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**Changes in Herbaceous Plant
Diversity in an Old-Growth Ohio
Forest Before and After Emerald
Ash Borer Invasion**



Honors Thesis

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Department: Biology

Advisor: Ryan W. McEwan, Ph.D.

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Abstract

The herbaceous layer of eastern North American deciduous forests is an important contributor to biodiversity in this region. One of the greatest threats to herbaceous plant diversity is the introduction of invasive species, which can suppress native species and alter local environmental conditions. *Agrilus planipennis* (emerald ash borer) is a non-native insect pest that has caused a mass death of ash trees (*Fraxinus* spp.) in North America since its introduction to the United States. The resultant changes in canopy structure may affect local conditions and thus have indirect impacts on herbaceous layer composition. Drew Woods State Nature Preserve is a 6-ha old-growth forest fragment in Darke County, Ohio that has recently experienced EAB-related ash mortality. Our goal was to understand how herbaceous layer diversity has been changing through time in response to this sitewide canopy disturbance. Annual surveys of herbaceous biodiversity were conducted across 32 1-m² sampling plots from 2012 to 2017. Species richness, total cover, Shannon Diversity, and species evenness were calculated for each plot by year, and beta diversity (Bray-Curtis Dissimilarity) was used to assess community turnover through time. Repeated measures ANOVA was used to test for significant changes over this period, and regression analyses were used to understand relationships between diversity and environmental variables (canopy cover, soil moisture, and distance to forest edge). Species richness and herbaceous cover tended to be higher in more recent sampling years. There was a temporally consistent north-south gradient where diversity tended to be greater toward the southern edge of the stand. These results suggest that EAB-induced ash mortality is increasing light availability via canopy gap formation, which is a driving factor of herbaceous diversity. The full impact of EAB is not yet clear, but will likely extend beyond ash mortality and have important indirect effects on other parts of forest ecosystems.

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Introduction

The herbaceous layers of deciduous forests are some of the most species rich communities in North America (Ricketts et al. 1999, Gilliam and Roberts 2003a, Gilliam 2007). Species composition and functional group abundance in these communities is affected by the presence or absence of canopy cover via competition for water and nutrients (Dubbart et al. 2014). Canopy cover is important in regulating temperature in the understory, where tree cover has been linked to greater herbaceous diversity and cooler temperatures (Zihan et al. 2015). In general, overstory trees influence herbaceous species distributions on both local (Croizer and Boerner 1984) and stand-level scales (Brewer 1980, Whitney and Foster 1988, Ford et al. 2000, Gilliam and Roberts 2003b). In addition, canopy composition has been shown to affect light availability for the herbaceous layer, where decreased light correlates with decreased herbaceous growth (Wulf and Naaf 2009). In addition, herb distributions have been related to microtopography, gradients of soil fertility, and moisture (Bratton 1976, Thompson 1980, Hutchinson et al 1999, Small and McCarthy 2005). There is evidence that soil moisture is imperative for herbaceous growth (Whittaker 1956, Runkle and Whitney 1987, Hutchinson 1999, Leuschner and Lenszion 2009). Other environmental factors affecting the herbaceous layer are nitrogen content (Aber et al. 1989, Small and McCarthy 2005, Gilliam 2007 Hofmeister et al. 2009) and soil pH (Wulf and Naaf 2009, Yu and Sun 2013).

In general, biodiversity can be greatly reduced by the invasion of non-native species via competition for nutrients and light (Collier et al. 2002). *Agrilus planipennis* Fairmaire, commonly known as emerald ash borer (EAB), originated in Asia and is thought to have been brought to the United States in 2002 via international trade through a port in Detroit, Michigan (Poland and McCullough 2006). EAB is extremely detrimental to ash trees (*Fraxinus* spp.) in the U.S., as the larvae consume the phloem and cambium and adults eat the foliage (Poland and McCullough 2006). Although EAB eventually causes death, the implications of these losses are largely unknown. Ash trees are important contributors to leaf litter inputs that are necessary to maintain quality topsoil (Langenbruch et al 2011). Light availability is a main component of invasive species' success (Brothers and Spingarn 1992) and can function as a limiting factor. In

this context, EAB is thought to help invasive species by creating canopy gaps, allowing more light to reach species in lower levels of the forest (Herms and McCullough 2014).

In addition, *Alliaria petiolata* Bieb, commonly referred to as garlic mustard, is a nonnative herbaceous plant that originated in Europe and Asia and affects North American deciduous forest ecosystems (Nuzzo 1999). *A. petiolata* can live in both shade and sunlight, prefers basic and moist soils, and thrives in disturbed areas (Grime et al. 2014). Light availability has been shown to be an important factor in *A. petiolata*'s success in these ecosystems (Meekins and McCarthy 2000). Contrary to previous findings, Phillips-Mao et al. (2014) found that light negatively impacts garlic mustard seedlings' ability to establish due to competition with native plants, a trait that could be imperative to maintaining herbaceous layer biodiversity.

Drew Woods State Nature Preserve (DWSNP) is an old-growth forest fragment in west central Ohio that was largely untouched by EAB effects in initial floristic surveys done in 2012 and tree surveys conducted in 2011. *Alliaria petiolata* had a heavy presence in previous floristic surveys (Chapman et al. 2014). EAB has since invaded the area, causing a mass death of ash trees throughout the forest. This area provides a unique environment to study *A. petiolata* and EAB's impacts, as one of few remaining old-growth forests in the Midwest. As a forest fragment, DWSNP is more susceptible to invasion by nonnative species because it has four exposed edges (Honnay et al 2005). The objectives of this study were to (1) examine changes in the herbaceous layer composition over a six-year period, and (2) if detectable changes exist, determine whether those changes correlate with changes in the canopy, specifically due to EAB-induced ash tree mortality. It was hypothesized that (H₁) herbaceous layer richness, cover, Shannon diversity, and evenness would vary through time as EAB-induced ash tree mortality would leave gaps within the overstory and alter the understory environment, (H₂) the temporal turnover of herbaceous communities (beta diversity) would increase through time with the loss of *Fraxinus* spp., (H₃) relationships between herbaceous layer composition and environmental gradients would be altered by changing canopy structure, and (H₄) measured changes in canopy cover would relate directly to beta diversity as well as changes in richness, cover, Shannon diversity, and evenness.

Methods

Study Site

Drew Woods State Nature Preserve (DWSNP, 40°15'N, 84°39'W) is located in Darke County, Ohio and managed by Darke County Parks (Figure 1). The topography is relatively flat with less than 5 m change in elevation, and the climate is hot, humid summers and cold, dry winters. Mean annual precipitation is 95.5 cm and mean annual temperature is 10.2 °C (National Climatic Data Center 2012). Boerner and Kooser characterized the soil as Glynwood silt loam and Blount silt loam (1991). DWSNP is in the Central Ohio Clayey Till Plain region (ODGS 1998), and the overstory is dominated by *Acer saccharum*, *Carya* spp., *Fraxinus* spp., and *Quercus* spp. (Goins et al. 2013, Boerner and Kooser 1991).

Data Collection

The herbaceous layer (non-woody species) was surveyed annually in early May from 2012 to 2017 using 32 circular 1-m² plots previously established by Goins et al. (2013). All species within a plot were identified to species and percent cover was estimated using a modified Domin scale (<1%, 1 – 5%, 6 – 10%, 11 – 25%, 26 – 35%, 36 – 50%, 51 – 75%, 76 – 90%, 91 – 100%). Surveys were conducted in early May to capture the phenological overlap of spring ephemeral and summer green species, which creates a seasonal peak in species richness during this time (Chapman et al. 2014). *Alliaria petiolata* was recorded and subsequently removed from study plots each year. Soil moisture content (%) was measured in 2014 using a HydroSense volumetric water content probe (Campbell Scientific, Inc.), taking four readings per plot and calculating a mean value. Plot coordinates were collected using a Garmin eTrex Legend GPS Receiver (Garmin International, Inc.), then imported into ArcGIS to determine the distance in meters of each plot from the northern, southern, eastern, and western edges of DWSNP. In 2012 and 2017, canopy images were taken in the center of each plot using a CID-120 Canopy Imager (CID Bio-Science, Inc). Botanical nomenclature follows Jones (2005) and USDA Plants Database (<https://plants.usda.gov>).

Data Analysis

Relative importance values (RIV) were calculated for each species by averaging the relative cover and relative frequency within each year. Species richness, cover, Shannon diversity (presented as species equivalent values), and Pielou's evenness were calculated for all plots in each sampling year. Repeated measures ANOVA was used to test for differences in these four metrics across sampling years. Linear regression was used to test for significant relationships between environmental variables (soil moisture, canopy cover, distance to forest edge) and richness, cover, diversity, and evenness. Canopy images were used to obtain leaf area index (LAI) values for each plot, representing the canopy cover (area of sky obscured by leaves). Linear regression was also used to test for significant relationships between changes in canopy cover and changes in richness, cover, diversity, and evenness. Changes in canopy cover were calculated by subtracting the 2012 LAI values from the 2017 values. Plot-level changes in richness, cover, Shannon diversity, and evenness were calculated by subtracting 2012 plot values from the 2017 values. Temporal turnover (beta diversity) of the herbaceous layer between years was calculated using the Bray-Curtis dissimilarity index, which ranges from 0 to 1 where values closer to 1 indicate greater change in species composition (greater dissimilarity). Beta diversity values were also compared to environmental variables using linear regression. All analyses were performed using the R statistical programming language version 3.4.3.

