

The effects of invasive slender false-brome (*Brachypodium sylvaticum*) on forest  
ecosystem function in western New York

by

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## Abstract

The interconnectedness of the modern world has led to the spread of species outside of their normal range. Some species become invasive and can impact ecosystems by changing soil, water, and nutrient dynamics. Disrupting these important ecosystem processes can facilitate further invasion. Slender false-brome (*Brachypodium sylvaticum*) is an exotic bunchgrass that is invasive in North America. Its encroachment into forest understories may have implications for ecosystem processes and characteristics. The goal of this study was to understand the impacts of slender false-brome on forest ecosystem function. This study took place within two forests in western New York, one at Taughannock Falls State Park (TFSP), Trumansburg, and one in Danby State Forest (DSF), Danby. Replicate paired plots with and without *B. sylvaticum* were selected in each forest; each pair was matched by canopy cover and canopy type. In plots I measured vegetation, soil physical and chemical characteristics, soil moisture, soil respiration, and decomposition of leaf litter. I used generalized linear mixed models to determine variables that were the strongest predictors of soil nutrients, soil respiration, and leaf litter decomposition. All soil characteristics measured were significantly different between invaded and uninvaded plots except bulk density. At TFSP, invaded plots were enriched with organic matter (OM) and total nitrogen (TN). At DSF, invaded plots were enriched with phosphorus (P). Invaded plots at both sites had greater cation (Mg, Ca, K) concentrations, pH, and bulk density, and soil respiration and decomposition rates also increased in response to *B. sylvaticum* invasion. My results demonstrate that *Brachypodium sylvaticum*

invasion significantly alters ecosystem processes, although initial site conditions do affect the magnitude and trend of some changes. Overall, *B. sylvaticum* has impacts on ecosystem processes like other flagship invasive species, however the impacts seem to change based on initial site conditions. I found that sites like Danby State Forest and Taughannock Falls State Park are at risk of changes in soil nutrients, soil respiration, and decomposition. A greater diversity of sites needs to be investigated to determine if other types of ecosystems are at risk from *Brachypodium sylvaticum*.

## Introduction

Invasive animals and plants have become widespread issues due to increased global connectivity and human introductions of invaders (Vitousek *et al.* 1997a, Vitousek *et al.* 1997b, Wilcove *et al.* 1998, Pimentel *et al.* 1999, Hulme *et al.* 2009, and Seebens *et al.* 2017). An invasive species is a nonnative organism that impacts or has the potential to impact humans or native species or ecosystems in a negative way (Simberloff 1996, Sakai *et al.* 2001). There are hundreds of these species in each country, with an apparent correlation with total area (Vitousek *et al.* 1997). The economic and ecological damages caused by invasive species are difficult to quantify, but each species can cost thousands of dollars to control per acre, with some species costing millions to control across many acres (Jardine and Snachirico 2018). Invasive species' impact ranges from damaging important sectors of the U.S. economy to changing fundamental ecosystem processes (Pimentel *et al.* 2005). Ecosystem processes are functions performed by biota within an ecosystem that transfer nutrients, water, and energy between plants and soils (Chapin III *et al.* 2011).

The movement of nutrients through plants and soils in ecosystems is an essential process that can be altered by invasive plants (Ehrenfeld 2003). Invasive plants have been noted to change nitrogen, phosphorus, and major cation abundance in soils, elements which are cited as nutrients that can individually or co-limit plant growth (Tilman 1985, Chapuis-Lardy *et al.* 2006, Thorpe *et al.* 2006, Rodgers *et al.* 2008, Vitousek *et al.* 2010). Invasive species typically increase nutrient pools and rates of nutrient cycling (Belnap and Phillips 2001, Ehrenfeld 2003). Increases in

nutrients due to invaders can potentially cause ‘invasional meltdown’ (Simberloff and Von Holle 1999), which is a positive feedback loop, or a facilitative relationship, between plant invasion and nutrient enrichment.

Although invasive species are often thought to increase nutrient availability (Rodgers *et al.* 2008,), impacts of invasive species on soil nutrients are not always consistent between species or even between sites within a species. For example, soil nitrogen is often considered the most important nutrient in limiting plant and microbial growth. Although soil nitrogen changed in response to invasion in numerous studies, a 2003 meta-analysis noted the lack of a clear pattern in the change in nitrogen post-invasion (Ehrenfeld 2003). The annual invader cheatgrass (*Bromus tectorum*), increased nitrogen content in grasslands it invaded in Canyonlands National Park, Moab, Utah (Belnap and Phillips 2001). However, the same invader had an insignificant effect on soil nitrogen in another study (Bolton *et al.* 1993). These contrasting impacts of cheatgrass are exemplary of the importance of site and species-specific studies investigating the impacts of invasive species.

Invasive species alter soil nutrient contents, but they also alter physical characteristics of soils by changing water uptake. The water usage patterns, and different root structures of plant functional groups, including invasive and native species, can have implications for total water used and transpired by plants (Cline *et al.* 1977, Ehrenfeld *et al.* 2001, Sardans and Penuelas 2014). Effects of invasive species on soil moisture have been observed which was attributed to dense growth patterns causing shading of the soil surface and increased soil moisture (Crooks

2002). Specifically, a study examining the effects of removal of invasive purple-fountain grass (*Pennisetum setaceum*) found that when the grass was removed, water availability was increased, and seedling regeneration increased as well. The implication of this result is that invasive grasses, at least in this case, compete by using up mass amounts of water and deprive competitors of this essential resource (Thaxton *et al.* 2012).

Invader impacts on soil chemistry, moisture, and nutrient content can ultimately affect microbial communities and function. The rate of microbial respiration can depend on soil nutrients, soil pH, and water availability (McCulley *et al.* 2004, Simpson *et al.* 2012), and these can all be altered by invasive species. For example, the nutrient enrichment caused by Japanese stiltgrass (*Microstegium vimineum*) and Japanese barberry (*Berberis thunbergii*) in north eastern hardwood forests leads to increased soil microbial activity underneath the invasive plants (Kourtev *et al.* 2002). Common forest invaders have caused increases in soil pH which, for some ecosystems, can facilitate microbial respiration, thus increasing speed of nutrient cycling (Ehrenfeld *et al.* 2001). Soil pH influences bacterial community diversity and abundance (Zhalnina *et al.* 2014). Studies have found a significant influence of pH and soil moisture on soil respiration, but the results varied based on habitat type (Reth *et al.* 2005). The direct influence of soil abiotic factors on soil microbe function supports the idea that invasive species can change microbial-mediated functions such as soil respiration and decomposition.

Changes in soil respiration can be related to decomposition rate, as soil fauna are responsible for the breakdown of organic material. The difference between native and invasive species growth can lead to changes in biomass quantity and quality that fuels microbial decomposition (Arthur *et al.* 2012). Increased biomass production in invaded areas is a common effect of invasive plants (Sakai *et al.* 2001, Ehrenfeld 2003, Aguilera *et al.* 2010). When large amounts of invader leaf litter are input into the system, depending on the invader and study sites, decomposition can either be sped up or slowed down (Allison and Vitousek 2004, Ehrenfeld 2003, Evans *et al.* 2001). Increased rates of decomposition are often linked to higher quality leaf litter (increased nutrient content and lower carbon complexity) entering the system (Arthur *et al.* 2012). However, slowed decomposition has also been observed in invasive species research where the invasive species had a high lignin content (Godoy *et al.* 2010). Invasive species do not only change the type and quantity of litter input to systems but also the conditions where litter is decomposing. Plots dominated by either native or invasive vegetation can chemically change soils and create a different assemblage of soil fauna (Ashton *et al.* 2005). For example, if there is a monoculture of an invasive species in one plot, but not another, the massive amounts of different quality leaf litter can facilitate bacterial and fungal growth by adding a surplus of nutrients that the uninvaded plot does not have. Furthermore, soils under a monoculture of invasive plants can retain more moisture than uninvaded plots by preventing evaporation and increasing shading of the soil surface. As with invasive species impacts on nutrients, the effects of any one invader depends on its

characteristics and those of the invaded system. This leads to a lack of consistent patterns of impacts to decomposition caused by invasive species (Ashton *et al.* 2005, Godoy *et al.* 2010).

### *Study species*

A perennial bunch grass, slender false-brome (*Brachypodium sylvaticum*) is a species native to Europe, Asia, and North Africa that is an expanding problem in the United States and Canada (Holmes *et al.* 2009, Rosenthal *et al.* 2008, Miller *et al.* 2011). The first herbarium specimen of *B. sylvaticum* was collected in Oregon in 1939 and it is hypothesized it escaped from an agriculture research site (Rosenthal *et al.* 2008). In New York State, *B. sylvaticum* was first found in the 1990s, but was not properly identified, it has been found in many ecosystems including forests, retired railroad beds, and wetlands. One infestation of *B. sylvaticum* is at Bergen Swamp, Genesee County where it has been present since the 1990s (Daniel and Werier 2010, Miller *et al.* 2011). Another infestation discovered by Daniel and Werier (2010) is in Tompkins County. *Brachypodium sylvaticum* has the potential for considerable impact on Eastern temperate forest ecosystems.

In both its native and invaded range, *B. sylvaticum* is found in forest understories, field edges, and wet to upland conditions (Holmes *et al.* 2009, Miller *et al.* 2011, Roy 2019). Although *B. sylvaticum* is found in both sun and shaded sites, studies have shown that *B. sylvaticum* thrives in forest understories (Holmes *et al.* 2009) and sees higher recruitment of seedlings under coniferous overstories (Taylor and Cruzan 2015). One paper noted the prominence and aggressive growth that *B.*

*sylvaticum* sometimes exhibits in its native range, the effects of this are smothering cooccurring species with mass amounts of biomass and outcompeting the same species for resources (Corney et al. 2008). This impact of *B. sylvaticum* is important because it is a species that is largely spread by humans and animals (Heinken and Raudnitschka 2002). The dense growth pattern of *Brachypodium sylvaticum* has serious implications for communities and ecosystem processes in invaded sites. When *B. sylvaticum* success was compared with native vegetation, researchers found that presence of *B. sylvaticum* was negatively correlated with percent cover of shrubs, ferns, and other grasses (Taylor and Cruzan 2015). The results of these studies show how forested areas that are disturbed by humans, like public parks and nature preserves, are particularly vulnerable to *B. sylvaticum* propagule pressure. The impact of *B. sylvaticum* on vital ecosystem processes such as soil nutrient content, decomposition, and nutrient cycling are not currently known, as they have not been studied yet.

