

An investigation into the presence of slender false brome (*Brachypodium sylvaticum*) and its relationship with plant communities in New York State

By

Megan Evelyn Aubertine

A thesis submitted to the Department of Environmental Science and Ecology of

The College at Brockport

in partial fulfillment of the requirements for the degree

of

Master of Science

August 5, 2022

Copyright

by

Megan Evelyn Aubertine

2022

Department of Environmental Science and Ecology
Thesis Defense

Megan Aubertine

Thesis defense date 5-03-22

Thesis seminar date 5-23-22

Master's Degree Advisory Committee

Approved Not Approved

[Signature]
Major Advisor

X _____

[Signature]
Committee Member

✓ _____

[Signature]
Committee Member

✓ _____

[Signature]
Graduate Director

5-23-22
Date

[Signature]
Chair, Environmental Science & Ecology

5-26-22
Date

Acknowledgments

First, I'd like to thank my graduate advisor, Dr. Kathryn Amatangelo for her endless support and guidance through the development and execution of my thesis project. I'd like to thank my committee members, Dr. Rachel Schultz and Ms. Andie Graham, for their support and feedback. I'd additionally like to thank Andrew Leonardi, Jess DeToy, Aubrey Franks, Kati Gierlinger, Zac Falconer, Rachael Ezzzew, Claire Hartl, and many more for assisting with data collection and other aspects of my research as I could not have done it without them. I'd also like to recognize the Bergen Swamp Preservation Society, Genesee Valley Conservancy, Monroe County and New York State Parks Departments and several private landowners for site access. Finally, I'd like to thank my friends, family, fiancé and dogs for their love, support and continuous encouragement along the way.

This study was funded by the New York State Department of Environmental Conservation, the SUNY Department of Environmental Science and Ecology Graduate Student Fund, and the SUNY Distinguished Professors Graduate Student Research Award.

Table of Contents

Abstract	1
Introduction	3
Methods	13
<i>Study Sites</i>	13
<i>Field Methods</i>	14
<i>Greenhouse Methods</i>	16
<i>Statistical Analyses</i>	17
<i>Brachypodium sylvaticum presence</i>	18
<i>Brachypodium sylvaticum Impact and Community Composition</i>	19
<i>Greenhouse Competition Experiment Analyses</i>	24
Results	24
<i>Brachypodium sylvaticum Presence</i>	25
<i>Brachypodium sylvaticum Impact and Community Composition</i>	26
<i>Greenhouse Competition Experiment</i>	29
Discussion	30
Literature Cited	42

List of Tables

Table 1. Study site locations, environmental variables, and descriptions. Ber=Bergen, NY, DSF = Danby State Forest; Tag = Taughannock falls State Park. Sites are ordered from west to east.	53
Table 2. Community characteristics of each site, large-scale samples. Sites are ordered from west to east. The dominant herbaceous species are the top 3 most frequently observed aside from <i>B. sylvaticum</i>	54
Table 3. Top GLM for among site data predicting <i>B. sylvaticum</i> cover.	56
Table 4. Best fit generalized linear models for predicting <i>B. sylvaticum</i> cover at sites with at least 10 quadrats containing <i>B. sylvaticum</i>	57
Table 5. Final generalized linear model for among invaded site data predicting species richness.	61
Table 6. Best fit generalized linear models (GLM) within each site predicting species richness at invaded (BerA, BerB, BerC, TagU, TagW, DSFA, DSFF, and IFNP) and uninvaded sites (UDan, UGCP, UBCP).....	62
Table 7. C-scores for all sites.	68
Table 8. Observed and simulated C-scores in intact and invaded areas at each site for large scale samples. N for invaded and intact plots are listed with site (N invaded, N intact).....	69

Table 9. Species associated and disassociated with *B. sylvaticum* based on the *Pairs*
analyses..... 70

List of Figures

- Figure 1. Map of the study site locations..... 73
- Figure 2. Average *B. sylvaticum* cover among soil types present within the invaded sites. Soils are grouped by drainage: well drained (WD), moderately well drained (MWD), somewhat poorly drained (SPD), poorly drained (PD), and very poorly drained (VPD). 74
- Figure 3. Average native and exotic species richness within invaded and uninvaded quadrats in invaded sites. 75
- Figure 4. Trends of soil moisture against *Brachypodium sylvaticum* percent cover within each invaded site. Dashed lines indicate the significant trend direction. 76
- Figure 6. NMDS ordination of community composition of all invaded sites. Symbols indicate the counties site is located within..... 78
- Figure 7. Non-metric multidimensional scaling (NMDS) plots of fine-scale community data in invaded and uninvaded quadrats at BerB (A), IFNP (B), BerC, (C), and TagU (D). *Brachypodium sylvaticum* was excluded from these analyses. All 3D NMDS are represented as 2D plots for clarity. Species significant at that site were presented in bold. Species not significant at that site but present within the site was listed not in bold..... 79

Figure 8. Growth parameters of *Dactylis glomerata* when grown with and without *B. sylvaticum*. 80

Figure 9. The differences in growth parameters of *Geum canadense* when grown with and without *B. sylvaticum*. 81

Figure 10. The differences in *Brachypodium sylvaticum* growth parameters when grown in monoculture, or in competition with *Dactylis glomerata* (DG), or *Geum canadense* (GC). 82

List of Appendices

Table 1. Study sites and the transect and quadrat spacing used. Sites where additional fine-scale sample took place are marked.	83
Table 2. Dates of environmental data collection at fine scale quadrats at BerB, BerC, TagU, and IFNP	84
Table 3. Soil types (Web Soil Survey 2022) located within the sample sites. Included is the soil taxonomy of each soil type, soil drainage, and the average percent cover of <i>B. sylvaticum</i> within the plots located within the soil types.	85

Abstract

Globalization has led to an increased frequency of biological introductions. These introductions have the potential to progress into invasions that negatively impact the recipient communities. However, not all species may have large impacts on native species or community assembly patterns. By understanding where invaders are likely to establish and their impacts, we can better allocate resources for early detection and rapid response to prevent future invasion. *Brachypodium sylvaticum* is an invasive grass in North America that is native to Eurasia and North Africa. First introduced in the Pacific Northwest, it has since made its way to the East Coast and western New York. As a relatively new invader, little is known about its environmental preferences, potential impact on communities, and its competitive ability. My study investigated these questions. In the first portion of my study I conducted vegetation surveys and environmental measurements in eight invaded and three uninvaded communities that varied in *B. sylvaticum* population size, environmental conditions, and forest types. As predicted, I found that water content and canopy cover determined *B. sylvaticum* abundance. It preferred drier soils within wetter sites, and wetter soil within drier sites. Contrary to my expectations, I found that *B. sylvaticum* abundance was not dependent on canopy type. *Brachypodium* is associated with lower species richness, which provides evidence that the invader is negatively impacting communities. However, impacts on recipient communities are limited to changes in richness as I did not find significant difference in community structure or assembly patterns between invaded and uninvaded quadrats. In the second portion of

my study, I conducted a greenhouse competition experiment in which I selected species from my co-occurrence analyses to grow in competition with *B. sylvaticum*. I found that *B. sylvaticum* is not a strong competitor against another exotic grass. Combined, my studies indicate that *B. sylvaticum* may not be a strong competitor on the east coast and may instead be a passenger of already degraded communities.

Introduction

Globalization has led to an increased frequency of biological introductions. Species have been introduced outside of their native ranges through human transport both intentionally and unintentionally. Common pathways of introduction include horticulture, soil contamination, the pet trade, shipping commerce, and agriculture (Keller and Lodge 2007, Visser *et al.* 2017). Introduced species have the potential to become invasive in their new range. Invasive species are defined as non-native species that have a negative impact on ecosystems, human health, or the economy and spread away from the initial site of introduction (Mack *et al.* 2000, Colautti and MacIsaac 2004, McDonald *et al.* 2008). Because of their negative impacts, research to identify key parameters that allow invasive species to be successful in their invaded ranges is important. The relationship of invader establishment and success depends on the invader's traits, site environmental conditions, and characteristics of the recipient community.

Invasive species often have traits that make them successful in their invaded ranges. Species invasiveness can be attributed to competitive advantages including greater genetic diversity, higher growth rates, nitrogen use efficiency, water use efficiency, or the ability to tolerate a wide range of environmental conditions (Anderson *et al.* 1996, Labrinos 2002, Matzek 2011, Van Kleunen *et al.* 2011). Generally, invasive species produce more biomass, have higher specific leaf area, and produce heavier seeds than their competitors (Pfeifer-Meister *et al.* 2006, Van

Kleunen *et al.* 2011, Bottolier-Cortet *et al.* 2013, Divisek *et al.* 2018). Invasive species success could also be related to phenotypic plasticity and tolerance of different environments. For example, Liu *et al.* (2015) identified that when grown at different light levels, invasive species showed higher plasticity than native species. These characteristics of invasive species often allow them to have a greater competitive ability than species in the recipient community.

Site conditions including resource availability, disturbance history, and the amount of stress, can also influence the success of an introduced species. Areas with high resource availability are often more susceptible to species invasion (Liu *et al.* 2015, Searle *et al.* 2018). However, while invasive species may be able to take advantage of available resources, they may be hindered by environmental stress. For example, frequent inundation may inhibit terrestrial invaders if they are not adapted to it (Berg *et al.* 2016). Communities that have a high degree of disturbance are more susceptible to invasion. Disturbances such as logging, frequent trafficked parks, increased herbivory, and soil disturbance increase the introduction, emergence, and establishment of invasive species (Knight *et al.* 2009, Davalos *et al.* 2015, Taylor and Cruzan 2015, Orban *et al.* 2021). Increased herbivory within a community suppresses native species' presence and opens room for invasive species to invade. Knight *et al.* (2009) and Davalos *et al.* (2015) identified that high white-tailed deer populations in communities facilitated the invasion of garlic mustard (*Alliaria petiolata*) and Japanese stiltgrass (*Microstegium vimineum*).

Invasion success may also depend on characteristics of the recipient plant community (Labrinos 2002, Matez-Mouro 2010). Already-invaded communities are more likely to be invaded by new species, a process called ‘invasional meltdown’ (Heimpel *et al.* 2010, Green *et al.* 2011). Studies have shown that invasion success increases in communities with other exotic species that have similar phylogenetics and traits to the new invader. Invasion success is also more likely when the invader has very different evolutionary history and traits than the native species present within the recipient community (Sheppard *et al.* 2018). The same invader can have different establishment success based on differences in recipient plant community alone (Rojas-Bostero 2022)

Once established, invasive species can negatively impact recipient communities (Mack *et al.* 2000, Haines *et al.* 2018). Species invasions are associated with the loss of biodiversity at local scales and lead to homogenization of landscapes. Invaded communities typically have lower species richness, diversity, and evenness than intact communities (Hejda *et al.* 2009, Matez-Mouro *et al.* 2010, Fu *et al.* 2018, Khan *et al.* 2021). Native species growth rate is significantly reduced by the presence of invasive plants (Schultheis and MacGuigan 2018). Not all species have equal effects; Schultheis and MacGuigan (2018) found that invasive members of Poaceae and Asteraceae had the greatest competitive impact on native plant communities.

In addition to the reduction of biodiversity, invasive species also alter community assemblage patterns. Researchers have used co-occurrence analyses to

investigate community assembly and the patterns associated with competition and facilitation within communities. Co-occurrence analyses evaluate the frequency in which species co-occur within a site and assess whether the species tend to aggregate, segregate or associate randomly within each other. More recently, co-occurrence analyses have been used to investigate how invasive plants impact assemblages within invaded communities. Assemblages or assembly patterns are determined by competitive interactions and habitat filtering (Diamond 1975, Reshi *et al.* 2008, Gotzenberger *et al.* 2012, Trivallone *et al.* 2017, Flint 2018). When an invasive species is successful within a community, it interrupts competitive interactions between and among native species, disassembling assembly patterns (Sanders *et al.* 2003, Reshi *et al.* 2008, Santoro *et al.* 2012, Kuebbing *et al.* 2014, Fu *et al.* 2018). The disassembly of co-occurrence patterns is when species no longer aggregate or segregate more than expected by chance. Instead, these patterns move toward random co-occurrence. The loss of competitive interactions among species can be attributed to the addition of a new, potentially stronger competitor.

Even though invasive species are often regarded as strong competitors that alter ecosystem processes and communities, researchers have worked to identify if invasive species are drivers or passengers of community changes. Drivers are species with novel traits and characteristics that allow them to invade, outcompete other species, and potentially alter ecosystem processes and community composition. Passengers are species that take advantage of an already degraded system with underlying conditions that are causing the loss of biodiversity (HillerRisLambers *et*

al. 2010, Bauer 2012). Passenger species often do not have superior competitive ability compared to species within a recipient community (HillerRisLambers *et al.* 2010). Evaluating whether an invasive species is a passenger or a driver is crucial to determining the amount of resources that should be allocated towards control and eradication.

Brachypodium sylvaticum

Slender false brome (*Brachypodium sylvaticum*) is a perennial bunchgrass native to Eurasia and North Africa. In its native range *B. sylvaticum* is present in multiple habitats ranging from full sun to deep shade. It occurs in temperate forested environments but may also be found in open grasslands and along roadsides (Grime *et al.* 1988). It is found in shallow, rocky limestone soils and rocky outcrops (Merton 1970). It prefers moist soils and frequently grows along steep slopes where talus is present (Grime *et al.* 1988). However, despite the variability in habitat conditions within its native range, it is largely absent from wetland areas and riparian areas (Holten 1980, Grime *et al.* 1988). It is also uncommon in open, dry soils as germination of seedlings is hindered in these environments (Evans and Etherington, 1990). It has also been noted that *B. sylvaticum* is able to tolerate low light conditions where other species may not be successful (Merton 1970, Haeggstrom and Skyten 1996). Its tolerance of stress-inducing environments, such as arid climates with prolonged drought conditions, gives it potential to invade different ecosystems.

In North America, *Brachypodium sylvaticum* is highly invasive in the United States and Canada. It has spread rapidly, forming dense monocultures (Holmes *et al.* 2010, Fjeran 2014). It was first introduced to the Pacific Northwest in Eugene, Oregon during the late 1930s by the United States Department of Agriculture experimentally as a more productive rangeland grass (Fjeran 2014, Rosenthal *et al.* 2008). In California, Johnson (2004) observed this species producing seeds year-round in optimal conditions, increasing its potential to be introduced elsewhere.

In the Pacific Northwest, the establishment of *B. sylvaticum* has been shown to be influenced by vegetation and disturbance. *Brachypodium sylvaticum* is associated with areas of high disturbance such as recently logged forests and multi-use parks, growing along trails and roads eventually spreading into less disturbed areas (Holmes *et al.* 2010, Kim 2015, Taylor *et al.* 2015). It has been most abundant in coniferous forests with dense canopy cover, shorter or limited understory vegetation, and compacted soils (Holmes *et al.* 2010, Taylor *et al.* 2015, Taylor and Cruzan 2015). Populations have been identified in both deciduous and coniferous forest but are more prominent in conifer-dominated forests (Daniel and Werier 2010, Taylor *et al.* 2015, Taylor and Cruzan 2015). *Brachypodium sylvaticum* appears to be more successful in conifer forests as deciduous forest contains deep leaf litter that has been found to hinder the germination and establishment of seedlings (Taylor *et al.* 2015, Taylor and Cruzan 2015). However, once this grass is established, the presence of deciduous leaf litter has a positive impact on the growth of *B. sylvaticum*, likely due to an increase in soil moisture retention (Taylor *et al.* 2015).

Abiotic factors such as soil moisture and soil type are likely to influence the presence and establishment success of *B. sylvaticum*. Marchini et al. (2018) evaluated traits of drought tolerance in contrasting water environments in *B. sylvaticum* individuals within its invaded (Pacific Northwest) and native ranges to further understand its success as an invader. Their study showed that there was no difference in traits or growth between the water-available and water-limited treatments, suggesting no phenotypic plasticity in either native or invaded ranges. They also identified that water availability is likely a selective pressure in *B. sylvaticum* populations in its invaded range. Traits related to water stress in the arid climate were present within invaded-range individuals and not native range individuals. These traits make *B. sylvaticum* more adapted to survive in arid climates and become more drought tolerant. The authors suggest that this local adaptation and divergence of drought-tolerant traits may lead to the rapid evolution of *B. sylvaticum* in its invaded range. It is not currently known what soil moisture regimes *B. sylvaticum* tolerates in the Northeastern America range, as this has not yet been studied. As moisture retention varies among soil types and may contribute to plant hypoxia or wilting, soil characteristics may also contribute to the success of this species. In the Pacific Northwest, soil type has been recorded within *B. sylvaticum* study areas but has not been studied in direct relation with *B. sylvaticum* success in any part of its invaded range.