The presence of the invasive herb species *Alliaria petiolata* in DWSNP was a concern for interpreting our results because of its capacity to create dense localized populations, as evidenced by the 2012 survey where a few plots had very high cover values due to *A. petiolata*. While the overall abundance of *A. petiolata* has decreased in DWSNP over the years because of targeted removal efforts (J. Chapman, pers. comm.), we felt it necessary to perform all analyses twice, including *A. petiolata* and excluding it, to assess whether temporal changes in herb layer diversity and cover were due to re-invasion by *A. petiolata* or other causes, particularly changes in the overstory related to EAB-induced *Fraxinus* mortality.

Results

Relative Importance Values

In 2012, *Alliaria petiolata* was the most important herb species in DWSNP (15.44), but its importance decreased by almost half in the 2013 survey (8.87; Table 1). The importance of *A. petiolata* continued to decrease over time (Figure 2), while *Sanicula odorata* progressively increased in importance beginning in 2013 and became the most important species in 2017 (19.36). *Floerkea proserpinacoides* was the most dominant herb species in 2013 (13.01) and 2014 (10.27), and was the second most common species in 2015 (11.35), only behind *S. odorata*. There were no species that experience consistent increases each year over the six surveys, and only one species decreased each successive year (*Symphytotrichum lanceolatum*). From 2012 to 2017, numerous species experienced increases in RIV, including *S. odorata*, *Geranium maculatum*, *F. proserpinacoides*, *Claytonia virginica*, *Dentaria laciniata*, *Allium tricoccum*, and *Erythronium. sp.* (Table 1).

Temporal Changes in Diversity and Cover

There were significant year-to-year changes in richness, cover, and evenness both with and without the inclusion of *A. petiolata*, but significant changes in Shannon diversity were only detected when *A. petiolata* was removed from analysis (Table 2). In general, species richness decreased significantly from 2012 to 2013, remained constant from 2013 to 2015, increased significantly in 2016, then decreased slightly in 2017 (Figure 3). Total cover decreased significantly from 2012 to 2013, remained constant from 2013 to 2015, and increased significantly in 2016 and 2017 (Figure 4). The increases in 2016 and 2017 were the same whether *A. petiolata* was included or not, so we are confident that these changes are not due to re-invasion of plots by *A. petiolata*. Shannon diversity showed no significant differences between any year-to-year comparisons with *A. petiolata* included (Figure 5a), but there were slight differences in diversity between 2016 and 2017 when *A. petiolata* was excluded (Figure 5b). Species evenness had overall significance ($f = 5.50, p < 0.0001$). With *A. petiolata* included, evenness increased significantly from 2012 to 2013, remained constant from 2013 to

2015, and decreased somewhat in 2017 (Figure 6a). With *A. petiolata* excluded, evenness was consistent from 2012 through 2016 and decreased significantly in 2017 (Figure 6b).

Beta Diversity

The amount of temporal turnover (beta diversity) varied significantly ($f = 35.27$, $p < 0.0001$) among the sampling intervals (Table 2). Beta diversity for 2012–2013 interval was significantly higher than all subsequent intervals (2013–2014, 2014–2015, 2015–2016, and 2016–2017), regardless of whether *A. petiolata* was included (Figure 7). The lowest amount of compositional change occurred between 2014 and 2015 (Figure 7). There were no significant differences in beta diversity among the 2013–2014, 2015–2016, and 2016–2017 intervals (Figure 7). There was a high level of turnover comparing 2012 to 2017, which exceeded all of the smaller, consecutive intervals except for 2012–2013 (Figure 7).

Environmental Variables: Soil Moisture, Distance to Edge, and Canopy Cover

Higher soil moisture content tended to decrease richness, cover, and Shannon diversity, although moisture lower than 20 percent and higher than 85 percent did not exist in the surveyed areas (Figure 8). Soil moisture did not significantly affect cover, evenness, or beta diversity (Figure 8, Table 3). Richness was positively impacted by lower soil moisture in 2012 ($p = 0.0268$), 2014 ($p = 0.0190$), 2015 ($p = 0.0097$), 2016 ($p = 0.0140$), and 2017 ($p = 0.00296$), but not in 2013; in addition, Shannon diversity followed this trend and had significant correlations with soil moisture in 2014 ($p = 0.0138$), 2015 ($p = 0.0128$), 2016 ($p = 0.0113$), and 2017 ($p = 0.0295$), but not in 2012 or 2013 (Figure 8, Table 3).

A north-south gradient was identified, with species richness increasing with distance from the northern edge for each year, 2012 ($p = 3.28E-5$), 2013 ($p = 0.0027$), 2014 ($p = 0.0014$), 2015 ($p = 0.0020$), 2016 ($p = 0.0023$), 2017 ($p = 0.0019$) (Figure 9, Table 3). Cover had a slight tendency to increase moving away from the northern edge of DWSNP, but only 2015 ($p = 0.04662$) and 2016 ($p = 0.0367$) were significant (Table 3). Shannon diversity significantly followed this trend in 2012 ($p = 0.0099$), 2013 ($p = 0.0236$), and 2014 ($p = 0.0149$) (Figure 9, Table 3). Evenness and beta diversity did not

follow this gradient and had no significance any year, except 2016-2017 ($p = 0.0237$) for beta diversity (Table 3). No east-west gradient was identified (Figure 10).

Soil moisture did not significantly affect beta diversity (Figure 10, Table 3). Beta diversity did not follow the north-south gradient, nor did it have any significant correlation to soil moisture (Figure 11).

Negative LAI change indicates the canopy was more open in 2017 than it was in 2012 (loss of canopy cover). Positive LAI change (increased canopy cover) correlated with lower richness, Shannon diversity, and evenness differences, indicating an inverse relationship; the canopy was more open where each of these three metrics were higher. Cover showed the opposite, where negative LAI change correlated with a higher change in cover, meaning cover decreased with canopy opening (Figure 12). Beta diversity showed no significant associations with change in LAI (Figure 13).

In addition to LAI, basal area ($\text{m}^2 \text{ha}^{-1}$) of dead and living *Fraxinus* spp. trees were calculated for 2011 and 2017 (Figure 14). In 2011, most ash trees located in DWSNP were living ($151.40 \text{ m}^2 \text{ha}^{-1}$) and some had begun to die ($33.51 \text{ m}^2 \text{ha}^{-1}$). When compared to 2017 basal area calculations, nearly all were dead ($132.32 \text{ m}^2 \text{ha}^{-1}$) and living ash trees were nearly nonexistent ($1.68 \text{ m}^2 \text{ha}^{-1}$).

Discussion

Richness, cover, Shannon diversity, evenness, and beta diversity significantly varied over the course of this 6-year study. These changes can be linked to overstory alterations due to falling ash trees leaving gaps in their wake, which allows for increased light exposure (Herms and McCullough 2014), an important component of herbaceous success (Wulf and Naaf 2009). In addition, the observed herbaceous layer changes could be in part due to the nutrient (N and P) inputs of decomposing trees (Johnson et al. 2014). The absence of a west-east gradient coupled with the presence of a north-south gradient is likely due to DWSNP's location in the northern hemisphere (Palik and Murphy 1990); greater species richness was found in the southern area of the forest, which is consistent with previous findings in DWSNP (Chapman et al. 2014). A north-south gradient of herbaceous species richness and Shannon diversity was observed in another old-growth

Ohio forest that was partially attributed to less moist soil on the southern side (Murphy and McCarthy 2013), which was also observed in Drew Woods (H₁).

An increase in beta diversity was observed throughout the study period; turnover and increase in diversity has been shown to be driven by canopy gaps (Jimenez-Alfaro et al. 2014) (H₂). Canopy cover changes did not correlate with an increase in beta diversity, contrary to predictions, which is likely due to other environmental factors that were not analyzed (H₄).

Six previous herbaceous surveys conducted at DWSNP in 2012 identified the invasive plant *Alliaria petiolata* as a dominating species (Chapman et al. 2014), which has been found to thrive in highly disturbed forests and remain more controlled in forests with low levels of disturbance (Nuzzo 1999). A probable cause for this disturbance was the introduction of the emerald ash borer. EAB presence typically goes undetected after the initial invasion because ash tree mortality does not begin until 3 to 4 years post-invasion (Siegert et al. 2007). In 2012, Goins noted *Fraxinus* spp. was the third largest contributor to overstory basal area in DWSNP (2013), indicating a mass ash tree death had not yet begun. In the years since, it has been observed that ash trees are dying at a rapid rate in DWSNP, indicating the disturbance caused by EAB likely led to *Alliaria petiolata* success and downfall, as well. Nearly no living ash trees remain in DWSNP. Falling trees are a notable disturbance via gap-dynamics in old-growth forests (Runkle 1982), and the increased light availability after these trees began to fall, likely negatively impacted seedling *A. petiolata* plants' ability to grow (Phillips-Mao et al. 2014), allowing native plants to bounce back. No documents describing an *A. petiolata* presence prior to 2012 when it was noted in Chapman et al. (2014) have been found.

