</i>	0	0.028
<i>Oxalis</i> sp.**	1.722	0	<i>Carpinus caroliniana</i>	1.639	1.36
<i>Phytolacca americana</i>	0.087	0.123	<i>Carya cordiformis</i>	0.149	0.126
x <i>Pilea pumila</i>	0.028	0	x <i>Carya glabra</i>	0.028	0.028
<i>Polygonum hydropiperoides****</i>	2.75	0.034	<i>Carya ovata</i>	0.142	0.061
<i>Sanguinaria canadensis**</i>	0.75	0.028	x <i>Cornus alternifolia</i>	0.007	0
<i>Solidago</i> sp.	0.023	0.127	<i>Frangula alnus</i>	0.113	0.037
<i>Tiarella cordifolia****</i>	30.168	16.917	<i>Fraxinus americana****</i>	0.706	1.983
<i>Trientalis borealis***</i>	0.199	2.958	x <i>Fraxinus nigra</i>	0	0.028
<i>Trillium cernuum</i>	0.688	0.516	<i>Hamamelis virginiana</i>	0.2	0.026
x <i>Viola canadensis</i>	0.083	0	<i>Juglans cinerea*</i>	5	0
<i>Viola pubescens</i>	1.068	0	x <i>Juniperus communis</i>	0.007	0
x <i>Viola sororia</i>	0.028	0	<i>Lindera benzoin</i>	0.291	0.078
Shrubs			<i>Liriodendron tulipifera</i>	0.169	0.032
<i>Ilex verticillata</i>	0.194	0.139	<i>Ostrya virginiana</i>	0.1	0.057
<i>Lycopodiaceae</i> sp.	0	0.282	<i>Pinus strobus***</i>	0.017	0.993
x <i>Nemopanthus mucronata</i>	0	0.056	x <i>Prunus pensylvanica</i>	0.014	0.014
<i>Parthenocissus quinquefolia**</i>	0.339	0.794	<i>Prunus serotina****</i>	1.666	0.628
<i>Ribes lacustre</i>	0.414	1.24	<i>Prunus virginiana</i>	0.45	0.28
<i>Rubus</i> sp.****	1.07	3.778	<i>Quercus rubra</i>	0.047	0.078
x <i>Sorbus americana</i>	0	0.028	x <i>Quercus velutina</i>	0.028	0.014
x <i>Spiraea</i> sp.	0	0.028	x <i>Tsuga canadensis</i>	0	0.028
<i>Toxicodendron radicans*</i>	0.174	0.436	<i>Ulmus americana</i>	0.086	0.269
<i>Vaccinium angustifolium</i>	0	1.412	Ferns		
<i>Viburnum acerifolium*</i>	0	1.241	x <i>Dennstaedtia punctilobula</i>	0	0.028
x <i>Viburnum alnifolium</i>	0.028	0.028	<i>Dryopteris</i> sp.	0.648	1.183
<i>Vitis riparia</i>	0.11	0.183	<i>Equisetum arvense</i>	0	0.506
Grasses			<i>Onoclea sensibilis</i>	2.333	1.687
<i>Carex</i> sp.****	1.126	11.25	<i>Osmunda cinnamomea**</i>	1.722	3.806
x <i>Scirpus atrovirens</i>	0.069	0	x <i>Polystichum acrostichoides</i>	0.151	0