I hypothesized that invasion of *Brachypodium sylvaticum* will increase nutrient pools and rates of nutrient cycling within those pools due to increased quantity and quality of leaf litter. This increase in biomass will result in increased microbial activity and faster decomposition of leaf litter in invaded plots. The increased density of vegetation will increase soil moisture, which will also contribute to increased soil respiration. The increased microbial activity caused by higher quality litter and wetter plots will increase nitrogen and phosphorus concentrations in plots. Invasion of *Brachypodium sylvaticum* will also increase bulk density of soils and increase pH of soils.

## Methods

We implemented this study in Danby State Forest (DSF, 18T, 378180.56E, 4685769.12N, Danby, New York) and Taughannock Falls State Park (TFSP, 18T, 368658.12E, 4711155.26N, Ulysses, New York). The average precipitation for nearby Ithaca, New York is 94.7cm with average annual high and low temperatures of 13.9°C and 2.7°C respectively ([www.usclimatedata.com](http://www.usclimatedata.com)). At each site, fifteen invaded plots were paired with fifteen uninvaded plots. Pairs were matched for canopy cover and canopy type. The invaded plots (*Brachypodium* plots) were 3x3m areas with *Brachypodium sylvaticum* covering at least 50% of the ground. Uninvaded plots (control plots) were 3x3m areas with less than 5% *Brachypodium sylvaticum* cover and at least 50% cover of other species. I also identified whether canopy species were deciduous or coniferous since soil processes under consideration could also be affected by tree type. Within DSF, five plot pairs had deciduous canopies, five pairs had coniferous canopies, and five pairs had mixed canopies. Preliminary site visits showed the dominant tree species at DSF were *Acer saccharum* and *Fagus grandifolia*. At TFSP, 20 plots were deciduous, and 10 plots were mixed canopy with *Acer saccharum* and *Pinus strobus* as the dominant tree species.

### *Vegetation data*

Ground-layer vegetation was quantified in each plot in 2019. I calculated percent cover of vegetation in six categories: *B. sylvaticum*, invasive shrub, native shrub, invasive herb (including graminoids and ferns), native herb, and bare in 15 pairs of *Brachypodium* vs. Control plots. Shrubs were defined as woody species with a diameter

at breast height (DBH) greater than 3 cm. Although both nonnative and native herb percent cover was initially estimated, the categories were combined because of a misidentified grass and to combat zero inflated data. Finally, the bare category included any area within the plots that was exposed soil, rock, or leaf litter. Canopy openness was assessed using hemispherical photos taken with a Nikon D3300 camera with a Rokinon aspherical fish-eye lens. The camera was connected to a 3-axis tripod that was leveled when placed in the center of each plot. Gap Light Analyzer (Simon Frazer University and Cary Institute of Ecosystem Studies) was used to quantify canopy openness (Frazer *et al.* 1999).

#### *Bulk density*

A steel collar with an interior diameter of 5.27 cm and a length of 10.13 cm was used to facilitate the determination soil bulk density (Klute 1986). The collar was hammered into the soil until the top was flush with the ground, at which time a small spade was used to extract the collar while retaining all soil within it. All the soil within the collar was put into a clean and labelled plastic bag. The samples were dried in an oven at 60°C for 48 hours and were subsequently weighed using an analytical balance. The sample mass was divided by the volume of the collar to obtain bulk density in grams per centimeters cubed ( $\text{g}/\text{cm}^3$ ).

#### *Soil moisture*

Soil moisture was measured using Decagon ECH2O soil moisture probes and Em50 data loggers which were programmed using the ECH2O Utility software (METER Group 2019). Hoboware microstations were also used to collect moisture

data, which used the same ECH2O moisture probes (Onset Corporation 2020). Moisture probes were inserted horizontally into the soil profile at 10 cm depth. These probes measured moisture volumetrically every hour with the earliest measurement starting on 21 August 2019 and the latest ending on 23 October 2020. The data loggers were removed from the field from 23 November 2019 to 31 March 2020 to prevent any damage from freezing. We collected data for twelve plots at DSF and fourteen plots at TFSP. Some of the data were lost because of destruction of probes by mice, and two probes were moved to new plots at both DSF and TFSP because of mouse presence in the area.

#### *Soil nutrient content*

Soil samples were collected within all plots at DSF and TFSP on 20 August 2019. The upper layer of undecomposed organic layer of the soil (generally 1-5cm of undecomposed leaf litter/twigs) was moved out of the way to expose bare soil before taking the soil samples to prevent organic matter levels from being skewed by leaf litter or twigs. Three replicates were taken in each plot and then homogenized. Each replicate was an 8.57cm diameter by 10.16cm deep soil core that was taken within each of the sixty 3x3m plots. Samples were then put through a 2mm (size 20) sieve and dried at 60°C for 72 hours.

Soils were sent to the Wisconsin Soil and Forage Lab for soil texture analysis, total nitrogen, carbon analysis, available phosphorus, pH, available potassium, organic matter, and total leachable mineral analysis. Source for all soil analysis methods was the University of Wisconsin Soil and Forage Lab website at (Peters 2013, [UW Soil](#)

[Lab](#)). Soil texture was examined using the hydrometer method (outlined in Buoyoucos 1962), which separates soil particles into three categories: sand (2.0 - 0.05 mm), silt (0.05 - 0.002 mm), and clay (< 0.002mm). Total nitrogen in my samples was determined using the Kjeldahl method, which analyzes digested samples with a Lachat 8000 (Lachat Instruments 1995). Total carbon in the soil samples was determined using a combustion method using a LECO CNS-2000 analyzer (LECO Corporation 2002, Matejovic 1997). Brays method for plant available phosphorus and potassium content in soils was developed in the 1940s and the digestion was used for flow injection analysis (FIA) on a Lachat (Bray and Kurtz 1945). The pH of my samples was determined using a 1:1 water method using a pH electrode, but if the pH of a sample was below 6.6, the Sikora buffer method employed to analyze the samples, this method is used by the lab because it uses less hazardous chemicals than the traditional SMP buffer (Sikora 2006, Laboski *et al.* 2006).

A sub sample of the sent-out soil samples were also used to determine soil organic carbon (SOM) using the loss-on-ignition (LOI) method (Salehi *et al.* 2011). The furnace used for this analysis was a Thermolyne benchtop muffle furnace (Model no. F30428C; Barnstead International 2001). The soil was air dried in the lab and then put through a 2mm stainless-steel sieve. After drying in the oven at 105°C for 48 hours, the samples were placed in a desiccator for 10 minutes followed by weighing to obtain the pre-ignition weight. The samples were then put in a muffle furnace for 2 hours at 360°C, which are parameters proposed by Salehi *et al.* in their 2011 analysis of organic matter in soils via loss-on-ignition. Once samples were removed from the muffle

furnace, they were put back into the oven at 105°C, and then into the desiccator for 10 minutes prior to weighing.

I conducted a web soil survey using a database upkept by the USDA National Resource Conservation Service that has soil data from 95% of counties in the USA. This data is upkept and updated regularly.

### *Soil respiration*

Soil respiration was measured using the LICOR 6400 (LiCor 2011) with a soil respiration chamber attachment. The target value was set to 400 ppm CO<sup>2</sup>, which was approximately equal to ambient CO<sup>2</sup> levels at each site. The delta CO<sup>2</sup> value was set to 15 ppm, which is used to prevent abnormal fluxes from significantly altering respiration rates. A 9 cm Ø PVC tube was inserted 2 cm into the soil surface in each plot a week before starting measurements to prevent influence of inserting the soil chamber into the soil (LiCor 2011, Wang *et al.* 2005). Respiration rates were measured every three weeks from 5 May 2020 to 1 November 2020. Soil temperature was measured simultaneously because there is a strong correlation between respiration rate and soil temperature (Lloyd and Taylor 1994).

We quantified the rainfall of the week before each soil respiration measurement (Angers and Caron 1998, Davidson *et al.* 2002, Moyano *et al.* 2013). Data were downloaded from weather stations near DSF and TFSP from <https://www.ncdc.noaa.gov/>. The ground-based weather stations used for DSF and TFSP were the NEWFIELD 2.5 S, NY US US1NYTM0015 and Trumansburg 0.4

WNW, NY US US1NYTM0038 respectively. Since DSF and TFSP are in different hardiness zones (6a and 5b respectively), two different frost-free growing seasons were used when organizing moisture data for analysis. The growing season for DSF lasted from 23 May 2020 to 23 September 2020 while TFSP growing season lasted from 9 May 2020 to 4 October 2020.

### *Decomposition experiment*

In the Fall of 2019, freshly fallen leaves from *Acer saccharum*, and *Fagus grandifolia* were collected from Danby State Forest, DSF. Leaf litter from *B. sylvaticum* was collected from DSF and TFSP by clipping at the base of the plant. Whatman 42 filter paper was also included as a low-nutrient baseline. Filter paper and litter from each species were air dried for 72 hours following collection and was cut into smaller pieces (estimate size), and mixed (within species) to ensure each species pool was homogenized across the sites. Litter bags were constructed out of 1mm fiberglass mesh (window screen) sealed into 16cm<sup>2</sup> squares. Two grams of leaf litter were added to each bag. Litter bags were placed experimental plots on 29 March 2020 (DSF) and 31 March (TFSP) 2020. Harvests were collected at 5, 10, 20, and 39 weeks.. There were four replicates of each species per plot per harvest. The litter remaining after each harvest was placed in the drying oven at 60°C for 72 hours and weighed. The decomposition rate was calculated using the formula  $kD = (-\ln (Lt/L0))/t$  where  $kD$  is decomposition rate,  $t$  is time,  $Lt$  is leaf litter weight at time  $t$ , and  $L0$  is initial leaf litter weight.