The type of forest and relative canopy openness are essential for determining the composition of the herbaceous layer (Yu and Sun 2013). There was a general trend of many species increasing RIV immediately following 2012, then settling out, which is likely due to *A. petiolata*'s sudden decreased presence. *Sanicula odorata* became the dominating species, which thrives in partial sun, not complete shade (Pryer and Phillippe 1989). *Floerkea proserpinacoides* is in direct competition with *A. petiolata*, and significantly increased in abundance after 2012, likely due to the lower level of competition in its preferred wetter soils (Voss and Reznicek 2012). *Claytonia virginica*

is a hardy species that happily grows in most forested areas and can persist even in open spaces, explaining its relative consistency and subsequent increase by the last survey (Voss and Reznicek 2012). Interestingly, the only species to decrease in RIV across all six years was *Symphytichum lanceolatum*, which typically thrives in shade. This decrease can be explained by its preference for moist soils that would be drier due to the open canopy as a result of fallen ash trees (Voss and Reznicek 2012). These are the more notable changes, as biodiversity is not stagnant and is capable of bouncing back quickly from disturbance (Gilliam 2007) (H₃).

Conclusion

This six-year survey shows the variability that can occur in the herbaceous layer over time when influenced by outside forces. Emerald Ash Borer appears to be the main cause of disturbance in Drew Woods State Nature Preserve, most likely via canopy opening. With this opening comes increased light and alteration of soil fertility, forcing the herbaceous layer to change in response. Further studies must be undertaken to ensure *Fraxinus* spp. loss via EAB is solely responsible for this shift in biodiversity, but it is at least partially liable for the documented temporal changes.

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Figures and Tables

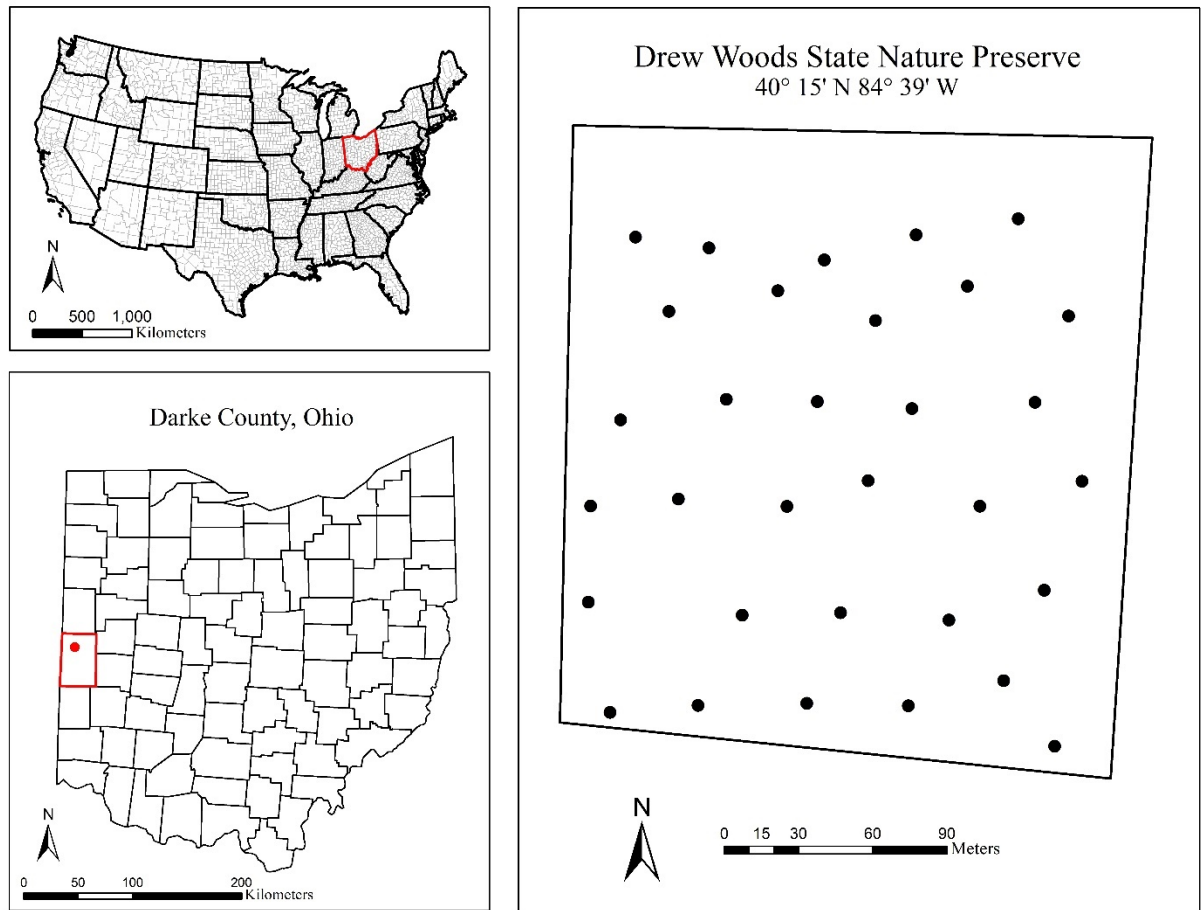
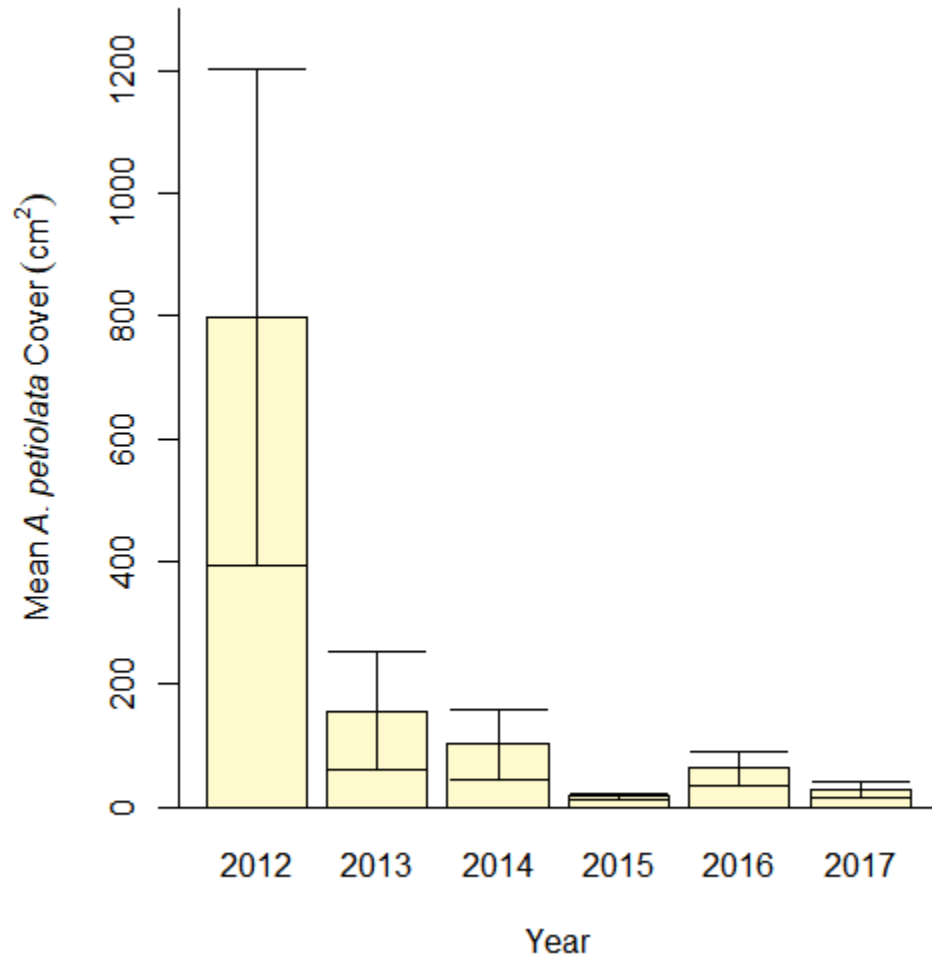


Figure 1: Location of DWSNP within the continental United States (top left) and Ohio (bottom left). The 32 1-m² plots located within Drew Woods are shown as black dots (right). These dots are not to scale.



