

Plant species co-occurrence and plot-level temporal instability

By

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Abstract

There is a large body of research investigating drivers of compositional change in plant communities through time. Communities that experience a significant amount of compositional change through time can be described as unstable. My goal was to investigate the role of co-occurrence patterns within a plant community as a source of instability across three successive years. I developed an approach to examining the relationship between instability and co-occurrence patterns that also accounted for several other potentially important community features that may impact community stability, including functional diversity, the abundance of exotic species, protection from herbivory, phylogenetic diversity, and the evenness of species abundance within plots. I monitored instability as variation in species abundance in two groups of 75 experimental treatment plots in an old-field plant community: a control group and a caged group, with the intent of reducing herbivory within the caged plots. Although the model developed did not fit the data for species experiencing reduced herbivory and co-occurrence patterns fluctuated without direction within both treatment groups across time, significant predictors of temporal instability emerged in the final years within the control plots. Overall, I found no clear impact of pairwise co-occurrence patterns on temporal instability, despite incorporating several community aspects that have been previously shown to impact stability. This indicates that the factors driving temporal change were not adequately captured by the model.

Introduction

A plant community can be considered stable when the community composition remains essentially unchanged through time, or if it can return to a similarly unchanging state after a disturbance that pushes it away from equilibrium (Botkin and Sobel 1975; Connell and Sousa 1983; DeAngelis and Waterhouse 1987; Gigon 1983; Stohlgren 2006). Thus, any characteristic of a community which increases its ability to resist perturbation contributes to its stability. Several community attributes have been investigated as possibly impacting stability, including the susceptibility to herbivores (Rees and Brown 1992; Olff and Ritchie 1998; Heard and Sax 2013; Engelkes et al. 2016), the presence of dominant or exotic species (Lodge 1993; Kennedy et al. 2002; Myers and Bazely 2003; van Ruijven et al. 2003; Valone and Balaban-Feld 2018), the evenness of relative abundance within a community (Kirwan et al. 2007; Hillebrand et al. 2008), and the distribution of functional traits (Mason et al. 2005; Villéger et al. 2008; Laureto et al. 2015).

Numerous studies have shown that grazing can significantly impact the diversity of a plant community, with the impact from herbivory being related to herbivore body size and the spatial scale of the plant community being considered. Although sporadic foraging from smaller herbivores can increase the diversity of plant communities studied at a smaller, plot-level scale by reducing species abundance without severely reducing species richness (Grime 1973; Huston 1979; Gibson and Brown 1991), the same effect on diversity may not hold for plant communities studied in a larger area (Chaneton and Facelli 1991; Gibson and Brown 1991; Glenn and Collins 1992; Olff and Ritchie 1998). The importance of spatial scale may not hold for all herbivores, as previous work has shown that groups of large grazing herbivores increase the

diversity of a plant community through the reduction of dominant plant species irrespective of spatial scale. (McNaughton 1985; Milchunas et al. 1988; Crawley 1989; Huntly 1991; Belsky 1992; Root 1996).

As recently noted by Valone and Balaban-Feld (2018), a number of studies found that small-scale experimental communities that displayed high diversity and evenness also tended to be more stable (Cardinale et al. 2006, 2012; Gross et al. 2014; Tilman et al. 2014). However, this relationship between diversity and stability may not carry over into natural communities, which tend to exhibit lower evenness (Eisenhauer et al. 2016; Wardle 2016). In the case of natural communities, the persistence of the most dominant species may be a more significant contributor to temporal stability than community diversity (Grime 1998; Polley et al. 2007; Sasaki and Lauenroth 2011). It is also noteworthy that herbivores tend to preferentially graze on plant species indigenous to their native range, thereby suppressing dominance when the most abundant plants are native species (Myers and Bazely 2003). This suppression mechanism is typically absent for introduced plant species, so communities dominated by introduced species may be higher in stability and lower in diversity than communities dominated by native species (Ives et al. 1999).

Competitive interactions among plants have received considerable attention with regard to general community functioning (reviewed in Callaway and Walker 1997; Cavieres and Badano 2010), but competitive interactions do not take place in isolation of facilitative interactions. In the event of release from stabilizing mechanisms (such as through a natural disturbance or protection from herbivory), a previously rare or absent species may be able to seize the opportunity to establish itself in high abundance (Olf and Ritchie 1998; Keane and

Crawley 2002; Shea and Chesson 2002; Sasaki and Lauenroth 2011), possibly with the assistance of positive interactions with so-called “nurse species”, meaning plants that aid in the germination and establishment of neighbours (Flores and Jurado 2003; Gómez-Aparicio et al. 2004; Padilla and Pugnaire 2006). In the case of drastic changes in community constituents and relative abundance, a plant assemblage may require considerable time to strike a new balance between competition and facilitation before the community composition stabilizes. This is, of course, but one potential outcome resulting from a disturbance, and association with a nurse species is not a requirement for establishment. If the succeeding plant is an exotic species characterized by a high rate of growth or strong competitive ability for soil nutrients, it may be able to take root in the community without the assistance of nearby nurse species (Aerts 1999). It is also possible that a large and diverse seed bank of native species may be present in the soil, and this natural diversity within the recovering community is shielded from invasion due to a potential invader being unable to out-compete several native species simultaneously for resources (Peter and Burdick 2010).