Leaf/filter paper subsamples were ground to 2 mm with a Thomas Scientific Wiley Mill for nutrient analyses at the Wisconsin Soil and Forage Lab. Total nutrient analysis, which consists of N, P, K, Ca, Mg, S, Zn, Mn, B, Cu, and Fe, was measured using two methods, Kjeldahl (N and P) and a dry-ash method (all other minerals, Isaac and Johnson 1985). Total carbon was determined using a combustion method using a LECO CNS-2000 analyzer (LECO Corporation 2002). Lignin content of leaves was determined gravimetrically using a solution made of homogenized leaf litter dissolved in 72% sulfuric acid (Helrich 1990). Leaves were also analyzed for total nutrient content after they were decomposed, lignin was left out of the post-decomposition analyses. Leaf litter was homogenized across plot types, site, and species (ie *A. saccharum* leaves that were decomposed in *Brachypodium* plots at Danby were combined).

### *Statistical analyses*

IBM SPSS Statistics 25 (IBM Corp 2017) and Minitab 18 were used for analyses (Clark 2020). All data were first checked for normality using Q-Q plots, Shapiro-Wilkes tests, Kolmogorov-Smirnov tests, skewness statistics, and distribution histograms to examine assumptions for parametric statistics.

I used a Friedman test for vegetation data to determine differences between the different layer types, plot types, and sites. Multiple comparisons were accounted for using Holms-Bonferroni correction (Holm 1979). Vegetation categories were also compared to canopy openness to see if there were any significant correlates between the variables.

Spearman's rho correlation matrices were used to assess the relationships between response variables and fixed effects. Predictor variables that had higher correlations with the response variables (Soil respiration/decomposition rate) would likely perform best in predictive generalized linear mixed models. When assessing the relationship between soil moisture or rainfall and soil respiration, I found that the best water availability predictor was rainfall one week before soil respiration measurement with correlation coefficients of -0.132 at DSF and -0.308 at TFSP. Of litter nutrients, total nitrogen had the highest correlation coefficient of 0.892. The relationships between these response variables and their respective predictors led me to use them as factors in generalized linear mixed models.

I used a Kruskal Wallace one-way analysis of variance to test differences among the leaf nutrient profiles of the *Acer saccharum*, *Fagus grandifolia*, and *Brachypodium sylvaticum* from both DSF and TFSP. The filter paper control was unincluded because it is assumed to be different compared to actual leaf litter.

I developed generalized linear mixed models to examine the influence of site (DSF vs. TFSP), plot type (*B. sylvaticum* invaded vs. control uninvaded), canopy openness, and other fixed effects specific to each response variable.

All generalized linear mixed models used a gamma probability distribution with a log link to examine how predictor variables influenced each response variable with plot number as a random effect block. The variables were selected for each model using a backwards selection method in conjunction with Akaike's Information

Criterion (AIC, Akaike 1973, Burnham and Anderson 2002). This method is performed by adding in all important variables, removing the least significant variable, with a p value of 0.15 or more, until the AIC value increases. The goal of this method is to use the simplest model to achieve the lowest possible AIC value.

For the respiration model, I used log transformed soil efflux ( $\text{CO}_2/\text{m}^2/\text{s}^{-1}$ ) as the response variable. I input site, plot type, julian date (sample number 1 – 12), canopy openness, average soil moisture week before, bulk density, and canopy type (DSF only) and two-way interactions between them as fixed effects. Soil respiration was also separated into two different models based on relative soil moisture, dry models contained respiration samples from 6 July 2020 to 23 October 2020, while wet models contained respiration samples from 5 May 2020 to 16 June 2020.

For nutrient content and soil density models I chose plot type, site, canopy openness, total vegetation cover, and their two and three-way interactions as fixed effects in

The generalized linear mixed model that I developed for decomposition included site, plot type, total nitrogen, and a two-way interaction as predictor variables for decomposition constant (kD).

## Results

### *Vegetation*

The amount and type of vegetation cover differed between the two sampled sites in control plots. Control plots had over twice as much bare ground at Danby State

Forest (DSF) than at Taughannock Falls State Park (TFSP, 47.7% vs 21.3%,  $Z = -2.927$ ,  $p = 0.003$ ), 11x the native shrub density (12.3% vs. 1.1%,  $Z = -3.109$ ,  $p = 0.002$ ), and half the total herb density (33.7% vs. 68.7%,  $Z = -2.900$ ,  $p = 0.004$ ). Control plots at both sites had less than 1% *B. sylvaticum* cover ( $Z = -1.000$ ,  $p = 0.317$ ), and similar invasive shrub density ( $Z = -1.925$ ,  $p = 0.054$ , figure 1). *Brachypodium* plots at DSF and TFSP both had >50% *B. sylvaticum* cover but cover at TFSP was higher ( $Z = -3.191$ ,  $p = 0.001$ ). At DSF, control plot herb and bare ground percent cover was 33.7% and 37.7% respectively while *Brachypodium* plot herb and bare ground percent cover was 6.8% and 8.6% respectively. At TFSP, a similar reduction in herb and bare ground cover occurred between control and *Brachypodium* plots (herb cover 68.7% to 5.2%, bare ground cover 21.3% to 3.13%)

### Soils

Soil textures were similar when compared across plot types; however, subtle differences can change the soil type and drainage patterns of soils. A web soil survey at (<https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>) revealed similar soils between the sites with silt-loams as the dominant soil texture at both sites. Soils at TFSP also ranged from well-drained to moderately well-drained and soils at DSF ranged from poorly drained to well-drained, indicating similarities between the sites, but a reduction in drainage within some DSF soils. Soils at DSF were relatively similar with 7.7% greater clay content in *Brachypodium* plots. However, silt content at TFSP was only 4.7% greater in control plots (table 1).

All modeled soil characteristics except soil phosphorus differed significantly between sites, and site was the most common predictor variable in the soil GLMMs (table 2). Danby State Forest had significantly higher organic matter ( $F = 12.133$ ,  $df_1 = 1$ ,  $df_2 = 46$ ,  $p = 0.001$ , figure 2a) and total nitrogen ( $F = 12.924$ ,  $df_1 = 1$ ,  $df_2 = 48$ ,  $p = 0.001$ , figure 2b), while TFSP had significantly higher pH (6.23 vs 5.18,  $F = 4.770$ ,  $df_1 = 1$ ,  $df_2 = 50$ ,  $p = 0.034$ , figure 2c) and cations (1.04 % vs 0.57%,  $F = 7.617$ ,  $df_1 = 1$ ,  $df_2 = 47$ ,  $p = 0.008$ , figure 2d). Site was the only variable that significantly affected bulk density; TFSP had significantly denser soils (0.927 g/cm<sup>3</sup> vs. 0.803 g/cm<sup>3</sup>  $F = 10.3$ ,  $df_1 = 1$ ,  $df_2 = 58$ ,  $p = 0.002$ ; figure 2e).

*Brachypodium* plots differed from control plots for all soil models except bulk density, although plot type effects were often site dependent. Compared to control plots, *Brachypodium* plots were significantly enriched in nitrogen and organic matter at TFSP and reduced at DSF (figure 2a, 2b). As a result, differences between organic matter and total nitrogen between sites were smaller in *Brachypodium* plots than control plots, resulting in significant site\*plot type interactions for both variables in their respective models ( $F=8.887$ ,  $df_1 = 1$ ,  $df_2 = 46$ ,  $p = 0.005$ ,  $F=14.964$ ,  $df_1 = 1$ ,  $df_2 = 2$ ,  $p = 0.000$ , table 2). Soil phosphorus was significantly greater in *Brachypodium* plots at DSF, but not at TFSP (figure 2f). Since P values were similar in control plots between the sites, this resulted in a significant site\*plot interaction ( $F = 6.563$ ,  $df_1 = 1$ ,  $df_2 = 55$ ,  $p = 0.013$ ) and plot type effect ( $F = 8.983$ ,  $df_1 = 1$ ,  $df_2 = 55$ ,  $p = 0.004$ ) in the model (table 2).

At both DSF and TFSP, *Brachypodium* plots were significantly enriched in cations ( $F = 5.300$ ,  $df1 = 1$ ,  $df2 = 47$ ,  $p = 0.026$ , figure 2d) and had increased pH ( $F = 4.603$ ,  $df1 = 1$ ,  $df2 = 50$ ,  $p = 0.037$ , figure 2c). The lack of a plot type \* site interaction indicated the effect of plot type was consistent across DSF and TFSP. Soil moisture changed predictably on a diel cycle and following rain events (figure 3). In the spring, average soil moisture was at its highest around 0.400% v/v with a steady decrease until mid-June and early July where it stayed around 0.200-0.300% v/v for the remainder of the study. At DSF, *Brachypodium*-invaded plots were, on average, moister than control plots with few times where the inverse was true (0.235% v/v vs. 0.217% v/v). Conversely, at TFSP control plots were often wetter than *Brachypodium* plots (0.279% v/v vs. 0.239 % v/v, figure 3). Soil moisture models indicated plot type was an important factor at DSF, but not at TFSP ( $F = 13.372$ ,  $df1 = 1$ ,  $df2 = 69$ ,  $P = 0.000$ ). At both sites sample number, openness, and bulk density were also significant predictors of soil moisture (table 3).

There were no common significant predictor variables for soil respiration between DSF and TFSP. This is evident not only in the separated models, but also in the combined models where site became a significant factor when interacting with plot type, sample number, and canopy openness (table 4). In DSF, *B. sylvaticum* plots had higher respiration rates than control plots (17.1 mol  $\text{CO}_2/\text{m}^2/\text{s}$  vs. 8.3 mol  $\text{CO}_2/\text{m}^2/\text{s}$ , figure 4), and plot type was the strongest predictor of respiration in the model.

At TFSP, plot type was not a significant predictor of soil respiration. Instead, important predictor variables were sample number, canopy type, average soil moisture

the week before, and bulk density (table 4). Sample number was effectively time of year, with the highest efflux at four samples between 16 June 2020, and 18 August 2020 (26.4, 21.5, 22.8, and 23.6 mol CO<sub>2</sub>/m<sup>2</sup>/s) and the lowest efflux on 5 May 2020 (5.9 mol CO<sub>2</sub>/m<sup>2</sup>/s, figure 5). Canopy type also significantly altered soil carbon dioxide efflux at TFSP with deciduous canopies supporting higher respiration than mixed canopies (16.6 vs. 13.5 mol CO<sub>2</sub>/m<sup>2</sup>/s). Higher efflux was associated with lower soil moisture and greater bulk density. At DSF, soil moisture was positively correlated with respiration rate, while at TFSP soil moisture was negatively correlated with soil respiration rate, neither of which were statistically significant (figure 6).