*Figure 2: Average *Alliaria petiolata* cover for each plot by year throughout the 6-year study period, measured in cm².*

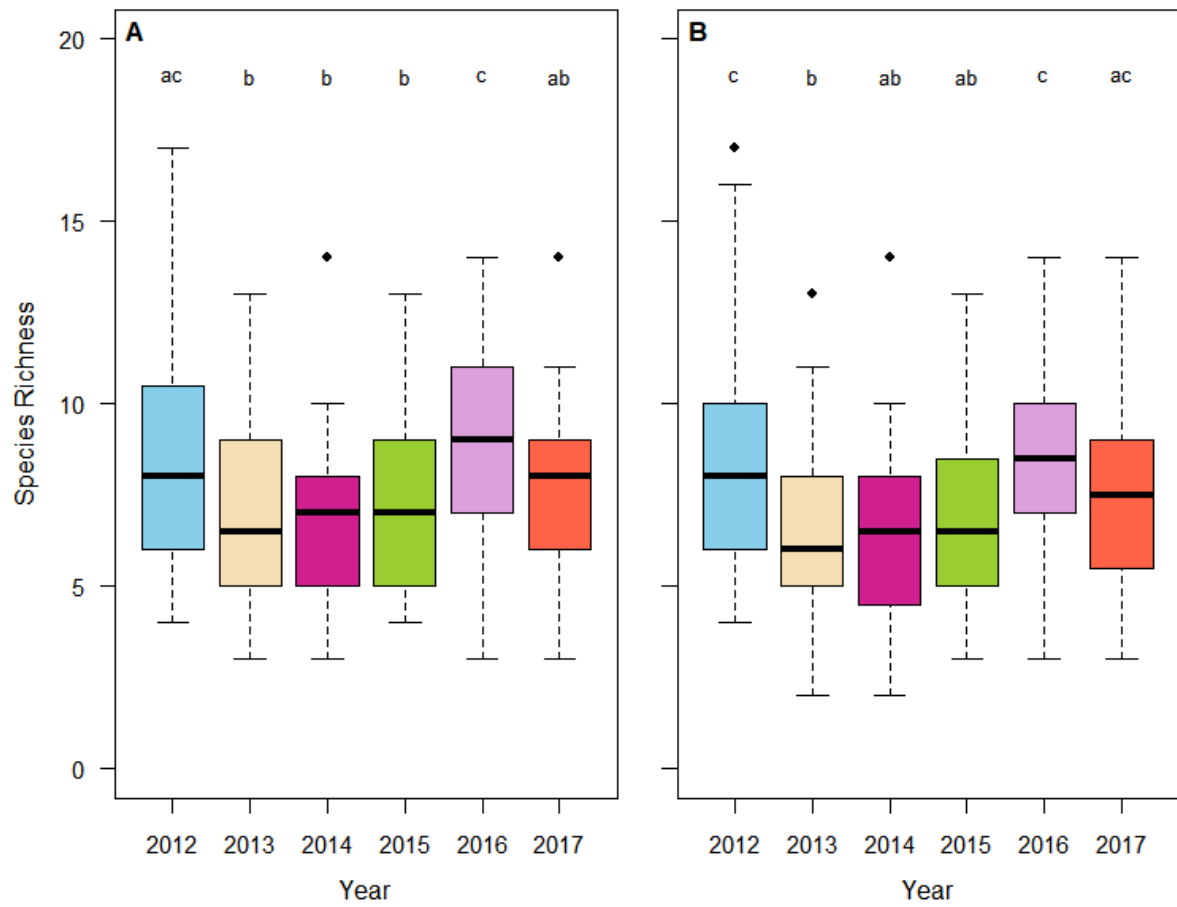


Figure 3: Species richness calculated for each plot every year, including (A) and excluding (B) *Alliaria petiolata*. Letters indicate significant difference.

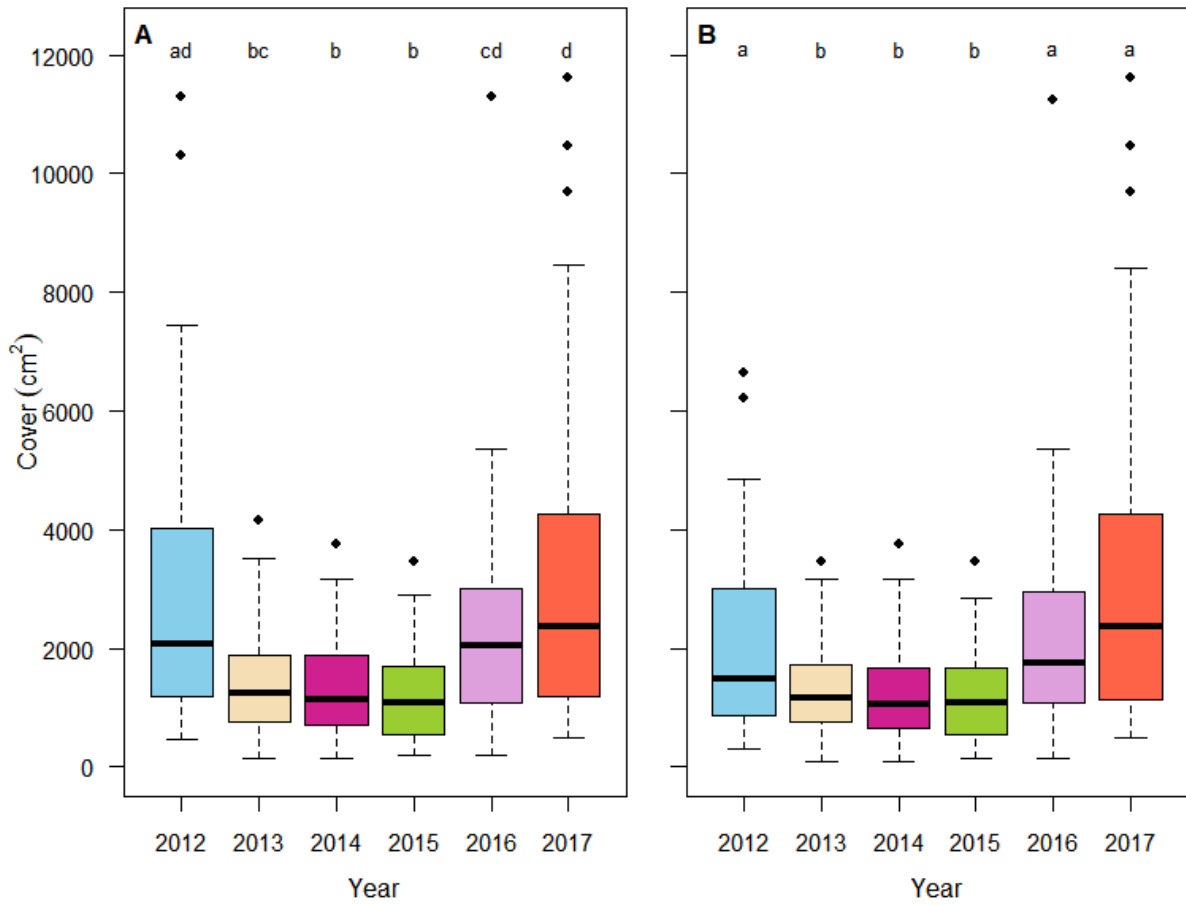


Figure 4: Plot cover by year shown both with (A) and without (B) *Alliaria petiolata*. Letters represent significant difference.

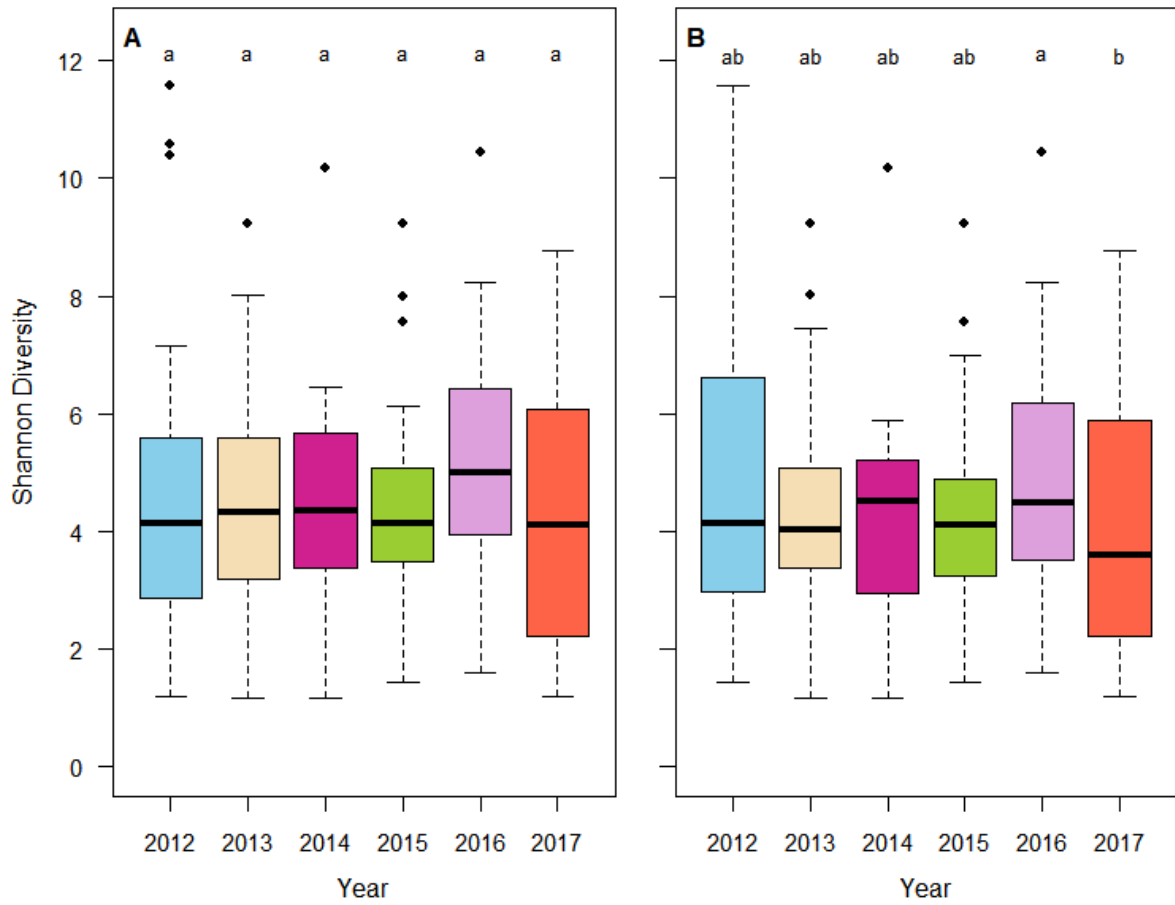


Figure 5: Shannon diversity was calculated on a logarithmic scale and corresponds to abundance differences within plots. *Alliaria petiolata* was included (A) and removed (B) for calculations. Letters indicate significant difference.