Although competition has previously gained more attention than facilitation (Bertness and Callaway 1994; Brooker and Callaghan 1998; Cavieres and Badano 2010), the presence of competition does not by itself exclude the possibility of facilitative interactions, and there are a considerable number of ways in which plants can positively impact neighbouring species beyond serving as nurse species (Callaway 1995; Bruno et al. 2003; Cavieres and Badano 2010). It has been theorized that communities that feature a high degree of facilitation are expected to be more stable due to a positive feedback loop wherein a community member that promotes the continued existence of neighbouring species is in turn promoted by those same

neighbours through niche complementarity, but this theory has yet to gain substantial support for natural communities (Hector et al. 1999; Loreau and Hector 2001; Ashton et al. 2010).

Plants may enhance the growth, survival, or reproductive success of neighbouring plants by ameliorating stressors associated with the environment or herbivory (Callaway and Walker 1997). These facilitative mechanisms can include increasing soil nitrogen (Ledgard 2001) and providing shade, which in turn can reduce temperature and dehydration stress associated with reduction in evapotranspiration (Holmgreen et al. 1997; Stachowicz 2001; Michalet 2006).

Plants lacking in physical defense mechanisms such as thorns, insect repellent compounds, or secondary metabolites that reduce palatability may benefit from growing close to plants that exhibit these features (Atsatt and O'Dowd 1976; Hay 1986; Gross 2008). Plants with low stress tolerance can increase their success by growing in association with other plants that are more stress-tolerant (Michalet et al. 2006). Logically, it follows that the relative competitive and facilitative effectiveness of an individual plant species can be examined by quantifying aspects of its physiology in the form of functional traits (Westoby 1998; Díaz and Cabido 2001; Lavorel and Garnier 2002; Westoby and Wright 2006; Kraft et al. 2015; Kuntsler et al. 2016).

Several traits can be used to assess the relative competitive ability of an individual plant species relative to community-wide traits (Gaudet and Keddy 1988; Leibold 1998; Cornwell et al. 2006), but if one attempts to list all of the plant traits that may play a role in shaping co-occurrence patterns, the list will rapidly become impossibly long. For this reason, I focused on only a few standard plant traits that have been linked to stability, diversity, or interspecific interactions. These traits are seed mass, maximum plant height and biomass, specific leaf area, leaf dry matter content, leaf lobation, and support fraction.

Seed mass may potentially serve as an influential trait with regard to pairwise co-occurrence patterns as there is some evidence that plants with larger seeds have a greater competitive effect on neighbouring species (Goldberg and Fleetwood 1987). This trait may also play an important role when viewed under the general lens of community temporal stability as it has been shown to have a significant relationship with seed persistence in soil (Thompson et al. 1993; Leishman et al. 2000). Plants that produce smaller seeds tend to produce more of them, and a community composed of species that deposit large seed banks in the soil may more readily recover from a disturbance, with the succeeding community being of similar composition to the pre-disturbance community (Guo et al. 2000; Leishman et al. 2000).

Maximum plant height and biomass may play a complex role in co-occurrence patterns. Taller, larger plants may compete with each other for light and may out-compete shorter, smaller plants that are not shade-adapted in successional communities (Werger et al. 2002; Craine and Dybzinski 2013), contributing to negative species co-occurrence between large and small plants after a disturbance. It is worth noting, however, that smaller plants tend to be more abundant than larger species and are able to make use of micro-habitats within communities (such as gaps between larger plants where resources and physical space are too low for bigger species), therefore playing an important role in community diversity and stability by sheer abundance (Aarssen et al. 2006). Additionally, shade-adapted species may contribute to positive co-occurrence by relying on the microclimate in the understory of taller species (Tewksbury and Lloyd 2001; Falster and Westoby 2003; Gómez-Aparicio et al. 2004; Westoby and Wright 2006; Kraft et al. 2015).

Specific leaf area and leaf dry matter content are two commonly used measures that have been shown to be related to each other in plant assemblages found in cool, temperate regions (Pérez-Harguindeguy et al. 2013). Although specific leaf area can vary between co-occurring species, species growing in resource-rich environments generally show higher specific leaf area values. Specific leaf area can also serve as an indirect measure of growth as it is positively related to relative growth rate across several species (Díaz et al. 1998; Pérez-Harguindeguy et al. 2013). Higher values for leaf dry matter content usually indicate tougher leaves that are more resistant to herbivory and other environmental sources of damage, such as wind (Pérez-Harguindeguy et al. 2013). Leaf lobation is an important functional trait as it is used as a means of determining leaf shape, which is strongly correlated with climate (Peppe et al. 2011). Support fraction, which is the proportion of plant biomass dedicated to support structures such as stems and leaf midribs, was included as it provides a measure of physical strength and resistance to damage. Plants with higher values for support fraction should exhibit higher stability and lower mortality.