### *Litter*

*Brachypodium sylvaticum* leaf litter was more N- and P-rich and had lower carbon and lignin than co-occurring *A. saccharum* or *F. grandifolia*, although differences were not always statistically significant (table 5). Leaf litter calcium, magnesium, and lignin were all lower in *B. sylvaticum* than tree counterparts, however the magnitude of differences were inconsistent (table 5). *Brachypodium sylvaticum* litter collected from TFSP had the lowest C:N, C:P, and N:P ratios. N:P was not significantly different between species while DSF *B. sylvaticum* C:N was significantly lower than *A. saccharum* and TFSP *B. sylvaticum* C:P was significantly lower than *F. grandifolia* (table 5).

Of the ten metrics correlated with decomposition rate via Spearman's Rho, only phosphorus and nitrogen were still significant after a Holms-Bonferroni correction (table 6). Total nitrogen was used as a predictor variable rather than

phosphorus because nitrogen is often cited as an important predictor of leaf litter decomposition. Decomposition rate increased exponentially with increased soil nitrogen (figure 7). The significant predictors of decomposition rate were site, plot type, total nitrogen, and plot type \* total nitrogen (table 7). Decomposition rate was significantly higher at TFSP (average  $k_d = 1.98$  vs. average  $k_d = 1.18$ ,  $F = 24.854$ ,  $df_1 = 1$ ,  $df_2 = 620$ ,  $p = 0.000$ , Figure 8). At both sites *Brachypodium* plots had faster decomposition rates than control plots overall, and plot was a significant predictor of decomposition constant ( $F = 9.202$ ,  $df_1 = 1$ ,  $df_2 = 620$ ,  $p = 0.003$ ). Total nitrogen content conditionally influenced decomposition rate based on plot type, which is shown through the plot type \*total nitrogen interaction (table 5). *Brachypodium* plots had higher decomposition rates ( $k_d$ ) at low total nitrogen concentrations, which were the filter paper and tree litter types, and for TFSP *B. sylvaticum* litter. However, for DSF *B. sylvaticum* litter, the most nitrogen-rich litter type, control plots had similar or faster decomposition rates (Figure 8). Site had no significant interactions with plot type, or total nitrogen, indicating variables influenced decomposition rate similarly between DSF and TFSP (table 7).

## Discussion

Despite attempts to find general patterns of invasive species impacts on ecosystem function (Ehrenfeld 2003, Liao *et al.* 2008), additional research is important and ongoing as invasive species effects are nuanced and often site-specific. My study investigating an invasive species' impacts on soil nutrients and soil processes exemplifies this conclusion. The invasion of *B. sylvaticum* into forested ecosystems

had a significant impact on soil properties in both sampled state parks, as I hypothesized. Every parameter measured was affected by invasion in one or both sites. Overall, *B. sylvaticum* invasion in these sites is partially consistent with previous work that suggests that invasive species typically increase nutrient pools and rates of nutrient cycling (Belnap and Phillips 2001, Ehrenfeld 2003). The impact that invaders have on ecosystems depends on initial site characteristics, invader ecology, and differences in resource utilization (Vitousek 1990, Liao *et al.* 2008). My results, like previous studies, indicate the influence of site must be considered when examining invasion impact (Vanderhoeven *et al.* 2005, Dasonville *et al.* 2008, Rodgers *et al.* 2008). Fundamental differences between sampled sites in control plots affected the degree, direction, and significance of *B. sylvaticum*'s impact on some ecosystem properties. Nonetheless, five of the ecosystem properties measured here were consistently affected by *B. sylvaticum* in direction of effect, regardless of site differences.

My study found both an increase in soil cations and soil pH, which supported by hypotheses. Weathering of parent material and atmospheric inputs are often cited as main sources of cations (Chapin *et al.* 2011), however we can assume that the parent material and atmosphere are the same within respective sites because of the proximity and paired placement of study plots. The significant difference in cations between *Brachypodium* and uninvaded plot types can then most likely be caused by the difference in prevailing vegetation. This change in soils has also been noted in invasive garlic mustard (*Alliaria petiolata*, Ehrenfeld *et al.* 2001, Rodgers *et al.* 2008). Although *A. petiolata* is a biennial herb and *B. sylvaticum* is a perennial bunch grass, they

apparently alter hardwood-conifer forest soil cations and pH similarly. Ehrenfeld noted an increase in pH as being consistent in invaded systems that were also nitrogen enriched, which is another change in soil caused by *B. sylvaticum* in my study. Another potential explanation was proposed by Rodgers *et al.* who hypothesized the increase in pH under *A. petiolata* was caused by root exudates. Since *B. sylvaticum* is a perennial that competes fiercely in its invaded region, there may also be root exudates playing a role in its success.

Decomposition, an ecosystem function that relies on soil nutrients and leaf litter nutrients (Ashton *et al.* 2005), was significantly influenced by invasion at both sites. In my study the decomposition rate was significantly higher in *B. sylvaticum* invaded plots. The cause of this change may be attributed to the nutrient enrichment of the soils under the invaders and the change in microhabitat factors like soil moisture and fine root biomass. Increased soil moisture and fine root biomass are important for decomposition rate because increased root exudates and water speed up microbe function (Reth *et al.* 2005). The ability of invasive species to alter decomposition rates has been studied extensively and often invasive species have been found to decompose more readily than natives. A meta-analysis found invasive species often had performance-enhancing traits related to leaf chemistry and structure (Van kleunen *et al.* 2010), which enhance decomposability by being nutrient rich, and lower in recalcitrant compounds like lignin (Ashton *et al.* 2005, Cornwell *et al.* 2008). Species included in my study were from different functional groups, different invasion status, and different vegetation layers. However, pale swallowwort, which was found

alongside *B. sylvaticum* at TFSP also had significantly faster decomposition rates than some native counterparts (Leonardi and Amatangelo unpublished data). These results agree with existing research and support my hypotheses that invasive litter would be higher quality and that it would decompose faster than native litter.

Soil respiration was consistently enriched in *Brachypodium* plots at both sites when compared to control. The change in pH may have been the cause of the increase in soil respiration. As previous research found, pH levels along a gradient create unique bacterial and fungal communities (Zhalnina *et al.* 2014), so the 0.3 greater pH in invaded plots may be a contributing factor to its heightened soil respiration. Other studied species like *A. petiolata* and *B. thunbergii* have also been noted to change pH and soil nutrients which altered soil respiration (Kourtev *et al.* 2002). The changes in soils *B. sylvaticum* can be linked to multiple variables, such as nutrient enrichment, changes in pH and water availability, which are all viable explanations for the changes seemingly caused by differences in prevailing vegetation. While the effect of *B. sylvaticum* on soil respiration at TFSP was statistically significant, it was less of an effect than plots experienced at DSF. This may be due to the heavy presence of pale swallowwort at TFSP, which has known allelopathic root exudates that inhibit fungi function and leaf consumers (Mogg *et al.* 2008). Soil moisture is often cited as an important factor mediating soil respiration (McCulley *et al.* 2004, Simpson *et al.* 2012); however, it was insignificant in the DSF generalized linear mixed model, while it was significant in the combined model and at TSF where impacts on respiration were much

smaller. This may be due to the lack of replicates and lack of data, as many of the soil moisture probes were predated by mice.

Contrary to my hypotheses, soil organic matter, soil phosphorus, and soil nitrogen content did not have consistent effects from invasion across sites. One of my two sites, TFSP exhibited the expected pattern of significant enrichment in organic matter and total nitrogen with invasion, while phosphorus was significantly enriched only at DSF I expected there to be a significant difference between these soil nutrients because of the increase in higher-quality leaf litter, increased fine root biomass, and previous studies found similar impacts from other invaders. At DSF, nitrogen and organic matter contents were statistically equal between plot types, contrary to my predictions. I anticipated soil to be significantly enriched because uninvaded plots had an average of ~47% bare ground compared to ~8% bare ground in invaded plots and leaf litter additions following invasion are cited as contributors to impacts on soils (Allison and Vitousek 2004). It is possible increased plant cover did not translate to increased fine root biomass in the plots, or that the fine root biomass had not yet been incorporated into soil pools. Interestingly, soil respiration was significantly higher (~51%) in invaded plots at DSF, and the amplification of respiration was much greater than at Taughannock where nitrogen and organic matter were significant. Lack of difference between organic matter and total nitrogen of soils at DSF indicates they are not limiting microbial activity. The fundamental differences between the control and *Brachypodium* plots could have been a contributing factor to an inconsistent effect of invasion between sites, particularly in the impact of invasion on respiration. Vegetation

cover on the ground was much lower in control plots at Danby than at Taughannock. Increased fine root biomass and root exudates could prime soil respiration (Bird *et al.* 2011).

Another factor that could contribute to heightened soil respiration in invaded plots at DSF is canopy openness. One study found that temperature and water content of soils induced by canopy cover (opposite of canopy openness) had a more significant impact on soil respiration than leaf litter or fine-root biomass by showing that soil respiration was positively related to soil moisture until saturation, where respiration then decreased. (Liu *et al.* 2014). At DSF, canopy openness was close to being a significant predictive variable in the soil respiration model. Although the difference between openness above the invaded plots was less than 1% greater (11.25% vs 10.65%) than the canopy above uninvaded plots, the factor was still included in the model, which suggests it has some predictive ability as a factor.

Initial site conditions may be predictive of an invader's effect on an ecosystem's structure and function. Previous studies have found significant site-specific effects from invasion that influenced soil enrichment of sites (Vanderhoeven *et al.* 2005). One study (Dassonville *et al.* 2008) found different responses to invasion based on initial site soil nutrients. This 2008 study by Dassonville *et al.* showed sites that were initially nutrient rich or nutrient deficient experienced equalizing effects where the rich sites had reduced soil nutrients and deficient sites had soils enriched with nutrients (Dassonville *et al.* 2008). If the control plots in my study are used as a proxy for "plots before invasion", there is a similar type of equalizing effect on organic matter, total

nitrogen, and calcium when *B. sylvaticum* invaded where dissimilar control plots begin to look more similar following invasion (Figure 3). The contrasting effects of *B. sylvaticum* at DSF and TFSP stress the importance of replicating studies across sites and initial site conditions. Invasive species often produce far more biomass than native species (Sakai *et al.* 2001, Ehrenfeld 2003, Aguilera *et al.* 2010) which can lead to differential resource usage by invaders.