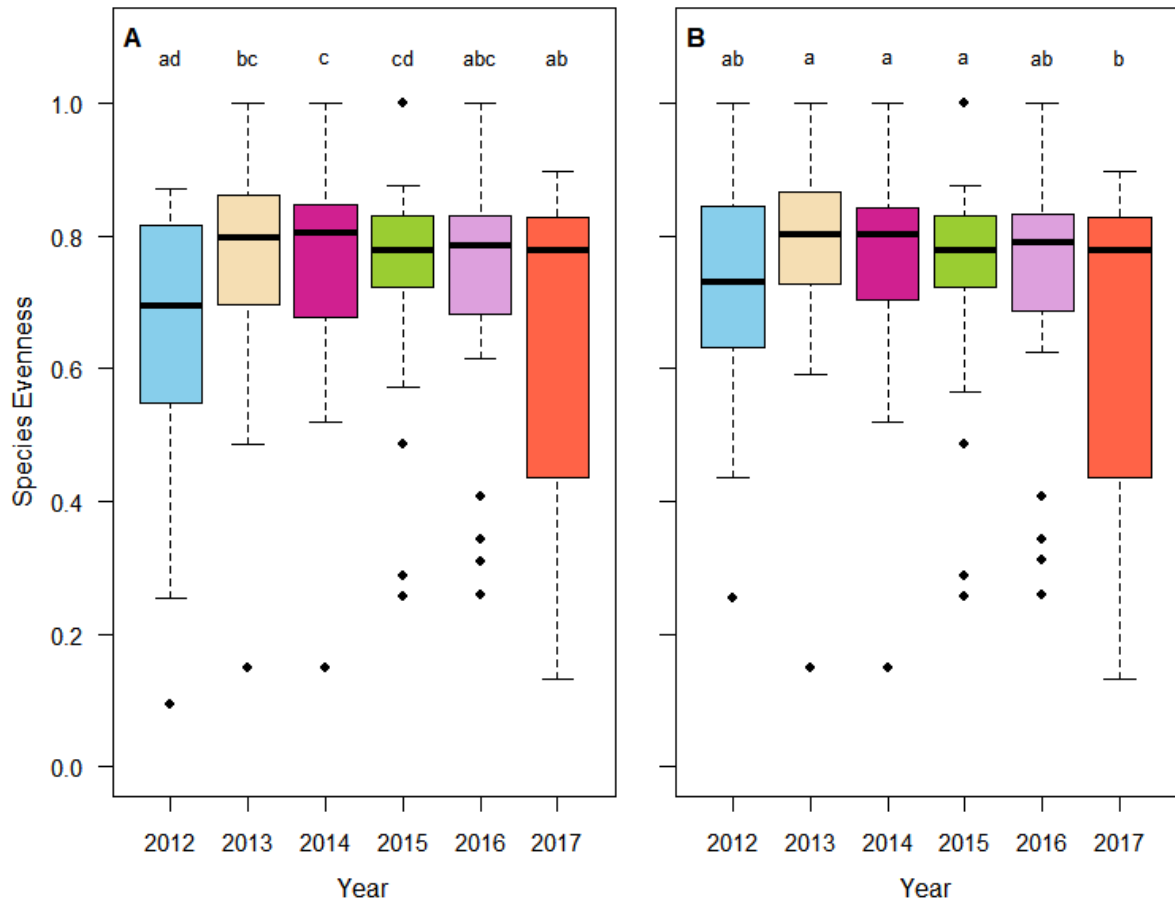


Figure 6: Evenness was used to represent the distribution of species throughout plots with (A) and without (B) *Alliaria petiolata* each year at DWSNP. Letters represent significant difference.

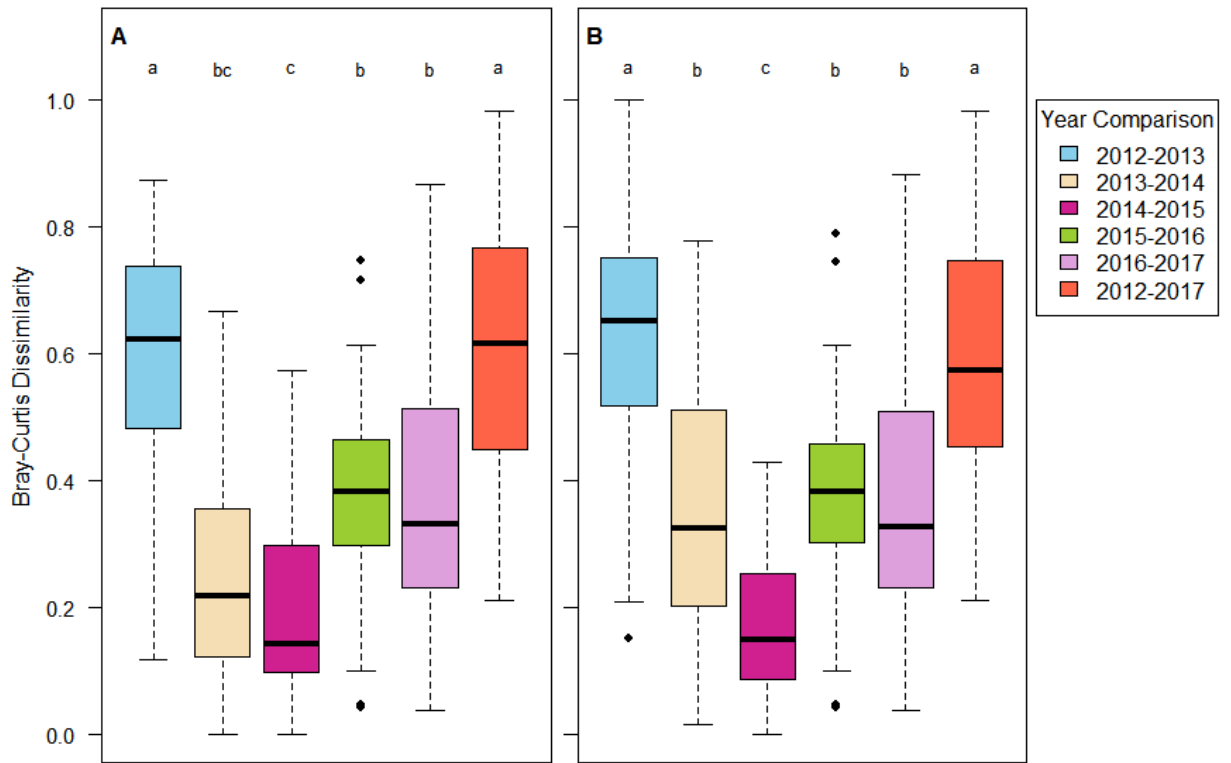


Figure 7: Bray-Curtis Dissimilarity was used to calculate beta diversity from year to year at DWSNP with (A) and without (B) *Alliaria petiolata*. Letters indicate significant difference. Note x-axis labels are located in the legend.