In addition to the individual effects of specific traits on the competitive and facilitative potential of a species, a collection of traits can be used to calculate the niche volume of the community as a whole. Communities that exhibit higher niche volume are expected to be more even, diverse, and stable over time as they leave less room for the establishment of new additions to the community. Communities with lower niche volume leave a wider array of resources open for potential invaders to exploit (Berendse 1994; Díaz and Cabido 2001; Donohue et al. 2001; Drenovsky et al. 2012), and as a result are expected to be less stable over time. A similar relationship can be found between phylogenetic diversity and stability;

communities that are composed of closely related species are more likely to share niche requirements and leave more resources open to exploitation from other species (Cadotte et al. 2012).

The concept that the stability of a community is tied to its diversity is one that has been a mainstay in ecology for a considerable amount of time (MacArthur 1955; Elton 1958; Lodge 1993; Ives et al. 1999). Despite the persistence of the diversity-stability concept, a plethora of definitions and measures exist for both terms. Grimm and Wissel (1997), for example, found 163 definitions of stability and over 40 different ways to measure stability. Diversity also encompasses a wide range of definitions and corresponding measures. Diversity may mean anything from simply the number of species within an area to more complex concepts and measures such as the genetic variation within an assemblage (Hill et al. 2005) or the range of functional traits distributed across the constituents in a given area (Mason et al. 2005). The Shannon-Weiner index and Simpson index are examples of frequently used measures of diversity (Hill 1973; Magurran 2004; Hill et al. 2005), although one should exercise caution in using a common measure simply because it is commonly used. Considering the high degree of variation in methods and terminology in the study of diversity and instability, one should clearly define each term from the outset.

In this study, I define instability as mean temporal variation in the relative abundance of individual species within individual experimental plots. The three types of diversity I have measured in this study are species richness, phylogenetic diversity, and functional diversity. It is important to note that although physical proximity may be a common requirement of facilitation and competition in sessile organisms like plants, probabilistic positive and negative

co-occurrence are not direct measures of competition or facilitation. In this study, I estimated positive and negative spatial co-occurrence, with the reasonable assumption that at least some of these co-occurrence patterns are indicative of competition and facilitation (Gotelli and McCabe 2002).

The main goal of this study was to develop a comprehensive approach to examining potential sources of the temporal instability of a natural plant community. This approach incorporated a variety of intrinsic community aspects that may influence instability, such as variations in plant functional traits, species evenness, the abundance of exotic species, phylogenetic diversity, and probabilistic co-occurrence patterns. Additionally, I tested for differences in co-occurrence patterns between plant assemblages sheltered from herbivory and those left exposed to herbivores. This study was designed to evaluate two hypotheses. Firstly, it was hypothesized that reduction in herbivory impacts co-occurrence patterns, which in turn leads to changes in temporal instability. The second, main hypothesis of this study was that co-occurrence patterns affect the temporal stability of a plant community, and as a result, can be used in conjunction with other community attributes to predict stability.

Materials and methods

Study site

This study was conducted in an old-field plant community at the Ontario Ministry of Natural Resources Arboretum in Sault Ste. Marie, Ontario (coordinates: 46°32'34.1" N 84°27'37.4" W) from 2013 to 2015. A total of 150 plots measuring 50 cm in diameter were randomly assigned to two treatment groups: a control group and a caged group, with 75 plots per group. Each plot

contained an average of 6.8 species, with a variance of 3.2 in the caged plots and 3.5 in the control plots. Both caged and control plots contained a large proportion of exotic species, with a higher proportion of exotic species in the caged plots (88% in the caged plots and 83% in the control plots). A slightly higher number of native species were present in the control plots (17% in the control plots and 12% in the caged plots).

Experimental design

To evaluate the hypothesis that herbivory impacts pairwise co-occurrence patterns, the 75 plots assigned to the caged group were surrounded by exclusion cages composed of 1 cm gauge fencing. The fencing extended approximately 15.2 cm below ground and 45.7 cm above ground to reduce small mammalian herbivore access to the plots. The cages were left open on top to allow for unrestricted vertical plant growth. Control plots were left open and undisturbed. A full census of each plot was conducted once per year between May to September for three consecutive years (2013 to 2015).