Research regarding the impacts of *B. sylvaticum* is mainly focused on control efforts and community level impacts, however my work indicates there might be soil impacts caused by this invasive grass. Future research should focus on active/soluble soil nutrients rather than total nutrients because my work may not have shown the complete story of how *B. sylvaticum* alters soil chemistry. Measuring root biomass changes in invaded areas should also be studied. The possibility of root exudates interfering with soil microbial communities is a long-term impact of *B. sylvaticum* that can condition soils for years even if the species is removed.

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Tables

Table 1. Summary of soil texture analysis via hydrometer. A Wilcoxon signed rank test examined differences between plot types within each site with no significant difference emerging. N = 3.

	<b>Danby</b>		<b>Taughannock</b>	
	<b>Brachypodium</b>	<b>Control</b>	<b>Brachypodium</b>	<b>Control</b>
<b>Sand</b>	27 ± 2%	32 ± 2%	25 ± 0.5%	25 ± 2%
<b>Silt</b>	39 ± 3%	42 ± 0.4%	39 ± 1%	44 ± 0.3%
<b>Clay</b>	34 ± 2%	26 ± 1%	35 ± 1%	31 ± 1%

Table 2. Summary of generalized linear mixed models made for major soil nutrients. A gamma distribution was used with a log link to assess factors influence on each response variable and plot number was included as a random effect block. All models started with the same four univariate factors and ten 2- or 3-way interactions. The backwards selection method was used with Akaike's Information Criterion corrected for small sample size (AICc) to determine the appropriate factors for each model.

	<b>Organic matter</b>		<b>Total nitrogen</b>		<b>Phosphorus</b>		<b>pH</b>		<b>Cations</b>		<b>Bulk density</b>	
<b>Model AICc</b>	<b>40.184</b>		<b>19.648</b>		<b>-46.751</b>		<b>160.911</b>		<b>62.150</b>		<b>-38.100</b>	
	<b>included</b>	<b>sig</b>	<b>included</b>	<b>sig</b>	<b>included</b>	<b>sig</b>	<b>included</b>	<b>sig</b>	<b>included</b>	<b>sig</b>	<b>included</b>	<b>sig</b>
<b>Type</b>	x		x		x	x	x	x	x	x		
<b>Site</b>	x	x	x	x	x		x	x	x	x	x	x
<b>Openness</b>	x		x				x	x	x			
<b>Total veg</b>	x		x		x		x		x	x		
<b>Type * site</b>	x	x	x	x	x	x	x		x			
<b>Type * openness</b>	x		x				x		x			

Type * Total veg	x						x		x	x		
Site * openness	x	x	x	x					x			
Site * total veg	x	x	x	x			x		x			
Openness * total veg	x		x						x	x		
Type * site * openness	x	x	x	x								
Type * site * total veg							x	x	x	x		
Type * openness * total veg	x								x	x		
Site * openness * total veg	x	x	x	x								

Table 3. Summary of soil moisture models. Danby State Forest indicated by DSF, and Taughannock Falls State Park indicated by TFSP. Sample variable was an indicator for time of season when a sample was collected.

Site	AICc	Variables	F	df1	df2	sig
<b>DSF and TFSP</b>	98.49	Plot type	12.27	1	146	0.001*
		Sample	23.82	9	146	<0.001*
		Bulk density	5.743	1	146	0.010*
<b>DSF</b>	46.94	Plot type	13.37	1	69	<0.001*
		Sample	15.44	8	69	0.001*
		Openness	3.623	1	69	0.061
		Bulk density	7.256	1	69	0.009*
<b>TFSP</b>	47.83	Sample	20.33	8	65	<0.001*
		Canopy	5.263	1	65	0.025*
		Openness	15.71	1	65	<0.001*
		Bulk density	37.01	1	65	<0.001*

Table 4. Summary of generalized linear models for soil carbon dioxide efflux with soil moisture as a predictor variable. A gamma distribution was used with a log link to assess factors influence on each response variable and plot number was included as a random effect block. Akaike's Information Criterion corrected for sample size indicated by AICc and F value as the test statistic. Asterisk \* represents predictor variables that reached the  $p < 0.05$  significance threshold.

Site	AICc	Variables	F	df1	df2	sig
<b>DSF and TFSP</b>	214.204	Site	2.298	1	133	0.132
		Plot type	32.98	1	133	0.000*
		Type * site	10.45	1	133	0.002*
		Julian	7.782	9	133	0.000*
		Site * julian	5.75	7	133	0.000*
		Openness	3.178	1	133	0.077
		Site * openness	4.436	1	133	0.037*
		Avg SM week before	7.657	1	133	0.006*
		Bulk density	5.645	1	133	0.019*
		Avg SM week before * bulk density	6.251	1	133	0.014*
		<b>DSF</b>	127.594	Plot type	35.76	1
Julian	1.878			8	66	0.078
Canopy type	1.537			2	66	0.223

		Openness	3.701	1	66	0.059
		Plot type*canopy	2.812	1	66	0.067
<b>TFSP</b>	54.665	Plot type	0.179	1	62	0.673
		Julian	14.91	8	62	0.000*
		Canopy type	13.12	1	62	0.001*
		Plot type*canopy type	2.57	1	62	0.114
		Avg SM week before	6.019	1	62	0.017*
		Bulk Density	20.93	1	62	0.000*
		Average SM week before* bulk density	5.516	1	62	0.022*

Table 5. Average nutrient contents with standard error of plant material of *Brachypodium sylvaticum* (BRSY(D)), *Acer saccharum* (ASCA), and *Fagus grandifolia* (FAGR) sourced from Danby State Forest and *Brachypodium sylvaticum* (BRSY(T)) sourced from Taughannock Falls State Park. Filter paper (FIPA) was used as a comparison. The direction of difference is indicated in the final column, which depicts which litters were significantly different from each other and the direction of that difference, with equal signs indicating no difference.

	<b>BRSY (D)</b>	<b>BRSY (T)</b>	<b>ACS A</b>	<b>FAG R</b>	<b>FIPA</b>	<b>Direction</b>
<b>Acid</b>	40.01 ±	38.93 ±	40.35	51.39	94.58	BRSY(T)<FAG
<b>Detergent</b>	0.51	0.43	± 0.6	± 0.54	± 1.71	R
<b>Fiber (ADF)</b>						
<b>Lignin %</b>	5.35 ±	3.07 ±	13.59	16.35	0.01 ±	BRSY(T)<FAG
<b>DM</b>	0.33	0.25	± 0.41	± 0.36	0	R
<b>Phosphorus</b>	0.17 ±	0.21 ±	0.12 ±	0.11 ±	0.01 ±	=
<b>% DM</b>	0.01	0.01	0.01	0.01	0	
<b>Calcium %</b>	0.38 ±	0.35 ±	1.58 ±	0.79 ±	0.04 ±	BRSY(T)<ACS
<b>DM</b>	0.02	0.04	0.05	0.01	0.01	A
<b>Potassium</b>	1.11 ±	1.23 ±	0.36 ±	0.67 ±	0.02 ±	BRSY(T)>ACS
<b>% DM</b>	0.04	0.11	0.02	0.02	0.01	A

<b>Magnesium</b>	0.13 ±	0.1 ±	0.17 ±	0.19 ±	0.01 ±	BRSY(T)<FAG
<b>% DM</b>	0.01	0.02	0.01	0.01	0	R
<b>Total</b>	1.87 ±	1.72 ±	0.97 ±	1.12 ±	0.28 ±	BRSY(D)>ACS
<b>Nitrogen %</b>	0.05	0.07	0.01	0.01	0.02	A
<b>DM</b>						
<b>Total</b>	40.43 ±	39.32 ±	44.74	45.67	42.05	BRSY(T)<FAG
<b>Carbon %</b>	0.36	0.43	± 0.11	± 0.1	± 0.25	R
<b>DM</b>						
<b>C:N</b>	21.67 ±	22.85 ±	45.96	40.9 ±	152.32	BRSY(D)<ACS
	0.73	1.17	± 0.27	0.19	± 8.92	A
<b>C:P</b>	233.42 ±	187.51 ±	384.0	403.62	4205 ±	BRSY(T)<FAG
	7.82	9.26	7 ±	±	25.06	R
			18.68	19.08		
<b>N:P</b>	10.78 ±	8.21 ±	8.36 ±	9.87 ±	27.67	=
	0.51	0.26	0.4	0.47	± 1.53	
<b>Lignin:N</b>	2.87 ±	1.78 ±	13.96	14.64	0.04 ±	BRSY(T)<FAG
	0.24	0.15	± 0.35	± 0.25	0	R

Table 6. Spearman's rho correlation matrix between decomposition rate and each leaf nutrient was deemed as potentially important. Sample size was five for each variable. A correction factor was used in the analysis as part of the Holms-Bonferroni correction to yield an adjusted p threshold. The variable that was still significant after the correction factor is indicated by an asterisk (\*).

	<b>P</b>	<b>TN</b>	<b>C:N</b>	<b>TC</b>	<b>ADF</b>	<b>DM</b>	<b>Cations</b>	<b>Lignin</b>	<b>Lignin:N</b>	<b>N:P</b>
<b>Correlation</b>	0.913	0.892	-0.583	-0.379	-0.306	0.108	0.059	0	0	0
<b>Coefficient</b>										
<b>Sig. (2-tailed)</b>	0.03*	0.042*	0.302	0.53	0.617	0.863	0.925	1	1	1

Table 7. Generalized linear mixed model summary of models using decomposition constant as the response variable. A gamma log distribution with a log link was used to assess the response variable and plot number was included as a random effect block. Akaike's Information Criterion corrected for small sample size (AICc) was a metric that helped assess model adequacy.