Brachypodium sylvaticum's impact on plant and insect communities in its invaded range has been widely observed but less frequently quantified and published.

Severns and Warren (2008) evaluated *B. sylvaticum*'s impact on *Plantago lanceolata* populations and a federally endangered butterfly (*Euphydryas editha taylori*) who utilizes it as a host. They found that the number of host plants declined in exotic grass dominated quadrats, in return leading to a lower number of larval butterflies. A study by Holmes *et al.* (2010) provided additional information on *B. sylvaticum*'s success and its competitive ability in its invasive range. The authors evaluated the competitive ability of *B. sylvaticum* against other species in a competition experiment, finding that the bunch grass produced less biomass when grown with other invasive grasses, indicating that *B. sylvaticum* may not be a strong competitor against other species. However, that study used only individuals of the same functional group from the Pacific Northwest. Additionally, Holmes *et al.* (2010) presented the effect of competition on *B. sylvaticum*, not the effect of *B. sylvaticum* on other species leaving room to question how *B. sylvaticum* altered their growth. A competition experiment with *B. sylvaticum* and other species from the Northeast would help us understand how *B. sylvaticum* interacts with and potentially impacts native species.

Brachypodium sylvaticum is a relatively new invader in eastern North America. It has been detected in Ontario, Canada, and in Michigan, Virginia, and New York, United States (Miller *et al.* 2011). In New York State it has been found in several counties including Genesee, Livingston, Monroe, Tompkins, Onondaga, and Dutchess (IMap Invasives, 2022). Little is known about its success in different environments or impact on plant communities in eastern North America. Throughout

central and western New York, populations ranging in size from a few square meters to hundreds of hectares have been observed throughout various environments including conifer and deciduous forests, wetland complexes and floodplains, and open fields. While it has been observed in a variety of habitats, there has been no published research on where it is most likely to occur or its environmental preferences in the Northeast. Often, when a new population is identified, it is beyond the point of extirpation and control is the only option of management, which becomes costly. My research aims to identify the environmental conditions in which *B. sylvaticum* is most likely to occur in the Northeast, so land managers are better able to allocate resources to early detection and rapid response. Additionally, there is no information on *B. sylvaticum*'s relationship and competitive interactions with communities in which it has invaded or if potential community resistance hinders this invader from establishing. In this study I work to identify what these relationships are and how *B. sylvaticum* interacts within its invaded communities.

Goals and Hypotheses

The goals of this study were threefold. First, I wanted to assess the environmental conditions in which *B. sylvaticum* is present within New York State. I hypothesized that *B. sylvaticum* cover would be greater in coniferous forests with high canopy cover. In relation to soil moisture, I hypothesized that *B. sylvaticum* would be most abundance in soils with a moderate soil moisture but not in saturated conditions. This prediction is based on research performed in its native range and its

preference for non-arid climates in its invaded range. I additionally hypothesized that soil type would be important for the presence of *B. sylvaticum* as soil type is heavily related to soil moisture content. To investigate the presence of *B. sylvaticum* throughout western and central New York, I used data collected during field surveys to build models identifying important variables.

Secondly, I evaluated *B. sylvaticum*'s impact on plant communities in the field. I hypothesized that *B. sylvaticum* would be a driving change of community composition and species richness, with heavily invaded areas having lower species richness than uninvaded areas and native species being more impacted than exotic species. Additionally, I hypothesized that community composition would be altered by *B. sylvaticum* invasion and that invaded areas would demonstrate a loss of competitive structure and a disassembly of co-occurrence patterns. I also expected that species associated with *B. sylvaticum* would be other invasives and generalist species, or species adapted to a wide range of environmental conditions, and species disassociated with *B. sylvaticum* would be species outcompeted by *B. sylvaticum*.

For the third portion of my thesis, I evaluated the competitive ability of *B. sylvaticum* within a greenhouse experiment using species from a field survey. A novel portion of my research included combining the results from the co-occurrence analyses with a competition experiment in a greenhouse setting. It is difficult to tease apart competition among species and environmental variables in the field. Paired controlled greenhouse experiments are used to identify competitive interactions

without environmental variation. Often, environmental treatments are added to further evaluate the competitive ability of invasive species among environmental gradients (Pfeifer-Meister *et al.* 2006). I selected two species, one significantly associated and one significantly disassociated with *B. sylvaticum*, to grow in a competition experiment with *B. sylvaticum*. This helps to illuminate if associations and disassociations were due to competition and facilitation or differences in environmental preference. I expected that *B. sylvaticum* would be a strong competitor against species with which it was disassociated, reducing their growth parameters when grown in competition. In contrast, I expected there to be no competition between *B. sylvaticum* and an associated species.

Methods

Study Sites

Sites were located throughout western and central New York (Table 1, Figure 1). Eleven sites were sampled: eight were invaded by *B. sylvaticum* and three were not. Three of the invaded sites were in Bergen, Genesee County, as part of a large wetland complex on private property. These sites are Bergen Private Site A (BerA), B (BerB), and C (BerC). Another invaded site was in Geneseo, Livingston County, at Indian Fort Nature Preserve (IFNP). Two sites were located within Taughannock Falls State Park, Tompkins County, one wetland site (TagW) and one upland site (TagU). The final two sites were located within Danby State Forest, one upland site (DSFA) and one site within a floodplain (DSFF).

The uninvaded sites were selected based on their proximity to and similarity in plant communities and environmental conditions to the invaded sites with the largest *B. sylvaticum* populations. Two uninvaded sites were in Monroe County. The first was within Greece Canal Park (UGCP). The site was adjacent a stream and contained similar plant species to those at the invaded sites located within Bergen, NY. The second site in Monroe County was in Black Creek Park (UBCP). This site was selected due to its proximity to Black Creek, representing the communities sampled within BerA, BerB and BerC, as the Bergen sites were also adjacent to Black Creek west of this site. The last uninvaded site was in Danby State Forest, southeast of the invaded Danby floodplain site (UDan). This site has the same plant community as the invaded floodplain site but has not been invaded by *B. sylvaticum*.

Field Methods

Vegetation sampling took place during the growing seasons (May-August) of 2019 and 2020. I used two scales when sampling: a large and a fine scale. The fine scale sampling was designed to closely capture environmental conditions within the sites. The large scale was designed to evaluate community composition and the presence of *B. sylvaticum* throughout each site. For both scales, I ran evenly spaced transects with evenly spaced 1 x 1 m quadrats along each transect. For the larger scale, spacing of transects and quadrat varied based on the size of the site, extent of *B. sylvaticum* invasion, and the location of the invasion within the site. Transects at BerA, TagU, TagW, DSFA, DSFF, IFNP and all uninvaded sites were spaced 25 m

apart with quadrats spaced 25 m apart. The transects at BerB were spaced 25 m apart with quadrats placed every 10 m along each transect. Quadrats were spaced closer together at this site to capture an existing environmental gradient to help predict the location of *B. sylvaticum*. Lastly, transects at BerC were spaced 75 m apart with quadrats placed every 25 m as this site contained the largest continuous invasion of *B. sylvaticum* (Appendix A, Table 1). At the large scale, the number of quadrats sampled ranged from 30 at the uninvaded sites to 188 at BerB. The fine scale sampling was conducted at four invaded sites: BerB and BerC, IFNP, and the TagU Site. Fine-scale sampling occurred within a subset of the overall sites to capture distinct environmental gradients. Transects were spaced 10 m apart with quadrats placed every 10 m. The number of quadrats sampled at the fine scale ranged from 30 quadrats at IFNP to 45 quadrats at BerC.

Within each quadrat I identified the vegetation down to the lowest possible resolution and visually estimated the percent cover for each of the taxa. I calculated canopy cover using a spherical densiometer (Taylor et al. 2015, Taylor and Cruzan 2015). Soil moisture (volumetric water content) and soil temperature data were collected using a Vernier Lab Quest 2 moisture probe. I collected soil moisture and soil temperature data once at the larger scale within each quadrat when vegetation sampling was conducted between June and August of 2019 and 2020. At the fine scale, I collected moisture and temperature data three times during the summer (Appendix A, Table 1).

Greenhouse Methods

To evaluate if *B. sylvaticum* is a strong competitor, I selected two species to grow with *B. sylvaticum* in a greenhouse competition experiment. The species selected were found to be significantly associated or disassociated with *B. sylvaticum* from my co-occurrence analyses (described below). Orchard grass (*Dactylis glomerata*) was selected as the significantly disassociated (segregated from *B. sylvaticum*) species, and white avens (*Geum canadense*) was selected to be the significantly associated (aggregated with *B. sylvaticum*) species.

Seeds were collected from each species from my study sites throughout the summer. *Brachypodium sylvaticum* seeds came from BerB, BerC, TagU, TagW and IFNP. They were cold stratified for 60 days at 4°C and then placed in the greenhouse to germinate (Holmes et al. 2010, personal communication with Brigitte Wierzbicki with NY State Parks). Due to a low germination rate of *B. sylvaticum*, individuals from the collected sites were pooled and selected at random for the experiment. When seedlings were at least 2 cm tall, randomly selected individuals from the different sites were transplanted into 17 cm diameter pots. A single density pot design was used with four individuals in each pot. Each pot was either a monoculture with four individuals of one of the three species, or a competition treatment with two *B. sylvaticum* and two of the other species.

Natural height (allowing leaves to droop), longest leaf and blade length, width, and plant health data were collected weekly for each individual plant. Plant

health was scored categorically as 1) dark green and producing new growth, 2) healthy appearance with medium green leaves and no new growth, 3) leaves yellowing, 4) leaves starting to brown and die back, 5) individual is dead. The number of leaves was recorded weekly for the first 8 weeks, then recorded monthly thereafter until the end of the experiment. One leaf from every individual was marked and checked weekly to monitor leaf longevity. Two leaves from each individual were cut one week before the end of the experiment to measure specific leaf area (SLA). Following the methods of Sugiyama (2005), leaves of *D. glomerata* and *B. sylvaticum* were cut at the ligule. Leaves were scanned immediately using a Canon CanoScan LiDE 110 scanner and imported into Image J (Rasband 1997) to calculate the surface area of the leaves. Once scanned, leaves were placed into a 70°C drying oven for 48 hours and weighed (Kluse and Allen-Diaz 2005, Holmes *et al.* 2010). Specific leaf area was calculated as surface area (cm²) divided by dry weight (g). Plants were harvested when rootbound after 100 days. Aboveground biomass was cut at the soil surface and placed in a drying oven at 60°C for 48h before being weighed (Holmes *et al.* 2010).

Statistical Analyses

While I sampled at two scales, the same patterns were shown within the fine and large scales, so the fine scale data is only presented for within-site NMDS ordinations to help illuminate the environmental variables and their relationship with

the communities. All analyses were performed in R Studio (RStudio Team 2020) or SPSS (IBM Corp 2020).

Brachypodium sylvaticum presence

I calculated the average soil moisture and canopy cover at each site within quadrats with more than 50% *B. sylvaticum* cover. Additionally, I calculated the average *B. sylvaticum* cover within each soil type listed by the United States Department of Agriculture (USDA) National Resource Conservation Service's (NRCS) Web Soil Survey (Web Soil Survey Staff, 2022).

Researchers have investigated the success of invasive species within varying environments and communities using exploratory methods such as generalized linear models (GLM, Gasso *et al.* 2012, Dechoum *et al.* 2015). This method helps to illuminate variables that are most important for predicting the presence of an invasive species (Dechoum *et al.* 2015). Before running the models, I checked that my data met the assumptions of GLMs including homogeneity for the variances and normality of the residuals using a series of Levene's test and Q-Q plots. To evaluate the predictors of *B. sylvaticum* cover, I ran GLMs for each site using a linear distribution after transforming the data using arcsine and square root transformations, as this was recommended for percent cover data. I included soil moisture, soil type, and percent canopy cover, with quadrat latitude and longitude added to account for spatial autocorrelation. Preliminary analyses showed that canopy type was not significant, therefore, it was not included. Two-way interactions were included in the models. I

used the backward method, entering all variables into the model and removing the variables with the highest Akaike information criterion (AICc) value, starting with the interactions first (Gao *et al.* 2018). Akaike information criterion is used to evaluate how well the model fits the data. The smaller the AICc, the better fit the model. I stopped removing variables when I had the lowest possible AICc I also evaluated how *B. sylvaticum* cover varied among all the invaded sites by using an additional GLM analysis with site also included in the model.

Brachypodium sylvaticum Impact and Community Composition

Richness

Generalized linear models are a commonly used method to evaluate parameters important for predicting community metrics such as species richness. This helps to identify if the presence of an invader or environmental variables are responsible for a response variable such as richness. A set of GLMs were also created to evaluate how *B. sylvaticum* cover and other measured variables predict species richness. These models used the Poisson distribution with a log link as this is the recommended method for count data. The models included *B. sylvaticum* cover as a predictor variable. All two-way interactions with *B. sylvaticum* were included in the model before backwards selection. I also evaluated how richness varied among all the invaded sites by using an additional GLM analysis with site also included in the model.

Co-occurrence Analyses

In addition to traditional community ecology methods such as ordination and diversity calculations, researchers have used co-occurrence analyses to evaluate the impact of invasive species on assembly patterns and community composition analyses (Gotelli and Arnett 2000, Sanders *et al.* 2003, Santoro *et al.* 2012, Flint 2018). Performing these types of analyses can provide additional nuance in understanding *B. sylvaticum*'s relationship with and impact on communities in its invaded range. I evaluated co-occurrence and species assemblage patterns within the sample sites at two levels: community and pairwise. Species co-occurrence patterns can be identified through the deviations from a null model. The null models are based on the randomization of ecological data and help us spot these patterns within a community (Gotelli 2001, Ulrich and Gotelli 2007, Flint 2018). This can be done using co-occurrence indices. The index that I used in this study was the C-score. A C-score is an average number of checkerboard units created for all possible species pairs (Stone and Roberts 1990, Gotelli and McCabe 2002, Flint 2018). Checkerboards are any submatrices of the following combinations, with presence being 1 and absence being 0:

$$\begin{array}{cc} 1 & 0 \\ 0 & 1 \end{array} \text{ or } \begin{array}{cc} 0 & 1 \\ 1 & 0 \end{array}$$

A C-score takes the average of all pairs of two species in a matrix and produces a value showing the aggregation or separation of those two species

(Gotelli and McCabe 2002, Li and Waller 2016). In a perfectly segregated matrix, multiple species pairs will form checkerboards as seen above where those species never co-occur (Ulrich and Gotelli 2007).

C-scores are calculated using the CS equation:

$$CS = \frac{2 \sum_{i=1}^{S(S-1)/2} (n_i - N_{ij})(n_j - N_{ij})}{S(S-1)}$$

Where S is the number of species, n_i and n_j are the number of occurrences of species i and j, and N_{ij} is the number of co-occurrences of each set of two species (Gotelli and McCabe 2002, Li and Waller 2016, Flint 2018).

I converted the percent cover data into presence-absence data. I only included taxa present in at least five percent of the quadrats as recommended by McCune and Grace (2002). Some individuals could only be identified to genus. For those identified to genus accounting for more than 25 percent of all samples within those genera, all taxa in that genera were lumped at the genus level. For different species within the same genera that occurred at more than one site, I combined the species at the genus level for comparability purposes among sites.

For all co-occurrence analyses, I used the fixed rows and fixed columns method for all the null models simulated for this study. Fixed rows (species) and columns (quadrats) means that the observed row and column totals are maintained in

the simulated matrices (null models). In other words, the number of occurrences of each species or the number of species in each quadrat is the same in the simulated matrices as the observed matrices (Reshi *et al.* 2008, Flint 2018). This method works well with the use of C-scores as it reduces Type I error (falsely rejecting a null hypothesis) and is the only method of null model randomization that does not create degenerate matrices (Flint 2018). A degenerate matrix is a matrix that contains “missing species” or “empty sites” meaning that at least one of the row or column totals is zero (Flint 2018).

To test for differences between invaded and uninvaded areas at each site, I followed the methods of Sanders *et al.* (2003) using the EcoSim 7.0 guild structure, grouping by region (invaded and intact quadrats). I used the presence of *B. sylvaticum* to determine the region of each quadrat. I then removed *B. sylvaticum* from the analyses (Gotelli and Arnett 2000, Sanders *et al.* 2003).