Hypothesis testing

To test the hypothesis that instability could be predicted using intrinsic community aspects for each assemblage in a plot, I developed a model that incorporated multiple plot-level measurements as independent variables and temporal instability as the dependent variable. I initially planned to utilize species richness, the abundance of introduced species and native species, height asymmetry, three measures of functional diversity, plot-level positive and negative co-occurrence scores, phylogenetic diversity, and species evenness as the

independent variables for this model. Species richness, abundance of native species, and height asymmetry were removed due to multicollinearity. Plot-level positive co-occurrence scores were also dropped from the model due to a lack of positive co-occurrence in the caged plots during 2014.

Species richness was calculated as the total number of species occurring within a plot (Magurran 2004). The abundance of introduced species was determined by first comparing the annual census data with the United States Department of Agriculture Plants Database (USDA, NRCS 2018) to classify each species as either exotic or native. I then calculated plot-level introduced abundance as the sum of the abundance of each species found within a plot that was listed as introduced in the database. Plots were also assessed for native species abundance using the same approach as introduced species.

For each species found within a plot, 25 representative plants were collected from the field surrounding the plots and assessed for seven functional traits: maximum height, maximum biomass, specific leaf area, support fraction, leaf dry matter content, leaf lobation, and seed mass. Functional trait data was averaged based on twenty samples of each species found in each plot type per year. For each trait and species, the data was standardized by subtracting the mean of all species from the trait value for a specific species and dividing the product by the standard deviation of the trait for all species. Maximum height data was used to quantify size asymmetry between species using the Gini coefficient (G), following the equation in Weiner (1990) where n is the number of species, X is maximum height, and i and j represent separate species:

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n(n-1)\bar{x}}$$

I performed this calculation using the “reldist” package in R (Handcock 2016, R Core Team 2017). Although the Gini coefficient was originally developed to measure inequalities in wealth distributions in economics, it has proven to be a useful tool for measuring size inequalities in ecology (Weiner and Solbrig 1984; Weiner 1990).

The three aspects of functional diversity I measured were functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). When the plant assemblage in a plot is envisioned as an n -dimensional space, with each dimension representing a different functional trait, FRic provides a measure of the total trait space occupied by the species in a plot, FEve determines how evenly the space is occupied by those species, and FDiv allows one to describe how spread out the constituents of a plot are with respect to their traits (Villéger et al. 2008; Mouchet et al. 2010).

I completed the calculations for FRic, FEve, and FDiv using the “FD” package in R (Laliberté et al. 2014, R Core Team 2017). FRic is calculated as:

$$FRic = \frac{SF_{ci}}{R_c}$$

Where SF_{ci} is the niche space filled by the community and R_c is the absolute range of traits used to determine the niche space (Mason et al. 2005). FEve is calculated as follows, where S is species richness:

$$FEve = \frac{\sum_{l=1}^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

With partial weighted evenness (PEW_l) calculated as:

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$$

Where weighted evenness (EW_l) is obtained as:

$$EW_l = \frac{dist(i,j)}{w_i + w_j}$$

Where $dist(i,j)$ is the Euclidean distance between any two given species in the community (designated species i and species j) and w_i and w_j represent the relative abundance of those species. The calculation of FEve results in a measure that is bound between zero and one, with one representing complete evenness (Villéger et al. 2008).

Like FEve, FDiv is bound between zero and one, with values closer to zero indicating that highly abundant species are located closer to the center of gravity relative to rare species. FDiv is calculated according to the following series of equations, where i is an individual species, k is a specific trait, T is the number of dimensions, S is species richness, and X_{ik} is the coordinate of a specific species on a specific trait (Villéger et al. 2008):

$$FDiv = \frac{\Delta d + \overline{dG}}{\Delta |d| + \overline{dG}}$$

Where Δd is the sum of the weighted deviances from the center of gravity, which is calculated as:

$$\Delta d = \sum_{i=1}^S w_i \times (dG_i - \overline{dG})$$

and \overline{dG} is the mean species distance to the center of gravity, calculated as:

$$\overline{dG} = \frac{1}{2} \sum_{i=1}^s dG_i$$

Where dG_i is the Euclidean distance to the center of gravity for each species, which is calculated as:

$$dG_i = \sqrt{\sum_{k=1}^T (x_{ik} - g_k)^2}$$

The Euclidean distance to the center of gravity for each species is calculated using the coordinates of each species (V) that form the vertices of the convex hull (g_k), which are found as follows,

$$g_k = \frac{1}{2} \sum_{i=1}^V x_{ik}$$

I identified positively and negatively co-occurring plant species using the “cooccur” package in R (Griffith et al. 2016; R Core Team 2017), which calculates the probability of two species co-occurring at a given number of sites as:

$$P_j = \frac{\binom{N_1}{j} \times \binom{N - N_1}{N_2 - j}}{\binom{N}{N_2}}$$

Where N_1 is the number of plots where species A occurs, N_2 is the number of plots where species B occurs, N is the total number of sites, and j represents co-occurring plots. Species pairs that did not consistently co-occur across years were discarded, on the basis that a one-time co-occurrence did not significantly contribute to the pairwise composition of each plot across time. I then discarded pairs that contained either a rare species (occurring in fewer than 10% of individual plots per treatment group in a given year) or a highly abundant species

