The effects of different disturbance regimes in a state park on plant community and invasion dynamics

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Riley Metz

Bachelor of Sciences

Submitted in partial fulfilment of the requirements for

College Honors

Departmental Distinction in Biology

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Title: The effects of disturbance regimes in a state park on plant community and invasion dynamics

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Abstract: Abiotic and biotic variables act as short-term drivers and long-term restraints on plant community succession and composition through time. Anthropogenic disturbance creates an emergence of new ecosystems that are often characterized by less predictable successional trajectories. In this study we characterize three disturbances within a State Park in PA in terms of abiotic and biotic variables which act as early successional drivers and determine vulnerability to invasion by *Microstegium vimineum*. We found that disturbed sites initially displayed peak diversity immediately post disturbance. These same sites displayed high richness once *M. vimineum* became more prominent. Abiotic restraints acted as a main determinant in species richness and composition within later successional sites due to light limitation. Light availability also provided a strong restraint in the colonization of *M. vimineum* within those sites. *M. vimineum* biomass was marginally correlated within nitrogen availability, therefore those disturbed sites which had high light regime and high nitrogen availability had more prominent *M. vimineum* presence due to increased photosynthetic capabilities. Biotic restraints also played an integral role in determining a disturbed site's vulnerability to invasion, the clear-cut disturbed sites displayed the lowest *M. vimineum* presence due to the prominent occurrence of a competitive *Poaceae* species which was planted to decrease the potential 'invasibility' of the newly disturbed site.

Introduction

Plant succession is the change in species composition over time within a community following a disturbance. This process is not random, but rather orderly in that the trajectory of the recovering plant community is often predictable. This is partly because the successional process eventually slows and the system reaches an equilibrium. This produces a self-maintaining system referred to as a climax community. Certain variables can hinder the predictability of this process which yields a novel trajectory of the developing plant community and consequently a potentially different climax community. In extreme cases factors can prevent the community from climaxing at all (Smith, 1996).

Modern successional pathways, which result from anthropogenic influences creating an emergence of novel ecosystems, are influenced by species pools, habitat conditions and biotic interactions that are novel in contrast to those that have previously shaped landscapes (Huebner et al. 2008). These various abiotic and biotic variables (*e.g.* organic matter, soil nutrients, plant community composition) have the potential to act as short-term drivers and longer-term constraints of succession (Walker & Wardle, 2014). The short term processes are defined as those that occur within the first few decades of succession and often fluctuate on a micro scale (*e.g.* as a matter of seconds, days or weeks) (Walker & Wardle 2014). These initial processes are characterized by an accumulation of biomass and are integral in determining the pattern and composition of plant colonizers which has the potential alter the first few stages of successional trajectory.

One concern in post disturbance management is colonization by invasive plant species. An invasive species is one that is not native and is often abnormally pervasive within an area (Smith, 1996). Although ecological disturbance is not necessary for exotic plant invasion, it has been identified as an indicator of invasion vulnerability. The unambiguous relationship between invasion prominence and disturbances has been attributed to variables within disturbed sites that pertain to resource availability and competition (Huebner et al. 2008). A site's susceptibility to invasion is dependent upon interspecific interactions in relation to competition for space. Susceptibility is determined by species richness, composition, and diversity. Although there are different views on how these biotic characteristics affect the 'invasibility' of a site (Didham et.al. 2005), there is agreement that they influence the abundance of invasive species that thrive in disturbed localities (Mack et al. 2000). Community-level theory predicts that most organisms are spatially discrete and are affected by other individuals within reasonable proximity. At the same time, no single species can fully occupy a site or niche, which leaves space open for other species to be recruited. Processes (*e.g.* timbering) that disrupt natural plant dispersal dynamics cause species abundance and compositional changes which increase the susceptibility of a site to be colonized, often by invasive species. This is a consequence of native species being limited by lower dispersal rates as opposed to invasive species which often have high dispersal capabilities (Tilman, 1997). Therefore recruitment limitations placed on invasive species are a reflection of community composition and maturity.

Commented [SGM1]: But this argument is based on dispersal dynamics… how do these relate to community composition and "maturity"? (What is maturity of a community?)

Disturbances often have the effect of the re-allocation of site nutrients; early in the successional process these nutrients act as driving factors for competition within colonizing plant communities. Invasions have the potential to alter vegetation patterns and recovery within disturbed sites through competition for newly allocated resources (Tognetti et al. 2009). Nutrient supply rates from the soil fluctuate on the micro time scale (Walker & Wardle, 2014). These supply rates dictate the relative success of species able to colonize a newly disturbed system (Walker & Wardle, 2014). Most terrestrial plant communities are limited by nitrogen as a resource. Metabolic processes, leading to increase in vegetation biomass, are dependent upon adequate supplies of nitrogen. Greater nitrogen availability yields greater photosynthetic capacity and leaf nitrogen content because 75% of leaf nitrogen is found in chloroplasts and is invested in ribulose biphosphate carboxylase, the main catalyst in the reaction of photosynthesis (Cechin & Fumis, 2004). Plants that are more efficient at sequestering nitrogen will be dominant within a newly disturbed community and display higher foliar nitrogen content and lower carbon to nitrogen ratios relative to the soil (Belligham et al. 2001). In primary succession, early colonist plants may alter community composition through the alteration of soil nitrogen content via nitrogen fixation which could perturb or facilitate the growth of other species (Belligham et al. 2001, Walker & Wardle, 2014).

Some invasive species, such as *Microstegium vimineum*, have been associated with fluctuating soil nitrogen levels. *M. vimineum* is a highly invasive, shade-tolerant C_4 grass distributed throughout the eastern United States (Flory et al. 2012). *M. vimineum* is believed to elevate nitrification potential in relation to co-occurring native plants, making nitrogen more available for *M. vimineum* leading to a positive feedback loop and increased persistence of the invasive species (Flory et al. 2012). Although it is associated with increased nitrate levels, it is unknown if *M. vimineum* is the cause of the elevated nitrogen content. Additionally the relationship between these elevated nitrogen levels and *M. vimineum* growth rate or biomass is poorly understood (Flory et al. 2012).

This study was designed to characterize the short-term successional drivers of plant community composition and susceptibility to invasive plant colonizers across differing disturbance regimes. Specifically we focused on the first 2 years of the plant successional process within sites that corresponded to natural and anthropogenic disturbance within a forested ecosystem. We hypothesized that biotic variables would be drivers in the earlier stages of succession and that this effect would be of greater magnitude in those sites that had less developed plant communities. These differences in abiotic variables would also be reflected in intra- and inter-annual variation within plant community composition. We also hypothesized that those communities that presented more biotic competition (*i.e.* had higher species community abundance, richness, and diversity already established) would be less susceptible to invasion.

Site Description

Nolde Forest State Park covers 665 acres comprised of a mix of even age and un-even age deciduous and conifer forest within Eastern Pennsylvania (Pennsylvania DCNR n.d) (Figure1). The Commonwealth has recently been forced to make some critical forestry management decisions due to storms and senescent stands of trees. The managers made the decision to clear storm debris interfering with trails and also took the opportunity to employ selective cutting within the park.

The clearing is designed to encourage re-growth of the forest and promote long-term forest health. Three park locations were cleared and replanted with various strategies. One area (clear cut) was clear cut and is being replanted with monoculture stands of *Pinus strobus* (White Pine) and *Larix laricina (*American Larch) to honor the tradition set by Jacob Nolde. A second area (select cut) was selectively timbered and has been replanted with a mix of native tree seedlings in accordance with modern approaches. The third area (blow-down) was partially cleared of Norway Spruce trees (*Picea aibes*) that were felled by tropical storm Sandy in October 2012. This plot had limited re-planting of native tree seedlings and much of the slash (woody debris) was left in place.

Methods

Data Collection

Data were collected between the months of May and August of 2013 and 2014. Four circular 10-m diameter plots were established within each of the disturbance types (clear-cut, select-cut and blow-down) and within control sites corresponding to each disturbance type (24 plots total). Abiotic measurements were taken from each plot: triplicate soil samples of 2 cm in depth were taken with the use of a corer for nitrogen and moisture content, light regime and relative humidity measurements were made using HOBO monitors, and canopy cover was quantified using a spherical densiometer. Biotic measurements included: identification, number, and diameter of trees (> 2 cm DBH) within each plot, vertical vegetation cover in 4 directions to be averaged using a cover board. Forest floor plant abundance (by species) was quantified within 4 randomly-placed permanent quadrats ($0.25m^2$) in each plot. Biotic measurements were taken once in 2013 and twice in 2014 to correspond with early and later growing seasons. To elucidate the relationship between soil nitrogen and invasive plant growth, biomass and nitrogen content of *Microstegium vimineum* (the dominant invasive plant) were measured from a minimum of 11 clip plots (0.10 m^2) including three plots from each disturbance type. The clip plots were quadrats of smaller size which were placed in area of *M. vimineum* cover. *M.* vimineum biomass was clipped and cleared from these clip plots and taken back to the lab for weights and nitrogen analyses. Plant tissue nitrogen and biomass were paired with a measure of soil nitrogen from each clip plot (analysis using a Perkin-Elmer Elemental Analyzer).