I evaluated patterns of species associations with *B. sylvaticum* within each site using the *Pairs* program (Ulrich 2008). This allowed me to identify species that were significantly associated or disassociated with *B. sylvaticum*.

Multidimensional Analyses

Nonmetric multidimensional scaling (NMDS) ordination analyses have been used to evaluate the difference in community composition in invaded and uninvaded areas (Khan *et al.* 2021). This method demonstrates differences in composition within and among communities. To evaluate the difference in plant communities among sites, I ran an NMDS ordination using plant frequency among 30 subsampled quadrats from the large-scale data at each site. Only species present in five percent of the quadrats were used in the ordination following the methods of McCune and Grace (2002) and Khan *et al.* (2021). *Brachypodium sylvaticum* was excluded from the ordination following Khan *et al.* (2021) as my goal was to examine community composition as a result of *B. sylvaticum* invasion. I used Bray-Curtis Dissimilarity Index to calculate the resemblances that were then used in the NMDS ordination.

To identify the differences in plant community composition within each site among invaded and uninvaded quadrats, I ran additional NMDS ordinations using data from the fine scale survey areas. I included species present in five percent of the quadrats in the ordinations per the recommendations of McCune and Grace (2002) and Khan *et al.* (2021). I excluded *B. sylvaticum* from the ordination. I used the Bray-Curtis Dissimilarity Index to calculate the resemblances. To identify if invaded and uninvaded quadrats were significantly different, I conducted a PERMANOVA analysis using the pairwise adonis function in R based on euclidean distances. I overlaid environmental conditions on each ordination by calculating the average soil

moisture and soil temperature among the three environmental sampling periods. I included latitude and longitude coordinates for the location of each quadrat as well to evaluate for spatial autocorrelation.

To further analyze *B. sylvaticum*'s relationship with other species, I overlaid the significantly associated and disassociated species from the co-occurrence analyses. For comparability purposes among sites, I included any species that was significant within the co-occurrence analyses and present within that site.

Greenhouse Competition Experiment Analyses

To assess the difference in the natural plant height, leaf length or width, number of leaves, above ground biomass, and SLA in *D. glomerata* and *G. canadense* when grown with and without *B. sylvaticum*, I ran a series of Mann-Whitney U tests. To evaluate the difference in the natural plant height, leaf length, number of leaves, above ground biomass, SLA and number of inflorescences among *B. sylvaticum* grown in monoculture or with one of its competitors, I ran a series of Kruskal-Wallis tests. Due to the low germination rate of *B. sylvaticum* and small sample size, we set alpha at 0.1 for this experiment.

Results

Each of the invaded sites has distinct community composition, invasion size of *B. sylvaticum*, and environmental conditions (Table 1, Table 2). Bergen Private site C has the largest invasion with *B. sylvaticum* present in 76% of the surveyed quadrats.

Indian Fort Nature Preserve had the smallest invasion with *B. sylvaticum* present in 19% of the surveyed quadrats. Green Ash (*Fraxinus pennsylvanica*) was the dominant canopy cover in 7 of the 11 sites, 5 invaded and 2 uninvaded. Sites all had similar average soil moisture ranging from 24% to 38%. The average site canopy cover was similar among sites ranging from 60% to 79% cover with Bergen Private Site B falling outside of that range at 30% cover.

Ontario loam and Palmyra and Arkport soil types had the highest average percent cover of *B. sylvaticum* (Figure 2, Appendix A, Table 1). Both variations of Ontario loam soils had an average 56% and 74% cover of *B. sylvaticum*. Palmyra and Arkport soils had an average of 84% cover of *B. sylvaticum*. The soil types with the least *B. sylvaticum* cover were Halsey silt loam with an average 0% *B. sylvaticum* cover and Edward muck with 4% *B. sylvaticum* cover.

Brachypodium sylvaticum Presence

Among sites, the top GLM model demonstrated that canopy cover ($p < 0.0001$) and site ($p < 0.0001$) were significant in predicting the presence of *B. sylvaticum* among invaded sites (Table 3). Canopy cover in plots with greater than 50% *B. sylvaticum* cover ranged from 9% to 97.92% with a 81% average. *Brachypodium sylvaticum* presence increases as canopy cover increases. There was a significant interaction between site and soil moisture ($p < 0.0001$). While soil moisture was not significant ($p = 0.943$), there was a negative trend between *B. sylvaticum* cover and soil

moisture. Soil moisture in plots with more than 50% *B. sylvaticum* cover ranged from 1% to 54% with a 24% average.

Within sites, *B. sylvaticum* cover decreased with increasing soil moisture at all sites except BerC (Figure 3). Soil moisture was present in 7 top within-site GLMs (Table 4). Soil moisture was found to be significant in predicting *B. sylvaticum* cover at 3 sites (BerB ($p < 0.0001$), TagW ($p = 0.041$), DSFF ($p = 0.002$)).

Trends of *Brachypodium sylvaticum* cover with canopy cover varied between sites. Canopy cover was present in all final models and was significant in all except for BerC and DSFA (Figure 4). *Brachypodium sylvaticum* cover increased with increasing canopy cover at BerA, TagU, and DSFF. Cover decreased with increasing canopy cover at BerB and TagW.

Brachypodium sylvaticum Impact and Community Composition

Richness

Richness varied between sites, with the lowest average richness of 5 at TagU and IFNP and highest of 10 at BerA and BerB within quadrats (Figure 5). Quadrat-level richness among sites was dependent on both abiotic and biotic variables. Site ($p < 0.0001$), canopy cover ($p = 0.004$), and soil moisture ($p = 0.073$), and *B. sylvaticum* cover ($p < 0.0001$) were important for predicting species richness among sites (Table 5). Richness increased with increasing soil moisture. Among sites, species richness was lower in quadrats with a higher percent cover of *B. sylvaticum*.

Brachypodium sylvaticum cover, soil moisture, canopy cover, and soil type were important when predicting species richness, though results varied between sites (Table 6). *Brachypodium sylvaticum* cover was in eight of ten of the final models. It was significant in predicting species richness in six of those models. In all the models, regardless of significance, species richness declines with increasing *B. sylvaticum* cover. Soil moisture and canopy cover were important for predicting species richness but varied between sites. Soil moisture was present in eight of the final models but was significant in predicting richness at one site, where richness increased with increasing soil moisture (Appendix A, Table 3). Canopy cover was present in eight models and found to be significant in five of those models. Sites with canopy cover in the best model included BerA ($p=0.839$), BerB ($p=0.863$), BerC ($p<0.0001$), TagU ($p=0.003$), DSFA ($p<0.0001$), and UBCP ($p=0.002$). Richness decreases with increasing canopy cover at BerA, BerC, TagU, and UBCP. At sites BerB and DSFA, richness increases as canopy cover increased.

Co-occurrence

All sites, except Indian Fort, had significantly higher C-scores than expected by chance indicating competitively structured communities (Table 7). The C-score for Indian Fort indicates the potential disassembly of co-occurrence patterns as it was not significant ($p=0.749$). In other words, there was a potential loss of competitive interactions.

There was no significant difference in community assembly patterns between invaded and intact quadrats for six of the eight sites (Table 8). BerB and BerC had lower observed C-scores than simulated C-scores in the invaded quadrats ($p < 0.05$, $p < 0.05$). BerC was marginally significant ($p = 0.07$) having lower observed C-scores than simulated C-scores.

Few species were found to be significantly associated with *B. sylvaticum* (Table 9). Those that were associated with *B. sylvaticum* were common, generalist species who have also have a wide tolerance of environmental conditions (enchanter's nightshade (*Circaea lutetiana*), white avens (*Geum canadense*), Virginia creeper (*Parthenocissus quinquefolia*), and jack-in-the-pulpit (*Arisaema triphyllum*)) or other invasive species (*Lonicera morrowii*). More species were found to be significantly disassociated with *B. sylvaticum* than associated. Species found to be disassociated with *B. sylvaticum* included fringed loosestrife (*Lysimachia ciliata*), rice-cut grass (*Leersia oryzoides*), multiflora rose (*Rosa multiflora*), spotted jewelweed (*Impatiens capensis*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), orchard grass (*Dactylis glomerata*), and hog peanut (*Amphicarpaea bracteata*).

Community Composition

Community composition among sites were most determined by region (Figure 6). The NMDS plots evaluating the similarity among sites demonstrated that sites grouped more by county and not by the presence of *B. sylvaticum*.

At three of four sites at which fine-scale data were collected, intact and invaded quadrats were distinct via NMDS ordination (Figure 7). However, PERMANOVA analyses showed the separation only statistically significant at the TagU site. Of the environmental variables overlaid on the ordinations, canopy cover was significant at two sites (p-values <0.05), soil moisture was significant at one site (p=0.028), and latitude and longitude were significant at three of the four sites.

Species found to be significantly associated with *B. sylvaticum* (*Circeae lutetiana*, *Geum canadense*, and *Parthenocissus quinquefolia*) were close to *B. sylvaticum* on the ordination. Likewise, species significantly disassociated with *B. sylvaticum* (*Dactylis glomerata*, *Acer saccharum*, and *Prunus serotina*) were further away from *B. sylvaticum* on the ordination.

Greenhouse Competition Experiment

Dactylis glomerata growth and traits were not impacted by the presence of *B. sylvaticum* (Figure 8). There was no difference in natural height (p=0.567), number of leaves (p=1.0), longest leaf length (p=0.567), SLA (p=1.0) or above ground biomass (p=0.567) between *D. glomerata* grown in a monoculture or in competition with *B. sylvaticum*. *Geum canadense*, when grown with and without *B. sylvaticum*, did not differ in the number of leaves (p=0.662), above ground biomass (p=0.699), or SLA (p=0.589, Figure 9). However, *G. canadense* individuals grown in competition with *B. sylvaticum* were shorter than those grown without *B. sylvaticum* (p=0.082) and had wider leaves (p=0.052).

There were significant differences in *B. sylvaticum*'s above-ground biomass ($p=0.08$), number of inflorescences produced ($p=0.08$), and longest leaf length ($p=0.02$) when grown in competition with *D. glomerata* and *G. canadense* (Figure 10). *Brachypodium sylvaticum* had significantly lower above-ground biomass ($p=0.1$), shorter leaf length ($p=0.07$), and produced fewer inflorescences ($p=0.1$) when grown with *D. glomerata* than *G. canadense*.

Discussion

Brachypodium sylvaticum is a recent plant invader into eastern United States terrestrial and wetland ecosystems, and our limited knowledge about its impacts and drivers is from research in the Pacific Northwest. My study aimed to identify the environments in which *B. sylvaticum* is present and its relationship with and potential impact on communities in central and western New York. My hypotheses about its relationship with soil moisture, canopy cover, and soil type were mostly supported, indicating that *B. sylvaticum* prefers dense canopy forested areas with mesic to wet mesic soil conditions. My hypotheses about *B. sylvaticum*'s impact on species richness, community composition, and assemblage patterns were less supported, indicating that *B. sylvaticum* may be a passenger rather than a driver of change in these systems.

Canopy species can alter characteristics that affect understory vegetation, and I expected that canopy type would affect the presence of *B. sylvaticum*. Previous studies have shown that *B. sylvaticum* has been more successful invading and

establishing within coniferous forests as the deep, dense leaf litter within deciduous forests hinders germination (Taylor *et al.* 2015, Taylor and Cruzan 2015). However, my hypothesis was not supported as *B. sylvaticum* cover did not differ among deciduous, coniferous, or mixed canopy types. Although canopy type may impact germination, Taylor *et al.* (2015) additionally concluded that once established, deciduous leaf litter has a positive effect on *B. sylvaticum* growth, likely due to the moisture retention of the litter. Additional research has also found that *B. sylvaticum* cover does not differ between mixed oak/fir and Douglas-fir forests within the Pacific Northwest (Holmes *et al.* 2010). My results are consistent with the findings of Taylor *et al.* (2015) and Holmes *et al.* (2010), but more research needs to be done to explain the discrepancies in the literature about *B. sylvaticum* and canopy type.

While there was no significant difference between forest canopy types, *B. sylvaticum* had a positive relationship with canopy cover, as I predicted since *B. sylvaticum* is commonly found in forested understories. Despite producing more biomass and growing larger in full sun treatments within a greenhouse experiment conducted by Holmes *et al.* (2010), open habitats do not appear to be suitable habitat for *B. sylvaticum*. *Brachypodium sylvaticum* was not common in open areas in my surveys. Its presence in open habitats appears to be dependent on the water availability in the soil. In its native range, *B. sylvaticum*, though considered a shade species, can be found in open areas where the soil remains moist (Roder *et al.* 2007). It is likely that *B. sylvaticum* is not found in open environments due to a lack of soil moisture.

Although *Brachypodium sylvaticum* is not found in dry, open habitats, the invader does have a wide range of soil moisture conditions in which it can survive. This pattern in *B. sylvaticum* presence is not surprising as invasive species are often able to tolerate wide ranges of environmental conditions (Matzek 2011). Areas with 50% cover of *B. sylvaticum* or more ranged in soil moisture from 1.48 to 54.1%. This range of tolerance is consistent with observations in individuals in the Pacific Northwest (Marchini *et al.* 2018). Based on preliminary observations in the field and previous studies, I had expected that *B. sylvaticum* cover would increase with increasing soil moisture but would not occur in saturated conditions. Despite its ability to establish a wide range of soil moisture conditions, my results suggest this grass has the highest cover within mesic to wet-mesic environments in western New York.

Due to the variability between sites in average soil moisture, I found that *B. sylvaticum*'s relationship with soil moisture depends on the site. The negative relationship *B. sylvaticum* had with soil moisture at the BerB and DSFF sites are likely due to the high amounts of saturated areas within the sites. In these areas, *B. sylvaticum* is present within the drier areas, becoming less frequent as soil moisture increases. *Brachypodium sylvaticum* was present in saturated areas or areas with standing water only due to the presence of microtopography. This pattern has been observed in other terrestrial invasive species as well. Berg *et al.* (2016) observed that glossy buckthorn (*Frangula alnus*) was able to invade wetland areas with saturated and inundated conditions by growing on hummocks within those areas. These

microhabitats provided by the microtopography may be the reason *B. sylvaticum* is able to invade these saturated areas. Additional research following the methods of Berg *et al.* (2016) would help better understand *B. sylvaticum*'s success in inundated areas as my results relating to soil moisture further show that *B. sylvaticum* does not prefer poorly drained soils. As predicted, soil type was significant within several models sites predicting *B. sylvaticum* cover. The soils with the highest percent cover of *B. sylvaticum* were well drained soils whereas soils with the lowest percent cover of *B. sylvaticum* were classified by the USDA NRCS as very poorly drained soils, including a muck. The significance of soil type appears to be related to soil moisture.

While *B. sylvaticum* cover was higher in drier locations within wetter sites, the opposite was observed within drier sites. Within drier sites such as TagU and TagW sites *B. sylvaticum* was present in areas with higher soil moisture becoming less frequent in areas with lower soil moisture. It is present within drier environments but prefers the areas with moist soil within those environments. *Brachypodium sylvaticum* has difficulty establishing in dry open environments in its native range as its germination is hindered by dry soils (Evans and Etherington 1990). This appears to be the case in the Northeast as *B. sylvaticum* presence was limited in open environments in this study.

Despite its absence from dry, open environments in its native range and the Northeastern United States portion of its invaded range, *B. sylvaticum* has invaded dry open environments in the Pacific Northwest. Marchini *et al.* (2018) found that

Brachypodium sylvaticum's wide tolerance is not due to phenotypic plasticity within its invaded or native ranges after inducing drought stress in a greenhouse experiment. They instead identified that that *B. sylvaticum* in its invaded range has developed drought tolerant traits such as high xylem vessel frequency and lower bulliform cell area potentially as a result of rapid evolution in populations located within arid climates. The development of these new traits may partially explain why *B. sylvaticum* has become such a prolific invader in the Pacific Northwest. My results suggest that these traits may not be present within individuals in the Northeast as *B. sylvaticum* is absent from open fields with low soil moisture and there is a lack of environmental pressure to influence the development of these traits. Further investigation is needed to better understand if natural selection due to environmental pressures is also present within populations of *B. sylvaticum* in the Northeast.