(occurring in greater than 90% of plots in a treatment group in a given year). Rare and highly abundant species were discarded in an attempt to compensate for a general limitation in calculations of co-occurrence. For rare and highly abundant species, co-occurrence calculations lack the power required to discriminate between positively, negatively, and randomly co-occurring pairs. Once recurring pairs with moderate abundance were identified, I then assigned separate positive and negative scores to each plot by dividing the sum of the abundances of paired individuals by the total plot-level abundance for all species.

I constructed a phylogenetic tree of all species included in the study using DNA sequences for the ribulose-1,5- biphosphate carboxylase/oxygenase large subunit (rbcl) gene. This gene was selected because it is a commonly used DNA barcoding sequence in plants, therefore allowing for the accurate identification and placement of species within the tree (Hasebe et al. 1994; Kress and Erickson 2007; CBOL Plant Working Group 2009). I obtained these sequences from the National Center for Biotechnology Information Nucleotide database (NCBI 2018). An additional species, *Isoetes hystrix*, a land quillwort belonging to the Isoetaceae family, was included as an outgroup. The rbcl sequences for each species were aligned and trimmed using the program MEGA 7 (Kumar et al. 2016). Because the sequences varied substantially in length due to differences in primers and sequencing techniques used, all sequences were trimmed to 550 base pairs from the gene origin to avoid including false divergence in the tree. The phylogenetic tree was then constructed in MEGA 7 using the default maximum parsimony method, with the phylogeny tested using a bootstrapping method of 500 replications (Kumar et al. 2016).

I used the branch lengths obtained from the phylogenetic tree to calculate mean nearest taxonomic distance (MNTD) for each plot. This allowed me to determine the average phylogenetic distance separating each of the species within each plot (Cadotte et al. 2012). A null model was constructed from this data and run 1000 times. The actual community was then compared to the model to determine which plots displayed phylogenetic evenness and which plots were clustered around specific portions of the tree. Phylogenetic evenness is indicated by positive observed MNTD values in the community and P-values greater than 0.95 when compared to the null model. Clustering is demonstrated when the observed community MNTD values are negative and P-values are lower than 0.05 when compared to the null model. This analysis was completed using the “picante” package in R (Kembel et al. 2010; R Core Team 2017).

Although a diversity index with a long history of use exists and is still widely used in ecology, namely the Shannon index (Lande 1996; Magurran 2004), I have not used this index to quantify diversity. Several conceptual issues exist with this index, such as the error that may arise when all possible species are not represented in a plot (Peet 1974; Magurran 2004), the loss of information regarding individual species (Yue et al. 2007; Barrantes and Sandoval 2009), and because it confounds species richness with evenness (Magurran 2004). In place of this measure, I used Smith & Wilson’s evenness index, referred to as E_{var} (Smith and Wilson 1996) to identify asymmetries in plant species abundance. Identification of rare species is necessary in this study because species rarity is generally positively correlated with extinction risk (Shaffer 1981; Pimm et al. 1988).

Evenness was calculated using E_{var} , where:

$$E_{var} = 1 - 2/\pi \arctan \left\{ \sum_{s=1}^S \left(\ln(x_s) - \sum_{t=1}^S \ln(x_t)/S \right)^2 / S \right\}$$

In this equation, S represents species richness, x_s is the abundance of an individual species and x_t signifies the abundance of a single species in a plot minus the total plot abundance. This equation examines proportional differences, without dependence on units, and is based on the variance of abundance. This index gives the proportional variance in species abundance in a plot and binds the result between one and zero, with one representing the maximum possible evenness (meaning all species are equally abundant) and zero indicating the minimum level of evenness (Smith and Wilson 1996; Magurran 2004).

I examined plot-level temporal stability using the Bray-Curtis dissimilarity index (β). I selected this index because it allows for the quantification of change in species abundance between two time points and because the index is bound between a fixed upper and lower value, providing an easy to interpret measure of change (Legendre and Legendre 1998; Magurran 2004; Barwell et al. 2015). Plots found to have a higher degree of dissimilarity over time will be considered less stable than plots that remain relatively unchanged across all times points. This definition of stability is in line with the definition of constancy put forth in Grimm and Wissel (1997). β is calculated as:

$$\beta = 1 - \frac{2W}{(A + B)}$$

In this equation, W is equal to the sum of the minimum abundances of each species, A is equal to the sum of species abundance at the first time point, and B is the sum of species abundance at the second time point. I calculated this value for each individual plot across time, resulting in two measures per plot (2013 to 2014, and 2014 to 2015). The maximum possible

value for any given plot is one (complete dissimilarity, interpreted as minimum stability) and the minimum possible value is zero, which indicates no plot-level change from one year to the next, meaning maximum stability (Legendre and Legendre 1998; Barwell et al. 2015; Magurran 2004).