	<b>AICc</b>	<b>Variable</b>	<b>F</b>	<b>df1</b>	<b>df2</b>	<b>p</b>
<b>DSF and TFSP</b>	1444.91	Site	24.854	1	620	0.000*
		Plot type	9.202	1	620	0.003*
		Total leaf nitrogen	694.537	1	620	0.000*
		Plot type * total leaf nitrogen	6.181	1	620	0.013*
<b>DSF</b>	766.823	Plot type	3.736	1	363	0.054
		Total leaf nitrogen	452.884	1	363	0.000*
		Plot type * total leaf nitrogen	2.752	1	363	0.098
<b>TFSP</b>	655.258	Plot type	5.874	1	254	0.016*
		Total leaf nitrogen	273.692	1	254	0.000*
		Plot type * total leaf nitrogen	3.852	1	254	0.051

Figures

Part one

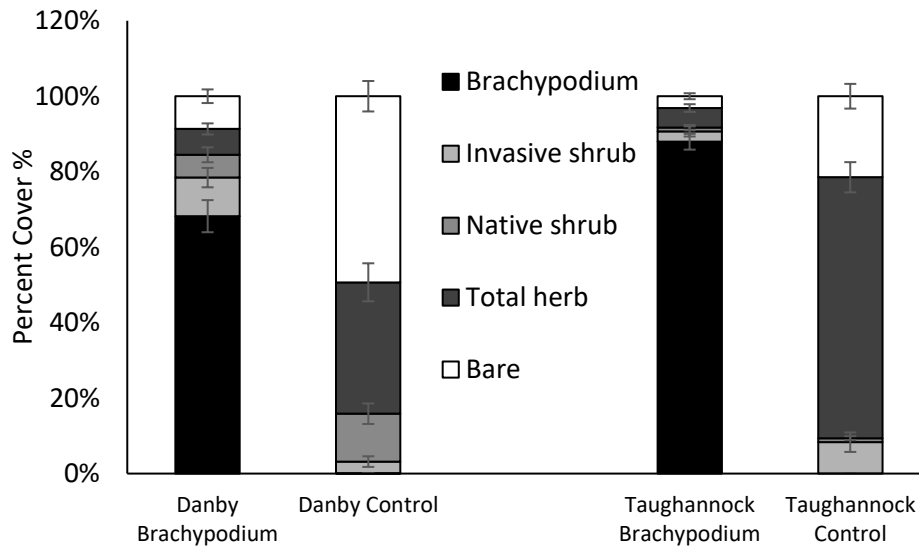


Figure 1. Vegetation categories compared across study site and plot type. Vegetation plot data was collected during the 2019 field season.

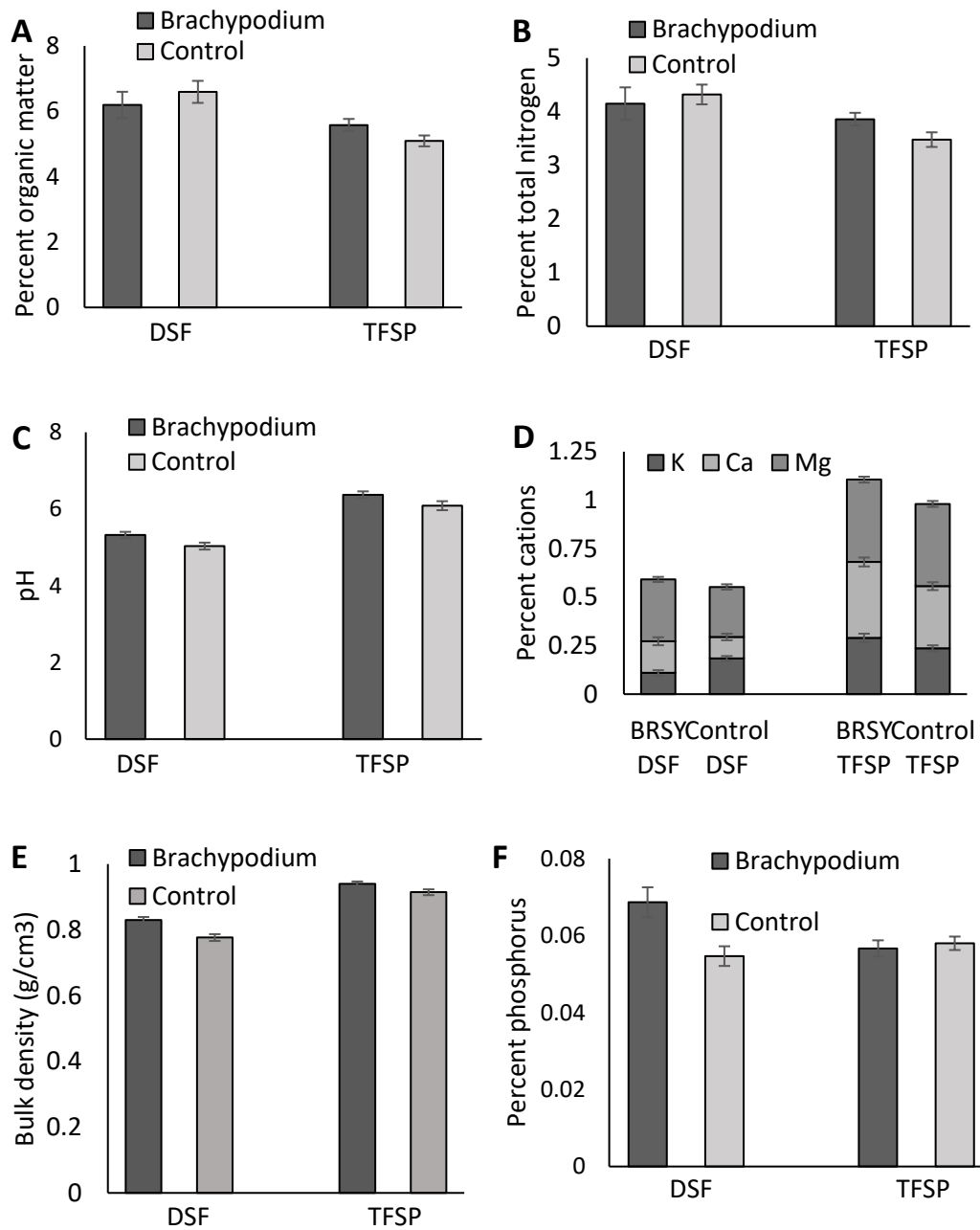


Figure 2. Panel diagram of the different soil metrics. Panels A-F are for soil parameters organic matter, total nitrogen, phosphorus, cations, pH, and bulk density respectively. Note different scales. Darker left bars are invaded plot averages while lighter right bars are uninvaded plot averages. Standard error bars used to account for sample size.

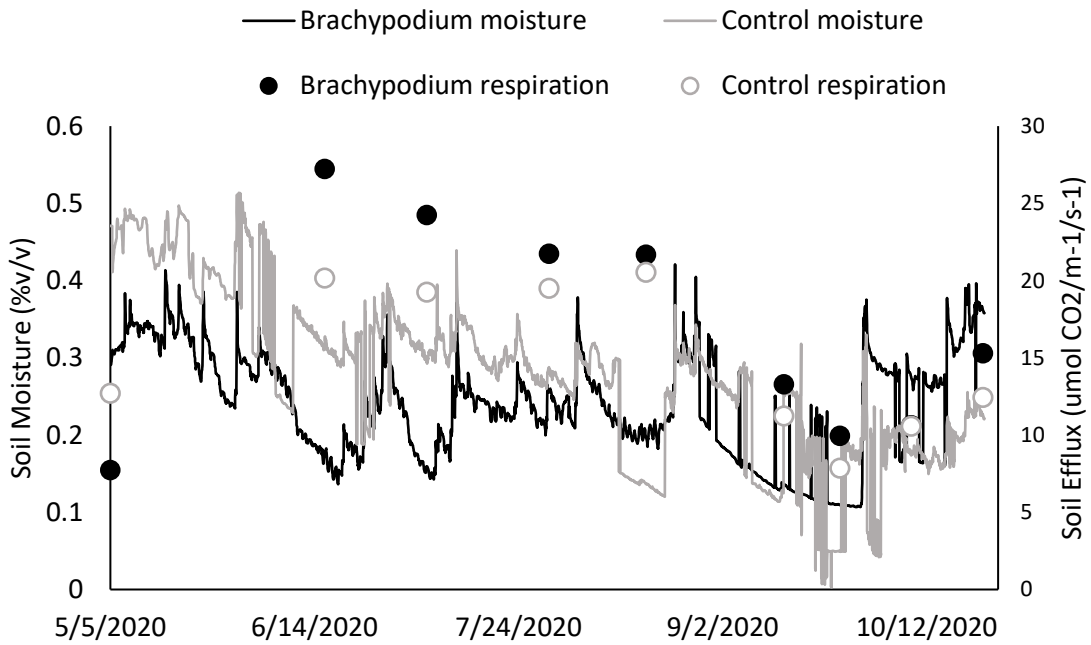
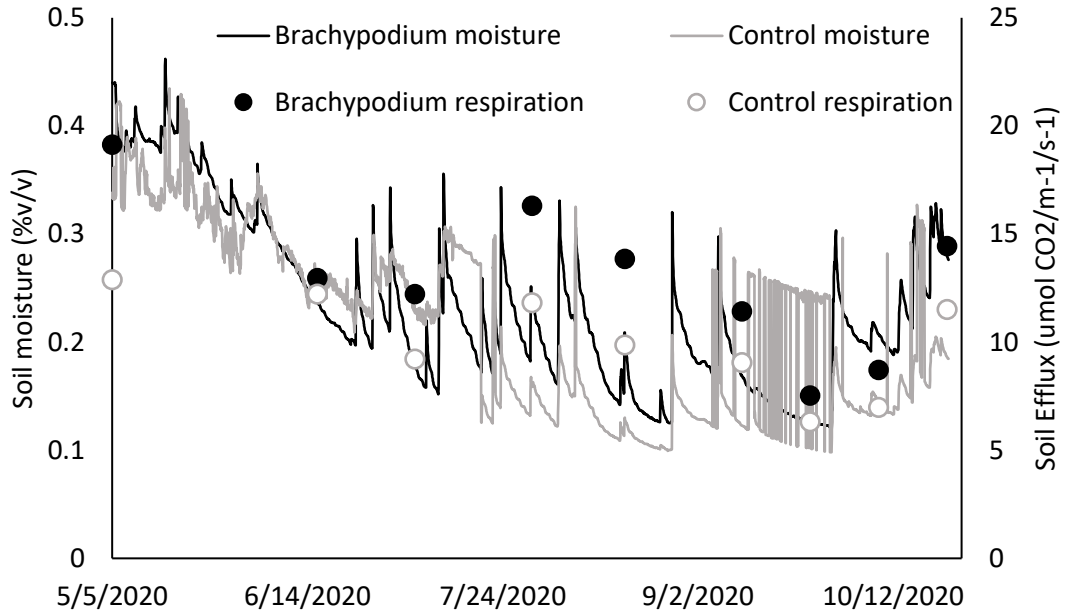


Figure 3. The top figure displays average moisture within Control and *Brachypodium* plots within Danby State Forest. The bottom figure shows the average moisture within

Control and *Brachypodium* plots within Danby State Forest. Data measured continuously throughout the growing season, with soil respiration measurements overlaid.