*P≤0.05, **P<0.01, ***P<0.001, ****P<0.0001

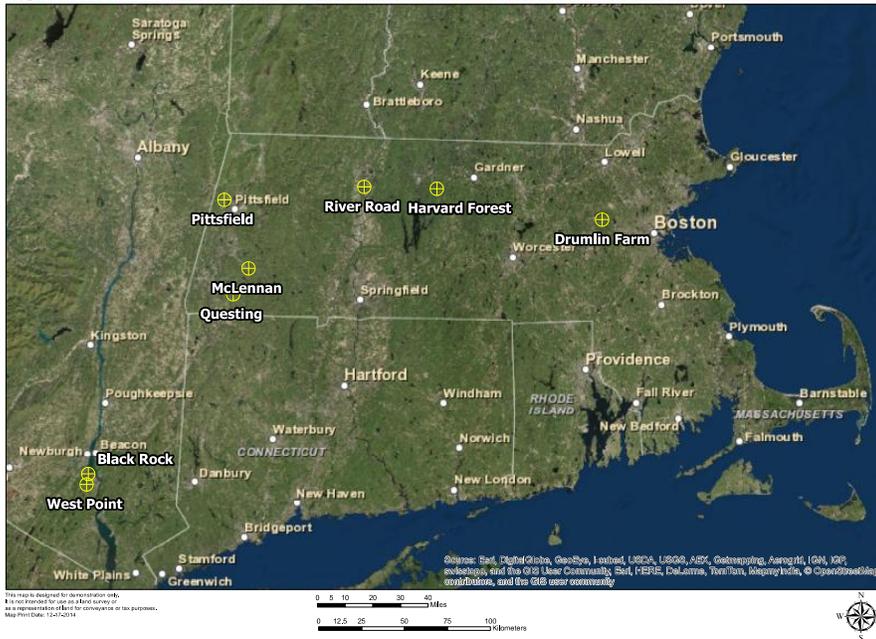


Figure 1. Locations of study sites.

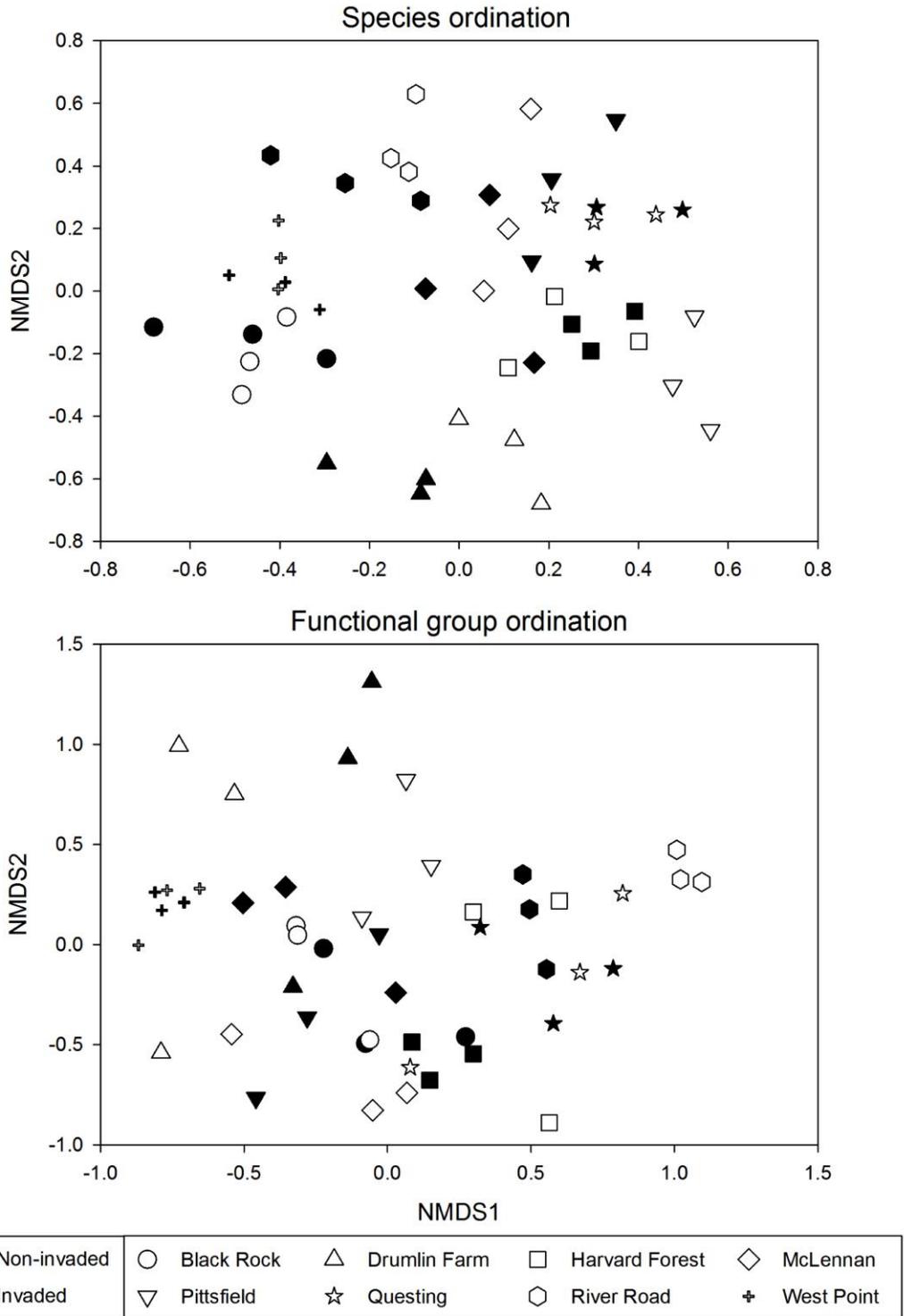


Figure 2. Nonmetric multi-dimensional scaling analysis for (A) species space and (B) functional group space of the eight study locations, at the plot level and separated by invasion status. The NMDS visually depicts differences the overlap in sites and the plot level