Data analysis

To test for a relationship between temporal instability and the plot-level measures previously described, I performed multiple regressions using temporal instability as the dependent variable. Prior to performing these analyses, I used Shapiro-Wilk tests to ensure the normality of the dependent variable and used log transformations of the Bray-Curtis dissimilarity values when needed to achieve normality. I assessed the independent variables for multicollinearity using the “cor” function in base R (R Core Team 2017). When two independent variables were correlated, I selected the measure that captured more information about the plant assembly. For example, I discarded the Gini coefficient in favour of functional diversity measures, as functional diversity incorporated maximum height along with all other functional traits. As a result, the final model consisted of the abundance of exotic species, negative co-occurrence plot scores, FRic, FDiv, FEve, MNTD, and E_{var} . After performing the multiple regressions, I applied the False Discovery Rate (FDR) technique developed by Benjamini and Hochberg (1995) to the obtained p -values to reduce type I error. I used base R to perform the multiple regressions and p -value adjustments (R Core Team 2017).

I performed Mann-Whitney U tests in SPSS with an α value of 0.05 to assess for differences in instability between the caged and control plots for each individual year. I used

this nonparametric method to compare instability between groups because log transformations were required to achieve normality for only some of these measures within groups (Tables 1 to 4). It would be statistically invalid to use a parametric approach comparing transformed and untransformed data.

Results

The multiple regressions did not reveal any consistent predictors of temporal instability. None of the independent variables were significant predictors of instability for either time point in the caged plots (Tables 1 and 2) or the first time point for the control plots (Table 3). Three significant predictors did emerge in the second time point for the control plots. The abundance of exotic species, F_{Div} , and E_{var} were significant in this case (all p -values < 0.05), but the abundance of exotic species was no longer significant after adjustment with the FDR method (Table 4).

The Mann-Whitney U tests showed that temporal instability was not significantly different between the caged and control plots for 2013 to 2014 ($U = 2304$, $p = 0.056$) or for 2014 to 2015 ($U = 2735$, $p = 0.772$, Figure 1).

Discussion

My results indicate that providing shelter from herbivory did not significantly impact temporal instability. The model that I developed for this study was not able to account for any

appreciable variation in temporal stability among both control and caged plots. Despite species evenness and functional divergence being significant predictors of instability in the final years of the control plots, a very low amount of variation in temporal instability (14.1%) was attributable to the variables used in the model.

Despite the long-standing hypothesis of a relationship between stability and diversity (Elton 1958, Campbell et al. 2011), there remains significant challenges in developing a standard approach to examining this proposed relationship. Although there have been numerous studies examining the effects of diversity on stability, comparisons between studies has been problematic due to the variety in definitions and methods used (Grimm et al. 1992; Grimm and Wissel 1997; Campbell et al. 2011). Several studies have relied on variations in biomass production rather than changes in species abundance as a means of exploring temporal stability of ecosystem functioning rather than the stability of community diversity. The goal in this study was to examine the stability of diversity while maximize ecological realism by reducing experimental disturbance, so variation in species abundance was used in place of biomass production. Although some studies of the stability of ecosystem function have incorporated separate measures for diversity, the differences in methods between those studies and the one described here make direct comparisons inappropriate.

The independent variables selected for the model were intended to capture the highest amount of information about individual species while using the lowest number of variables to retain higher degrees of freedom. It was for this reason that functional diversity was used in place of separate, individual traits. This approach allowed me to include information about each of the seven traits while using only three variables. This may have been a source of noise in the

model, reducing the explanatory power. It may be worthwhile to narrow the focus of each variable in an attempt to reduce noise. The Gini coefficient, for example, could be used to examine height disparity in isolation of the remainder of the functional traits, rather than relying on the inclusion of maximum height in the functional diversity measures.

Future work with this data could adopt a different approach to quantifying plot-level co-occurrence measures. The use of plot-level co-occurrence scores based on probabilistic pairwise co-occurrence patterns for moderately abundant species resulted in positive co-occurrence being removed from the model. Although the pairwise co-occurrence calculations did identify some positively co-occurring species in the caged plots during 2014, all of these species were too rare to be included in the plot scores. It is possible that positive co-occurrence is more strongly associated with temporal stability for rarer species, so the original census data could be partitioned into rare, moderately abundant, and highly abundant species for separate consideration.