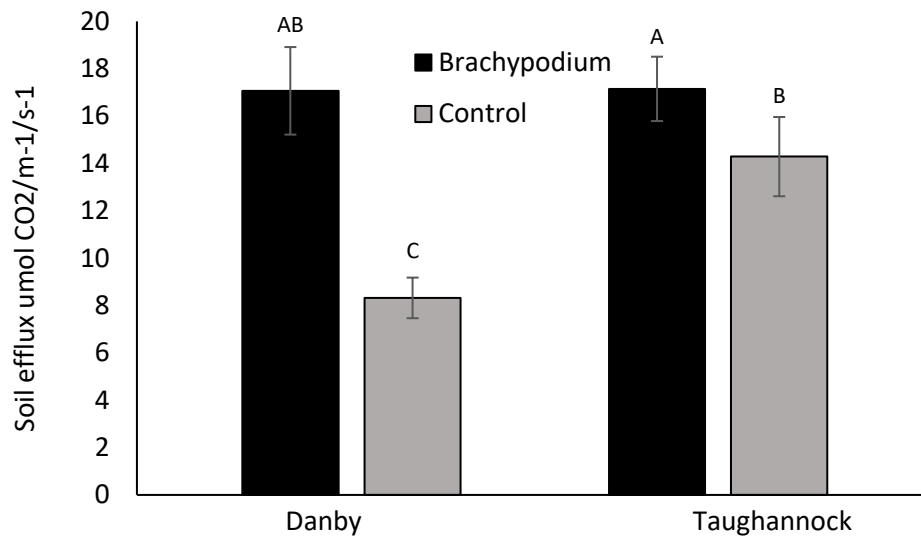


Figure 4. Average soil efflux (CO<sub>2</sub>/m<sup>-1</sup>/s<sup>-1</sup>) by sites and plot types. The left cluster of bars are Danby State Forest plots, right cluster of bars are Taughannock Falls State Park plots. Dark fill and dark lines are *B. sylvaticum* plots while grey fill and grey lines are uninvaded control plots. Standard error was used to correct for sample size.

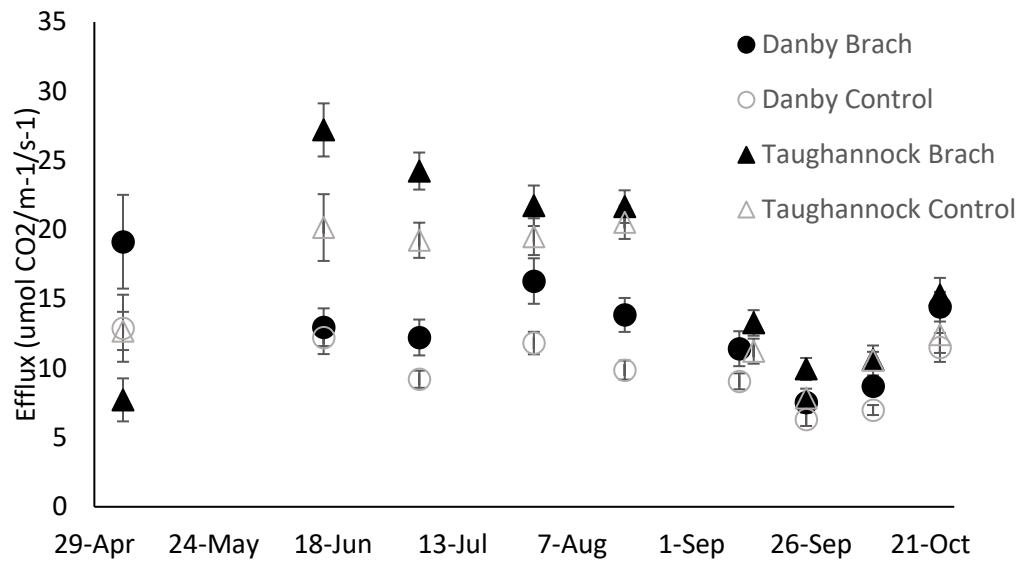


Figure 5. Soil respiration throughout the field season of this project. Each point, which corresponds to different site/plot combinations, represent average of all DSF *Brachypodium* plots at time of sample. Standard error bars applied to correct for sample size.

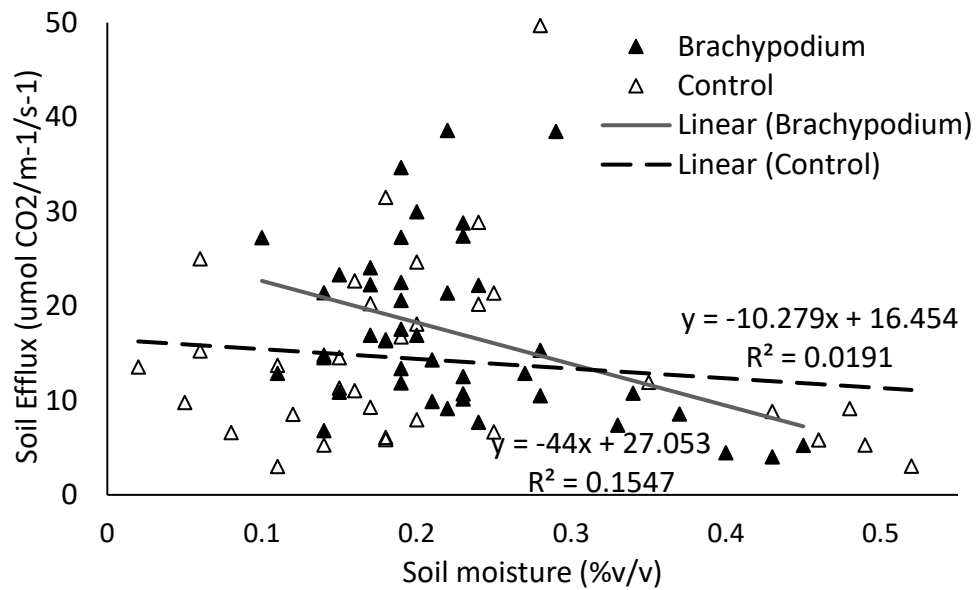
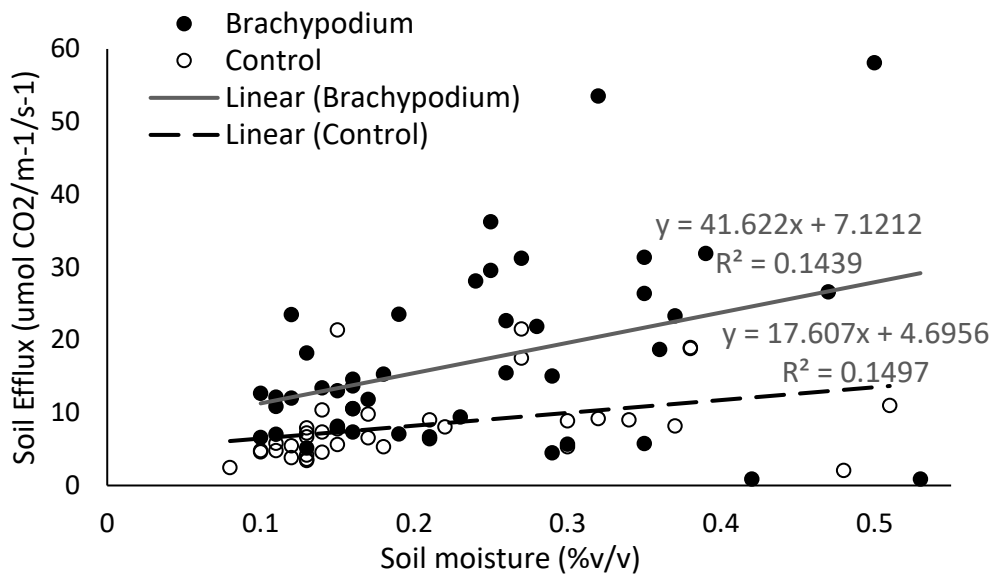


Figure 6. Soil respiration versus soil moisture. The top figure is for DSF, bottom figure shows TFSP.

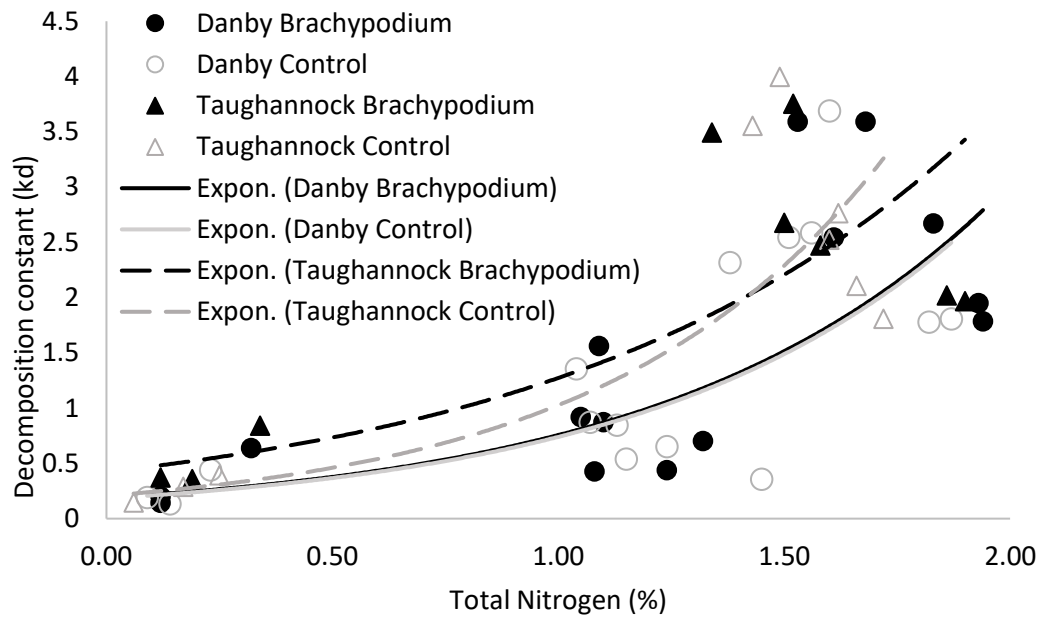


Figure 7. Decomposition constant and corresponding total nitrogen values for each litter nutrient sample. Different color/shape combinations indicate site and plot types.