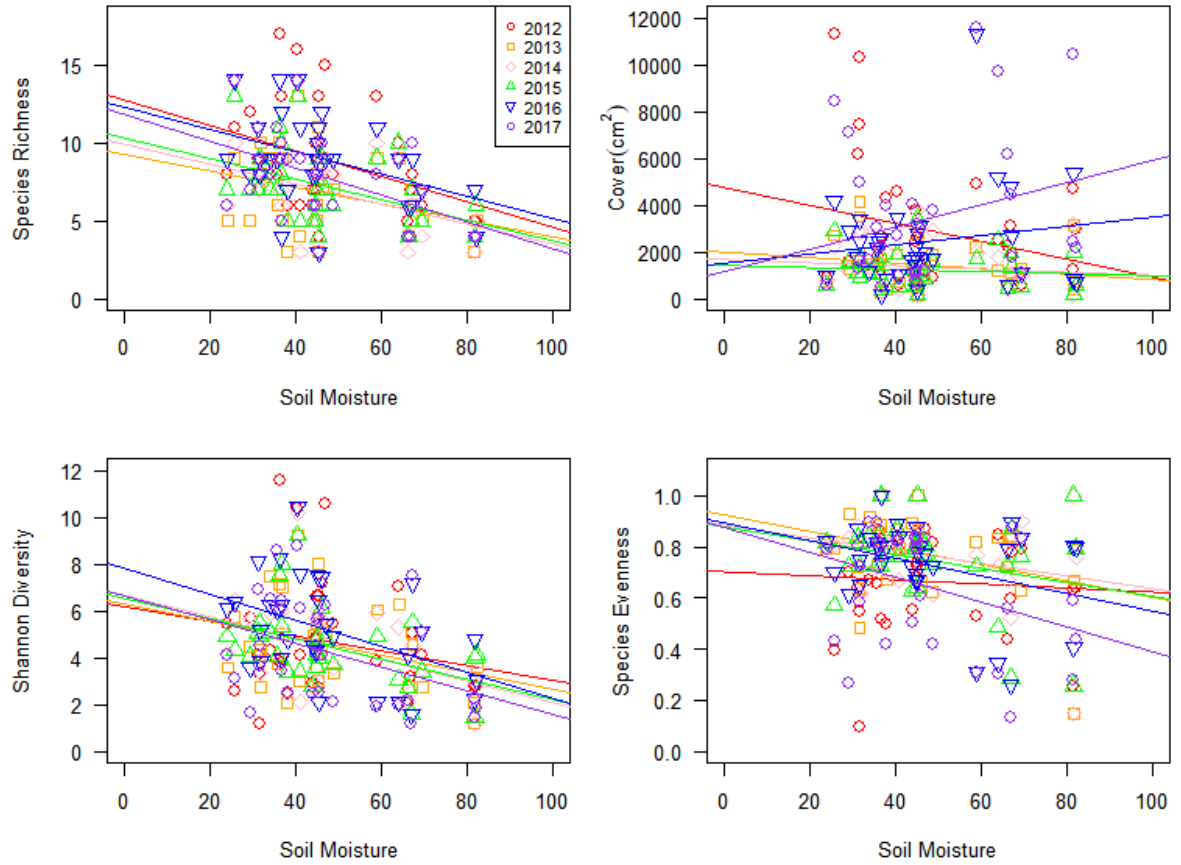


Figure 8: Soil moisture (%) by plot and year for richness, cover, Shannon diversity, and evenness (note the y-axes differences). Colors of regression lines correspond to symbol colors provided in the legend.

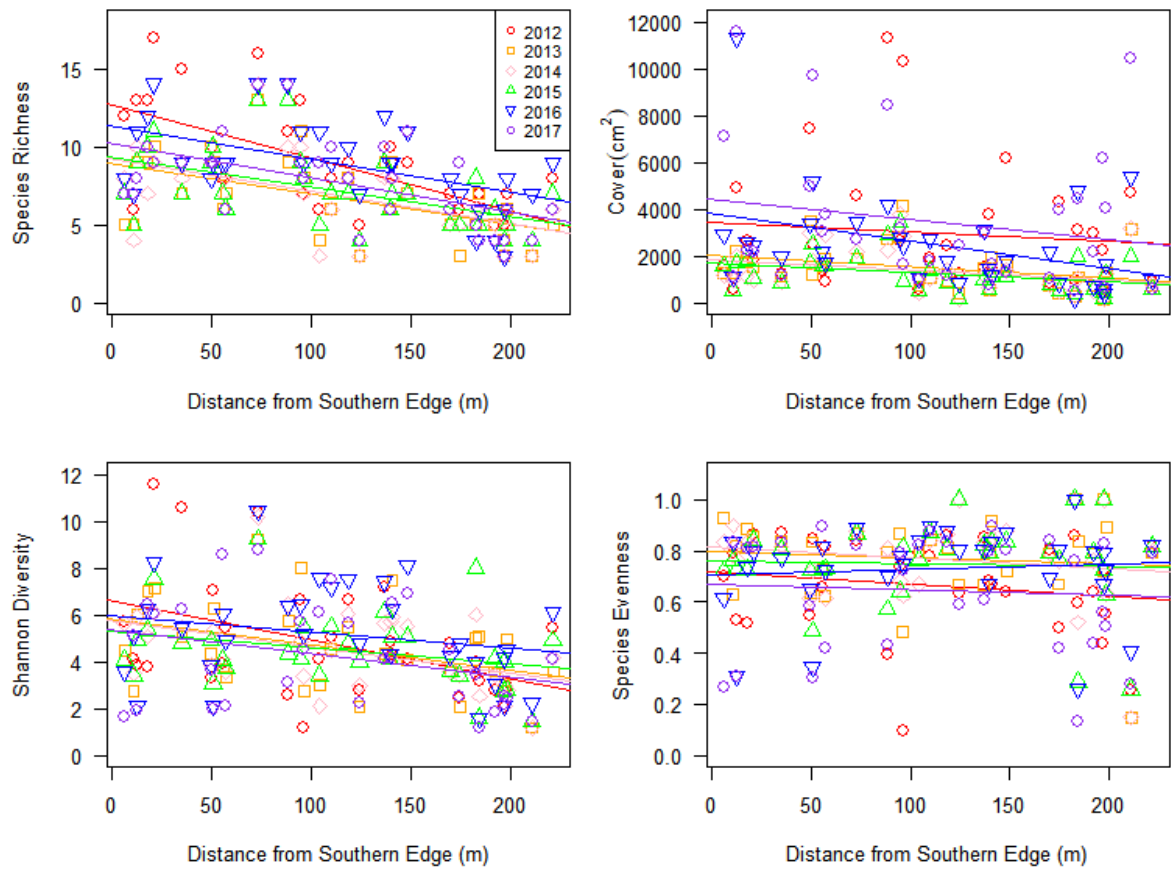


Figure 9: Environmental factors for each plot compared between years based upon the distance moving away from the southern edge of DWSNP. Regression line colors correspond to symbol colors provided in the legend. Note the different variables on the y-axes.

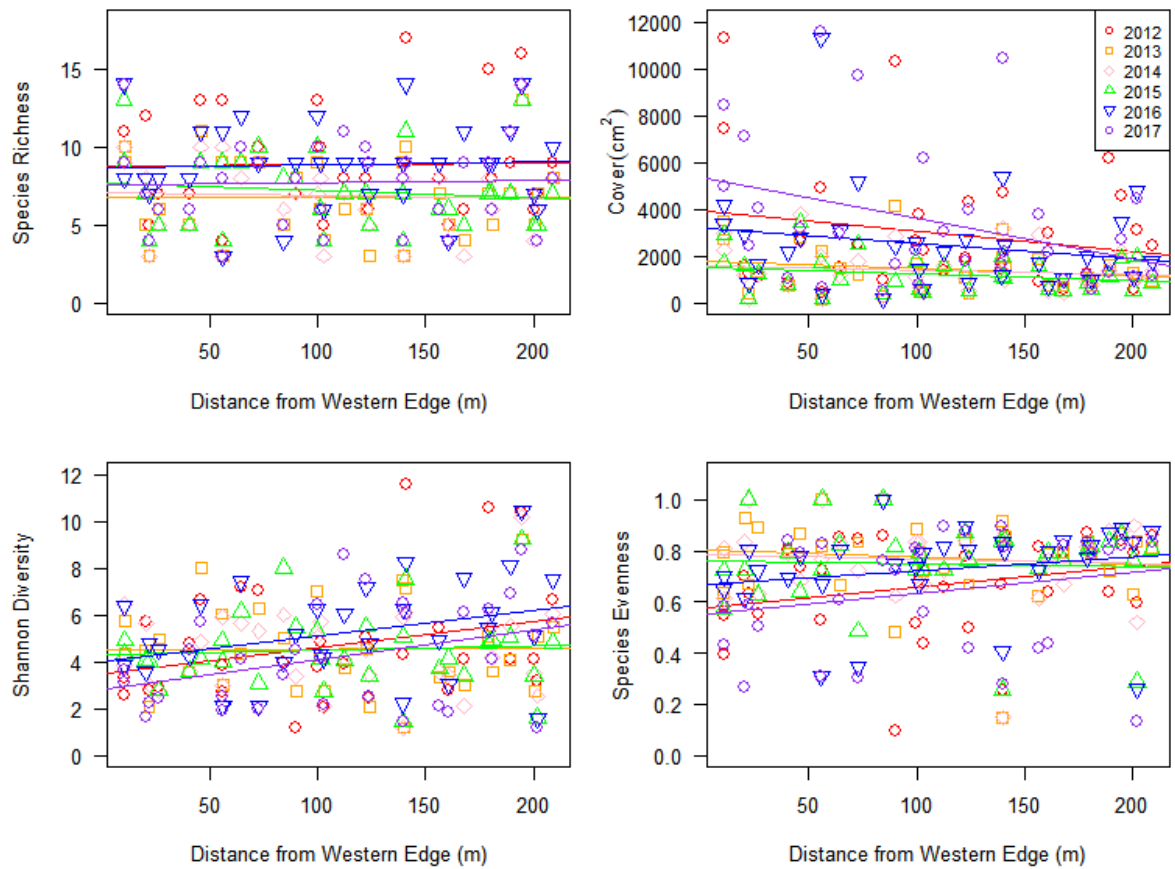


Figure 10: Environmental factors shown in relation to plot distances from the western edge of DWSNP. Regression line colors correspond with the legend. Note the different variables on the y-axes.