Data Analysis

Community metrics (*e.g.* Shannon Diversity) were calculated using standard calculations (Brower et al. 1998). The biotic and abiotic data at both the plot and quadrat level were analyzed using MANOVA models, a simple time series analysis was constructed by adding the year and time within the year as an additional variable. A series of protected ANOVAs were run after the MANOVA (Whitlock & Schluter, 2009). Tukey Kramer post hoc analyses were utilized to further refine differences. Plant biomass/plant nitrogen/soil nitrogen relationships were analyzed with multiple correlation analyses. All statistics were performed in the program “R i386” v3.0.1.

Results

Principle Component Analysis

Principle component 1 is characterized by the structural variables of vertical cover, which was split into two separate variables one pertaining to the 0 m level and the other to the 1 m level (Figure 1). Principle component 2 is characterized by the structural variable of percentage canopy cover and biotic measurement of complete individual abundance. These two components combined contribute to 84% of the variation in the data. Most all managed sites, regardless of site type and year, group within the lower right hand portion of the graphic displaying relatively low percent canopy and vertical cover. More than a majority of the sites (70%) which plot on the left-hand side of the graphic belong to the control sites. These sites display intermediate individual abundance and canopy cover and greater vertical cover. Blow-down sites within the year of 2014 group together with intermediate percent canopy cover and greater vertical cover and complete individual abundance (Figure 1). Those sites which plot with relatively lower percent canopy cover values are attributed to the blow-down and clear-cut disturbed sites, all within the year of 2013. Principle component 3 is also characterized by vertical cover (0 m), but also by complete individual abundance of plants within each species (Figure 2). Combined, principle components 1, 2 and 3 explain 97% of the variation in the data (Table 1). Along the axes of principle components 2 and 3 most of the variation is due to percent canopy with most sites plotting on the left half of the graph with intermediate values for vertical cover (0 m) and individual abundance and relatively high values for percent canopy cover. In general, those sites that were managed display lower percent canopy cover, further contributing to the variation patterns displayed on PC1 and PC2. Sites which displayed higher individual abundances tended to be those sites which were not managed (*i.e.* controls) (Figure 2). Those sites within the year of 2013 displayed low percentage canopy cover.

Abiotic and Structural Characteristics

Nitrogen, vertical cover (at 1 m and 0m above the ground), and percent canopy cover were different as a function of disturbance regime, year and management (Table 2). These variables also had a significant year by disturbance regime by management interaction (Table 2). Nitrogen varied as a function of year and disturbance regime with the select-cut sites and the year of 2013 displaying relatively higher nitrogen (*F_2 = 36.27, P<<0.0001; F_1 = 11.37, P=0.002)* (Figure 4). In general, control sites had significantly higher vertical cover at 0 m and 1 m above ground. Vertical cover at both levels was also greater within the year of 2014 relative to 2013 (*F_2 = 8.84, P = 0.005; F_2 = 3.29, P=0.008)* (Figures 5 & 6). Vertical cover was greatest within the blow-down disturbance regime regardless of management and year (*F_2 = 4.18, P = 0.02; F_2 = 7.77, P=0.002)* (Figures 5 & 6). There was a significant site by year interaction in terms of vertical cover at the 1 m level (*F_2 = 6.46, P=0.004)*. The blow-down sites had significantly higher vertical cover at 1 m than both the select-cut and clear-cut disturbance regimes within the years of 2014 and 2013. The blow-down sites within the year of 2014 had greater vertical cover (1 m) than the same sites within the year of 2013 (Figure 5). Vertical cover at 0 m above ground showed a significant disturbance regime by management interaction (*F_2 = 1.56, P=0.02)*. Vertical cover at 1 m above ground differed between cut and control sites. The blow-down sites had significantly higher 0 m cover in relation to the select-cut and the clear-cut sites regardless of year (Figure 6). The clear-cut sites also had significantly lower cover at 0 m in relation to corresponding controls (Figure 6). Percent canopy cover showed a significant interaction between disturbance regime and management (*F_1 = 0.63, P<<0.0001)*. The blow-down disturbed sites had greater canopy cover than the clear-cut disturbed sites and the corresponding blow-down controls within the year of 2013. Blow-down sites within 2014 also had significantly lower canopy cover than corresponding controls. Clear-cut sites had less canopy cover than corresponding controls and select-cut sites within the year of 2013.Clear-cut sites from 2013 also had significantly less canopy cover in relation to the same sites within 2014 (Figure 7).

M. vimineum biomass was significantly higher within the blow-down disturbed sites relative to the clear-cut disturbed sites ($F_2 = 4.01, P=0.03$) (Figure 14). It is important to note that control sites were not included in this analysis due to inability to collect clip plot samples because of sparse *M. vimineum* populations. Percent nitrogen within the plot was marginally correlated (r = 0.36, P=0.051) with *M. vimineum* biomass (Figure 15).

Biotic Community Metrics

Community metrics varied as a function of year, disturbance regime, and management (*e.g.* whether the site was cut or uncut) (Table 3). Diversity showed a significant disturbance regime and year interaction ($F_2 = 3.58, P=0.04$). The later growing season of 2014 had significantly lower plant diversity than the 2014 early growing season and the 2013 season within the blow-down and the select-cut sites. Within the clear-cut sites, the later growing season within 2014 had significantly lower diversity than the year of 2013, but was not different than the early 2014 growing season (Figure 8). Species richness within the later growing season of 2014 was significantly higher than the early growing season within 2014 and the season within 2013 ($F_2 = 2.58, P<<0.0001$) (Figure 9). The controls displayed significantly higher species richness than their corresponding cut counterparts ($F_1 = 7.73=6, P=0.01$) (Figure 9). The blow-down sites also displayed significantly higher species richness than both the clear-cut and select-cut sites ($F_2 = 14.06, P<<0.0001$) (Figure 9). The total percent area of the plant community attributed to *M. vimineum* was significantly higher in the managed sites in comparison to their unmanaged counterparts ($F_1 = 15.27, P=0.0005$) (Figure 10). The clear-cut sites displayed significantly less *M. vimineum* cover relative to the select-cut sites ($F_2 = 4.01, P=0.03$) (Figure 10).

Plant Community Composition (2014)

Each disturbance type and corresponding control had very different plant community compositions and prominent species with only a few species common between disturbed sites and controls. The only species which was present in all sites regardless of year, disturbance regime, and management was *M. vimineum. M. vimineum* had a much higher percent area cover within the plant community within the disturbed sites than the controls. *M. vimineum* was also lower in sites that were more diverse (had multiple species with more than 5% cover). The highest percent cover attributed to *M. vimineum* within the control sites was 11%. The clear-cut displayed the lowest percent cover of *M. vimineum* with the early 2014 sites' community containing 18% and the late 2014 sites containing 24%. All other disturbed sites, regardless of disturbance, had at least 42% *M. vimineum* by area (Figures 11-13). The select-cut disturbed sites displayed significantly higher *M. vimineum* biomass per area of *M. vimineum* covered relative to clear-cut sites which displayed the lowest amount of *M. vimineum* biomass (Figure 14). There was a marginally significant positive correlation ($P = 0.051$) between soil nitrogen content and *M. vimineum* biomass.

Discussion

Diversity and species heterogeneity is greatest within all of the disturbance regimes in contrast to their later successional counterparts. Furthermore, within these disturbance regimes, diversity is greatest within the year of 2013 as opposed to the early and later growing season of 2014. It is worthy of noting that this pattern may be a result of the compounding of later and early growing season within the year of 2013 which has the potential to increase diversity. This represents the immediate processes of bioaccumulation of all life forms post disturbance. The initial species distribution and diversity is a likely a consequence of unresolved competition due to the reallocation of resources and the availability of space that a disturbance yields (Schoonmaker & McKee, 1988; Walker & Wardle, 2014). This pattern is displayed within the first year of monitoring (2013) which was representative of 1 year post disturbance and is especially prominent in the blow-down natural disturbance regime. Species composition is most dynamic within the first 30 years of community re-establishment post disturbance (Schoonmaker & McKee, 1988). Typically, species diversity will peak several times during the successional process with the first peak corresponding to the first 15 years post disturbance with declines occurring shortly after canopy enclosure (Schoonmaker & McKee, 1988). Early peak diversity patterns have been found to occur as early as 2 years after anthropogenic and natural disturbances because the initial processes within early succession are characterized by an accumulation of biomass of all life forms due to the reallocation of space and resources (Schoonmaker & McKee, 1988; Walker & Wardle, 2014).

The newly available space and resources initiate biotic competition between colonizing species. Those species that are better at acquiring and utilizing the newly derived resources will become more prominent within the system and will ultimately decrease heterogeneity thus causing a peak in species richness relative to diversity (Huebner et al. 2008; Tilman, 1997). The increased dominance of invasive species often facilitates a switch between species diversity peaks and species richness peaks within the primary successional processes. This is because the invasive species become dominant without eliminating many other species thus causing the abundance of individuals within each species to decrease, but the richness to stay constant

(Schoonmaker & McKee, 1988). The blow-down disturbance regime displayed the highest Shannon Diversity value of 0.6 within the year of 2013 which corresponded to a percent cover attributed to *M. vimineum* of approximately 15%. Within the later growing season of 2014 the same sites displayed a diversity value of 0.4 and a percent cover attributed to *M. vimineum* of approximately 42%. The establishment and increasing prominence of *M. vimineum* within the disturbed community resulted in a decrease of heterogeneity and diversity within the plant community resulting in an increase in species richness within the 2014 sites in contrast to those within the year of 2013.