Although I attempted to account for a large number of variables that have been shown to affect either stability or diversity, there were some potentially important measures I was not able to incorporate into this study. I attempted to assemble a climate data set by aggregating precipitation and temperature data for each growing season obtained by an unrelated study being conducted near the study site and Environment Canada databases. Due to differences in the timing of the unrelated experiment and this study as well as local variation in precipitation, gaps and inconsistencies in the aggregated data rendered it inappropriate for use in this study. Direct measures of average daily temperature and precipitation taken at the study site would be a valuable addition to future work conducted in a similar manner to this study. Although the

inclusion of climate data would not likely improve predictions of plot-level instability due to all plots being exposed to the same weather patterns, annual variations in climate could potentially explain why some species appeared in particular years. For example, the perennial *Equisetum arvense* was found in both control and caged plots during the 2013 census, but was not found in any plots for the following years. Considering the high moisture needs of this particular species (USDA, NRCS 2018), the lack of *E. arvense* individuals in 2014 and 2015 may be related to a decline in precipitation rather than competitive exclusion. Quantification of the length of the growing season for each year could also help provide some insight into changes in species abundance. It is possible that the significant predictors that appeared in the control plots in the final measure of temporal instability were due to a reduction in the length of the growing season in 2015, but this remains unexamined as only anecdotal observations are available for this possibility.

Despite the lack of standard methods used in the study of the relationship between diversity and community stability, this remains an important area of research. Plant community composition has changed in response to climate change and land-use change, but the full implications of these changes are yet to be fully understood. As our understanding of diversity and community stability improve, so will our methods of accurately measuring both. By broadening our understanding of the relationship between community stability and diversity, we can create more effective conservation and rehabilitation policies (McKinney and Lockwood 1999; Srivastava and Vellend 2005; Cardinale et al. 2012).

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Tables

Table 1. Results of multiple regression for caged plots with the dependent variable of the log of the Bray-Curtis dissimilarity from 2013 to 2014.

Variable	Estimate	Standard error	<i>t</i> value	<i>p</i> -value	Adjusted <i>p</i>
Intercept	0.210	0.170	1.235	0.221	-
Exotic abundance	0.000	0.000	0.694	0.490	0.705
-ve plot score	0.782	0.506	1.547	0.127	0.445
FRic	0.003	0.008	0.371	0.712	0.712
FDiv	0.232	0.127	1.822	0.073	0.445
FEve	-0.086	0.166	-0.521	0.604	0.704
MNTD	1.875	2.824	0.664	0.509	0.704
<i>E_{var}</i>	0.267	0.268	0.998	0.322	0.704
<i>R</i> ²			0.107		
Adjusted <i>R</i> ²			0.012		
Degrees of freedom			66		
F-statistic			1.129		
<i>p</i> -value			0.356		

Table 2. Results of multiple regression for caged plots with the dependent variable of the log of the Bray-Curtis dissimilarity from 2014 to 2015.

Variable	Estimate	Standard error	<i>t</i> value	<i>p</i> -value	Adjusted <i>p</i>
Intercept	-1.529	0.822	-1.859	0.067	-
Exotic abundance	0.000	0.001	-0.680	0.499	0.943
-ve plot score	-0.052	0.728	-0.072	0.943	0.943
FRic	0.007	0.035	0.209	0.835	0.943
FDiv	0.337	0.647	0.521	0.604	0.943
FEve	-1.135	0.679	-1.672	0.099	0.943
MNTD	-1.396	6.739	-0.207	0.837	0.943
<i>E_{var}</i>	0.610	1.145	0.533	0.596	0.943
<i>R</i> ²			0.055		
Adjusted <i>R</i> ²			-0.046		
Degrees of freedom			66		
F-statistic			0.545		
<i>p</i> -value			0.797		

Table 3. Results of multiple regression for control plots with the dependent variable as the untransformed Bray-Curtis dissimilarity from 2013 to 2014.

Variable	Estimate	Standard error	<i>t</i> value	<i>p</i> -value	Adjusted <i>p</i>
Intercept	-1.526	0.361	-4.233	7.17 ⁻⁵	-
Exotic abundance	0.000	0.000	-0.831	0.409	0.573
-ve plot score	-1.089	0.613	-1.776	0.080	0.460
FRic	0.017	0.027	0.613	0.542	0.632
FDiv	0.327	0.289	1.129	0.263	0.460
FEve	0.022	0.440	0.050	0.960	0.960
MNTD	4.243	3.546	1.196	0.236	0.460
<i>E_{var}</i>	0.983	0.686	1.434	0.156	0.460
<i>R</i> ²			0.178		
Adjusted <i>R</i> ²			0.092		
Degrees of freedom			67		
F-statistic			2.072		
<i>p</i> -value			0.059		

Table 4. Results of multiple regression for control plots with the dependent variable of the log of the Bray-Curtis dissimilarity from 2014 to 2015.