Proportional Densities of Functional Groups and Species Richness of Functional Groups

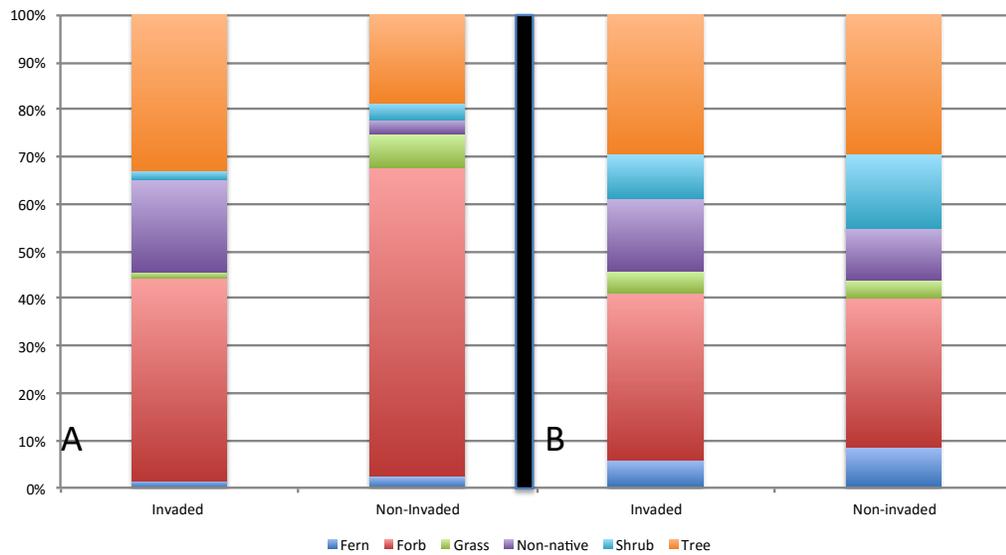


Figure 3. A. Proportional density of functional groups, by invasion status. B. Proportional density of species richness of functional groups by invasion status. The forb density was reduced in invaded plots, while richness remained about the same. Tree seedlings and non-native plants had greater densities in invaded plots, and while tree richness was similar non-native richness increased with invasion.

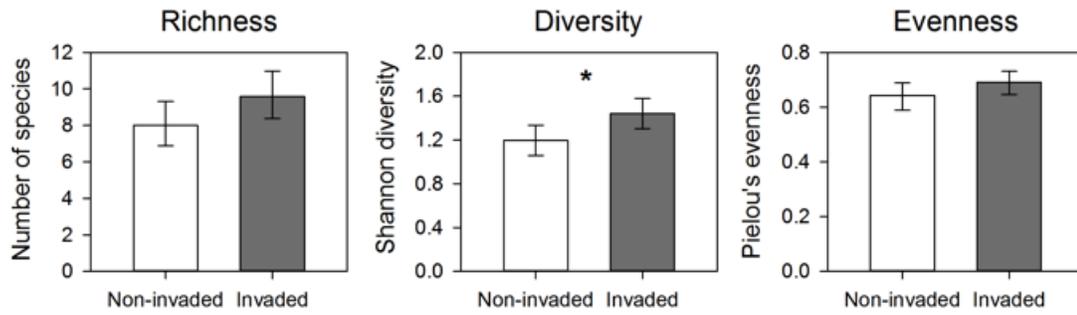


Figure 4. Diversity metrics by invasion status, across all sites. Species Richness, Shannon Diversity, and Pielou's Evenness all show a similar pattern of greater diversity in the invaded plots. Shannon Diversity is significantly greater ($P=0.05$) in invaded plots.

