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Are We Missing the Forest for the Trees? Quantifying the Maintenance of Diversity in Temperate Deciduous Forests

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ARE WE MISSING THE FOREST FOR THE TREES?:
QUANTIFYING THE MAINTENANCE OF DIVERSITY
IN TEMPERATE DECIDUOUS FORESTS

by

Kathryn E. Barry

A Dissertation Submitted in
Partial Fulfillment of the
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Doctor of Philosophy
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May 2016

ABSTRACT

ARE WE MISSING THE FOREST FOR THE TREES?: QUANTIFYING THE MAINTENANCE OF DIVERSITY IN TEMPERATE DECIDUOUS FORESTS

by

Kathryn E. Barry

The University of Wisconsin-Milwaukee, 2016
Under the Supervision of Professor Emily Latch

One of the most pressing questions of community ecology is: Why do we have so many species? Over 100 hypotheses have been proposed to answer this question for woody plants over the past 70 years, yet there remains no consensus among community ecologists. In this dissertation, I explore the evidence supporting several different hypotheses (Chapter 1). I provide evidence that negative density dependence, where individuals perform poorly near members of their own species, may only be relevant for canopy tree species (Chapter 2). Understory species do not demonstrate negative density dependence while canopy trees demonstrate negative density dependence that increases with plant size as predicted.

Furthermore, I examine the effect that disturbance and herbivory by large vertebrate herbivores have on negative density dependence in a fully-factorial experiment. I found that disturbance overrides negative density dependence and enhances diversity by 60% while herbivory strengthens negative density dependence (Chapter 3). These findings suggest that even where negative density dependence is present, it is modulated by disturbance.

I also explore the life-history strategies that determine the interplay between these mechanisms. Shade-tolerance, an important life history trade-off spectrum in temperate plants, did not significantly influence which mechanisms were relevant for diversity maintenance. Conversely, whether a plant was in the canopy or in the understory, a coarse metric that combines many trade-off spectra, was a good predictor of both the strength of negative density dependence and the effect of disturbance (Chapter 4). Understory plants demonstrated strong spatial clustering while canopy trees demonstrated strong negative density dependence. Disturbance randomized the spatial patterns of both understory and canopy plants.

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For my community:

Biological, ecological, and especially genetic

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LIST OF ABBREVIATIONS

NDD Negative density dependence

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Chapter 1: Maintenance of plant species diversity in forest ecosystems

Authors – Barry, Kathryn E. and Schnitzer, Stefan A.

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Abstract

One of the major questions in ecology is how plant species coexist and thus how diversity is maintained. While there are many theories to explain the maintenance of plant species diversity, compelling empirical support exists for very few of them. Here we summarize four major putative theories to explain the maintenance of forest plant species diversity, each of which have ample empirical support. These theories include: 1) niche differentiation; 2) negative density dependence; 3) disturbance; and 4) neutral dynamics with respect to competition. We also present a literature review that includes 51 studies that explicitly examined the maintenance of plant species diversity that were published between 2000 and 2015. In the literature review, we included only studies that stated either as part of their introduction or in clearly stated objectives that the hypothesis was a maintenance of diversity mechanism. We found that there has been a huge amount of progress in the research on the maintenance of species diversity. An overwhelming majority (all but 3) found significant evidence for the mechanism that they tested. The large majority (64%) of the studies were conducted in tropical regions (27% in Panama alone). Trees were the main focal group, comprising 75% of the studies, 14% focused on shrubs, and 7% on lianas. Only 4% of the studies focused on non-woody plants. Seedlings were also a main focus, and 61% of the studies focused explicitly on the seedling life stage.

Our findings lead us to conclude that the study of the maintenance of species diversity has progressed rapidly over the past 15 years. However, there is still a substantial amount of additional research to be done. Future studies may benefit from explicitly examining key theoretical requirements of the mechanism that they are examining. The use of spatial and temporal heterogeneity may be critical and, in many cases, would improve the precision of the study. Most tests have focused on single plant groups and single mechanisms for the maintenance of species diversity, but moving into the future a focus on multi-mechanism models for the maintenance of diversity using plant groups that differ in multiple axes of life-history strategy will be crucial to understanding how species coexist.