Variable	Estimate	Standard error	<i>t</i> value	<i>p</i> -value	Adjusted <i>p</i>
Intercept	-4.533	0.818	-5.543	5.6 ⁻⁷	-
Exotic abundance	0.002	0.001	2.267	0.027	0.06
-ve plot score	-2.542	1.708	-1.488	0.141	0.247
FRic	0.007	0.033	0.218	0.828	0.828
FDiv	1.593	0.521	3.057	0.003	0.020
FEve	0.660	0.596	1.108	0.271	0.380
MNTD	2.633	5.172	0.509	0.612	0.715
<i>E_{var}</i>	3.310	1.160	2.855	0.006	0.020
<i>R</i> ²			0.224		
Adjusted <i>R</i> ²			0.141		
Degrees of freedom			66		
F-statistic			2.719		
<i>p</i> -value			0.015		

Figures

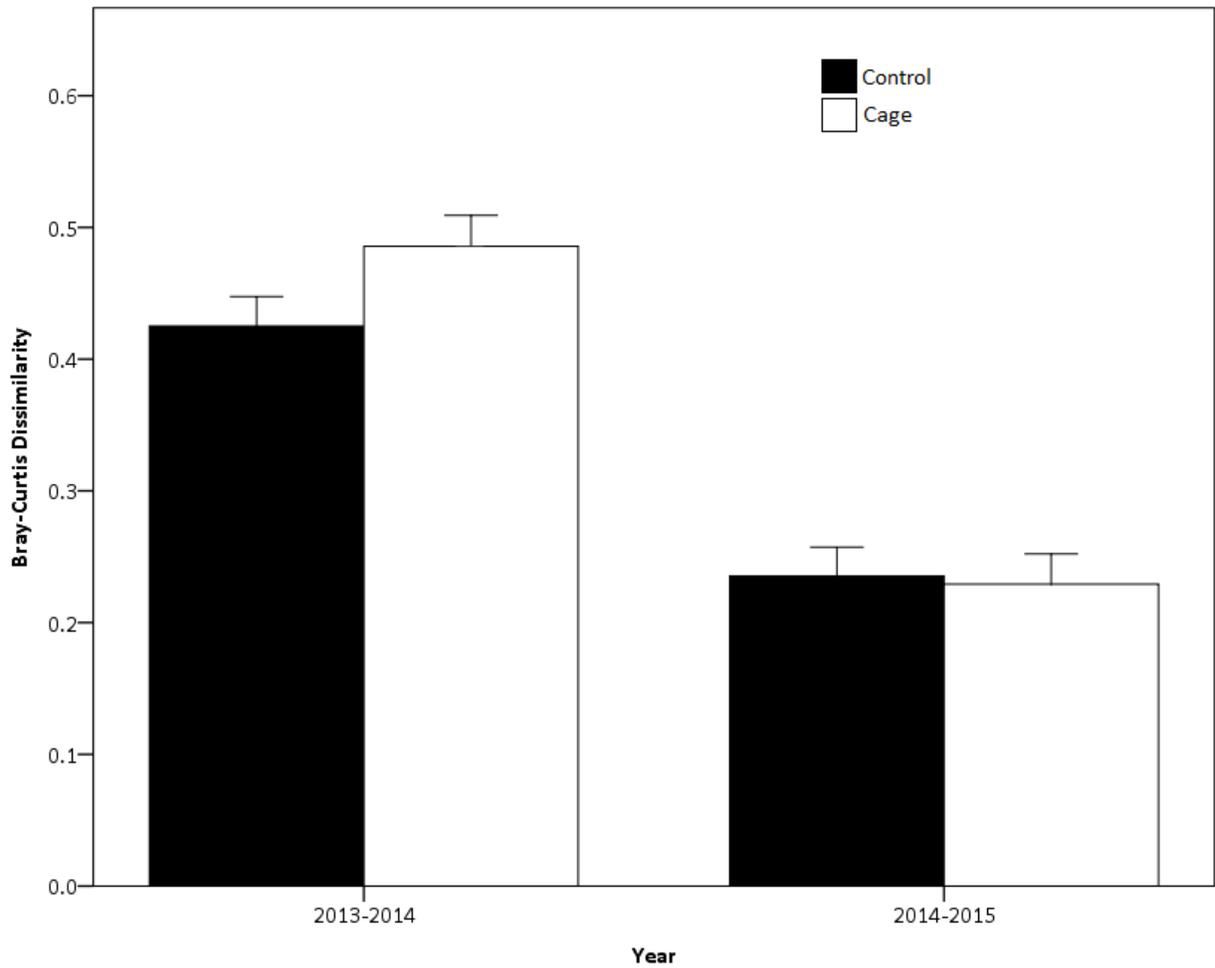


Figure 1. A bar plot illustrating the mean Bray-Curtis dissimilarity and standard error for control (black bars) and caged plots (white bars). There was no significant difference in temporal instability between the treatment groups in either time period (Mann-Whitney U ; $p > 0.05$).