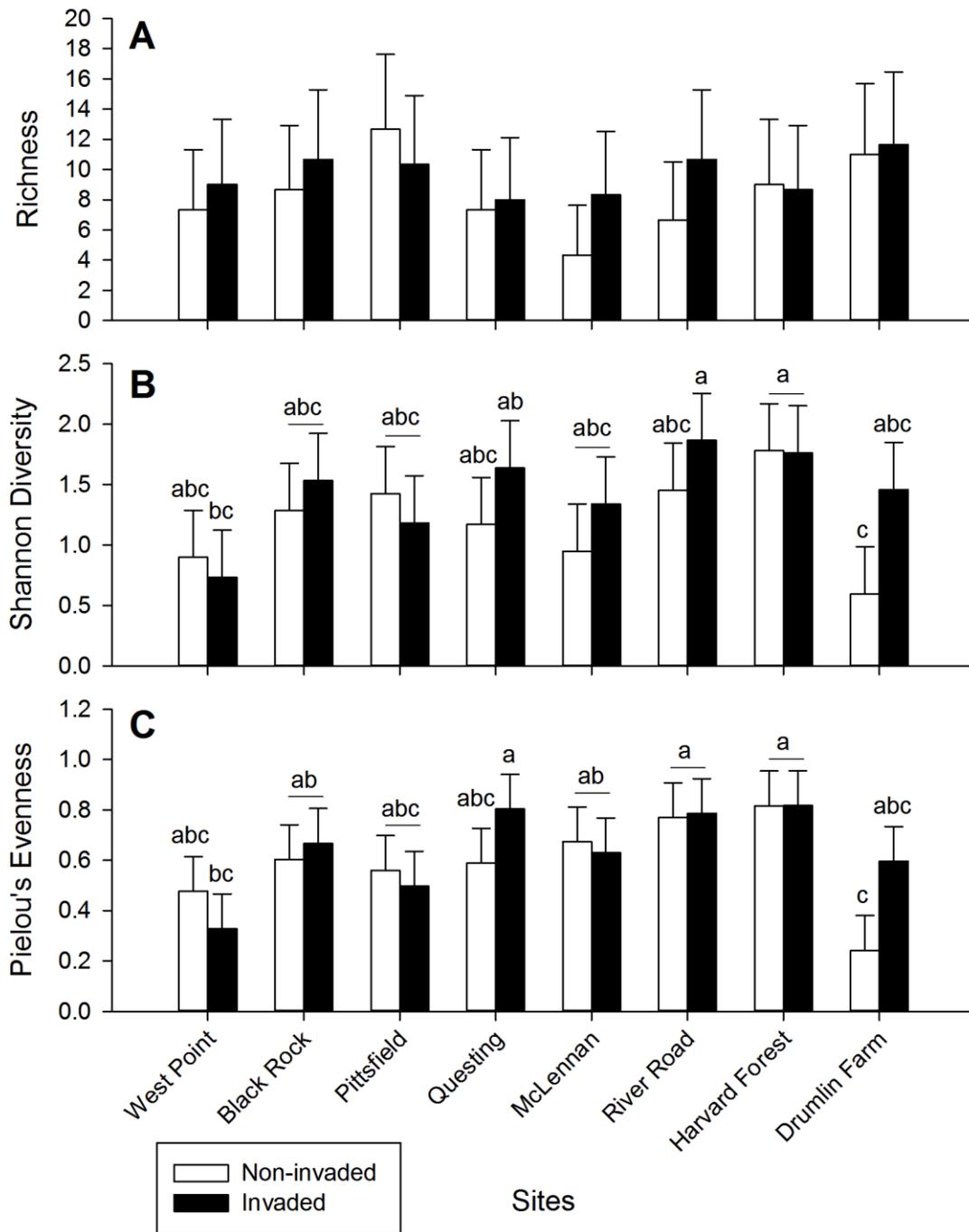


Figure 5. Diversity indices by invasion status and by Site. Differences are not significantly different at the site level or across sites. The opposite patterns found in Pielou's Evenness (C) is what is driving the significant interaction of Site and garlic mustard presence in the generalized linear model for Evenness.