1.1 Introduction:

Understanding the maintenance of diversity is one of the central goals of ecology. By understanding how species diversity is maintained, we gain valuable insight into the forces and mechanisms that determine the distribution of species, as well as how communities are assembled, regenerate, and function. Over the past century, more than 100 hypotheses have been proposed as potential explanations for the maintenance of species diversity (Palmer 1994), with the vast majority of these hypotheses aimed at understanding the coexistence of species within a single trophic level (Wright 2002).

For forest plants, the maintenance of species diversity can be reduced to four major theories for the maintenance of species diversity, which have been commonly tested empirically in temperate and tropical forests. The four theories are: niche differentiation, negative density dependence, disturbance, and a neutral dynamics model in terms of

species competition. While these theories have been examined numerous times, the extent of support that they have received relative to each other is not well known. That is, there is little information on which theories have received strong empirical support and which have not. By determining the level of support for each theory we can begin to determine which theories we should believe and which need more examination.

There are three other key issues that are also poorly understood, which can be summarized in the following questions. 1) Are the studies biased with regards to geographic region? Forests in different regions have very different dynamics. For example, currently some species are increasing in abundance in tropical forests that are experiencing more droughts while others are decreasing, which may change the species composition and richness differentially between geographic regions (Feeley *et al.*, 2011, Enquist and Enquist 2012; Schnitzer and Bongers, 2011). 2) Are the studies biased with regards to plant life-history stage? Mechanistic hypotheses on the maintenance of species are community level hypotheses that describe the ability of plant species to be maintained over long periods. Focusing on a single life history stage when a matrix of life history stages occur throughout the community and all must be maintained may lead only to proximate answers for the maintenance of diversity of a particular life-history stage (seedling, sapling, or adult) while losing sight of the community. 3) Are the studies biased with regards to functional group? Plants demonstrate a wide variety of functional traits that dictate how they interact with their environment. Groups of plants that demonstrate similar traits likely demonstrate similar mechanisms while other groups may not (McCarthy-Neumann and Kobe 2008). Focusing on a single group is limiting for maintenance of diversity studies as these groups may respond to different mechanisms.

In this chapter, we provide a description of the four key theories for the maintenance of species diversity. We then review the literature published over the past 15 years addressing these four diversity maintenance mechanisms. We used Google Scholar to search for studies using the following search terms: 1) “niche”, “maintenance of diversity”, forest; 2) “negative density dependence”, “maintenance of diversity”, forest; 3) “negative feedback”, “maintenance of diversity”, forest ; 4) “Janzen-Connell hypothesis”, “maintenance of diversity”, forest; 5) “disturbance” “maintenance of diversity”, forest. We restricted the publications to the years 2000 to 2015 (January 1, 2000 – January 1, 2015) and we excluded review articles or studies based strictly on mathematical modeling. We also excluded studies that were not testing the hypothesis as a maintenance of diversity mechanism, and any study that was not focused on a forest ecosystem.

1.2 Four Major Theories for the Maintenance of Forest Plant Species Diversity

1.2.1 Niche Assembly

A fundamental theory for the maintenance of species diversity is niche differentiation or niche assembly (e.g., Hutchinson, 1957, 1959; MacArthur and Levins 1967; MacArthur 1969, 1972). The theory states that no two species can coexist if they have the exact same niche requirements. Competition for shared resources results in the specialization of species on a unique combination of resources thereby allowing species to avoid competitive exclusion (or succumbing to competitive exclusion if the species does not specialize sufficiently). Thus, according to this theory, ecologically similar species are able to stably occupy the same community by specializing on a different set of resources and requirements (niches) and thereby limiting direct competition with similar species

(Hutchinson, 1957; Tilman, 1982). See Chase and Leibold (2003) for a detailed discussion on the definitions and importance of niches in ecology.