Higher species diversity perturbs invasion by providing effective biotic competition for newly allocated resources and space within a disturbed ecosystems (Tilman, 1997; Mack et al. 2000). The clear-cut disturbed sites displayed the least percent cover of *M. vimineum* which contributed 24% of the area within the 2013 and late 2014 growing seasons. This low invasive percent area cover may be a result of the effective competition yielded by the grasses that were planted within the clear-cut disturbed sites immediately post disturbance. This prominence of native grasses is a result of a grass seed mix which was planted immediately after timbering to perturb harmful colonizers (Linda Ingram pers. comm.). The clear-cut disturbed sites is reflected in this study to have relatively low diversity as a consequence of our inability to appropriately identify different species within the Poaceae family. These disturbed sites had a combination of approximately 10 different species of grasses which grew in approximately even densities and provided a fair amount of cover. This provided a biotic restraint on the developing community of *M. vimineum* through the occupation of space of a species which occupies a similar niche and can effectively compete for space and resources (Tilman, 1997).

In some systems late successional plant community composition reaches an equilibrium, usually resulting in a climax community, based on the abiotic characteristics of the system (e.g. light) (Smith, 1992; Schoonmaker & McKee, 1988). This causes certain later successional systems to display higher diversity than disturbed counterparts. However, some later successional systems display high richness and relatively lower diversity because they are restrained by certain abiotic characteristics of the system. Once canopy enclosure occurs it creates a uniform low-light environment within the understory of the forest structure which fewer understory plant species can tolerate (P. Schoonmaker & A. McKee, 1988). The eventual *penetration* of the later successional forested canopy by shade-tolerant sub-canopy species is a longer process that requires fragmentation of canopy structures and is beyond the scope of the time accounted for in our study (Schoonmaker & McKee, 1988).

The variation that existed between disturbance regimes and corresponding controls was mostly a result of characteristics pertaining to forest structure (*i.e.* vertical cover and percent canopy cover). The sites that represented later successional stages had higher percent canopy cover and higher vertical cover within 1 m and 0 m above the ground in addition to low species diversity, but relatively high species richness. This is a result of the abiotic restraint that is caused by a developed forest canopy within later successional stages. The controls' community composition had prominent shade tolerant species (*i.e. Lindera benzoin, Toxicodendron radicans, Rubus phoenicolasius*) (Rhoads & Block, 2000). At least 59% of area covered within the plant community of the select-cut, 42% within the blow-down, and 36% of clear-cut later successional sites within the late growing of 2014 was attributed to shade-tolerant species. The high percent canopy cover within the later successional sites limits the type of species that can be established within that community, but the species that are prominent are shade-tolerant shrubs which result in higher vertical cover and lower heterogeneity.

This high percent canopy cover within later successional sites also yields a very effective restraint against *M. vimineum* invasion. The greatest percent area cover of *M. vimineum* within the plant community corresponding to the late successional sites is 11% as opposed to the disturbed sites which all had greater then 40% *M. vimuneum* cover. *M. vimineum* is a C_4 grass which is characterized by high dispersal and reproductive rates. Because of the increased energy required to undergo the C_4 photosynthetic processes, *M. vimineum* is less effective at competing for resources within shady interior forested areas (Oswalt et al. 2007).

M. vimineum biomass per area of *M. vimineum* cover increased as the percent nitrogen within the soil increased. The select-cut and the blow-down sites displayed higher percent nitrogen, *M. vimineum* biomass and *M. vimineum* percent cover relative to the clear-cut sites. This means that not only did *M. vimineum* take up more space, but per unit area covered it was accumulating greater biomass. This led to greater cover and faster growth rates within those sites that also contained elevated nitrogen levels. Increases in nitrogen availability increase the growth of plants through the enhancement of photosynthetic capacity because it allows for elevated production of ribulose biphosphate carboxylase which increases metabolic processes and biomass production (Cechin & Fumis, 2003). Therefore, the increased nitrogen within the select-cut and blow-down sites further facilitates the production of *M. vimineum* biomass.

Nitrogen availability alone, however, does not always facilitate increased *M. vimineum* biomass. The select-cut sites displayed the highest nitrogen levels regardless of management, but higher *M. vimineum* cover and biomass was only displayed in the select-cut sites which were disturbed. This suggests that disturbance also facilitates establishment and sustained presence of *M. vimineum* because of the increased energy it takes for C_4 grasses to photosynthesize. Disturbances fragment forest canopy structures yielding optimal light regimes for plant photosynthesis. This further supports the strong abiotic restraint of forest canopy enclosure. However, this does suggest that a combination of elevated nitrogen levels and light availability due to disturbance produces a stronger and more prominent presence of *M. vimineum* within the community due to optimized conditions. These abiotic variables therefore are integral in determining the diversity, or lack thereof, within early successional sites.

Conclusion

Species diversity and richness peaks within plant community composition happen naturally within early succession as a result of unresolved and resolved conflict of newly allocated resources. Invasive species are defined by their ability to better exploit and utilize these resources which causes an invasive dominance within early plant communities. This dominance occurs without the full disappearance of other species which have also colonized the area causing a species richness peak and decreasing species heterogeneity within the newly disturbed system.

Abiotic and biotic variables have the ability to facilitate or perturb invasive prominence. Canopy enclosure can significantly decrease the supply of light to the plant community and also place a prominent restraint on invasive colonization. Nitrogen content within the soil is an integral facilitator to plant biomass production and growth. Furthermore, interspecific interactions of other species which occupy similar niches can provide an important outlet for competition for resources and decrease the colonization of invasive species.

This study has displayed very important principles in moving forward with forest management and timbering. Disturbance, regardless of type, results in a shift of community composition and reallocation of resources. More often than not, disturbance lone is enough for invasive species to dominate ecosystems. The managers at Nolde Forest State Park purposely replanted those sites which were a result of clear-cutting to decrease the amount of invasive colonization and that alone was enough to remediate those sites to a plant community composition which was ore representative of native species.

Table 1: A Principle Component Analysis displaying the proportion of variance and the cumulative proportion attributed to the first three components.

	PC1	PC2	PC3
Standard Deviation	43.51	26.23	14.52
Proportion of Variance	0.64	0.23	0.07
Cumulative Proportion	0.64	0.87	0.94

Table 2: A MANOVA table of the abiotic metrics (*i.e.* vertical cover, canopy cover and soil nitrogen content) as a function of year, disturbance regime, and management.

Independent Variable	Df	Pillai	F	Numerator Df	Denominator Df	P value
Year	1	0.85	24.56	7	30	9.00×10^{-11}
Site	1	0.30	1.88	7	30	0.10
Mgmnt	2	1.05	4.92	14	62	5.13×10^{-6}
year x Site	1	0.37	2.55	7	30	0.03
year x Mgmnt	2	0.81	3.00	14	62	0.001
Site x Mgmnt	2	0.33	0.88	14	62	0.58
year x Site x Mgmnt	2	0.34	0.92	14	62	0.54

*Where year includes 2014 early, 2014 late, and 2013. Site refers to the disturbance regime and Mgmnt refers to whether the site was cut or left uncut (control)

Table 3: A MANOVA table of the community metrics (*i.e.* Shannon's Diversity Index, Simpson's Dominance, total Abundance, and Species Richness) as a function of year, disturbance regime, and management.

Independent Variable	Df	Pillai	approx F	Numerator Df	Denominator Df	P value
Site	2	0.59	3.49	12	98	2.54×10^{-5}
Year	2	1.15	11.12	12	98	1.10×10^{-13}
Mgmnt	1	0.47	7.24	6	48	1.52×10^{-5}
year x Site	4	0.52	1.28	24	204	0.17
year x Mgmnt	2	0.25	1.19	12	98	0.29
Site x Mgmnt	2	0.17	0.78	12	98	0.67
year x Site x Mgmnt	4	0.28	0.64	24	204	0.90

*Where year includes 2014 early, 2014 late, and 2013. Site refers to the disturbance regime and Mgmnt refers to whether the site was cut or left uncut (control)

FIGURE LEGEND

Figure 1: A map portraying the locations of the timbering sites, disturbance sites and corresponding controls within Nolde Forest State Park.

Figure 2: A graphic displaying the principle component analysis with principle component 1 plotted on the x-axis being represented by vertical cover both at 0 & 1 m increasing in the negative direction and principle component 2 plotted on the y-axis being represented by percentage canopy cover increasing in the negative direction. Together PC1 & PC2 contribute to 84% of the variation between sites, years and management regimes.

Figure 3: A graphic displaying the principle component analysis with principle component 2 plotted on the x-axis being represented by percentage canopy cover increasing in the negative direction principle component 3 plotted on the y-axis being represented by vertical cover at 0 m increasing in the negative direction and total plant abundance increasing in the positive direction. Together PC1, PC2 & PC3 contribute to 94% of the variation between sites, years and management regimes.

Figure 4: A bar graph displaying the mean and standard error of percent nitrogen as a function of disturbance regime, time frame and management.

Figure 5: A bar graph displaying the means and standard errors of vertical cover (1 m) as a function of disturbance regime, time frame and management.

Figure 6: A bar graph displaying the means and standard errors of vertical cover (0 m) as a function of disturbance regime, time frame and management.

Figure 7: A bar graph displaying the means and standard errors of percent canopy cover as a function of disturbance regime, time frame and management.