Brachypodium sylvaticum impacts on plant communities

Species richness is often lower in invaded communities after plant invasion has occurred (Hejda *et al.* 2009, Matez-Mouro *et al.* 2010, Fu *et al.* 2018, Khan *et al.* 2021). For this reason, I predicted that areas invaded by *B. sylvaticum* would have lower species richness. Other studies have identified that *Brachypodium sylvaticum* is associated with lower species richness (Severns and Warren 2008, Holmes *et al.* 2010). My results are consistent with these studies as quadrats with high cover of *B. sylvaticum* had lower species richness. When predicting species richness among sites, *B. sylvaticum* was found to be significant. Additionally, I expected native species

would be more impacted than exotic species, defining exotic species as any non-native species. Species richness of native species was higher in quadrats without *B. sylvaticum* at six of the eight invaded sites. These results supported my initial predictions, demonstrating that *B. sylvaticum* may be influencing species richness within invaded communities.

My results did not show a significant difference in community composition among invaded and uninvaded quadrats as I had expected. While there was some degree of separation among the invaded and uninvaded quadrats, the separation was only significant at the TagU site. This contrasts with other studies that have found significant differences in community composition invaded and uninvaded areas (Khan *et al.* 2020). The significant separation at the TagU site may be related to competition between *B. sylvaticum* and *Dactylis glomerata* at the site as these species were significantly disassociated from each other, meaning they did not often occur together within the same quadrats.

I expected *B. sylvaticum* to alter community assemblage patterns in invaded communities similarly to what other researchers have found with other invasive species. Invasive species often result in the disassembly of assemblage patterns by interrupting facilitative and competitive interactions (Sander *et al.* 2003, Reshi *et al.* 2008, Santoro *et al.* 2012). Within the co-occurrence analyses, this display of random assembly patterns is shown as a non-significant C-score. My results were not consistent with these other studies and did not fully support my hypothesis. However,

IFNP and the DSFF site did not have significantly higher C-scores than expected by chance, demonstrating that species assemblages are random within the communities. These results suggest that the invaded communities within these two sites may not be competitively structured.

Most of the sites I sampled did not have a significant difference in community structure based on co-occurrence patterns between invaded and uninvaded quadrats. I predicted that the invaded quadrats would be structurally different than the uninvaded sites. My results partially supported my hypothesis. Of the eight invaded sites, BerB and BerC were the only ones that had significant differences in community assembly patterns between invaded and uninvaded communities while BerA had marginally significant differences. At these sites, the observed C-scores in invaded areas were significantly lower than the simulated C-scores, suggesting the loss of competitive interactions among species. The Bergen Private Sites results reflect similarly to other studies evaluating the differences in structure between invaded and uninvaded communities (Sanders *et al.* 2003, Reshi *et al.* 2008). These results may be related to the size of the invasions. The Bergen Private Sites has the largest invasions with the highest cover of *B. sylvaticum*. The other sites had smaller invasions that were patchier throughout the sites and had a lower percent cover in some invaded areas. This difference in invasion size may be why a disassembly of competitive and facilitative interactions has not taken place. Resampling and further evaluation of the other sites as populations spread may help understand if this is the case.

Pairwise species interactions

Invasive species are often associated with other invaders or generalist species (Pfeiffer *et al.* 2008). *Brachypodium sylvaticum* was significantly associated with generalist species such as *Circaea lutetiana* and *Geum canadense* and invasive species such as *Lonicera morrowii*, supporting my hypothesis. This further supports my hypothesis that *B. sylvaticum* has a wide range of tolerated conditions that are often exhibited by many invaders. Species associated with *B. sylvaticum* tolerate similar conditions and are not strong competitors with the invasive species, and vice-versa. When grown with *G. canadense*, *B. sylvaticum* has larger leaves, produced more inflorescence, and produced more above-ground biomass than when grown by itself, although these differences were not significant. Although *B. sylvaticum* may be associated with declines in richness, these results suggest that *B. sylvaticum* is not a strong competitor with all species in invaded communities.

Species are significantly disassociated from each other due to either distinct habitat preferences or strong competitive interactions. I hypothesized that species that were disassociated with *B. sylvaticum* would be due to *B. sylvaticum* outcompeting those species. Generally, species that were disassociated with *B. sylvaticum* were wetland species such as jewel weed (*Impatiens capensis*) and fringed loosestrife (*Lysimachia ciliata*) These disassociations are likely due to differences in habitat preference and not due to competition as *B. sylvaticum* is less likely to be found in saturated and inundated environments or in dry open or edge habitats. Other

disassociated species were or other invasive species such as multiflora rose (*Rosa multiflora*), Orchard grass (*D. glomerata*), and pale swallow-wort (*Vincetoxicum rossicum*). These disassociations could be due to competition, since as invasive species they have wide environmental tolerances across the conditions in which *B. sylvaticum* is found.

Brachypodium sylvaticum was found to be disassociated with *D. glomerata* despite having similar habitat conditions. I had expected *B. sylvaticum*'s competitive ability to be the reasons for this disassociation. The results of my competition experiment demonstrated that this was not the case for *D. glomerata*. In fact, it appears that the disassociation with *D. glomerata* is due to *D. glomerata* outcompeting and resisting *B. sylvaticum*. When grown with *D. glomerata*, *B. sylvaticum* had shorter leaves, fewer inflorescence, and produced less above ground-biomass. This did not support my hypothesis. The disassociation between *D. glomerata* and *B. sylvaticum* could be attributed to the significant difference in invaded and uninvaded quadrats at the TagU site. According to Sheppard *et al.* (2018) alien species with similar genetics and traits to resident alien species have a greater change of establishment success. As *D. glomerata* and *B. sylvaticum* are both perennial bunchgrasses, this portion of my results contrast with this study. Nevertheless, these results are concurred with Holmes *et al.* (2010) as they found similar results when *B. sylvaticum* was grown with another invasive bunch grass in the Pacific Northwest. In their study *B. sylvaticum* produced less biomass when grown with tall rye grass (*Schedonorus arundinaceus*) regardless of environmental

conditions. It appears *B. sylvaticum* does not have a strong competitive ability and cannot invade areas when the niches are already filled by a prior invader with similar traits. Future research should study *B. sylvaticum*'s competitive abilities when grown with disassociated species from other functional groups.

My results suggest that *Brachypodium sylvaticum* acts as a back-seat driver instead of a passenger or driver within invaded communities (Bauer 2012). Bauer (2012) describes back-seat drivers as species that benefit from or require disturbance within an ecosystem to invade and cause additional disruptions once established. *Brachypodium sylvaticum* is associated with a decrease in species richness, specifically a decrease in native species richness. While it appears that abiotic and other biotic variables such as soil type, soil moisture, and canopy cover may also be important for predicting richness and community composition at invaded sites, *B. sylvaticum* has shown to also be an influence once established. *Brachypodium sylvaticum* invasion is likely facilitated by disturbances within the communities as it does not appear to be a strong competitor. In both the Pacific Northwest (Holmes *et al.* 2010) and now in New York, *B. sylvaticum* has been shown to not be a strong competitor against other alien species. At the TagU site, the difference in community composition appears to be related to community resistance against *B. sylvaticum* as a prior, stronger invader (*D. glomerata*) has already filled open niches *B. sylvaticum* would have filled otherwise.

Invasive species are often associated with areas of high disturbance, and *B. sylvaticum* is associated with disturbance in both its invaded and native range. In the Pacific Northwest, *B. sylvaticum* is commonly found in logged sites, along heavy use trails, or in multi-use parks (Holmes *et al.* 2010, Kim 2015, Taylor *et al.* 2015). In its native region, *B. sylvaticum* has been associated with changing communities due to sheep grazing disturbance. Haeggstrom and Skyten (1996) documented a shift from a forb-dominated community to a graminoid-dominated community with dominant *Brachypodium sylvaticum* due to the opening of resources. Sheep led to increased light levels as trees and shrubs were removed and increased nutrients from decaying tree and shrub roots.

The phenomena of increasing herbivore impacts relating to plant invasion is common. It has been widely observed with other invasive species throughout the United States. The facilitation of invasion through the disturbance of white-tailed deer (*Odocoileus virginianus*) has been observed with species such as garlic mustard (*Alliaria petiolata*) and Japanese stiltgrass (*Microstegium vimineum*; Knight *et al.* 2009, HilleRisLambers *et al.* 2010, Davalos *et al.* 2015). New York is largely overpopulated by white-tailed deer. Although my study did not directly observe herbivory of white-tailed deer, herbivory pressure studied in *B. sylvaticum*'s native range and within forest communities within New York has been shown to decrease the presence of native species and facilitate invasions. This may also facilitate the invasion of *B. sylvaticum* throughout New York.

Another factor that may be facilitating *B. sylvaticum* invasion and establishment within forests may be the presence of non-native earthworms. Previous studies in the Pacific Northwest have demonstrated that *B. sylvaticum* germination is hindered by deep leaf litter within broad-leaf deciduous forests (Taylor *et al.* 2015, Taylor and Cruzan 2015). My results did not show a difference in *B. sylvaticum* presence among forest community types. This could be attributed to the lack of leaf litter within deciduous forest as a result of non-native earthworms. The influence of deer herbivory and earthworm presence are factors that may need to be studied further to better understand if there is a relationship between herbivory and *B. sylvaticum* invasion.

My study illuminated the environments in which *B. sylvaticum* is commonly found within New York and its role as back-seat driver of change. My results suggest that while *B. sylvaticum* has a wide tolerance of environmental conditions and replaces species in communities it invades, it is not a strong competitor against similar species and may not invade areas with limited resources. My study has opened more questions about this invader and its presence in the Northeast. To better understand *B. sylvaticum*'s establishment and success as an invader, researchers should evaluate its genetics and traits, presence within microhabitats created by microtopography, and its relationship with herbivores and how they may facilitate invasion. By doing this, we may be able to further understand why makes this bunchgrass such a prolific invader in the Northeast.

Literature Cited

Anderson, R. C., S. S. Dhillon, and T. M. Kelley. 1996. Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in Central Illinois. *Restoration Ecology* 4:181-191.

Bauer, J. T. Invasive species: “back-seat drivers” of ecosystem change? *Biological Invasions* 14:1295-1304.

Berg, J. A., G. A. Meyer, and E. B. Young. 2016. Propagule pressure and environmental- conditions interact to determine establishment success of an invasive plant species, glossy buckthorn (*Frangula alnus*), across five different habitat types. *Biological Invasions* 18:1363-1373.

Bottollier-Curtet, M., A. Planty-Tabacchi, and E. Tabacchi. 2013. Competition between young exotic invasive and native dominant plant species: implications for invasions within riparian areas. *Journal of Vegetation Science* 24:1033-1042.

Colautti, R. J. and H. J. MacIsaac. 2004. A neutral terminology of define ‘invasive’ species. *Diversity and Distribution* 10:135-141.

Culley, T., G. N. Cameron, S. E. Kolbe, and A. L. Miller. 2016. Association of non-native Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) with other invasive plant species in eastern deciduous forests in southwestern Ohio. *The Journal of Torrey Botanical Society* 143:398-414.

- Davalos, A., V. Nuzzo, and B. Blossey. 2015. Single and interactive effects of deer and earthworms on non-native plants. *Forest Ecology and Management* 351:28-35.
- Diamond, J. M. 1975. Assembly of species communities. In: Diamond, J. M. and Cody, M. L., Eds., *Ecology and Evolution of Communities*, Harvard University Press, Boston, MA, 342-344.
- Daniel, S., and Werier, D. (2010) Slender false brome (*Brachypodium sylvaticum* spp. *sylvaticum*): a new invasive plant in New York. Albany, NY: New York Flora Association. 12 p
- Dechoum, M. S., R. D. Zenni, T. T. Castellani, S. M. Zalba, and M. Rejmanek. 2015. Invasions across secondary forest successional stages: effects of local plant community, soil, litter, and herbivory on *Hovenia dulcis* seed germination and seedling establishment. *Plant Ecology* 216:823-833.
- Divisek, J., M. Chytrý, B. Beckage, N. J. Gotelli, Z. Lososova, P. Pyšek, D. M. Richardson, and J. Molofsky. 2018. *Nature Communications* 9:4631.
- Evans, C. E. and J. R. Etherington. 1991. The effect of soil-water potential on seedling growth of some British plants. *New Phytologist* 118:571-579.
- Fu, D., X. Wu, N. Huang, and C. Duan. 2018. Effect of the invasive herb *Ageratina adenophora* on understory plant communities and tree seedling growth in *Pinus yunnanensis* forests in Yunnan, China. *Journal of Forest Research* 23:112-119.

Fjeran, T. 2014. Treatment options for controlling *Brachypodium sylvaticum* and impacts on native vegetation. Paper of Masters. Oregon State University, Corvallis, Oregon, United States.

Flint, A. 2018. A temporal and spatial analysis of species co-occurrence patterns within a chalk heath community. Ph.D. Dissertation. University of Brighton, Brighton, England, United Kingdom.

Gao, J., Y. Liu, and M. Bogonovich. 2018. Habitat is more important than climate and animal richness at shaping latitudinal variation in plant diversity in China. *Biodiversity and Conservation* 27:3679-3691.

Gasso, N., J. Pino, X. Font, and M. Vila. 2012. Regional context affects native and alien plant species richness across habitat types. *Applied Vegetation Science* 15:4-13.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606-2621

Gotelli, N. J. 2001. Research frontiers in null model analysis. *Global Ecology and Biogeography* 10:337-343.

Gotelli, N. J. and A. E. Arnett. 2000. Biogeographic effects of red fire any invasion. *Ecology Letters* 3:257-261.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091-2096.

Gotzenberger, L., F. de Bello, K. A. Brathen, J. Davison, A. Dubuis, A. Guisan, J. Leps, R. Lindborg, M. Moora, M. Partel, L. Pellissier, J. Pottier, P. Vittoz, K. Zobel, and M. Zobel. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews* 87:111-127.

Green, P. T., D. J. O'Dowd, K. L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nelly. 2011. Invasion meltdown: Invader-Invader mutualism facilitates a secondary invasion. *Ecology* 92:1758-1768.

Grime, J. P. 1988. Comparative plant ecology: a functional approach to common British species.

Haeggstrom, C. A. and R. Skyten. 1996. Flowering and individual survival of a population of the grass *Brachypodium sylvaticum* in Nato, Aland Islands, SW Finland. *Annales Botanici Fennici* 33:1-10.

Heimpel, G. E., L. E. Frelich, D. A. Landis, K. R. Hopper, K. A. Hoelmer, Z. Sezen, M. K. Asplen, and K. Wu. 2010. European buckthorn and Asian soybean aphid as components of an extensive invasion meltdown in North America. *Biological Invasions* 12:2913-2931.

Hejda, M., P. Pysek, and V. Jarosik. 2009. Diversity and composition of invaded communities. *Journal of Ecology* 97:393-403.

HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. California annual grass invaders: the driver or passengers of change? *Journal of Ecology* 98:1147-115

Holmes, S. E., B. A. Roy, J. P. Reed, and B. R. Johnson. 2009. Context-dependent pattern and process: the distribution and competitive dynamics of an invasive grass, *Brachypodium sylvaticum*. *Biological Invasions* 12:2302-2318.

Holten, J. I. 1980. Distribution and ecology of *Brachypodium sylvaticum*, *Bromus benekeni* and *Festuca altissima* in central Norway. *Blyttia* 38:137-144.

Johnson, J. 2004. *Brachypodium sylvaticum* (slender false brome). CAL-IPC (California Invasive Plants Council) News 11:10-11.

IBM Corp. Released 2020. INM SPSS Statistics for Windows, Version 27.0. Armonk, NY: IBM Corp.

Keller, R. P. and D. M. Lodge. 2007. Species invasions from commerce in live aquatic organisms: problem and possible solutions. *BioScience* 57:428-436.

Kerns, B. K., C. Tortorelli, M. A. Day, T. Nietupski, A. M. G. Barros, J. B. Kim, and M. A. Krawchuck. 2020. Invasive grasses: A new perfect storm for forest ecosystems? *Forest Ecology and Management* 463:117985

Khan, M. A., K. Hussain, and M. A. Shah. Ecological restoration of habitats invaded by *Leucantheumum vulgare* that alters key ecosystem functions. PLOS ONE

16:e0246665.

Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate plant success in a Pennsylvania forest understory. *Natural Areas Journal* 29:110-116.

Kuebbing, S. E., A. T. Classen, and D. Simberloff. 2014. Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. *Journal of Applied Ecology* 51:124-133.

Lambrinos, J. G. 2002. The variable invasive success of *Cortaderia* species in a complex landscape. *Ecology* 83:518-529.

Li, D., and D. Waller. 2016. Long-term shifts in the patterns and underlying processes of plant associations in Wisconsin forests. *Global Ecology and Biogeography* 25:516-526.