Niche differentiation has been found, to some degree, in nearly every ecosystem. For example, many tropical plants have known associations with specific microhabitat factors suggesting that they are specializing on that microhabitat niche (Clark *et al.*, 1998,1999; Svenning, 1999; John *et al.*, 2007). In Borneo up to 80% of tree species may be specialized on edaphic factors (Russo *et al.*, 2008). In a congener-rich oak dominated subtropical forest, Cavendar-Bares and colleagues (2004) found that oaks fell into three clear community types based on available soil moisture, nutrient availability, and fire regime. Experimental evidence from grasslands suggests that plants strongly partition resources, particularly resources that are limiting (Tilman and Wedin, 1991). Indeed, even among ectomycorrhizal fungal communities differentiation for vertical space on roots has been shown (Dickie *et al.*, 2002). While there is strong evidence for the existence of niche partitioning, it is still unknown whether the strength of niche differentiation as a central mechanism for the maintenance of species diversity has received more support than other diversity maintenance mechanisms.

1.2.2 Negative Density Dependence

Another leading hypothesis for plant diversity maintenance is negative density dependence (NDD) due to the presence of species-specific enemies (Janzen, 1970; Connell 1971). Theoretically, negative density dependence can maintain stable, community-level diversity because seedlings growing near conspecific adults suffer reduced growth and survival due to the accumulation of species-specific enemies (e.g., pathogens, parasites, and

herbivores) around the adult. The reduction of conspecific seedlings increases the probability that adults are replaced by a different (heterospecific) species. If adults are consistently replaced by heterospecific species than rare species are favored because there are a higher number of suitable recruitment sites, and dominant species are limited because there are fewer suitable recruitment sites. Both of these conditions are critical for community-level diversity maintenance (Mangan *et al.*, 2010).

There is now compelling evidence that negative density dependence (NDD) is operating in both temperate and tropical plant forests (Harms *et al.*, 2000; Packer and Clay 2000; Hille Ris Lambers *et al.*, 2002, Wright, 2002; Petermann *et al.*, 2008). A plethora of studies have confirmed the presence of negative density dependent patterns. For example, Connell and colleagues (1984) demonstrated that individuals near a member of their own species were more likely to suffer from increased mortality and decreased growth. Harms and colleagues (2000) found that all species in the Barro Colorado 50 ha plot demonstrated negative density dependence during recruitment. Indeed, both experimental and observational studies support the evidence of NDD (e.g., Comita *et al.*, 2010; Mangan *et al.*, 2010; Ledo and Schnitzer, 2014).

1.2.3 Disturbance

Disturbance may maintain plant species diversity in several different ways. For example, tree fall gaps and similar smaller scale disturbances may maintain diversity by providing an equilibrium state in which both late and early successional species co-exist, and the system remains in a stable dynamic state (Schnitzer *et al.*, 2008). The creation of a tree fall gap begins a process of succession. The persistence of tree fall gaps creates a

regeneration niche for shade intolerant species to persist in the population rather than becoming competitively excluded (Denslow, 1987; Swaine and Whitmore, 1988; Whitmore 1989; Dalling *et al.*, 2001). Disturbance may also alter the distribution of nutrients across both time and space creating a broad spectrum of disturbance niches for plants to capitalize on (Chase and Leibold 2003). This niche-driven disturbance approach provides an equilibrium based hypothesis that requires disturbance to create a gradient of resource availability from mid-gap to non-gap (Ricklefs, 1977; Denslow, 1987).

Another hypothesis for how disturbance enables the maintenance of plant species was formalized by Connell in 1978 as the “Intermediate Disturbance Hypothesis” (IDH). This hypothesis states that species diversity will be highest when disturbance is intermediate in size, in time since disturbance, and in frequency. The IDH relies on an intermediate amount of disturbance to provide disturbed habitat for early successional species, but not so much disturbance that late successional species cannot establish.

Disturbance may in fact maintain diversity in some plant groups but not in others. In Panama, lianas (woody vines) are able to capitalize treefall gaps (Schnitzer and Carson, 2000, 2001), but trees are not (Hubbell *et al.*, 1999, Brokaw and Busing, 2000). Obiri and Lawes (2004) examined the extent to which species richness in coastal scarp forests in South Africa was determined by specialization along a gap niche axis and found little evidence that competition for resources along a niche-forest gradient maintained the diversity of tree seedlings and saplings.