Figure 8: A bar graph displaying the means and standard errors of Shannon's Diversity Index as a function of disturbance regime, time frame and management.

Figure 9: A bar graph plot displaying the means and standard errors of Species Richness as a function of disturbance regime, time frame and management.

Figure 10: A bar graph displaying the means and standard errors of percent area of the plant community attributed to *M.vimineum* as a function of disturbance regime, time frame and management.

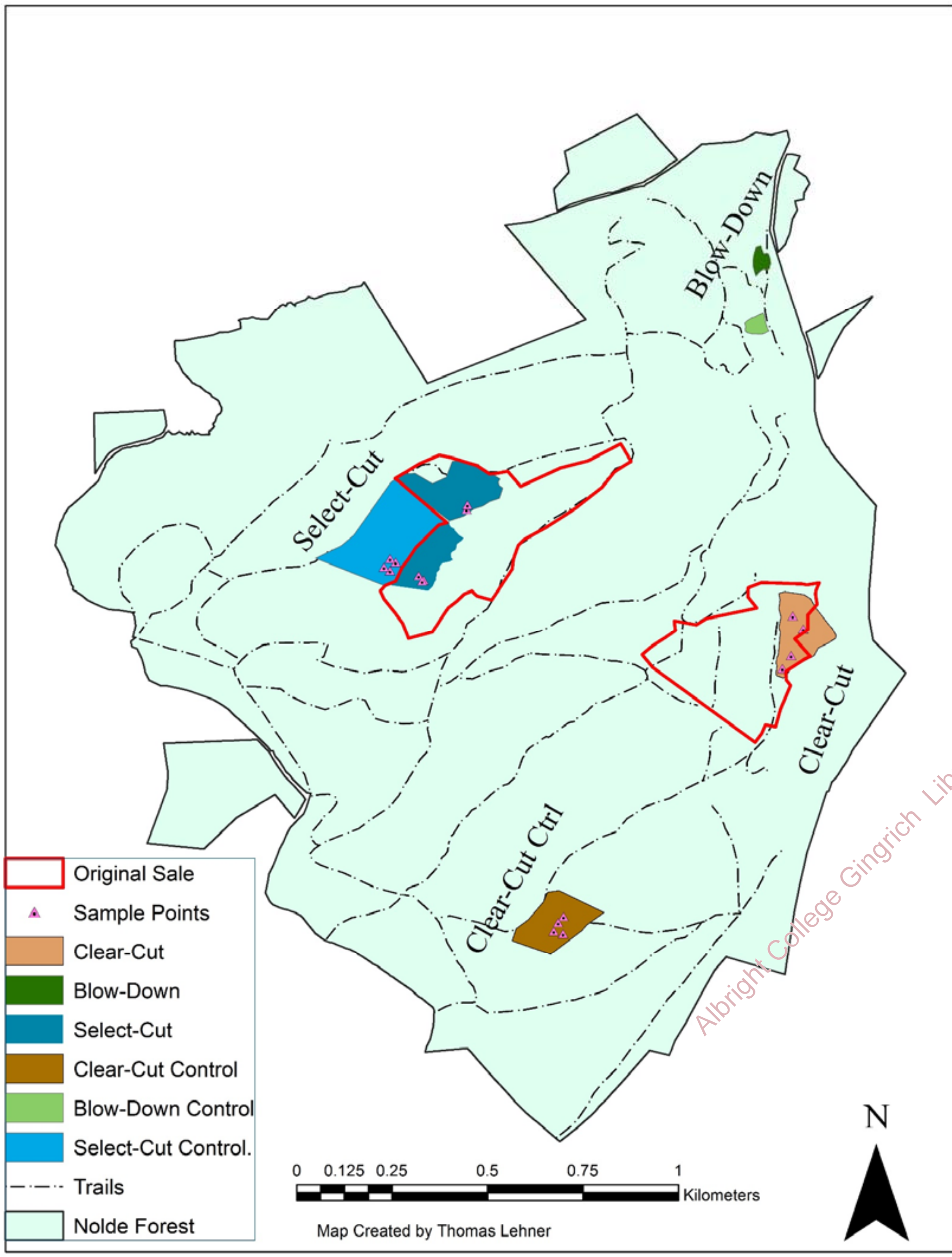
Figure 11: Pie charts depicting the percent area of the plant community attributed to each species within the early and late growing seasons of the control sites and corresponding select- cut managed sites. Any species that attributed less than 5% area was grouped in the “Others” category with the following number representing the number of species within the category.

Figure 12: A series of pie charts depicting the percent area of the plant community attributed to each species within the early and late growing seasons of the control sites and corresponding blow-down disturbed sites. Any species that attributed less than 5% area was grouped in the “Others” category with the following number representing the number of species within the category.

Figure 13: A series of pie charts depicting the percent area of the plant community attributed to each species within the early and late growing seasons of the control sites and corresponding clear-cut disturbed sites. Any species that attributed less than 5% area was grouped in the “Others” category with the following number representing the number of species within the category.

Figure 14: A mean point plot displaying the mean and standard error of *M. vimineum* biomass per area of *M. vimineum* cover within each of the disturbance regimes. Those sites that acted as controls are not included within this graph as there was only 1 measurement per control due to sparse population of *M. vimineum* within these sites.

Figure 15: A correlation plot of *M. vimineum* biomass and soil nitrogen where $y = -0.35 + 0.5$.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Blow-Down
Select-Cut
Clear-Cut Control
Blow-Down Control
Select-Cut Control.
Trails
Nolde Forest
0 0.125 0.25 0.5 0.75 1
Kilometers
Map Created by Thomas Lehner
N