Liu, S., Y. Luo, R. Yang, C. He, Q. Cheng, J. Tao, B. Ren, M. Wang, and M. Ma. 2015. High resource-capture and –use efficiency, and effective antioxidant protection contribute to the invasiveness of *Alnus formosana* plants. *Plant Physiology and Biochemistry* 96:436-447.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.

Maltez-Mouro, S., F. T. Maestre, and H. Freitas. 2010. Weak effects of the exotic invasive *Carpobrotus edulis* on the structure and composition of Portuguese sand-dune communities. *Biological Invasions* 12:2117-2130.

Marchini, G. L., C. A. Maraist, and M. B. Cruzan. 2018. Trait divergence, not plasticity, determines the success of a newly invasive plant. *Annals of Botany* 123:667-679.

Matzek, V. 2011. Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. *Biological Invasions* 13:3005-3014.

McCune, B. and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design. Glenden Beach, Oregon.

McDonald, R. I., G. Motzkin, and D. R. Foster. 2008. Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. *The Journal of the Torrey Botanical Society* 135:260-271.

- Merton, L. F. H. 1970. The history and status of the woodlands of Derbyshire limestone. *Journal of Ecology* 58:723-744.
- Orban, I., K. Szitar, T. Kalapos, and G. Korel-Dulay. 2021. The role of disturbance in invasive plant establishment in a changing climate: insights from a drought experiment. *Biological Invasions* 23:1877-1890.
- Pfeiffer, M., H. C. Tuck, T. C. Lay. 2008. Arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. *Ecography* 31:21-32.
- Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2007. Abiotic constraints on the competitive ability of exotic and native grasses in Pacific Northwest prairie. *Oecologia* 155:357-366.
- Rasband, W. S. 1997. ImageJ. U. S. National Institutes of Health. Bethesda, Maryland, USA. Available at: <https://imagej.nih.gov/ij/>
- Reshi, Z., I Rashid, A. A. Khuroo, and B. A. Wafai. 2008. Effect of invasion by *Centaurea iberica* on community assembly of a mountain grassland of Kashmir Himalaya, India. *Tropical Ecology* 49:147-156.
- Rojas-Botero, S., J. Kollmann, and L. H. Teixeira. 2021. Competitive trait hierarchies of native communities and invasive propagule pressure consistently predict invasion success during grassland establishment. *Biological Invasions* 24:107-122.

Rosenthal, D. M., A. P. Ramakrishnan, and M. B. Cruzan. 2008. Evidence for multiple sources of invasion and intraspecific hybridization in *Brachypodium sylvaticum* (Hudson) Beauv. In North America. *Molecular Ecology* 17:4657-4669.

RStudio Team. 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available at: <https://www.rstudio.com/>

Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. *PNAS* 100:2474-2477.

Santoro, R., T. Jucker, M. Carboni, and A. T. R. Acosta. 2012. Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. *Journal of Vegetation Science* 23:483-494.

Searle, C., B. R. Hochstedler, A. M. Merrick, J. K. Ilmain, and M. A. Wigren. 2018. High resource and infectious disease facilitate invasion by a freshwater crustacean. *Oecologia* 188:571-581.

Severns, P. M. and A. D. Warren. 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. *Animal Conservation* 11:476-483.

Schultheis, E. H. and D. J. MacGuigan. 2018. Competitive ability, not tolerance, may explain success of invasive plants over natives. *Biological Invasions* 20:2793-2806.

- Sheppard, C. S., M. Carboni, F. Essi, H. Seebens, D. Consortium, and W. Thuiller. 2018. It takes one to know one: similarity to resident alien species increases establishment success of new invaders. *Diversity and Distribution* 24:680-691.
- Stone, L. and A. Robert. 1990. The checkerboard score and species distributions. *International Association for Ecology* 85:74-79.
- Sugiyama, S. 2005. Developmental basis of interspecific differences in leaf size and specific leaf area among C3 grass species. *Functional Ecology* 19:916-924.
- Taylor, L. A. V. and M. B. Cruzan. 2015. Propagule pressure and distribution drive the invasion of perennial false-brome (*Brachypodium sylvaticum*). *Invasive Plant Science and Management* 8:169-180.
- Taylor, L. A. V., E. A. Hasenkopf, and M. B. Cruzan. 2015. Barriers to invasive infilling by *Brachypodium sylvaticum* in Pacific Northwest forests. *Biological Invasions* 17:2247-2260.
- Trivellone, V., S. Bougeard, S. Giavi, P. Krebs, D. Balseiro, S. Dray, and Marco Moretti. 2017. Factors shaping community assemblages and species co-occurrence of different trophic levels. *Ecology and Evolution* 7:4745-4754.
- Ulrich, W. 2008. Pairs – a Fortran program for studying pair-wise species associations in ecological matrices. www.uni.torun.pl/~ulrichw.

Ulrich, W. and N. J. Gotelli. 2007, Disentangling community patterns of nestedness and species co-occurrence. *Oikos* 116:2053-2061.

Van Kleunen, M., D. R. Schlaepfer, M. Glaetli, and M. Fischer. 2011. Preadapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range. *Journal of Biogeography* 38:1294-1304.

Visser, V., J. R. U. Wilson, K. Canavan, S. Canavan, L. Fish, D. L. Maitre, I. Nanni, C. Mashau, T. G. O'Connor, P. Ivey, S. Kumschick, and D. M. Richardson. 2017. Grasses as invasive plants in South Africa revisited: patterns, pathways and management. *Bothilia – African Biodiversity and Conservation* 47.

Tables

Table 1. Study site locations, environmental variables, and descriptions. Ber=Bergen, NY, DSF = Danby State Forest; Tag = Taughannock falls State Park. Sites are ordered from west to east.

	Site	Code	Invaded/Intact	Coordinates	Mean (SE) SM %	Mean (SE) % Canopy Cover
<i>Bergen Private Site A</i>	BerA		Invaded	Private	N/A	73.97
<i>Bergen Private Site B</i>	BerB		Invaded	Private	32.32	29.54
<i>Bergen Private Site C</i>	BerC		Invaded	Private	24.15	65.07
<i>Indian Fort Nature Preserve</i>	IFNP		Invaded	42.762987, -77.831999	18.93	75.00
<i>Greece Canal Park Intact</i>	UGCP		Uninvaded	43.199959, -77.743585	21.90	76.18
<i>Black Creek Park Intact</i>	UBCP		Uninvaded	43.074819, -77.813656	32.11	69.83
<i>Danby State Forest Abbot Loop Trail</i>	DSFA		Invaded	42.314186, -76.479417	19.42	72.98
<i>Taughannock Falls State Park Upland</i>	TagU		Invaded	42.541554, -76.598758	38.15	73.33
<i>Taughannock Falls State Park Wetland</i>	TagW		Invaded	42.536816, -76.603599	23.24	78.89
<i>Danby State Forest Floodplain</i>	DSFF		Invaded	42.304272, -76.481057	38.04	68.02
<i>Danby State Forest Intact</i>	UDSF		Uninvaded	42.289030, -76.490112	22.17	60.41

Table 2. Community characteristics of each site, large-scale samples. Sites are ordered from west to east. The dominant herbaceous species are the top 3 most frequently observed aside from *B. sylvaticum*.

Site	Number of Quadrats with <i>B. sylvaticum</i>	Average <i>B. sylvaticum</i> cover in invaded quads	Dominant Canopy Species	Dominant Herb Species
<i>BerA</i>	44 (54.32%)	32.61 (3.94)	<i>Pinus strobus</i> <i>Fraxinus pennsylvanica</i>	<i>Lysimachia nummularia</i> <i>Toxicodendron radicans</i> Carices
<i>BerB</i>	105 (56.15%)	35.36 (2.64)	<i>Populus tremuloides</i> <i>F. pennsylvanica</i> <i>Carpinus caroliniana</i>	<i>Impatiens capensis</i> <i>Onoclea sensibilis</i> <i>Parthenocissus quinquefolia</i>
<i>BerC</i>	129 (75.88%)	55.20 (2.55)	<i>Pinus strobus</i> <i>F. pennsylvanica</i> <i>A. saccharum</i>	<i>P. quinquefolia</i> <i>T. radicans</i> <i>Vincetoxicum rossicum</i>
<i>UBCP</i>	-	-	<i>A. rubrum</i> <i>Ulmus americana</i>	<i>P. quinquefolia</i> <i>Persicaria virginiana</i> <i>Geum canadense</i>
<i>UGCP</i>	-	-	<i>F. pennsylvanica</i> <i>Prunus serotina</i>	<i>P. quinquefolia</i> <i>P. virginiana</i> <i>T. radicans</i>
<i>IFNP</i>	6 (18.75%)	50.83 (16.45)	<i>F. pennsylvanica</i> <i>Juglans nigra</i> <i>Quercus rubra</i>	<i>G. canadense</i> <i>T. radicans</i> <i>Allaria petiolata</i>
<i>TagU</i>	40 (37.38%)	37.23 (5.02)	<i>A. saccharum</i> <i>P. serotina</i>	<i>Dactylis glomerata</i> <i>P. quinquefolia</i> <i>T. radicans</i>

<i>TagW</i>	22 (48.89%)	33.09 (6.57)	<i>A. saccharum</i> <i>Liriodendron tulipifera</i>	<i>P. quinquefolia</i> <i>Dactylis glomerata</i> <i>Circaea lutetiana</i>
<i>DSFA</i>	34 (60.71%)	28.82 (3.83)	<i>A. saccharum</i> <i>F. pennsylvanica</i> <i>Prunus serotina</i>	<i>Rubus pubescens</i> <i>Geum canadense</i> <i>Circaea lutetiana</i>
<i>DSFF</i>	11 (35.48%)	38.45 (9.08)	<i>Acer rubrum</i> <i>Tsuga canadensis</i> <i>C. caroliniana</i>	<i>L. nummularia</i> <i>Impatiens capensis</i> <i>Ranunculus septentrionalis</i>
<i>UDan</i>	-	-	<i>F. pennsylvanica</i> <i>A. saccharum</i>	<i>Symphotrichum preantoides</i> <i>L. nummularia</i> <i>Clematis virginiana</i>

Table 3. Top GLM for among site data predicting *B. sylvaticum* cover.

<i>Predictor Variable</i>	<i>Overall Model</i>	<i>AICC</i>	<i>df</i>	<i>p-value</i>	<i>Wald Chi-Square</i>	<i>Direction</i>
Site	<0.0001	28.706	7	<0.0001	27.316	
Soil Moisture			1	0.943	0.005	-
Canopy Cover			1	<0.090	2.866	No trend
Latitude			1	0.061	3.507	
Longitude			1	0.084	2.989	
Site *Soil Moisture			3	<0.0001	25.308	
Site* Canopy Cover			3	0.012	16.363	

Table 4. Best fit generalized linear models for predicting *B. sylvaticum* cover at sites with at least 10 quadrats containing *B. sylvaticum*.

Site	Predictor Variable(s)	Overall Model	AICC	df	p-value	Chi-Square	Direction
BerA Model 1	Canopy Cover	0.001	60.45	1	0.001	10.848	+
	Lat			1	0.186	1.747	
BerA Model 2	Canopy Cover	<0.0001	59.964	1	<0.001	13.881	+
BerB Model 2	Soil Type	<0.0001	103.765	5	0.006	16.481	
	Soil Moisture			1	<0.0001	20.783	-
	Canopy Cover			1	<0.0001	40.942	-
	Latitude			1	0.48	0.499	
	Longitude			1	0.049	3.887	
BerB Model 2	Soil Type	<0.0001	102.005	5	0.007	16.062	
BerB Model 2	Soil Moisture			1	<0.0001	24.04	-

	Canopy Cover			1	<0.0001	42.406	-
	Longitude			1	0.065	3.395	
BerC	Soil Type	<0.0001	114.878	10	<0.0001	78.989	
	Soil Moisture			1	0.289	1.125	-
	Canopy Cover			1	0.202	1.631	N/A
	Latitude			1	<0.0001	13.044	
	Soil Type*Canopy Cover			10	<0.0001	33.72	
	SoilType*Soil			11	<0.0001	36.913	
	Moisture*Canopy Cover						
TagU	Soil Moisture	0.092	53.594	1	0.065	3.416	+
	Canopy Cover			1	0.05	3.852	-
	SoilMoisture*CanopyCover				0.022	5.208	
TagW	Soil Type		46.819	4	<0.0001	41.746	
	Soil Moisture			1	0.041	4.184	+
	Canopy Cover			1	<0.0001	12.130	+

	Soil Type*Soil Moisture			4	0.006	14.574	
	Soil Type*Canopy Cover			4	<0.0001	35.638	
	Soil Moisture*Canopy			1	0.020	5.451	
	Cover						
DSFA	Soil Type	0.009	58.122	2	0.071	5.290	
	Soil Moisture			1	0.614	0.255	+
	Canopy Cover			1	0.559	0.341	-
	Latitude			1	0.012	6.287	
	Longitude			1	0.045	4.014	
	Soil Type*Soil Moisture			2	0.12	8.776	
	Soil Type*Canopy Cover			2	0.19	7.902	
	Soil Type*Soil			3	0.008	11.942	
	Moisture*Canopy Cover						
DSFF	Soil Type	0.002	32.053	2	0.005	10.571	
	Soil Moisture			1	0.002	9.935	-

Canopy Cover	1	0.008	7.091	+
Latitude	1	0.006	7.556	
Longitude	1	0.042	4.120	
Soil Type*Soil Moisture	2	0.012	8.883	

Table 5. Final generalized linear model for among invaded site data predicting species richness.

<i>Predictor Variable</i>	<i>Overall Model</i>	<i>AICC</i>	<i>df1</i>	<i>p-value</i>	<i>Wald Chi-Square</i>	<i>Direction</i>
<i>Site</i>	<0.0001	1077.274	6	0.041	13.157	
<i>BS Cover</i>			1	<0.0001	19.341	-
<i>Soil Moisture</i>			1	0.039	4.248	+
<i>Canopy Cover</i>			1	0.004	8.075	
<i>Longitude</i>			1	0.189	1.729	
<i>Site*BS Cover</i>			6	0.001	22.489	
<i>Site*Canopy Cover</i>			19	0.021	14.861	

Table 6. Best fit generalized linear models (GLM) within each site predicting species richness at invaded (BerA, BerB, BerC, TagU, TagW, DSFA, DSFF, and IFNP) and uninvaded sites (UDan, UGCP, UBCP).

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
BerA	BS Cover	0.019	447.295	1	71	0.014	6.347	-
	Canopy Cover					0.839	0.042	-
	Latitude					0.065	3.526	
	Longitude					0.049	4.006	
	Soil Type					0.036	2.728	
	BS Cover*Canopy					0.007	7.854	
	Cover							
BerB	BS Cover	<0.0001	986.756	1	169	0.509	0.476	-
Model 1								
	Soil Moisture					1.115	0.293	+
	Canopy Cover					0.354	0.863	+

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
	Latitude					0.052	3.838	
	Longitude					0.144	2.151	
	Soil Type					0.007	3.329	
	BS Cover*Soil Moisture					0.131	2.3	
	BSCover*Canopy Cover					0.399	0.714	
	Soil Moisture*Soil Type					0.003	3.771	
BerB	BS Cover	<0.0001	985.045	1	170	0.774	0.083	-
Model								
2								
	Soil Moisture					0.274	1.203	+
	Canopy Cover					0.184	1.775	+
	Latitude					0.04	4.301	
	Longitude					0.095	2.819	
	Soil Type					0.005	3.476	

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
	BS Cover*Soil Moisture					0.095	2.181	
	Soil Moisture*Soil Type					0.002	3.948	
BerC	BS Cover	<0.0001	847.638	1	153	0.001	11.306	-
	Soil Moisture					0.026	5.023	+
	Canopy Cover					<0.0001	19.743	-
	Latitude					0.24	1.393	
	Soil Type					0.001	3.067	
TagU	Soil Moisture	<0.0001	278.132	1	57	0.144	2.199	-
Model								
1								
	Canopy Cover					0.003	9.876	-
	Latitude					0.042	4.333	
	Longitude					0.23	1.471	

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
TagU Model 2	Soil Moisture	<0.0001	277.279	1	58	0.126	2.407	-
	Canopy Cover					0.001	11.842	-
	Latitude					0.003	9.426	
TagW	BS Cover	0.005	232.355	1	31	0.011	7.376	-
	Soil Moisture					0.301	1.107	-
	Latitude					0.012	7.181	-
	Soil Type					0.015	3.66	
	BS Cover*Soil Moisture					0.037	4.729	
	Soil Moisture*Soil Type					0.021	3.379	
DSFA	BS Cover	<0.0001	269.924	1	53	0.001	12.687	-
	Canopy Cover					<0.0001	17.872	+

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
DSFF Model 1	BS Cover	0.16	177.054	1	27	0.041	4.593	-
	Latitude					0.194	1.778	
	Longitude					0.447	0.597	
DSFF Model 2	BS Cover	0.101	175.367	1	28	0.052	4.137	-
	Latitude					0.207	1.672	
UBCP	Soil Moisture	0.004	171.015	1	24	0.002	12.137	+
	Canopy Cover					0.002	12.331	-
	Latitude					0.137	2.371	
	Longitude					0.091	3.098	

Site	Predictor Variables	Overall Model	AICC	df1	df2	p-value	F	Direction
	Soil Moisture*Canopy					0.001	13.383	
	Cover							
UGCP	Soil Moisture	0.82	148.702	1	28	0.82	0.053	
UDan	Longitude	0.129	161.039	1	27	0.129	2.447	

Table 7. C-scores for all sites.