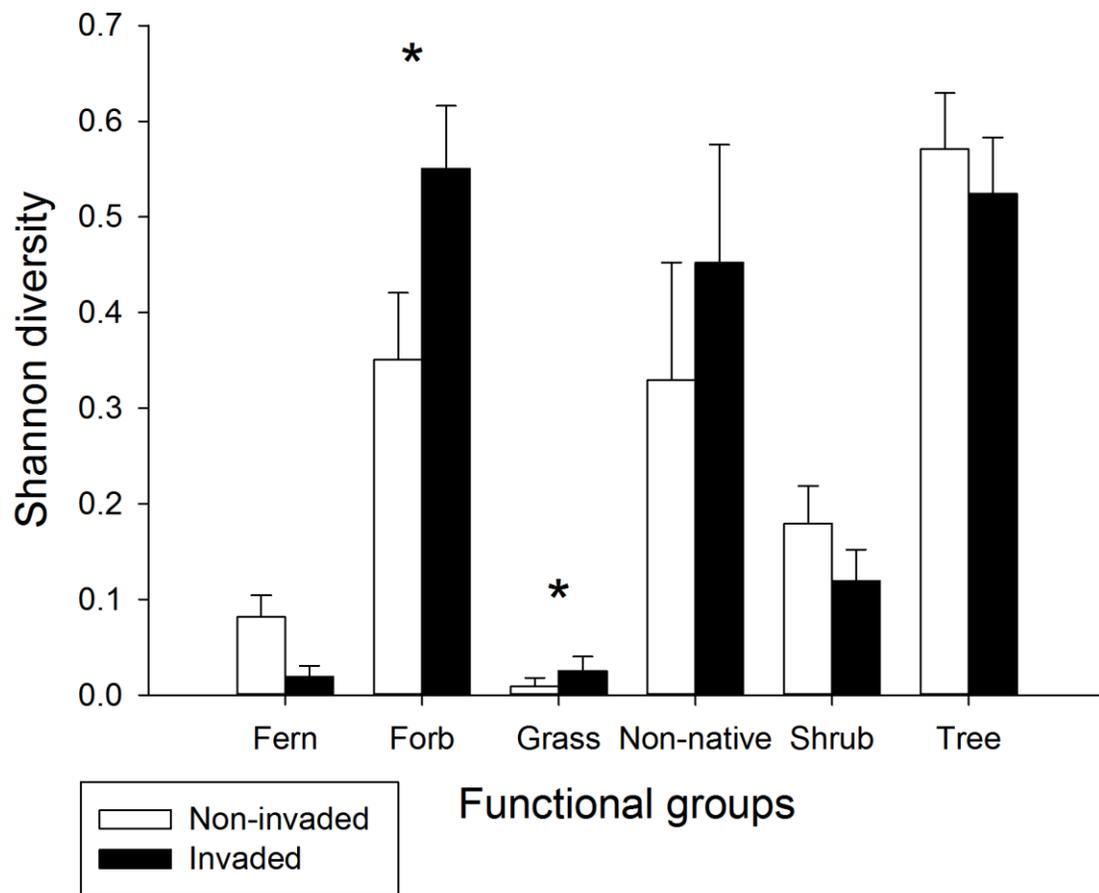


Figure 6. Differences in Shannon Diversity of the six functional groups averaged across all sites and compared by invasion status. The Shannon Diversity of the Forb group was significantly higher ($P=0.05$) in the invaded plots, the Grass group also showed a similar trend.

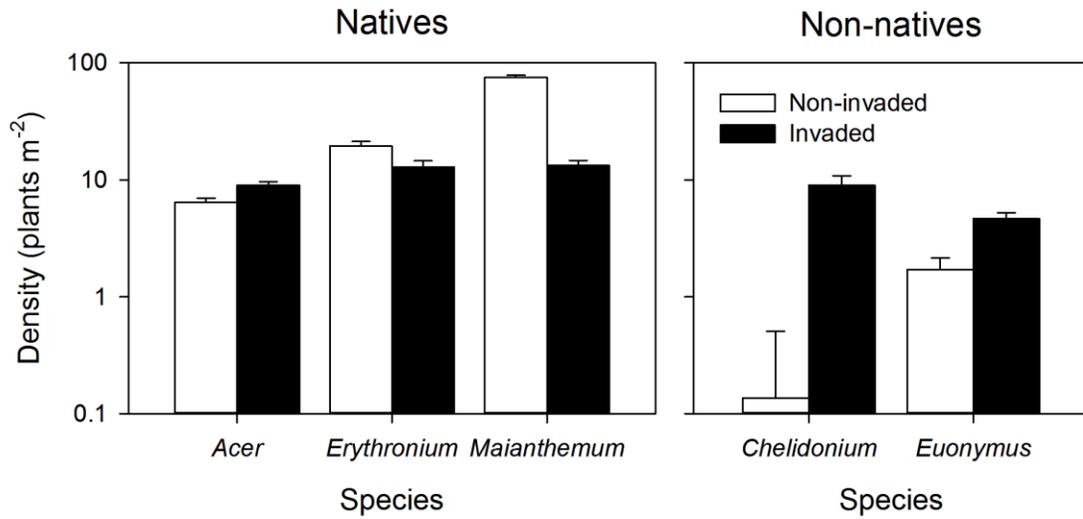


Figure 7. Density of the most abundant native (A) and non-native (B) species by garlic mustard invasion. Zero inflated Poisson distribution estimates compared using Tukey's HSD tests.

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