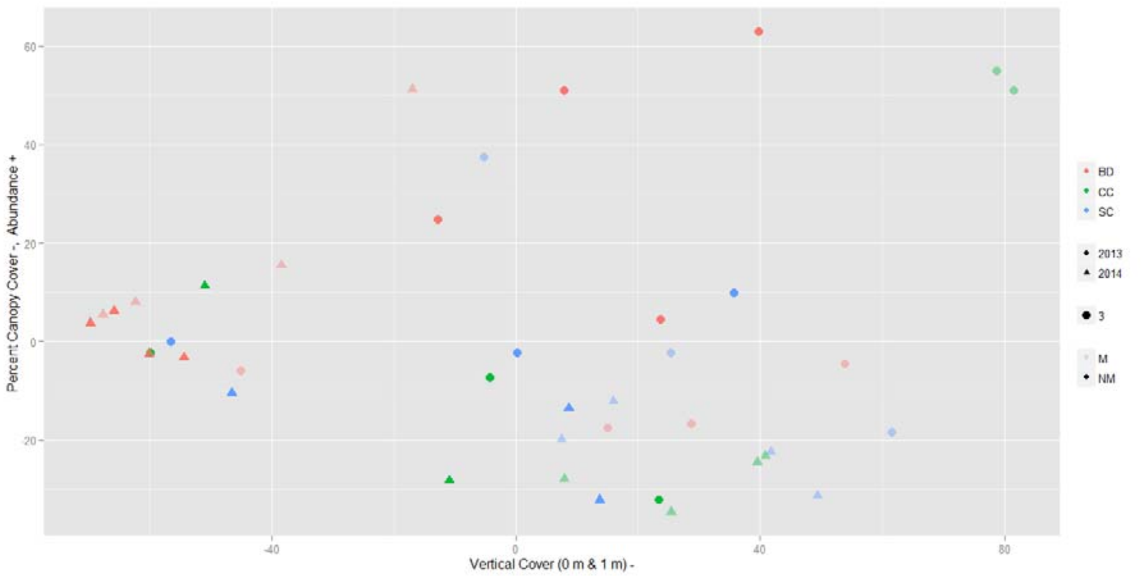


Figure 2.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

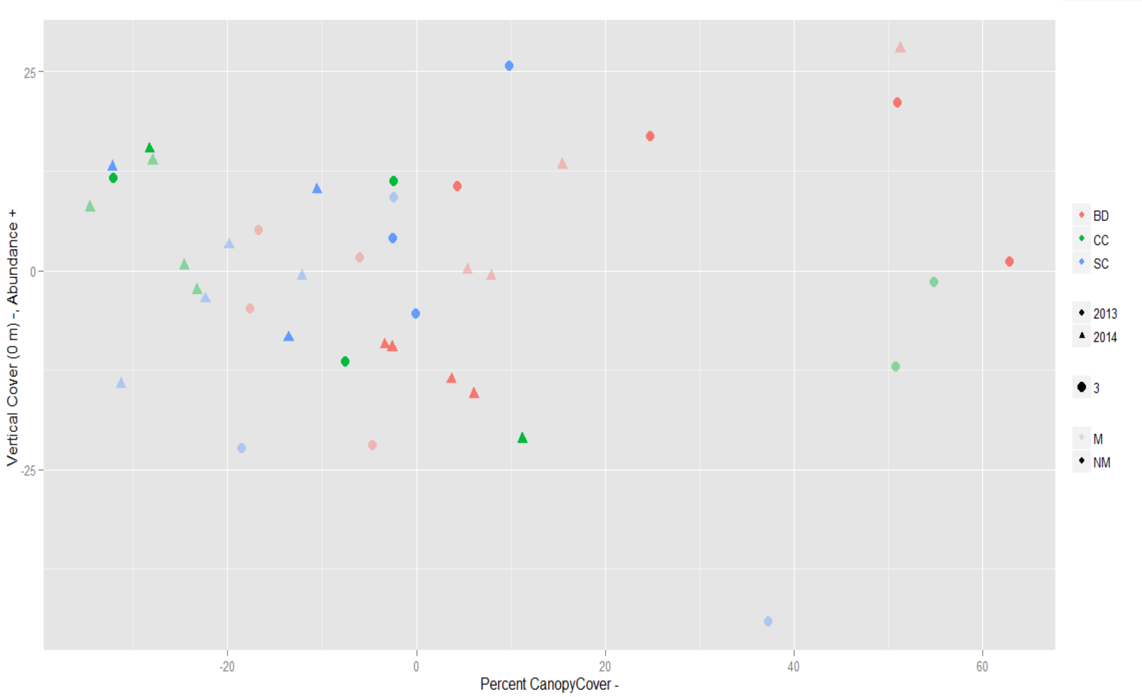


Figure 3.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

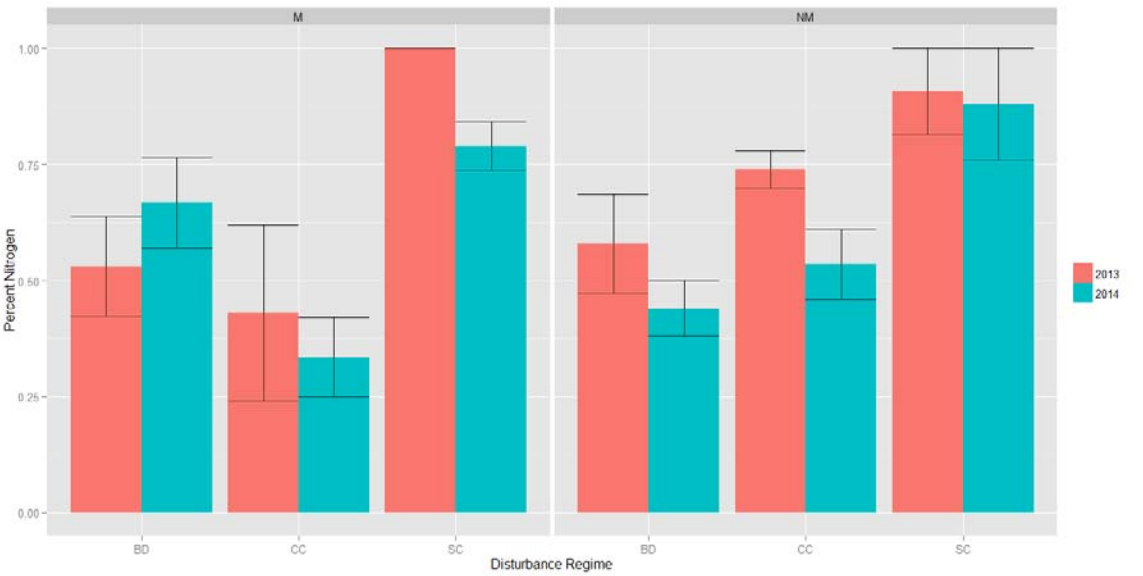


Figure 4.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

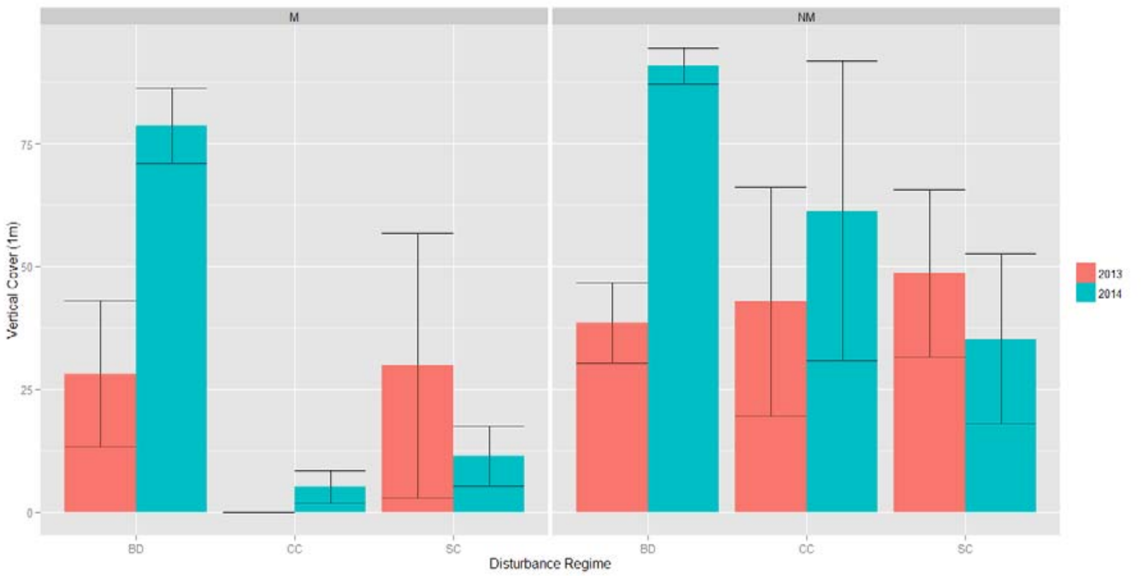


Figure 5.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

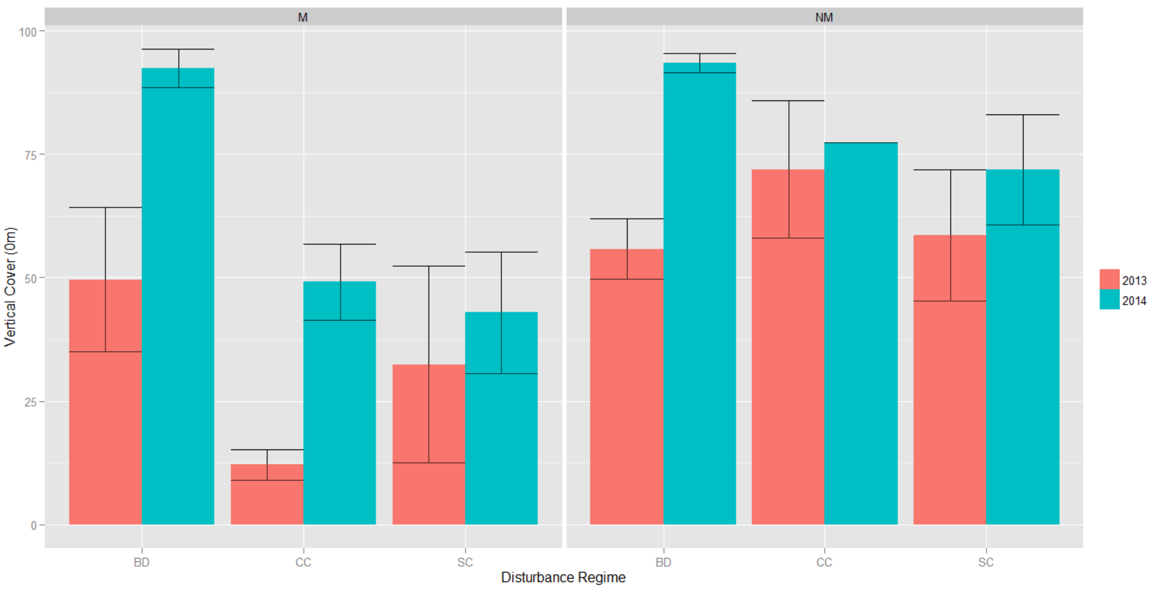


Figure 6.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