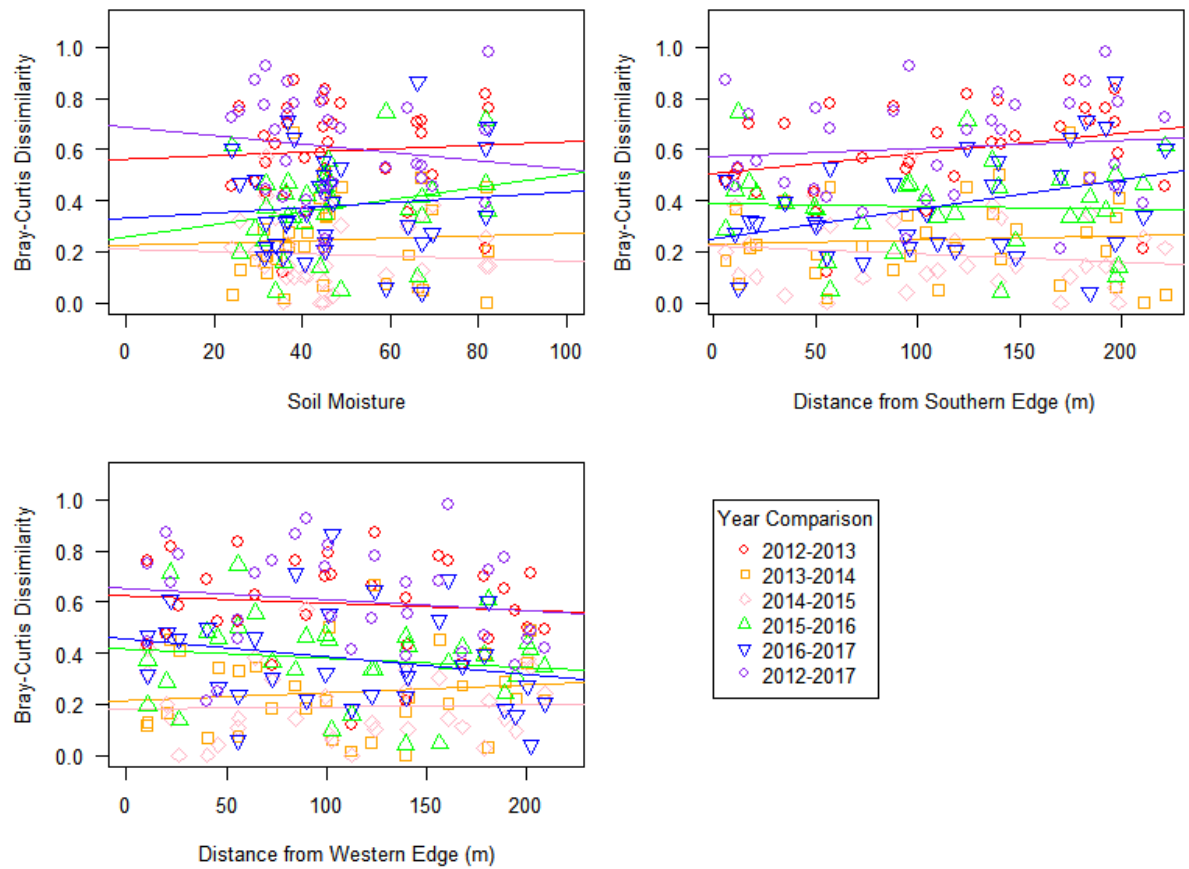


Figure 11: Beta diversity by plot and years shown compared to soil moisture and distance from the southern and western edges of DWSNP. Regression lines correspond with the symbol colors within the legend.

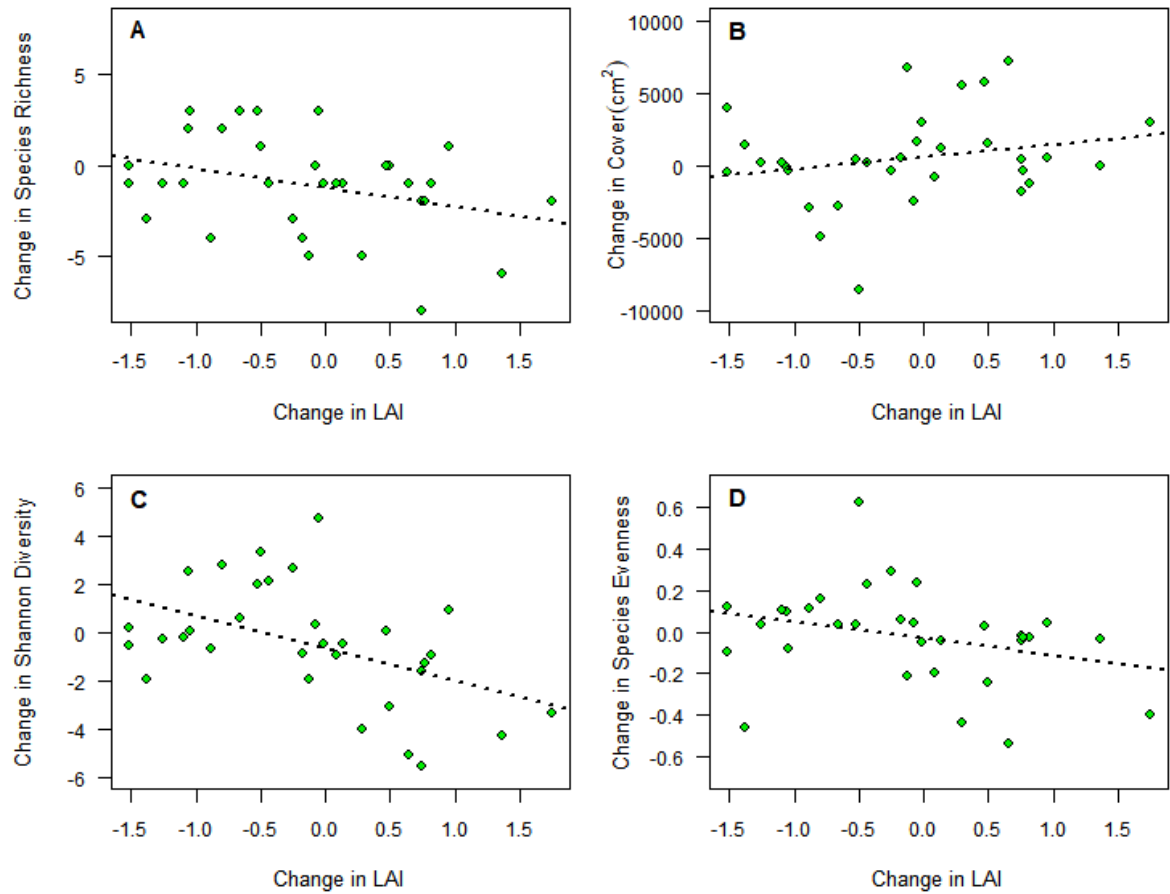


Figure 12: Richness (A), cover (B), Shannon diversity (C), and evenness (D) values from 2017 minus the 2017 values gave the differences, and are shown in relation to Leaf Area Index, which was calculated in the same manner.