1.2.4 Neutral Competition Dynamics

The idea that competitively neutral species could coexist was popularized by several authors, most notably and comprehensively by Hubbell in 2001 (but see also Hubbell, 1979, 1997; Bell, 2001). The "neutral model" provides both a hypothesis for the maintenance of species diversity and a potential null distribution for examining the validity of other mechanisms. The neutral model says that species diversity can be maintained simply through a combination of dispersal of propagules and mortality. In this model, space in a community is limited, and that space will be colonized by whichever species arrives in the space first. The space is then vacated when the species dies. The neutral model allows for diversity to be maintained through simple dispersal and local extinction with rare instances of speciation (Hubbell, 2001). This approach derives from models of island biogeography proposed by MacArthur and Wilson (1963, 1967) and much of the historical evidence for neutral processes in ecology comes from island communities. For example, Simberloff and Wilson (1970) found that in red mangrove islands that had been experimentally defaunated, species diversity was largely limited by area and distance from mainland populations, leading to the conclusion that these communities were largely dispersal assembled (see also Simberloff, 1974).

Many studies have reported that competitively neutral processes, such as recruitment limitation, rather than deterministic processes such as niche differentiation determine diversity (e.g., Hubbell *et al.*, 1999, Brokaw and Busing 2001; Obiri and Lawes, 2004). Furthermore, for tropical seedlings, species richness may be determined more by competitively neutral factors, such as proximity of seed sources, efficient dispersal mechanisms, and favorable establishment conditions, rather than deterministic processes (Denslow and Guzman 2000; Paine *et al.*, 2008).

1.3 Empirical Support for the Four Diversity Maintenance Theories

We reviewed the literature on the four diversity maintenance hypotheses and found 51 studies that met our criteria and were published between January 1st, 2000 and January 1st, 2015. We found that the most commonly invoked mechanism for the maintenance of species diversity was negative density dependence, which represented 73% of the studies included in this review (n=37). Niche differentiation comprised nearly 40% of tests (n=20), with neutral (n=11) and disturbance (n=4) representing a combined 30% of studies. Of the 51 studies, 29 (57%) examined the role of two mechanisms in maintaining diversity, and only two studies examined the role of 3 or more mechanisms.

1.3.1 Evidence for niche differentiation

Over the 14 years that we surveyed, several studies found compelling evidence for niche differentiation (Debski *et al.*, 2001; Newmaster *et al.*, 2003; Harms *et al.*, 2004; Gazol and Ibanez 2008; Paine *et al.*, 2008; Kraft *et al.*, 2008; Kursar *et al.*, 2009; Chuyong *et al.*, 2011; Metz, 2012). These studies fell into two general categories: 1) studies that utilized a trait based approach to understand how plants were adapted to utilize resources or defend against herbivory; and 2) studies that examined general spatial patterns of habitat specialization among species. For example, Kraft and colleagues (2008) found compelling evidence for niche differentiation in a diverse tropical forest in Yasuni, Ecuador using functional trait-based analyses. All traits measured, except for wood density, were more evenly distributed across species in a 25 hectare plot than would be predicted by a neutral model, suggesting that co-occurring species diverge in their strategies for coping with

limited resources, the cornerstone prediction of niche differentiation. Also in Parque Nacional Yasuni, Ecuador, Metz (2012) found that 90% of 136 species demonstrated habitat specialization during at least one time period over 9 years, and that 60% of the species had significant habitat associations during at least half of the census periods. Likewise, in the 50 ha plot on Barro Colorado Island in Panama, around 50% of the trees demonstrated habitat specialization with respect to soil chemistry (John et al. 2007). A study by Kursar and colleagues (2009) in both Panama and Peru found that coexisting adult plants within the genus *Inga* were more divergent in their defense strategies against herbivory than would be predicted by neutral dynamics. In Cameroon, 63% of tree species showed significant positive associations with at least one of five habitat types (Chuyong *et al.*, 2011). In adult understory trees in Malaysia, spatial point pattern analysis elucidated a similar pattern of significant habitat specialization that contributed to coexistence (Debski *et al.*, 2002). However, this pattern appears to vary across some plant groups. Dalling *et al.*, (2012) compare the degree to which lianas and trees specialize on topographic and soil chemistry habitats and found that significantly fewer lianas specialized on topographic (44%) or soil chemistry (21%) derived habitat values vs. 66% and 52% respectively for trees (see also Ledo and Schnitzer, 2014).