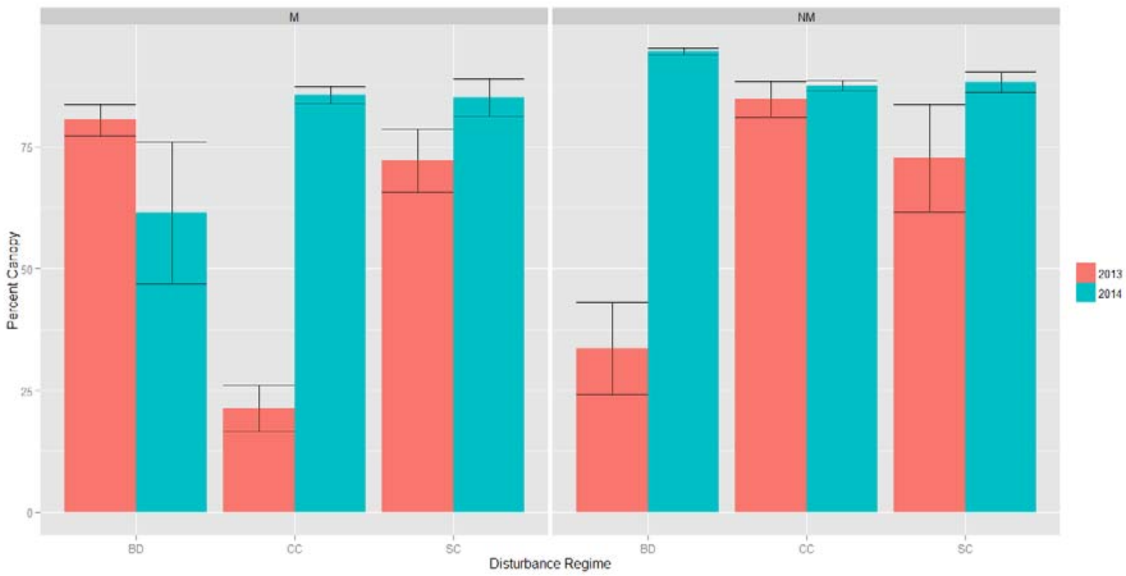


Figure 7.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

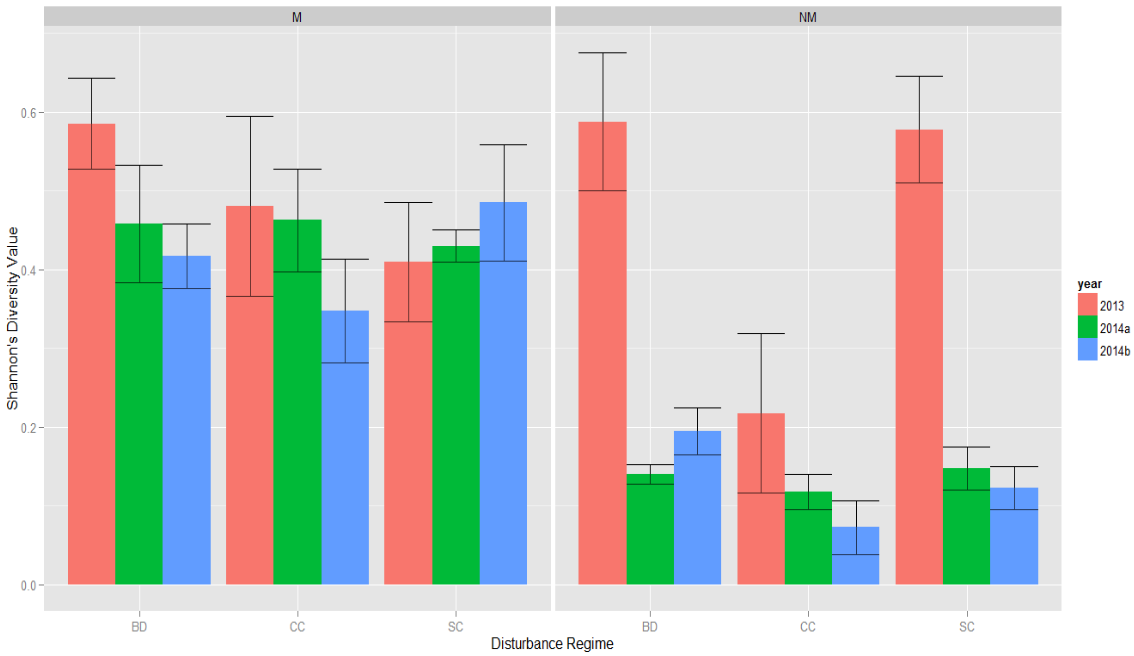


Figure 8

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

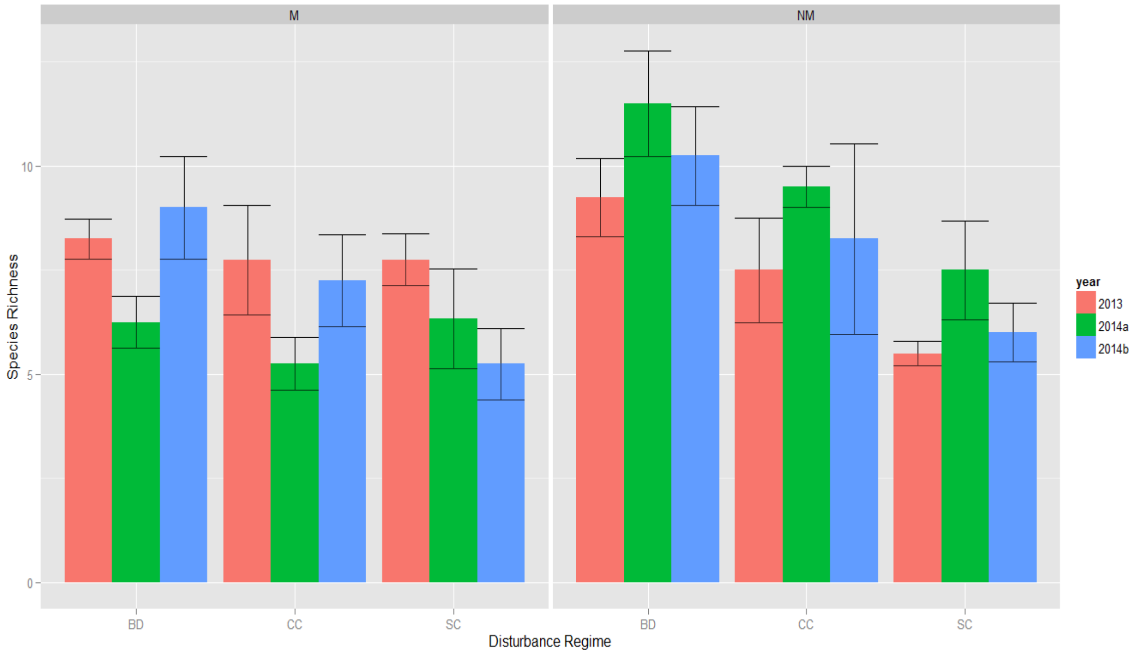


Figure 9.

*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

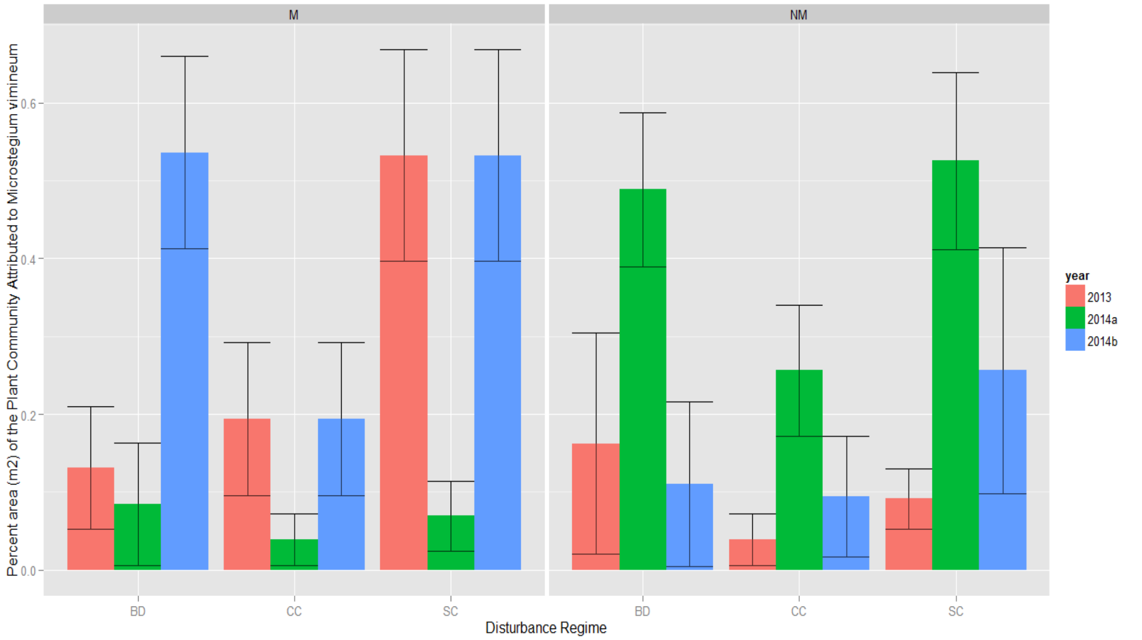
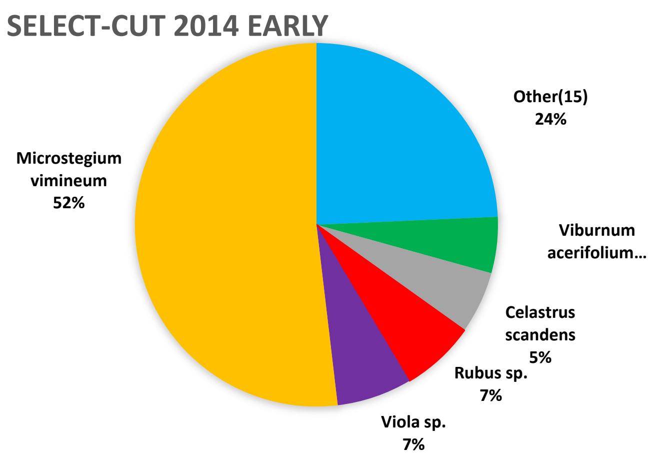
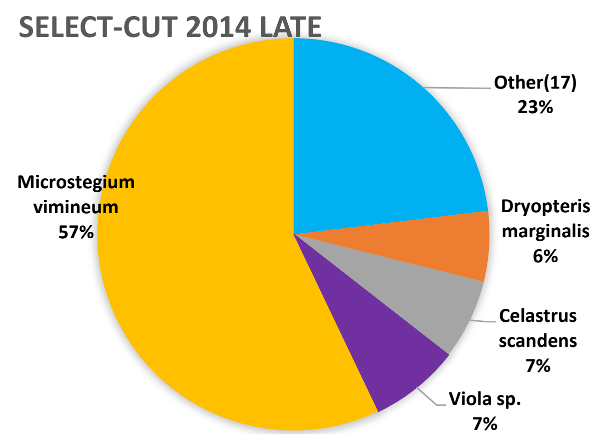
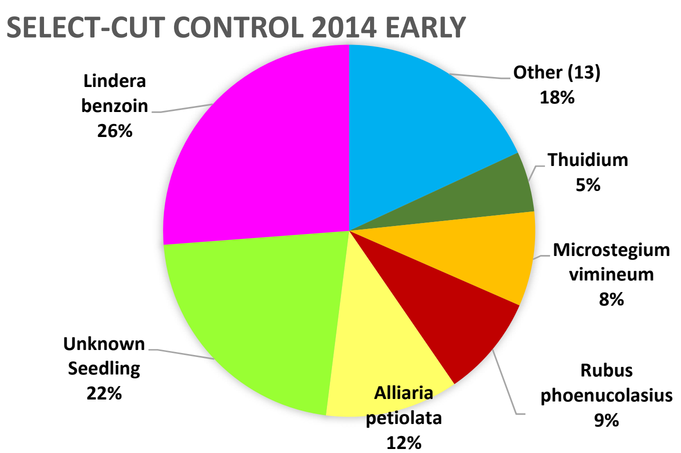