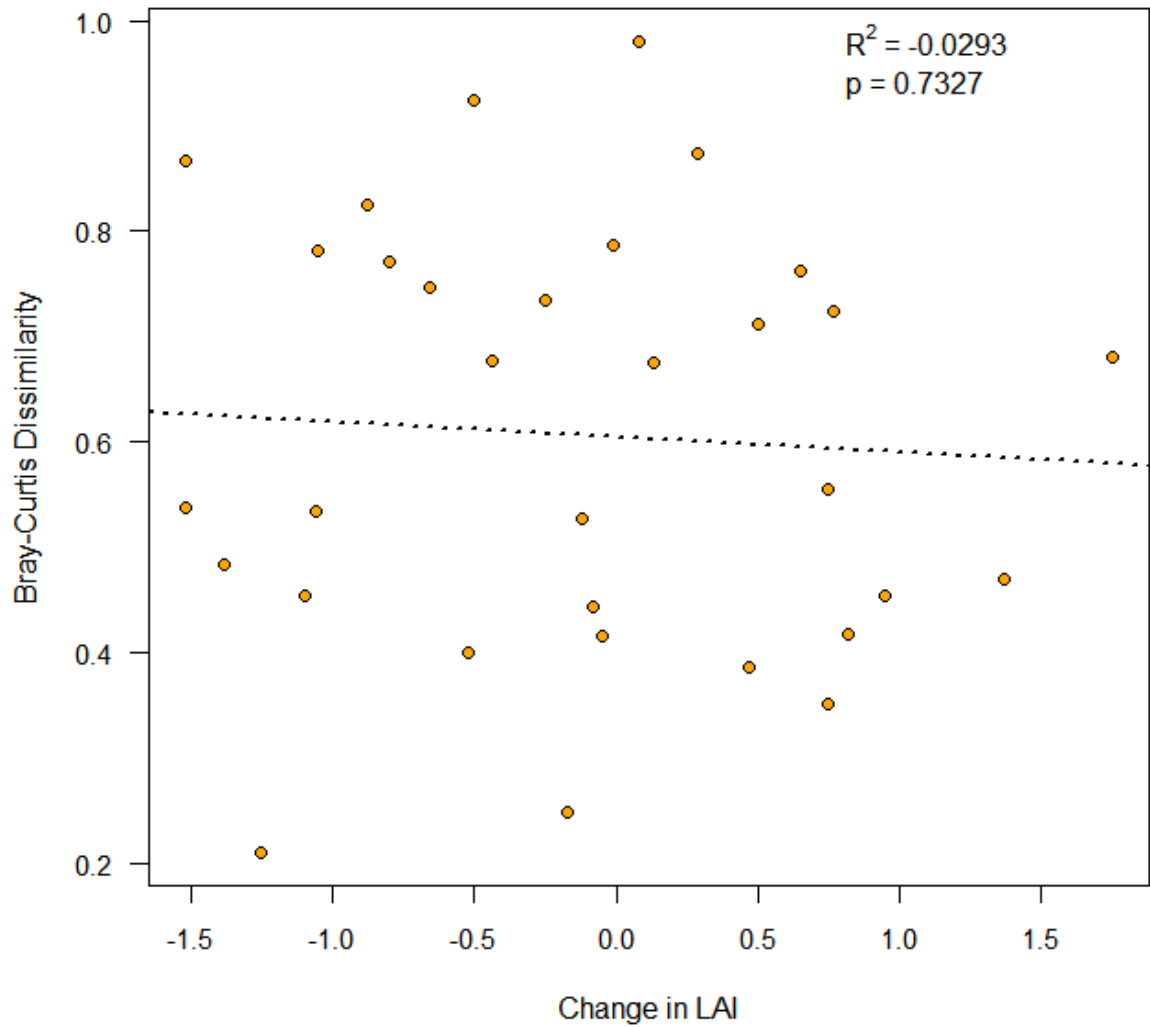


Figure 13: 2012 to 2017 beta diversity compared to Leaf Area Index (LAI) calculated from the difference between 2012 and 2017 LAI values.

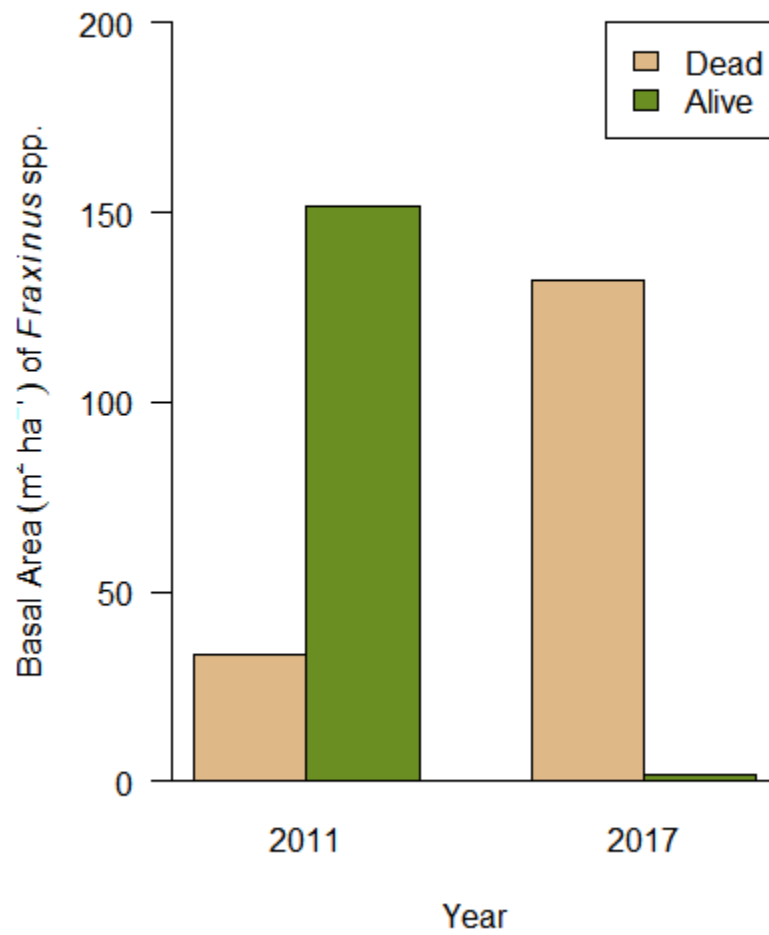


Figure 14: A comparison of living and dead ash trees in DWSNP in 2011 and 2012 using basal area ($\text{m}^2 \text{ha}^{-1}$) calculations.

Minor Species: *Actaea racemosa*, *Allium canadense*, *Carex albursina*, *Carex blanda*, *Carex jamesii*, *Cystopteris protrusa*, *Elymus hystrix*, *Eurybia divaricata*, *Festuca subverticillata*, *Galium circaezans*, *Laportea canadensis*, *Lithospermum latifolium*, *Lysimachia ciliata*, *Maianthemum racemosum*, *Osmorhiza claytonii*, *Phryma leptostachya*, *Phytolacca americana*, *Polygonatum biflorum*, *Prenanthes altissima*, *Solidago caesia*, *Solidago flexicaulis*, *Solidago ulmifolia*, *Sonchus arvensis*, *Teucrium canadense*, *Tradescantia virginiana*, *Triosteum aurantiacum*, Unknown, *Viola sp*

Table 2. Repeated Measures ANOVA was used to calculate *F*-values, *P*-values, and degrees of freedom (*df*) for each variable concerning species composition within the 32 1 m² plots from year to year in DWSNP. *Alliaria petiolata* was removed and values were recalculated, indicated by “No AP” following the respective variable. To obtain these measures, plot variables (richness, cover, Shannon diversity, evenness, beta diversity) were compared to the values obtained from all six years per plot, resulting in an *F*-value (higher values indicate increased significance). *P*-values less than 0.05 are significant.

	With Garlic Mustard			Without Garlic Mustard		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Richness	14.97	155	< 0.001	15.43	155	< 0.001
Cover	11.78	155	< 0.001	13.72	155	< 0.001
Shannon Diversity	1.87	155	0.103	3.00	155	0.013
Evenness	5.50	155	< 0.001	5.38	155	< 0.001
Beta Diversity	35.27	155	< 0.001	31.04	155	< 0.001

Table 3. The relationships between environmental variables and distance to southern and western edges (m), soil moisture, and Leaf Area Index (LAI) are shown by the adjusted R^2 value and P -value. LAI was collected in 2012 and 2017; therefore, there are no data for 2013-2016. Beta diversity and LAI regression was calculated using the difference of the two LAI measurements. P -values lower than 0.05 indicate significance.

	Distance to S Edge		Distance to W Edge		Soil Moisture		LAI	
	R ²	P	R ²	P	R ²	P	R ²	P
<i>Richness</i>								
2012	0.424	<0.001	-0.033	0.921	0.125	0.027	0.159	0.014
2013	0.237	0.003	-0.033	0.961	0.090	0.053	-	-
2014	0.269	0.001	-0.032	0.824	0.142	0.019	-	-
2015	0.251	0.002	-0.016	0.485	0.176	0.010	-	-
2016	0.247	0.002	-0.031	0.806	0.158	0.014	-	-
2017	0.255	0.002	-0.032	0.868	0.234	0.003	-0.031	0.809
<i>Cover</i>								
2012	-0.023	0.589	0.008	0.270	0.025	0.189	-0.028	0.685
2013	0.086	0.057	0.004	0.301	0.008	0.275	-	-
2014	0.064	0.088	-0.014	0.461	-0.019	0.515	-	-
2015	0.096	0.047	0.021	0.207	-0.025	0.616	-	-
2016	0.109	0.037	0.004	0.296	-0.008	0.391	-	-
2017	0.005	0.290	0.105	0.040	0.037	0.149	-0.023	0.584
<i>Shannon Diversity</i>								
2012	0.175	0.010	0.048	0.119	0.011	0.254	0.106	0.039
2013	0.132	0.024	-0.033	0.951	0.074	0.072	-	-
2014	0.155	0.015	-0.029	0.735	0.159	0.014	-	-
2015	0.049	0.118	-0.028	0.690	0.165	0.012	-	-
2016	0.017	0.223	0.076	0.069	0.169	0.011	-	-
2017	0.070	0.078	0.104	0.040	0.120	0.029	-0.025	0.633
<i>Evenness</i>								
2012	-0.003	0.349	0.044	0.130	-0.028	0.706	-0.017	0.499
2013	-0.023	0.583	-0.020	0.541	0.083	0.060	-	-
2014	-0.002	0.337	-0.028	0.703	0.035	0.156	-	-
2015	-0.031	0.808	-0.031	0.807	0.043	0.134	-	-
2016	-0.026	0.652	0.007	0.276	0.080	0.065	-	-
2017	-0.029	0.721	0.021	0.205	0.102	0.042	-0.033	0.942
<i>Beta Diversity</i>								
2012-2013	0.055	0.105	-0.023	0.586	-0.030	0.745	-	-
2013-2014	-0.028	0.697	-0.020	0.540	-0.031	0.787	-	-
2014-2015	-0.009	0.405	-0.032	0.838	-0.030	0.756	-	-
2015-2016	-0.032	0.825	-0.014	0.459	0.025	0.189	-	-
2016-2017	0.131	0.024	0.018	0.222	-0.026	0.646	-	-
2012-2017	-0.021	0.548	-0.014	0.453	-0.014	0.458	-0.029	0.733