Several studies clearly connected niche differentiation to the maintenance of species richness. Two studies of temperate zone forest sedges found that environmental heterogeneity and interspecific microhabitat preferences were important for the maintenance of local understory sedge species diversity. Furthermore, species diversity was greatest when the habitat was most variable (*i.e.* when there are the highest potential number of niches; Bell *et al.*, 2000, Vellend *et al.*, 2000).

1.3.2 Evidence for negative density dependence

The literature examined provides compelling evidence for both NDD (the pattern) and putative mechanisms in tropical and temperate trees, shrubs, and palms (Hubbell *et al.*, 2001; Blundell and Peart, 2004; Wyatt and Silman, 2004; Norghauer *et al.*, 2006; Comita and Hubbell, 2007; Queenborough *et al.*, 2007; Yamazaki *et al.*, 2009; Lan *et al.*, 2009; Chen *et al.*, 2010; Comita *et al.*, 2010; Mangan *et al.*, 2010; Bagchi *et al.*, 2010; Metz *et al.*, 2010; Bai *et al.*, 2012; Johnson *et al.*, 2012; Wang *et al.*, 2012; Jurinitz *et al.*, 2013; Meng *et al.*, 2014). Comita and colleagues (2010) found evidence for a pattern consistent with NDD in 180 tropical tree and shrub species at Barro Colorado Island, Panama. Furthermore, Comita and colleagues (2010) demonstrated that, contrary to the original predictions of Janzen (1970) and Connell (1971), relatively rare species experienced stronger NDD than more common species. John *et al.* (2002) found similar patterns in tropical dry forests in India. Mortality in small diameter trees (1-10 cm dbh) was negatively correlated with the abundance of conspecifics. In subtropical China, seedlings of legume species were less likely to survive in areas surrounding adults of their species (Liu *et al.*, 2012). In a temperate tree species (*Prunus serotina*), Packer and Clay (2000, 2004) demonstrated that seedlings were significantly less likely to survive near conspecific adults.

Soil microbes are a potential mechanism driving the presence of negative density dependent patterns. In Panama, Mangan and colleagues (2010) demonstrated that rare tree species experience stronger NDD than common ones, and that soil biota were responsible for the NDD pattern. Bagchi and colleagues (2014) removed insects and fungus using soil pesticide treatments and found that seedling diversity (in terms of the inverse Simpson index) was lower when soil fungi were eliminated. Xu and colleagues

(2014) tested NDD across an elevational gradient in subtropical China and found that negative feedback from soil-borne enemies caused significantly decreased growth and survival of seedlings, and that the effect of soil-borne enemies decreased with increasing elevation. In the temperate zone, Packer and Clay (2000) established that seedlings of the temperate tree species *Prunus serotina* were less likely to survive in the presence of a single soil pathogen further that this was a likely causative agent of NDD (2004).

Evidence from this review also suggests that life-history characteristics determine the strength of the NDD pattern. In a wet forest in Costa Rica, McCarthy-Neumann and Kobe (2008) found that shade tolerance interacted with the strength of negative density dependence. Specifically, seedlings of species with characteristics indicative of shade tolerance (high wood density, large seed size) tended to demonstrate weak or no NDD. Also in Costa Rica, Kobe and Vriesendorp (2011) reported that in seedlings of canopy, subcanopy and understory trees species, differences in negative density dependence were more strongly related to physiologically based life history traits than biotic feedback related to community abundance. Bai and colleagues (2012) reported that NDD was strongest in seedlings and saplings of trees and shrubs with gravity-dispersed seeds compared to wind and animal dispersed seeds and also that shrubs were significantly less likely to demonstrate NDD when compared to trees. Other factors such as drought, logging activity, and fire also seem to be negatively associated with the strength of NDD (John *et al.*, 2002; Bunker and Carson, 2005; Bagchi *et al.*, 2011).