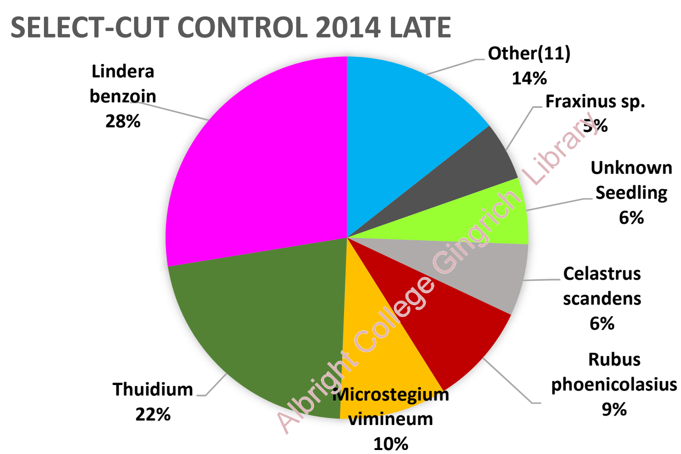
Figure 10.

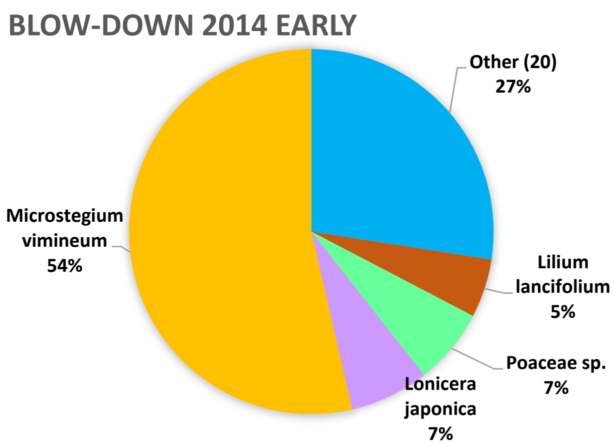
*Where year includes 2014 and 2013. Clear-cut, blow-down and select-cut site types are represented by CC, BD, and SC. And managed (cut) and unmanaged (controls) sites are represented by M and NM.

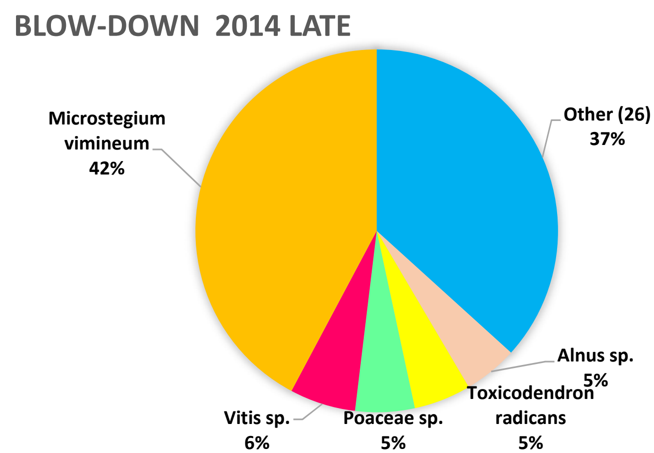

SELECT-CUT 2014 EARLY
Other(15) 24%
Viburnum acerifolium...
Celastrus scandens 5%
Rubus sp. 7%
Viola sp. 7%
Microstegium vimineum 52%

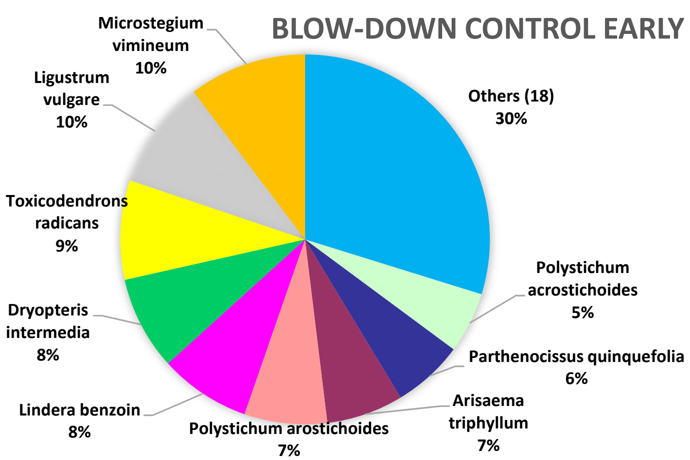

SELECT-CUT 2014 LATE
Other(17) 23%
Dryopteris marginalis 6%
Celastrus scandens 7%
Viola sp. 7%
Microstegium vimineum 57%

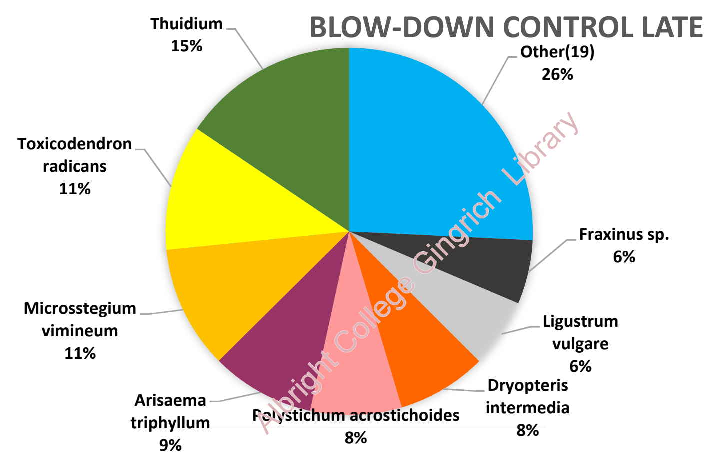

SELECT-CUT CONTROL 2014 EARLY
Other (13) 18%
Thuidium 5%
Microstegium vimineum 8%
Rubus phoenucolasius 9%
Alliaria petiolata 12%
Unknown Seedling 22%
Lindera benzoin 26%

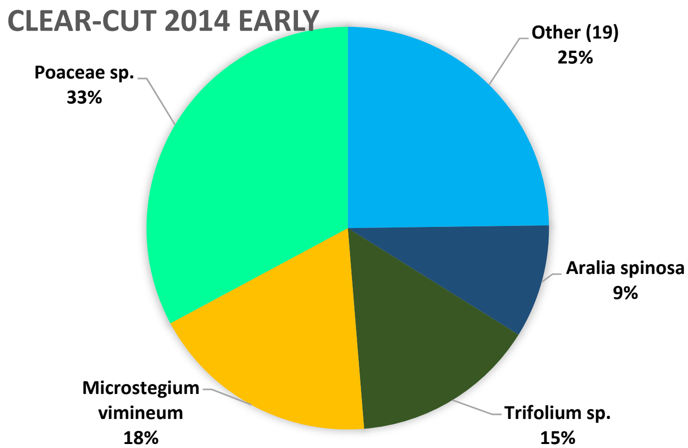

SELECT-CUT CONTROL 2014 LATE
Other(11) 14%
Fraxinus sp. 5%
Unknown Seedling 6%
Celastrus scandens 6%
Rubus phoenicolasius 9%
Microstegium vimineum 10%
Thuidium 22%
Lindera benzoin 28%

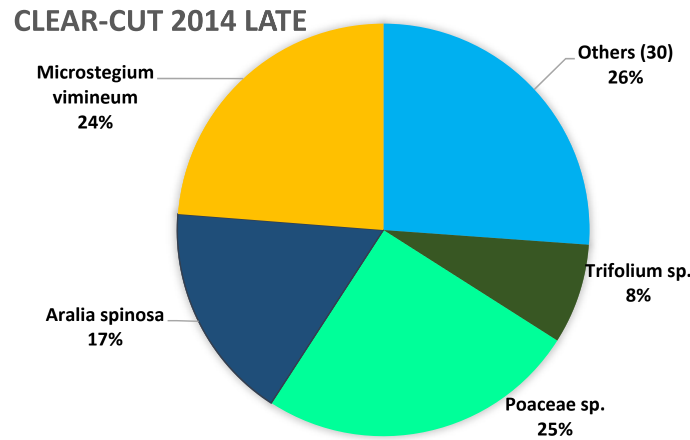

BLOW-DOWN 2014 EARLY
Other (20) 27%
Lilium lancifolium 5%
Poaceae sp. 7%
Lonicera japonica 7%
Microstegium vimineum 54%