<i>Site</i>	<i>Invaded</i>	<i>Observed Index</i>	<i>Simulated Index</i>	<i>p-value</i>	<i>SES</i>
<i>BerA</i>	Y	104.82	103.91	<0.001	2.645
<i>BerB</i>	Y	75.3	73.19	<0.001	5.583
<i>BerC</i>	Y	36.03	33.87	<0.001	6.121
<i>TagU</i>	Y	164.25	154.88	<0.001	8.553
<i>TagW</i>	Y	27.14	26.23	<0.001	4.211
<i>DSFA</i>	Y	49.66	48.07	<0.001	5.031
<i>DSFF</i>	Y	12.98	12.84	0.07	1.325
<i>IFNP</i>	Y	17.97	18.08	0.749	-0.69
<i>UBCP</i>	N	14.98	14.65	<0.001	3.173
<i>UGCP</i>	N	24.21	23.54	<0.001	4.613
<i>UDan</i>	N	14.54	14.25	<0.001	3.876

Table 8. Observed and simulated C-scores in intact and invaded areas at each site for large scale samples. N for invaded and intact plots are listed with site (N invaded, N intact).

<i>Site</i>	<i>Intact Area</i>		<i>Invaded Area</i>		Variance p-value
	Observed Matrix	Simulated Matrix	Observed Matrix	Simulated Matrix	
<i>BerA</i> (44, 37)	23.87	21.32	27.65	29.66	0.077
<i>BerB</i> (106, 81)	81.84	64.34	78.67	110.16	<0.0001
<i>BerC</i> (129, 41)	21.47	15.11	122.34	144.67	0.001
<i>TagU</i> (40, 67)	57.29	58.81	21.83	21.33	0.39
<i>TagW</i> (22, 23)	7.49	7.48	6.47	6.94	0.49
<i>DSFA</i> (34, 22)	9.17	8.22	16.65	18.08	0.20
<i>DSFF</i> (11, 20)	5.68	5.58	2.59	2.40	0.46
<i>IFNP</i> (6, 26)	13.22	11.82	1.09	1.29	0.965

Table 9. Species associated and disassociated with *B. sylvaticum* based on the *Pairs* analyses.

<i>Species</i>	<i>Site</i>	<i>Associated or Disassociated</i>	<i>z-score</i>	<i>Alpha</i>
<i>Circaea lutetiana</i>	IFNP	Associated	-2.21	0.027
	TagU	Associated	-1.65	0.098
	BerA	Associated	-2.21	0.027
	BerB	Associated	-3.48	0.0005
	BerC	Associated	-1.41	0.16
<i>Lysimachia ciliata</i>	BerA	Disassociated	4.45	<0.0001
<i>Leersia oryzoides</i>	BerB	Disassociated	10.27	<0.0001
<i>Geum canadense</i>	IFNP	Associated	-1.94	0.051
<i>Lonicera morrowii</i>	BerB	Associated	-2.33	0.019
<i>Rosa multiflora</i>	IFNP	Disassociated	2.68	0.007
<i>Impatiens capensis</i>	DSFF	Disassociated	3.07	0.002
	BerB	Disassociated	8.87	<0.0001
<i>Prunus serotina</i>	TagU	Disassociated	3.91	<0.0001

<i>Species</i>	<i>Site</i>	<i>Associated or Disassociated</i>	<i>z-score</i>	<i>Alpha</i>
<i>Acer rubrum</i>	TagW	Disassociated	3.56	0.0004
<i>Acer saccharum</i>	TagU	Disassociated	2.38	0.017
<i>Dactylis glomerata</i>	BerC	Disassociated	3.35	0.0007
	TagU	Disassociated	2.26	0.024
<i>Daucus carota</i>	BerC	Disassociated	3.89	<0.0001
<i>Anemone canadensis</i>	BerA	Disassociated	2.9	0.004
	BerC	Disassociated	3.44	0.0006
<i>Bidens frondosa</i>	BerA	Disassociated	2.69	0.007
<i>Fraxinus pennsylvsnica</i>	BerC	Associated	-2.22	0.026
	BerB	Associated	-3.32	0.0007
<i>Vincetoxicum rossicum</i>	BerC	Disassociated	3.01	0.003
<i>Onoclea sensibilis</i>	BerC	Disassociated	4.43	<0.0001
<i>Lysimachia nummularia</i>	BerC	Disassociated	2.77	0.006

<i>Species</i>	<i>Site</i>	<i>Associated or Disassociated</i>	<i>z-score</i>	<i>Alpha</i>
<i>Phleum pratense</i>	BerC	Disassociated	3.20	0.0013
<i>Amphicarpaea bracteata</i>	BerC	Disassociated	2.47	0.013
<i>Arisaema triphyllum</i>	BerB	Associated	-3.10	0.0019
<i>Euphorbia esula</i>	BerB	Disassociated	2.83	0.0045

Figures

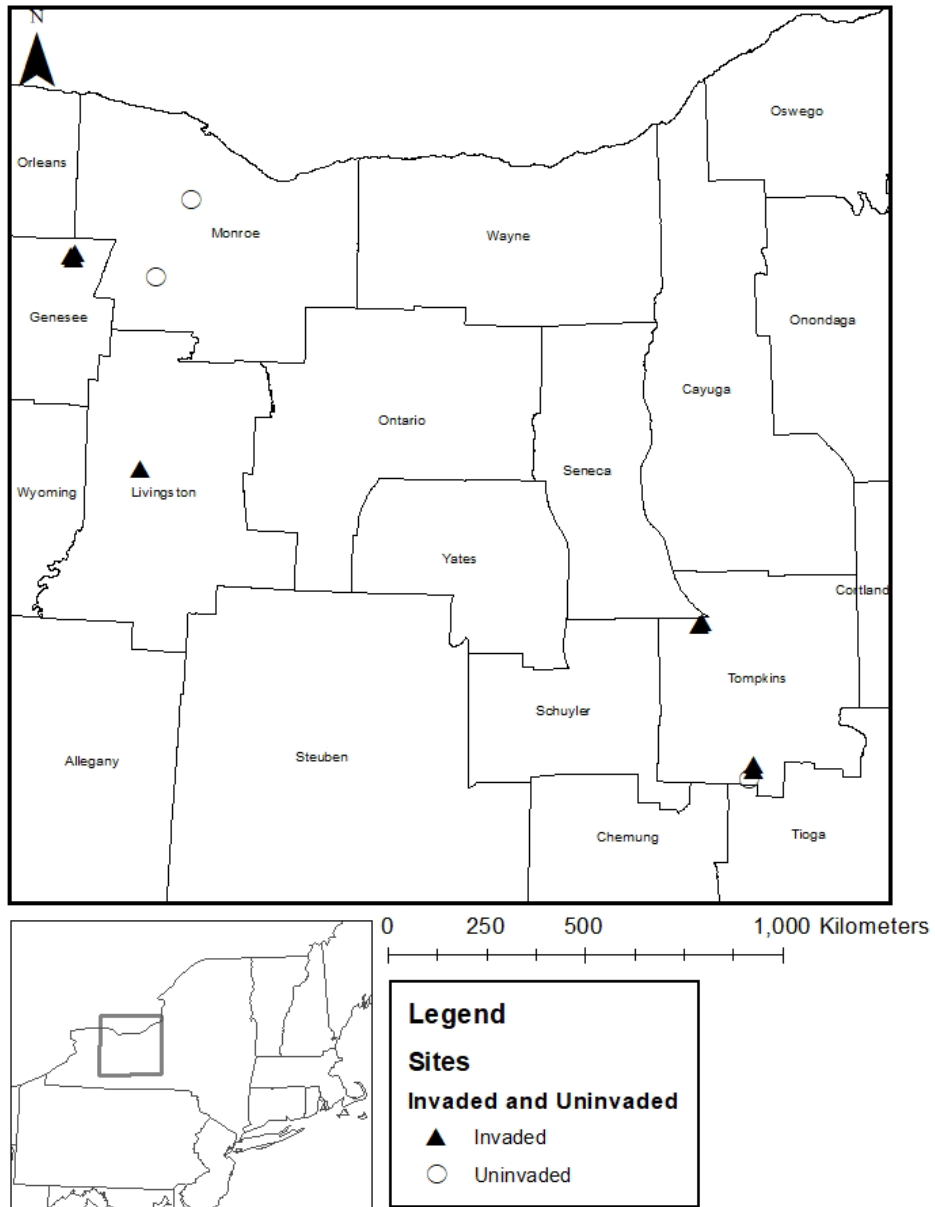


Figure 1. Map of the study site locations.

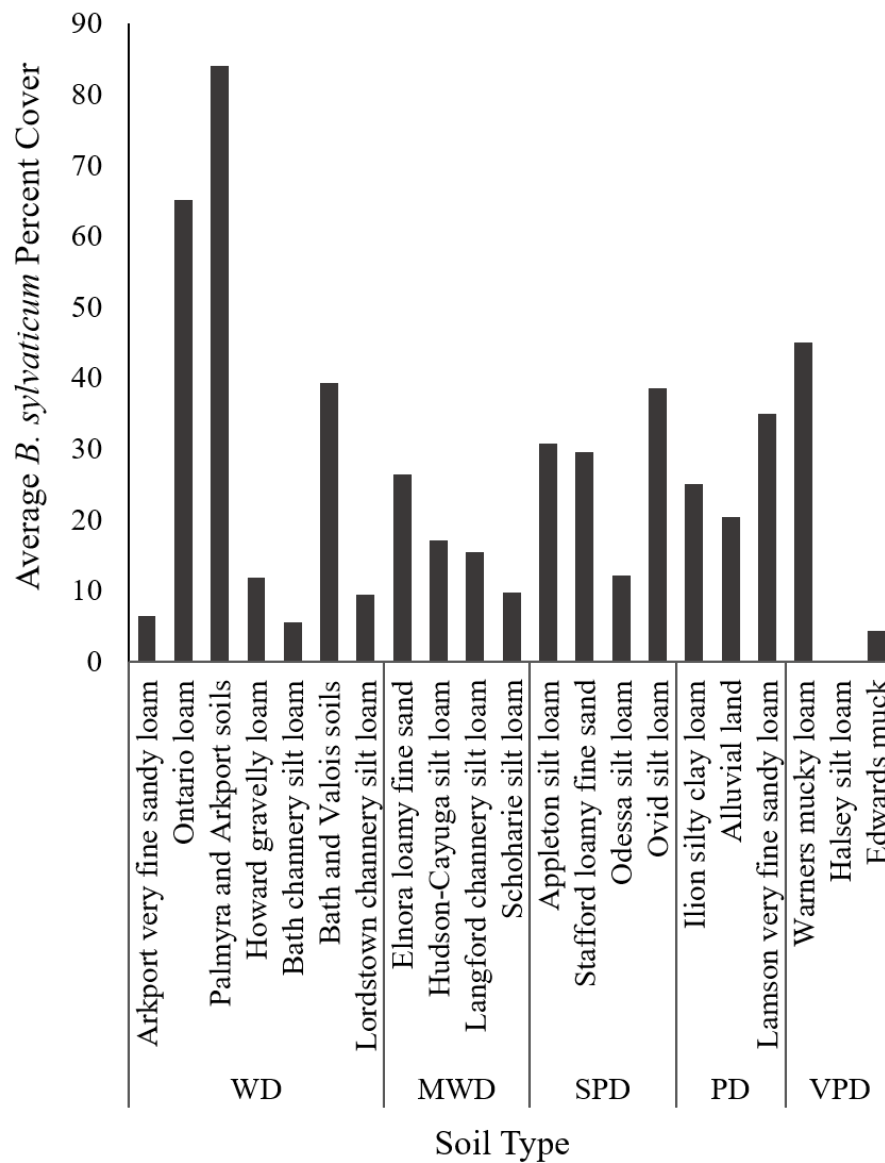


Figure 2. Average *B. sylvaticum* cover among soil types present within the invaded sites. Soils are grouped by drainage: well drained (WD), moderately well drained (MWD), somewhat poorly drained (SPD), poorly drained (PD), and very poorly drained (VPD).

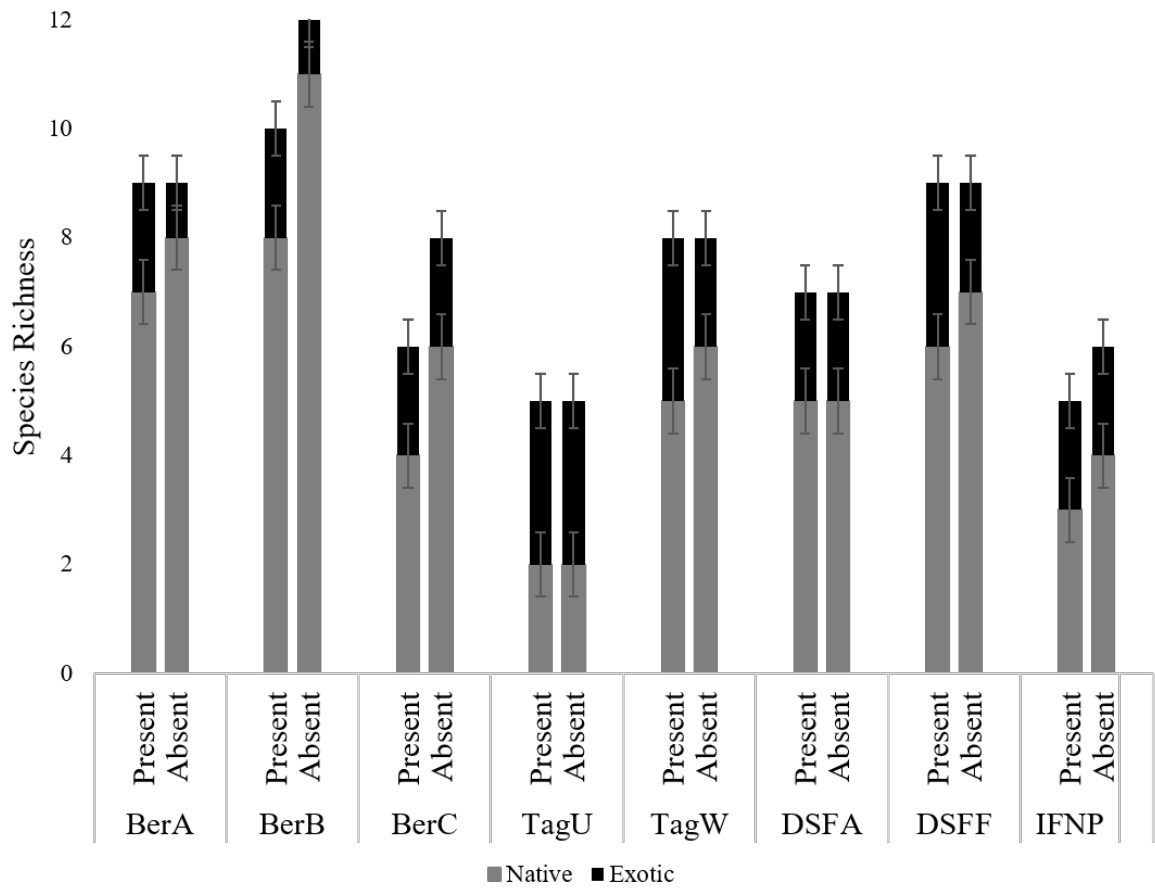


Figure 3. Average native and exotic species richness within invaded and uninvaded quadrats in invaded sites.