NDD does not appear to be associated with all growth forms. For example, in a forest in Panama, Ledo and Schnitzer (2014) found that lianas have a positive density dependent pattern (and thus are not maintained by NDD), whereas trees were consistently

negatively density dependent. Bai and colleagues (2012) found a similar result in temperate tree and shrub species in China. Tree seedlings and saplings were negatively affected by the presence of nearby conspecific adults, while shrub seedlings and saplings were far less likely to demonstrate this negative effect.

1.3.3 Evidence for disturbance hypotheses

Disturbance appears to maintain a portion of forest plant species diversity. For example, Schnitzer and Carson (2001) examined the extent to which disturbance maintains species diversity for lianas and reported that liana species diversity was higher in treefall gaps than in intact forest, even when controlling for liana density. Ledo and Schnitzer (2014) and Dalling *et al.* (2012) provided further evidence that lianas are maintained by disturbance events. Dalling and colleagues (2012) examined the degree to which lianas and trees specialize on specific habitat values and found that 63% of liana species had an affinity for areas of the BCI 50 ha plot in Panama with low canopy height indicative of recent canopy gap. Ledo and Schnitzer (2014) confirmed this finding using point pattern analysis to determine that only disturbance explained the distribution of lianas in the BCI 50 ha plot. Additionally, ter Steege and Hammond (2001) found that community attributes that are sensitive to disturbance such as seed mass and wood density are strongly correlated with tree diversity.

There is little evidence to suggest that disturbance maintains diversity in the way that Connell (1978) suggested in his intermediate disturbance hypothesis. Obiri and Lawes (2004) measured gap size and estimated time since gap creation and examined diversity patterns in the colonizing saplings of coastal scarp forests in South Africa. This study

reported only a slight (non-significant) increase in species diversity in gaps of intermediate size and time size creation. Furthermore, disturbance did not seem to maintain tree diversity. In the 50 ha plot on Barro Colorado Island (Panama), Brokaw and Busing (2001) found that tree seedlings appeared to colonize in gaps by chance dispersal and establishment rather than being particularly well-adapted to the gap environment. Additionally, Schnitzer and Carson (2001) found no difference in the species richness and density of shade tolerant non-pioneer tree species between gap and non-gap sites in the BCI 50 ha plot.

1.3.4. Evidence for neutral processes

Many studies during the time period of this survey provided evidence that neutral processes explain small parts of diversity maintenance patterns, but few provide compelling evidence that it is a major mechanism driving the maintenance of diversity. The findings of Comita *et al.* (2007) suggest that recruitment limitation determines which seedlings are able to establish in tropical tree and shrub communities in Panama. Obiri and Lawes (2004) also provide compelling evidence that neutral processes (i.e. recruitment limitation) determine the plants that colonize gaps in South Africa rather than specialization on a regeneration niche. Denslow and Guzman (2000) found that tropical tree seedling species richness was a function of not only seedling density, but the presence of proximate seed sources with efficient dispersal mechanisms and appropriate establishment conditions, suggesting that recruitment limitation plays a strong role in seedling community establishment. Siedler and Plotkin (2006) confirmed this finding in adults and saplings in Malaysia and Panama, documenting that both the extent and the scale

of conspecific spatial aggregation is strongly correlated with the mode of seed dispersal. By contrast, Uriarte and colleagues (2005) found that in a hurricane affected system in Puerto Rico, simple recruitment limitation was not sufficient to determine seedling species composition, and models that included NDD with recruitment limitation provided more explanatory power.

1.4 Bias in the maintenance of diversity literature

The studies included in our review were strongly biased towards tropical regions, with 64% of the studies being conducted in the tropics, 13% in the subtropics, and 22% in the temperate zone (Figure 1.1). Of the tropical countries, Panama was the largest contributor to this bias, accounting for 27% of the 51 studies. China contributed 16% of the studies, and Ecuador contributed 8% (Figure 1.2). Maintenance of diversity studies were biased on their selection of growth form. Three-quarters (38) of the studies sampled were conducted on tree species alone (Figure 1.3).