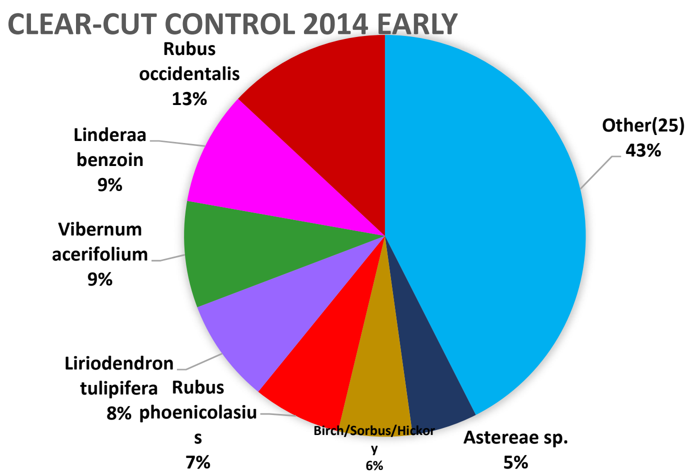

BLOW-DOWN 2014 LATE
Other (26) 37%
Alnus sp. 5%
Toxicodendron radicans 5%
Poaceae sp. 5%
Vitis sp. 6%
Microstegium vimineum 42%

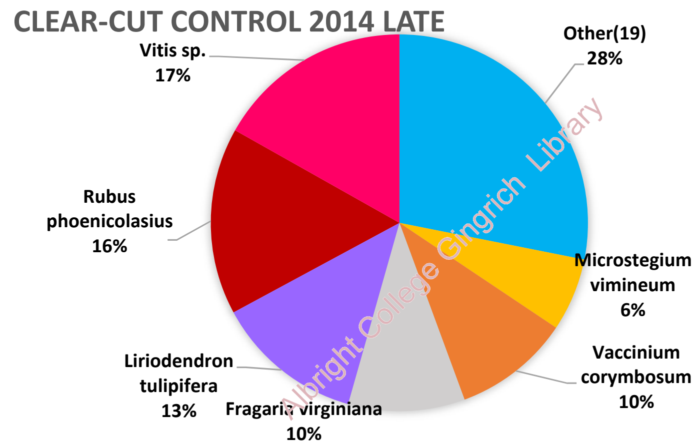

BLOW-DOWN CONTROL EARLY
Others (18) 30%
Polystichum acrostichoides 5%
Parthenocissus quinquefolia 6%
Arisaema triphyllum 7%
Polystichum arostichoides 7%
Lindera benzoin 8%
Dryopteris intermedia 8%
Toxicodendrons radicans 9%
Ligustrum vulgare 10%
Microstegium vimineum 10%


BLOW-DOWN CONTROL LATE
Other(19) 26%
Fraxinus sp. 6%
Ligustrum vulgare 6%
Dryopteris intermedia 8%
Polystichum acrostichoides 8%
Arisaema triphyllum 9%
Microsstegium vimineum 11%
Toxicodendron radicans 11%
Thuidium 15%


CLEAR-CUT 2014 EARLY
Other (19)
25%
Poaceae sp.
33%
Aralia spinosa
9%
Microstegium
vimineum
18%
Trifolium sp.
15%


CLEAR-CUT 2014 LATE
Others (30)
26%
Microstegium
vimineum
24%
Trifolium sp.
8%
Aralia spinosa
17%
Poaceae sp.
25%


CLEAR-CUT CONTROL 2014 EARLY
Rubus
occidentalis
13%
Linderaa
benzoin
9%
Other(25)
43%
Vibernum
acerifolium
9%
Liriodendron
tulipifera
8%
Rubus
phoenicolasiu
s
7%
Birch/Sorbus/Hickor
y
6%
Astereae sp.
5%


CLEAR-CUT CONTROL 2014 LATE
Other(19)
28%
Vitis sp.
17%
Rubus
phoenicolasius
16%
Microstegium
vimineum
6%
Vaccinium
corymbosum
10%
Liriodendron
tulipifera
13%
Fragaria virginiana
10%

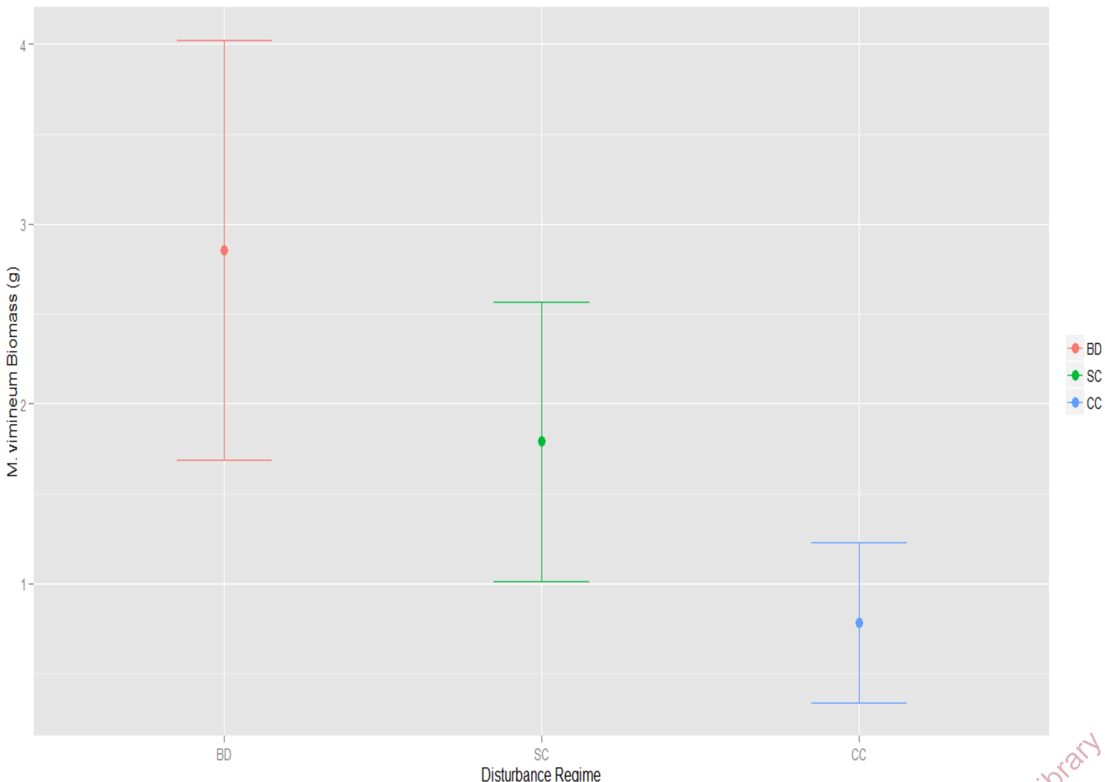

M. vimineum Biomass (g)
4
3
2
1
BD
SC
CC
Disturbance Regime
BD
SC
CC

Figure 14.

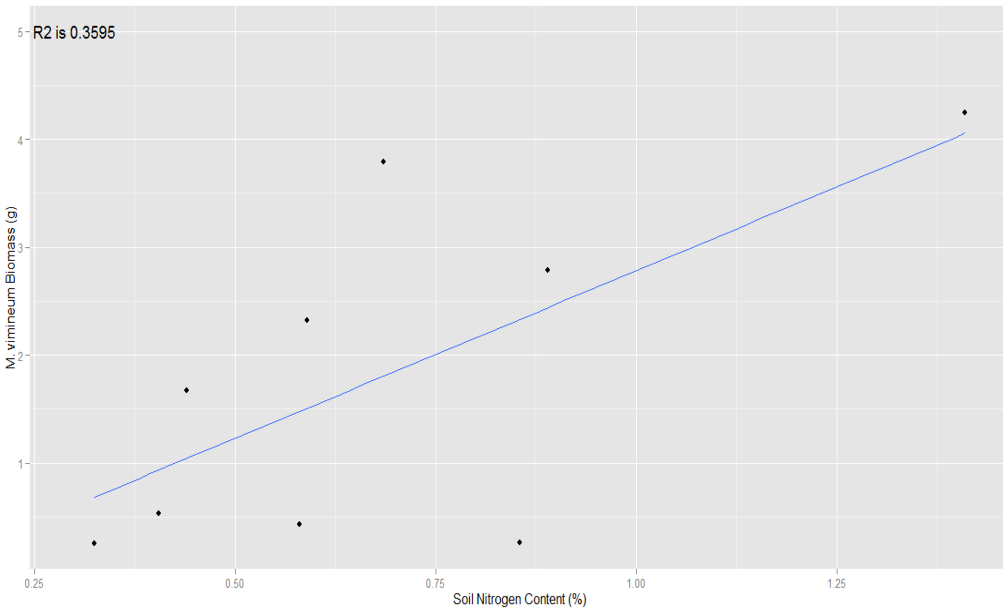

R2 is 0.3595
M. vimineum Biomass (g)
Soil Nitrogen Content (%)
5
4
3
2
1
0.25
0.50
0.75
1.00
1.25

Figure 15.

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