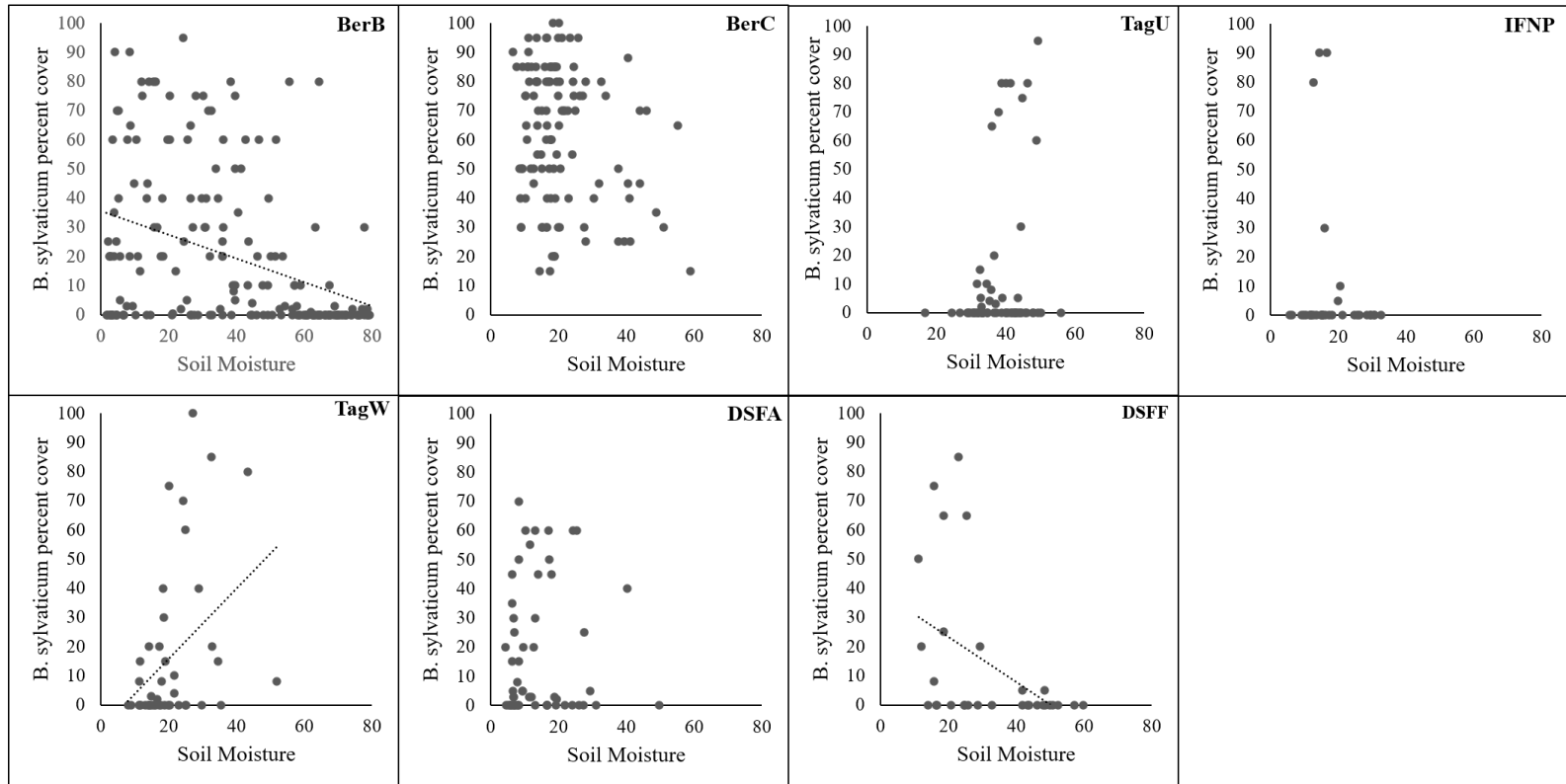


Figure 4. Trends of soil moisture against *Brachypodium sylvaticum* percent cover within each invaded site. Dashed lines indicate the significant trend direction.

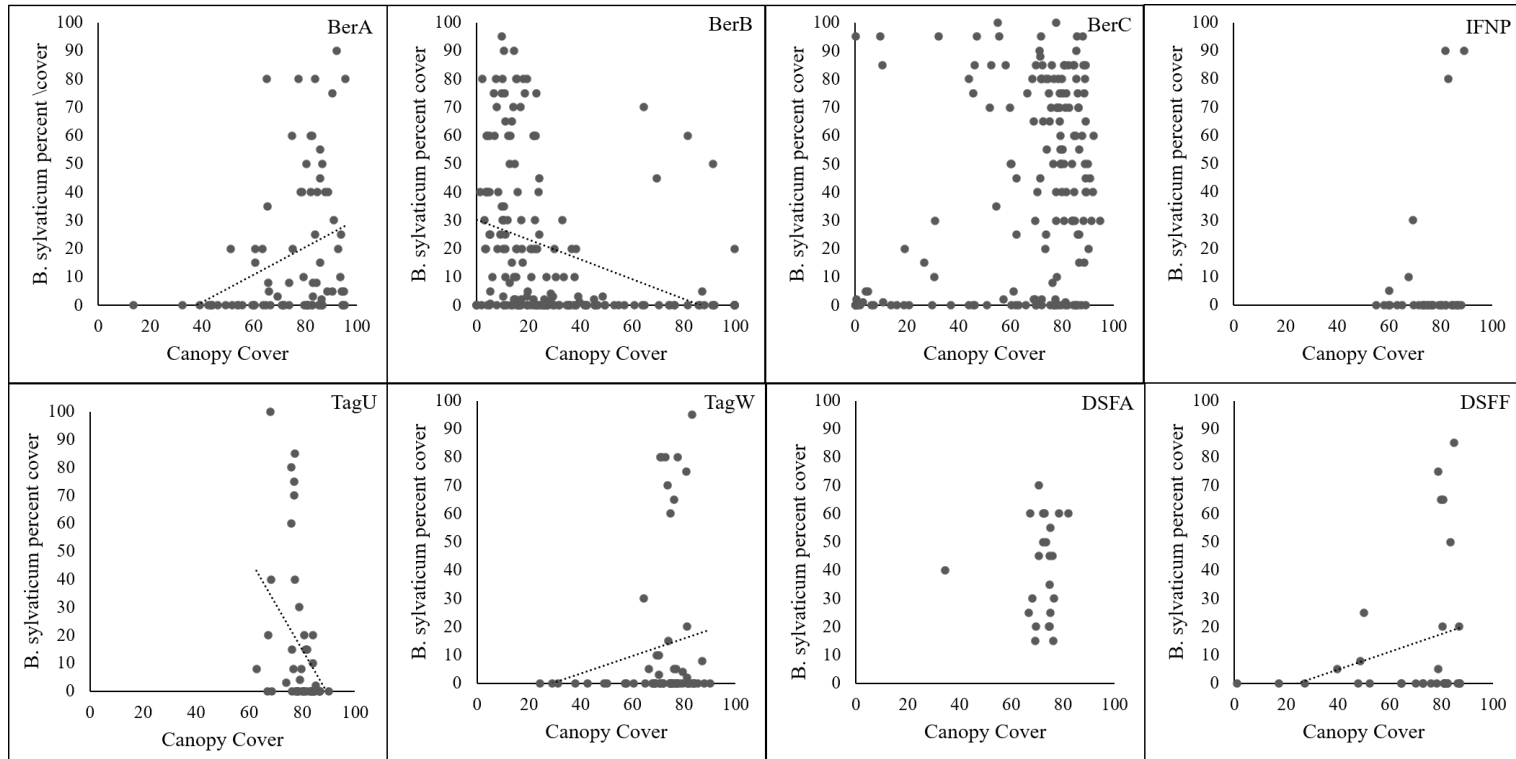


Figure 5. Trends of canopy cover against *Brachypodium sylvaticum* percent cover within each invaded site. Dashed lines indicate the significant trend direction.

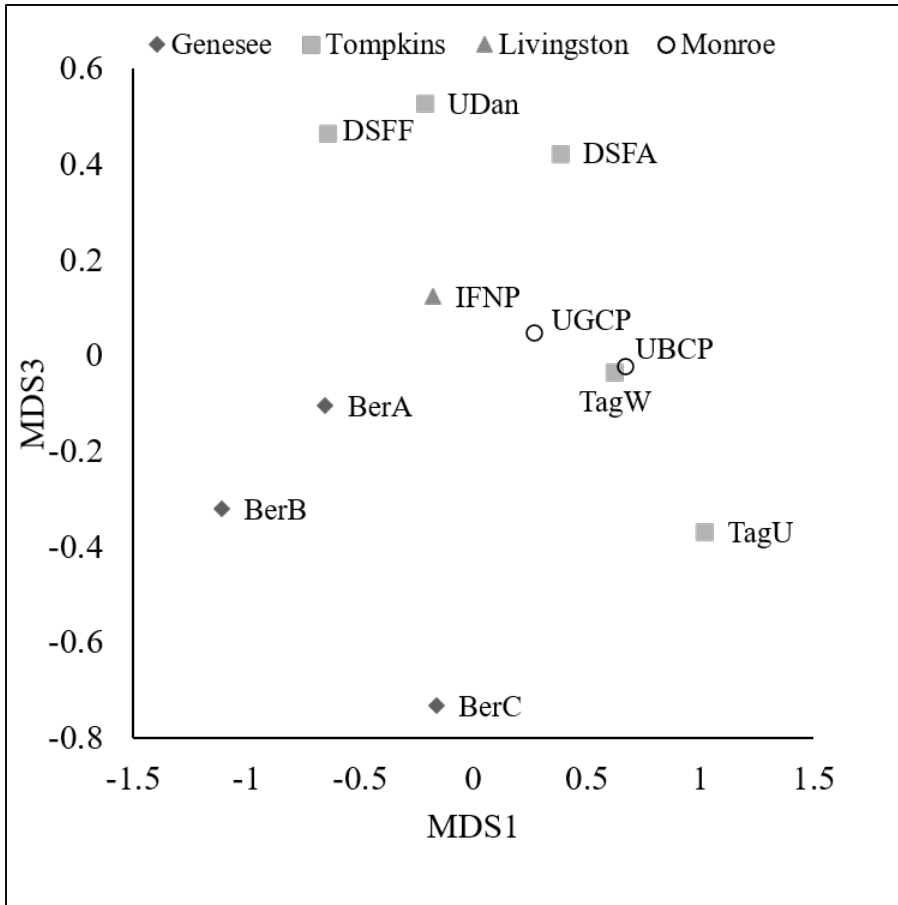


Figure 6. NMDS ordination of community composition of all invaded sites. Symbols indicate the counties site is located within.

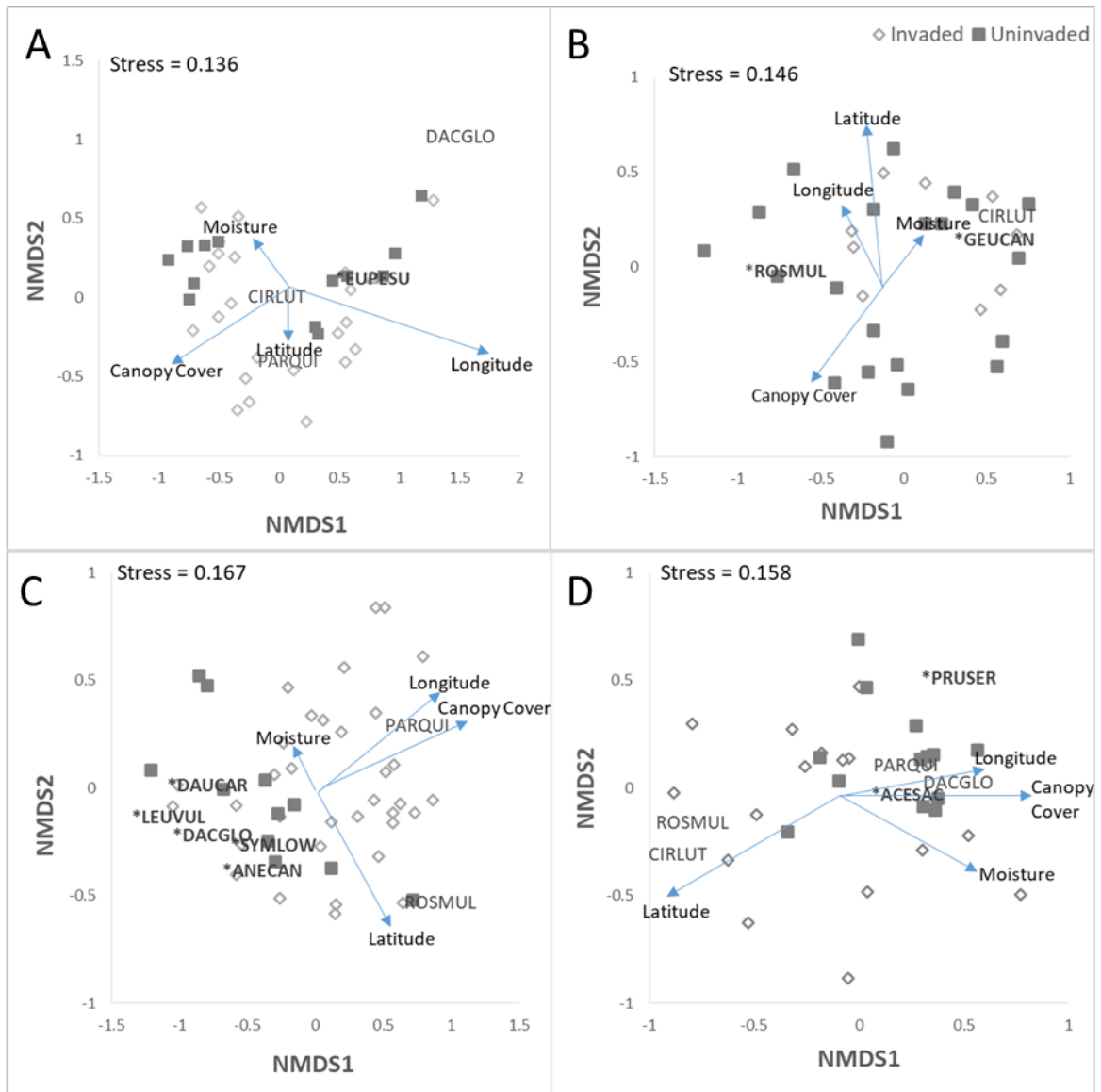


Figure 7. Non-metric multidimensional scaling (NMDS) plots of fine-scale community data in invaded and uninvaded quadrats at BerB (A), IFNP (B), BerC, (C), and TagU (D). *Brachypodium sylvaticum* was excluded from these analyses. All 3D NMDS are represented as 2D plots for clarity. Species significant at that site were presented in bold. Species not significant at that site but present within the site was listed not in bold.