The bias towards tree species may be a limiting factor for a general understanding diversity maintenance. In tropical forests, tree species represent a small fraction of vascular plant species diversity (Gentry and Dodson 1987). Tree diversity in temperate forests is less than 20% of vascular plant species diversity (Gilliam, 2007), which is even higher than in tropical forests. Recent evidence presented by Schnitzer and Ledo (2014) shows that tropical tree species in the 50 ha plot on Barro Colorado Island (Panama) are maintained in the community via a combination of niche differentiation and negative density dependence. By contrast, liana species diversity is maintained by a different set of mechanisms and most lianas species tended to have a clumped rather than an

overdispersed distribution that is consistent with negative density dependence. Shrubs in the 50 ha plot on Barro Colorado Island were also significantly clumped rather than overdispersed (Hubbell, 2001).

Species' functional traits may determine their susceptibility to specific mechanisms (Denslow and Guzman, 2000; Siedler and Plotkin, 2006; McCarthy-Neumann and Kobe, 2008). Dispersal ability provides an ultimate limit to how far individuals may be from one another. Species with shorter dispersal distances would not persist in a community if they were not adapted to the heightened pest and pathogen pressure near their parent plants. Thus, dispersal ability may be a large determinant of whether a species demonstrates NDD (Denslow and Guzman, 2000; Siedler and Plotkin, 2006). Different growth forms tend to have different suites of traits, and thus they may respond differently to the mechanisms that their maintain diversity.

Studies on the maintenance of plant species diversity tended to focus on seedlings, and over 60% of these studies utilized only individuals that had been established for less than one year (Figure 1.4). The bias towards seedlings may be particularly problematic.

The seed to seedling stage represents an ephemeral transition in the life history of a plant community. Many seedlings recruit into a community only to perish within the first several years after establishment. Seedlings have poorly developed root systems and little storage, and thus are especially vulnerable to the vagaries of temporal variation. The vulnerability to temporal variation in climate, as well as stochastic events, makes it especially important for studies to incorporate data from over many seasons. One-third of the studies examined seedling growth and mortality over multiple years. For example, Metz and colleagues (2010) reported that the strength of NDD and niche differentiation on

seedling recruitment varied annually. Similarly, Zhu and colleagues (2013) found that all studied species were associated with at least one environmental variable during at least one of their life stages, but that the frequency of habitat association and negative density dependence decreased with plant age.

1.5 Conclusion

Ecologists have made great advances in determining the factors and mechanisms responsible for the maintenance of species diversity. The positive signal found for multiple mechanisms suggests that many mechanisms are working at different scale (Metz, 2012) and may combine to maintain diversity (Wills *et al.*, 2006). However, there are still a number of issues yet to be resolved about the strength of diversity maintenance mechanisms. Few studies have accounted for multiple life history stages and multiple growth forms. Even fewer studies have compared the relative strengths of diversity maintenance mechanisms in a single study. Only two studies that we are aware of combines both of these approaches (e.g., Dalling *et al.*, 2012, Ledo and Schnitzer, 2014), and found evidence for multiple mechanisms that interact to maintain diversity differentially for different plant groups. Furthermore, only 3 studies focused on non-woody species, which represent the largest portion of diversity in all forests. Consequently a more well rounded approach to testing diversity mechanisms is necessary to understand how diversity is maintained.

Figure 1.1: Ecosystem type used to test four putative theories for the maintenance of species diversity. The vast majority of studies were performed in tropical regions (64%).

We categorized the studies based on author classification. Some studies identified the ecosystem as a subregion of the broader ecosystem type: subtropical montane (1 study), subtropical monsoon (1 study), and tropical dry (1 study). Data are from a review of 51 studies published between 2000 and 2015 that tested one or more of the four main hypothetical mechanisms for the maintenance of forest diversity.