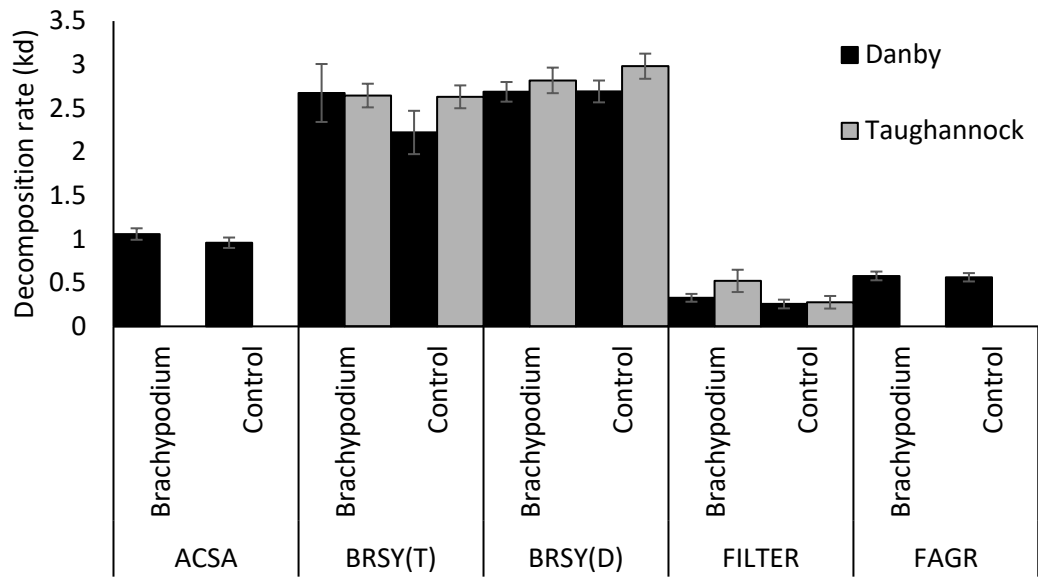


Figure 8. Decomposition constants (kd) measured for each species that was used in the litterbag experiment within the two plot types at both DSF and TFSP.

Part two:

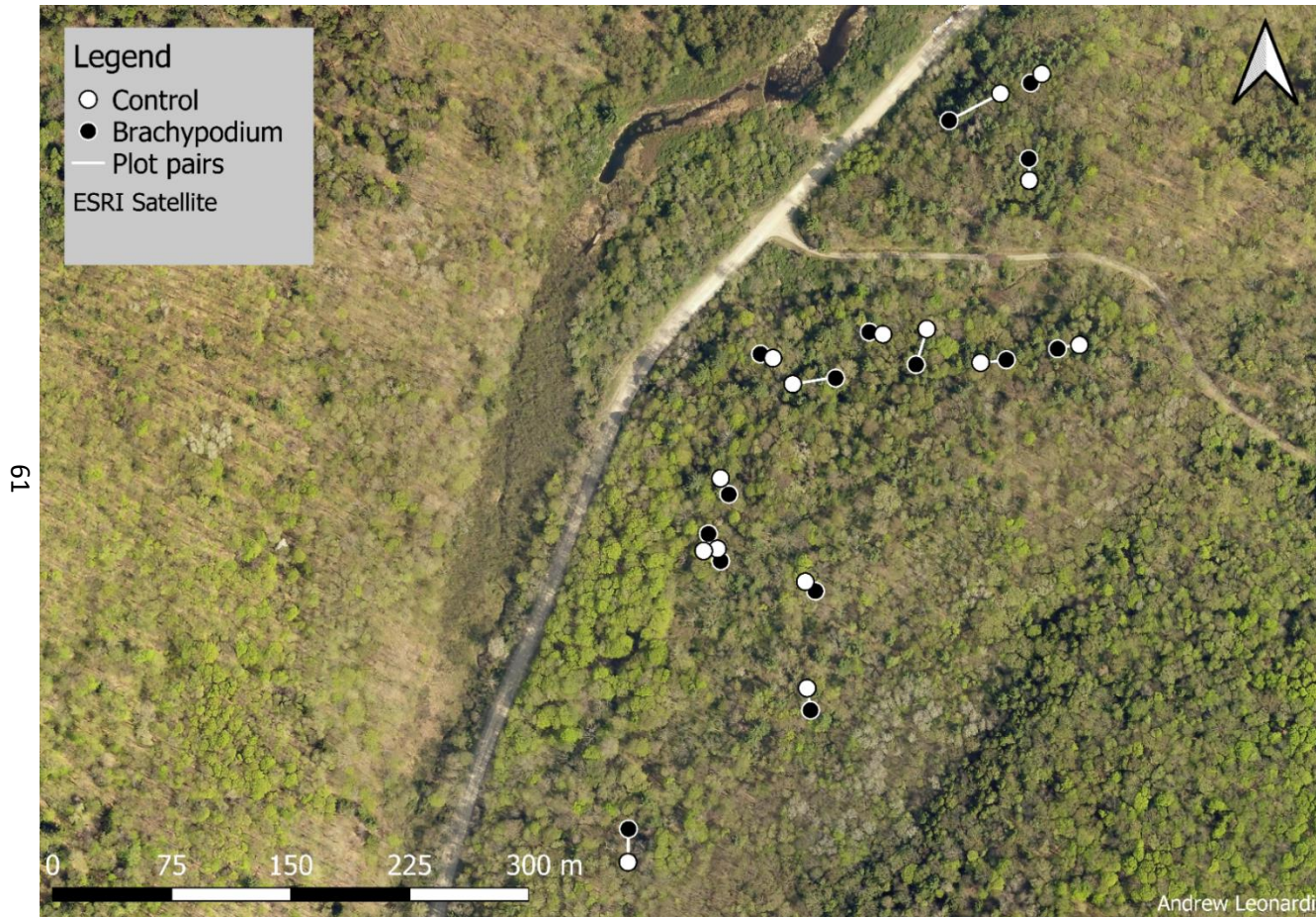


Figure 9. Map of experiment site at Danby State Forest.

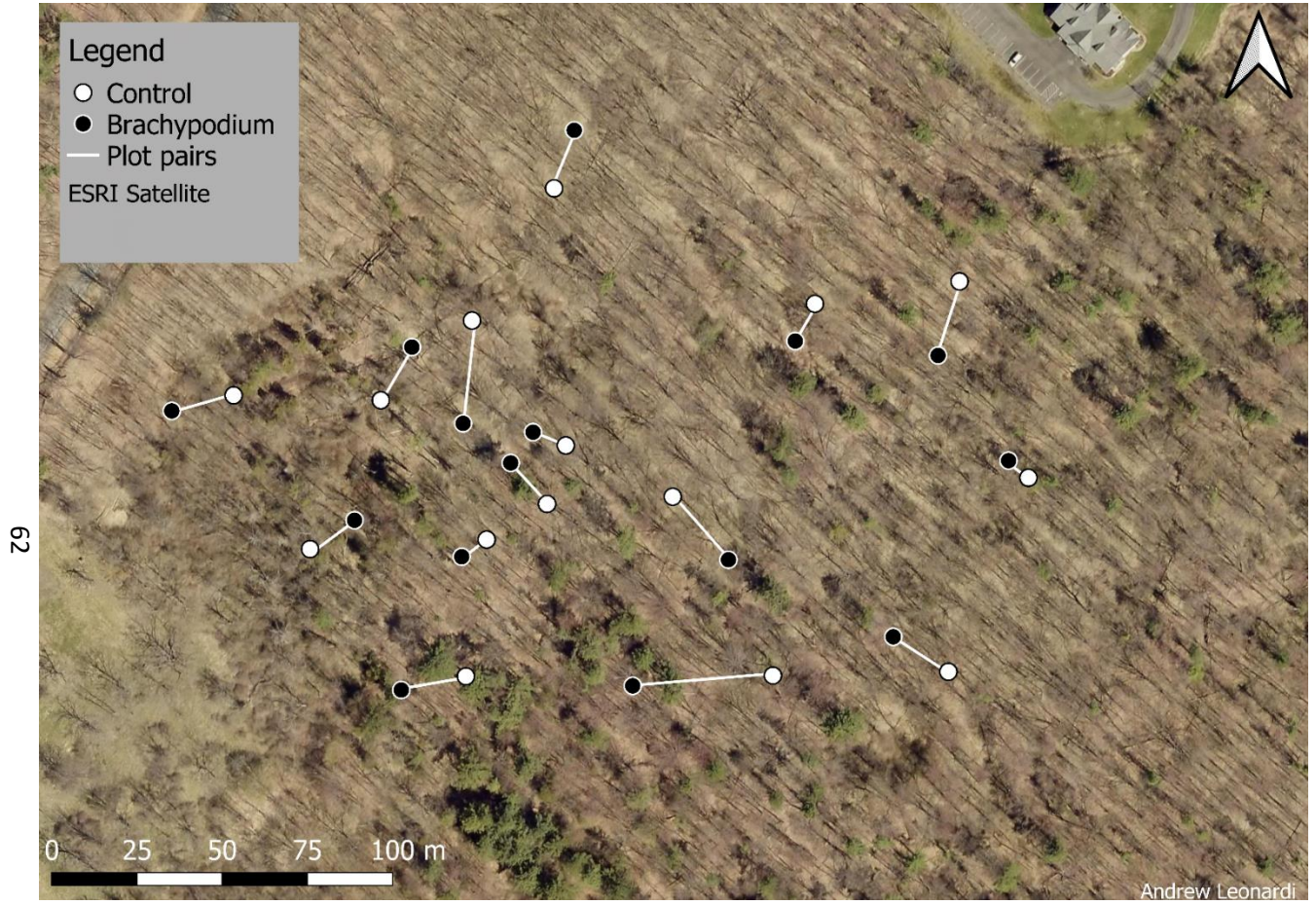


Figure 10. Map of experiment site at Taughannock Falls State Park.