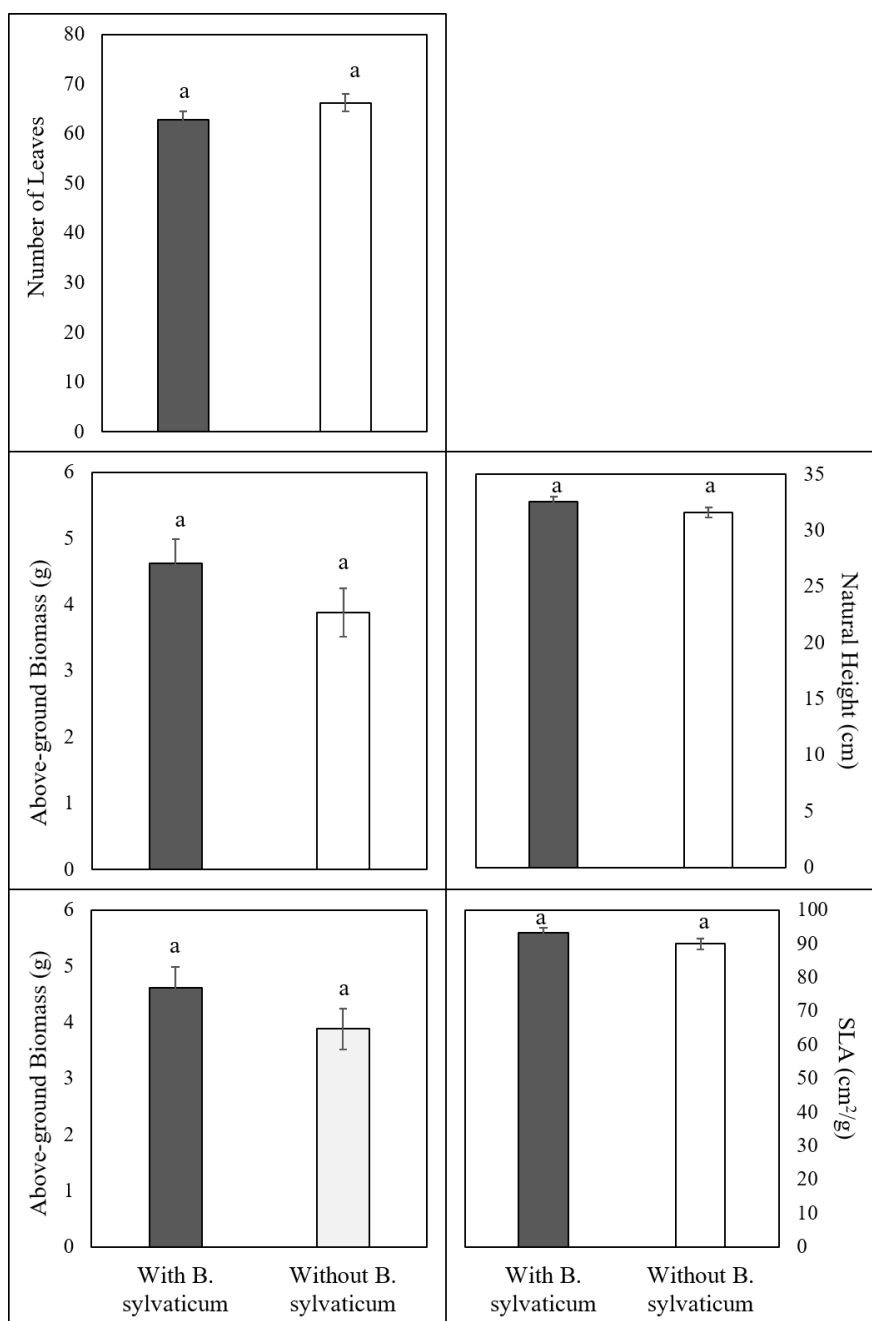


Figure 8. Growth parameters of *Dactylis glomerata* when grown with and without *B. sylvaticum*.

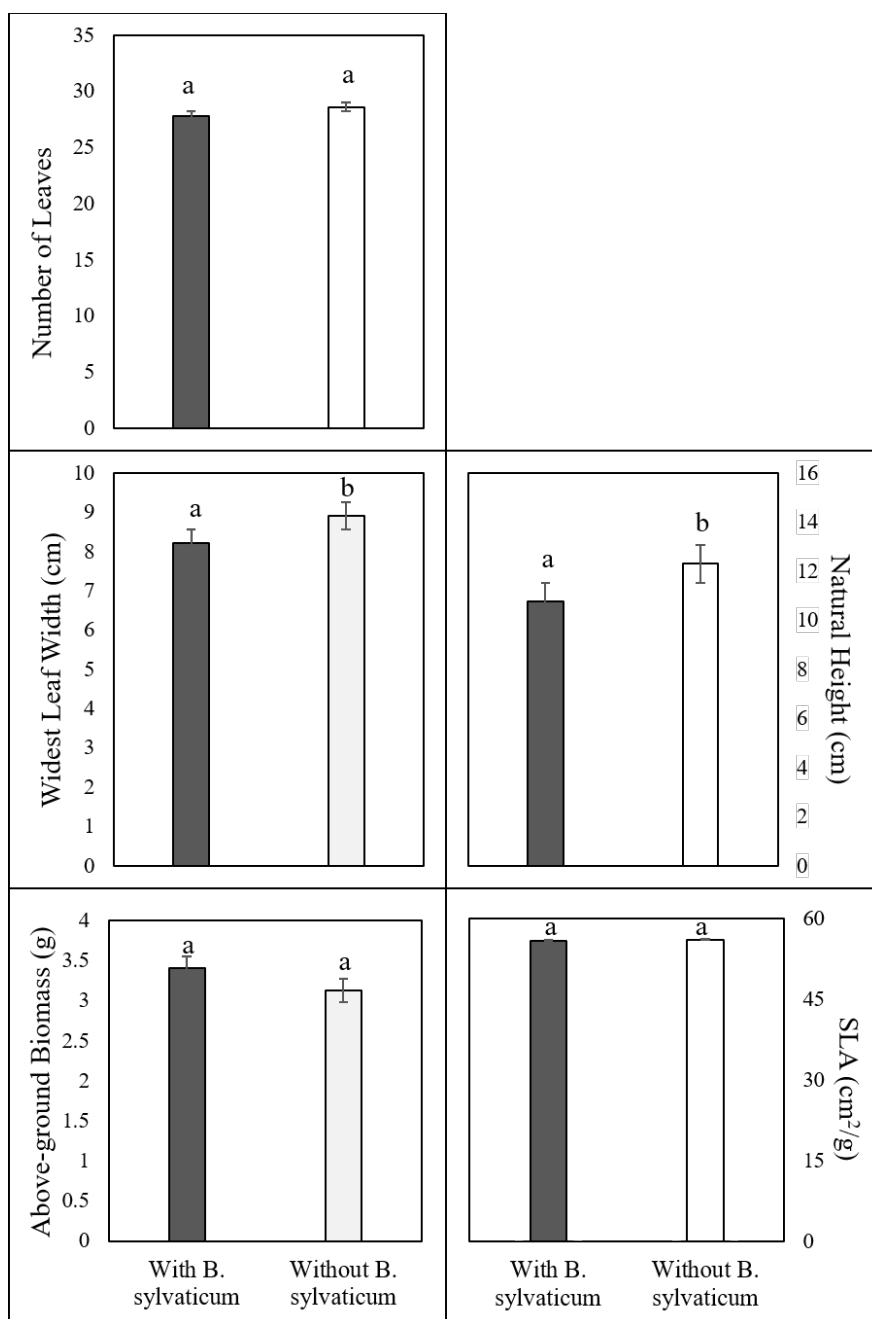


Figure 9. The differences in growth parameters of *Geum canadense* when grown with and without *B. sylvaticum*.

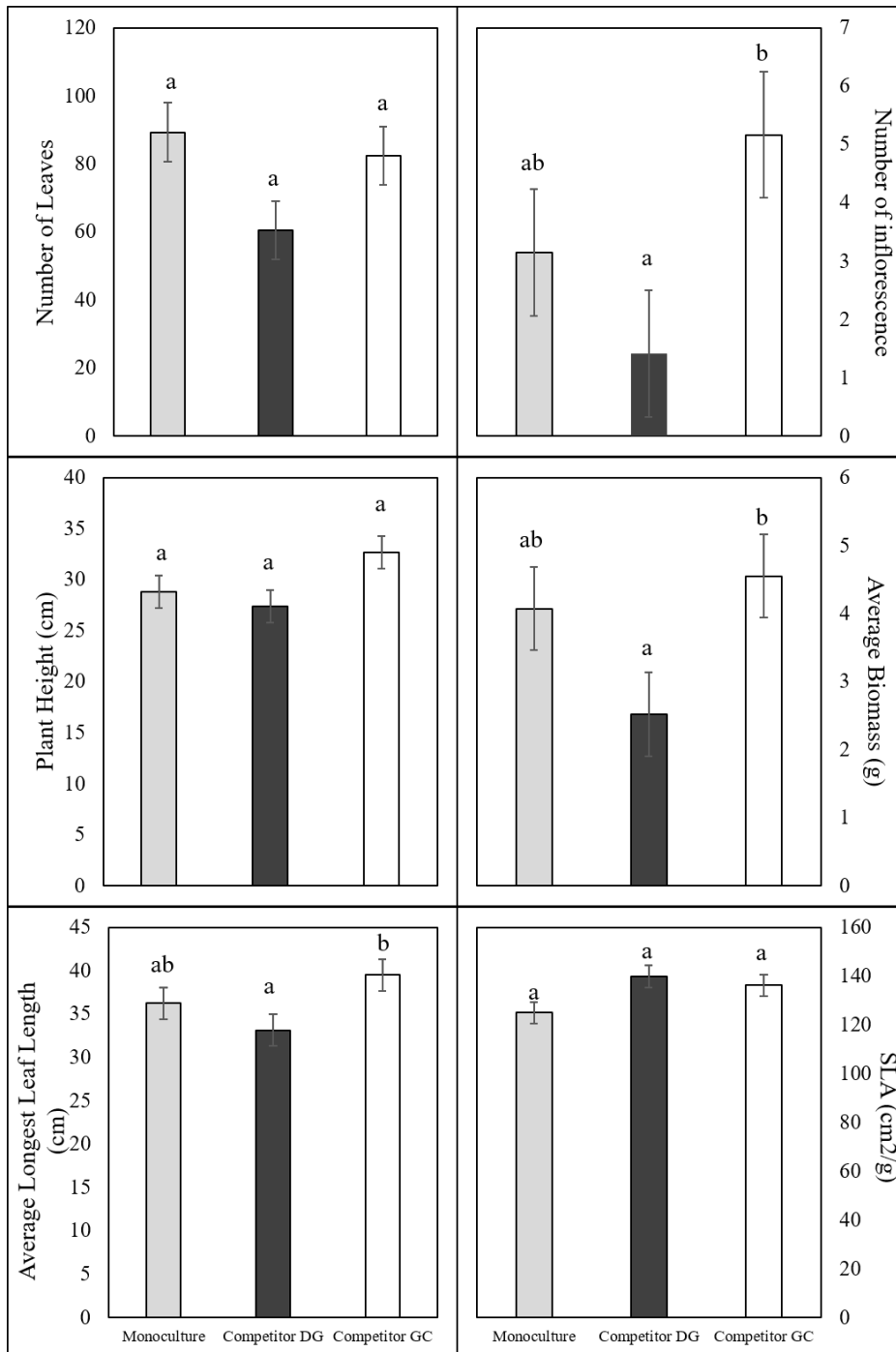


Figure 10. The differences in *Brachypodium sylvaticum* growth parameters when grown in monoculture, or in competition with *Dactylis glomerata* (DG), or *Geum canadense* (GC).

Appendix A

Table 1. Study sites and the transect and quadrat spacing used. Sites where additional fine-scale sample took place are marked.

<i>Site</i>	<i>Transect Spacing (m)</i>	<i>Quadrat Spacing (m)</i>	<i>Fine-scale sampling</i>
<i>BerA</i>	25	25	
<i>BerB</i>	25	10	X
<i>BerC</i>	75	25	X
<i>UBCP</i>	25	25	
<i>UGCP</i>	25	25	
<i>IFNP</i>	25	25	X
<i>TagU</i>	25	25	X
<i>TagW</i>	25	25	
<i>DSFA</i>	25	25	
<i>DSFF</i>	25	25	
<i>UDan</i>	25	25	

Table 2. Dates of environmental data collection at fine scale quadrats at BerB, BerC, TagU, and IFNP.

<i>Site</i>	<i>First Sample</i>	<i>Second Sample</i>	<i>Third Sample</i>
<i>BerB</i>	07-02-2019	07-26-2019	08-15-2019
<i>BerC</i>	07-06-2020	07-21-2020	08-07-2020
<i>TagU</i>	07-15-2020	08-07-2020	08-20-2020
<i>IFNP</i>	6-30-2020	07-20-2020	08-10-2020

Table 3. Soil types (Web Soil Survey 2022) located within the sample sites. Included is the soil taxonomy of each soil type, soil drainage, and the average percent cover of *B. sylvaticum* within the plots located within the soil types.

<i>Sites</i>	<i>Soil Type</i>	<i>Name</i>	<i>Soil Taxonomy</i>	<i>Drainage*</i>	<i>Hydric</i>	<i>BS Cover</i>
<i>BerB</i>	ApA	Appleton	Fine-loamy, silt loam mixed, active, mesic Aeric Endoaqualfs	SPD	No	30.7
<i>BerA</i> , <i>BerB</i> , <i>BerC</i>	StA	Stafford	Mixed, mesic loamy fine sand Typic Psammaquents	SPD	No	29.5
<i>BerA</i> , <i>BerB</i> , <i>BerC</i>	EiB	Elnora	Mixed, mesic loamy fine sand Aquic Udipsammets	MWD	No	26.4
<i>BerB</i>	Wr	Warners	Fine-silty, mucky loam carbonatic, mesic Fluvaquentic Endoaquolls	VPD	Yes	45.0
<i>TagW</i>	ArB	Arkport	Coarse-loamy, very fine sandy loam mixed, active,	WD	No	6.5

<i>Sites</i>	<i>Soil Type</i>	<i>Name</i>	<i>Soil Taxonomy</i>	<i>Drainage*</i>	<i>Hydric</i>	<i>BS Cover</i>
			mesic Lamellic Hapludalfs			
<i>BerA</i>	HaA	Halsey silt loam	Coarse-loamy over sandy or sandy-skeletal, mixed, active, nonacid, mesic Typic Humaquepts	VPD	Yes	0.0
<i>BerA</i>	OdA	Odessa silt loam	Fine, illitic, mesic Aeric Endoaqualfs	SPD	No	12.1
<i>BerC</i>	OnC	Ontario loam	Fine-loamy, mixed, active, mesic Glossic Hapludalfs	WD	No	56.3
<i>BerC</i>	OnB	Ontario loam	Fine-loamy, mixed, active, mesic Glossic Hapludalfs	WD	No	73.8

<i>Sites</i>	<i>Soil Type</i>	<i>Name</i>	<i>Soil Taxonomy</i>	<i>Drainage*</i>	<i>Hydric</i>	<i>BS Cover</i>
<i>BerC</i>	PkD	Palmyra and Arkport soils	Fine-loamy over sandy or sandy skeletal, mixed, active, mesic Glossic Hapludalfs, and Coarse-loamy, mixed, active, mesic Lamellic Hapludalfs	WD	No	84.0
<i>BerB</i>	Ed	Edwards muck	Marly, euic, mesic Limnic Haplosaprists	VPD	Yes	4.4
<i>TagU,</i> <i>TagW</i>	HdC	Howard gravelly loam	Loamy-skeletal, mixed, mesic Glossoboric Hapludalfs	WD	No	11.8
<i>TagU,</i> <i>TagW</i>	HuB	Hudson- Cayuga silt loams	Fine, Illic, mesic Glossoboric Hapludalfs	MWD	No	22.3

<i>Sites</i>	<i>Soil Type</i>	<i>Name</i>	<i>Soil Taxonomy</i>	<i>Drainage*</i>	<i>Hydric</i>	<i>BS Cover</i>
<i>TagU</i>	HuC3	Hudson-Cayuga silt loams	Fine, Illic, mesic Glossoboric Hapludalfs	MWD	No	18.6
<i>TagW</i>	OaA	Ovid silt loam	Fine-loamy, mixed, mesic Aeric Ochraqualfs	SPD	No	38.6
<i>TagW</i>	IcB	Ilion silty clay loam	Fine-loamy, mixed, mesic Mollic Ochraqualfs	PD	Yes	25.0
<i>DSFA</i>	LaB	Langford channery silt loam	Coarse-loamy, mixed, active, mesic Typic Fragiudepts	MWD	No	15.5
<i>DSFA</i>	BaC	Bath channery silt loam	Coarse-loamy, mixed, active, mesic Typic Fragiudepts	WD	No	5.5
<i>DSFA</i> , <i>DSFF</i>	BoE	Bath and Valois soils	Coarse-loamy, mixed, active,	WD	No	39.3

<i>Sites</i>	<i>Soil Type</i>	<i>Name</i>	<i>Soil Taxonomy</i>	<i>Drainage*</i>	<i>Hydric</i>	<i>BS Cover</i>
			mesic Typic Fragiudepts			
<i>DSFA,</i> <i>DSFF</i>	Ab	Alluvial land		PD	Yes	20.4
<i>BerC</i>	Ld	Lamson very fine sandy loam	Coarse-loamy, mixed, active, nonacid, mesic Aeric Endoaquepts	PD	No	35.0
<i>DSFF</i>	LoF	Lordstown channery silt loam	Coarse-loamy, mixed, active, mesic Typic Dystrudepts	WD	No	9.4
<i>IFNP</i>	236C	Schoharie silt loam	Fine, Illic, Mesic Oxyaquic Haplalalfs	MWD	No	9.8

*Drainage codes are provided from Web Soil Survey and are as follows: well drained (WD), moderately well drained (MWD), somewhat poorly drained (SPD), poorly drained (PD), and very poorly drained (VPD).