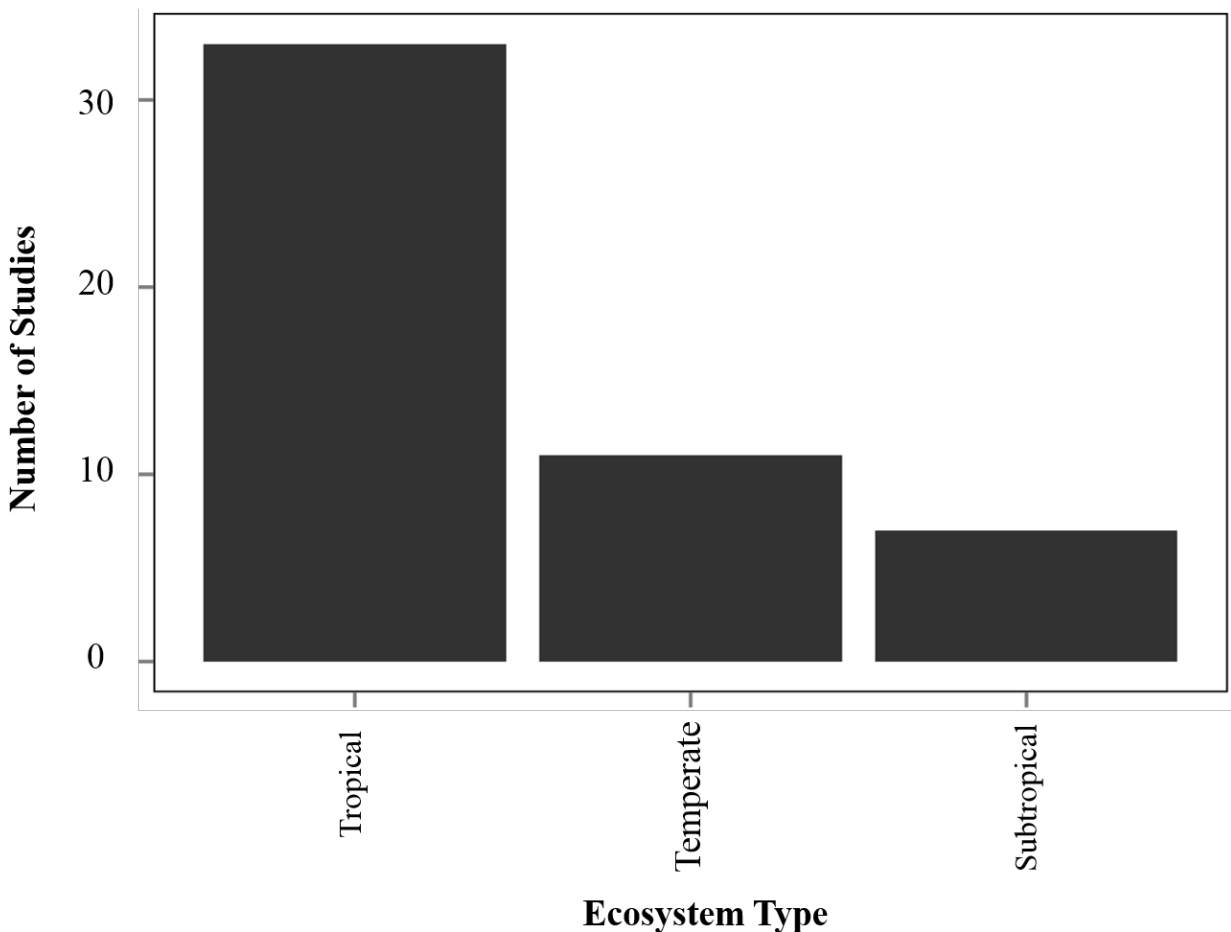


Figure 1.2: The country in which the four major hypotheses for forest plant diversity maintenance were tested. Panama represented the highest proportion of the documented study sites (27%). All studies that reported results from two separate countries were counted towards both countries separately, with the exception of the one study that reported results from major countries worldwide. Data are from a review of 51 studies examining four major hypotheses of diversity maintenance published between 2000 and 2015.

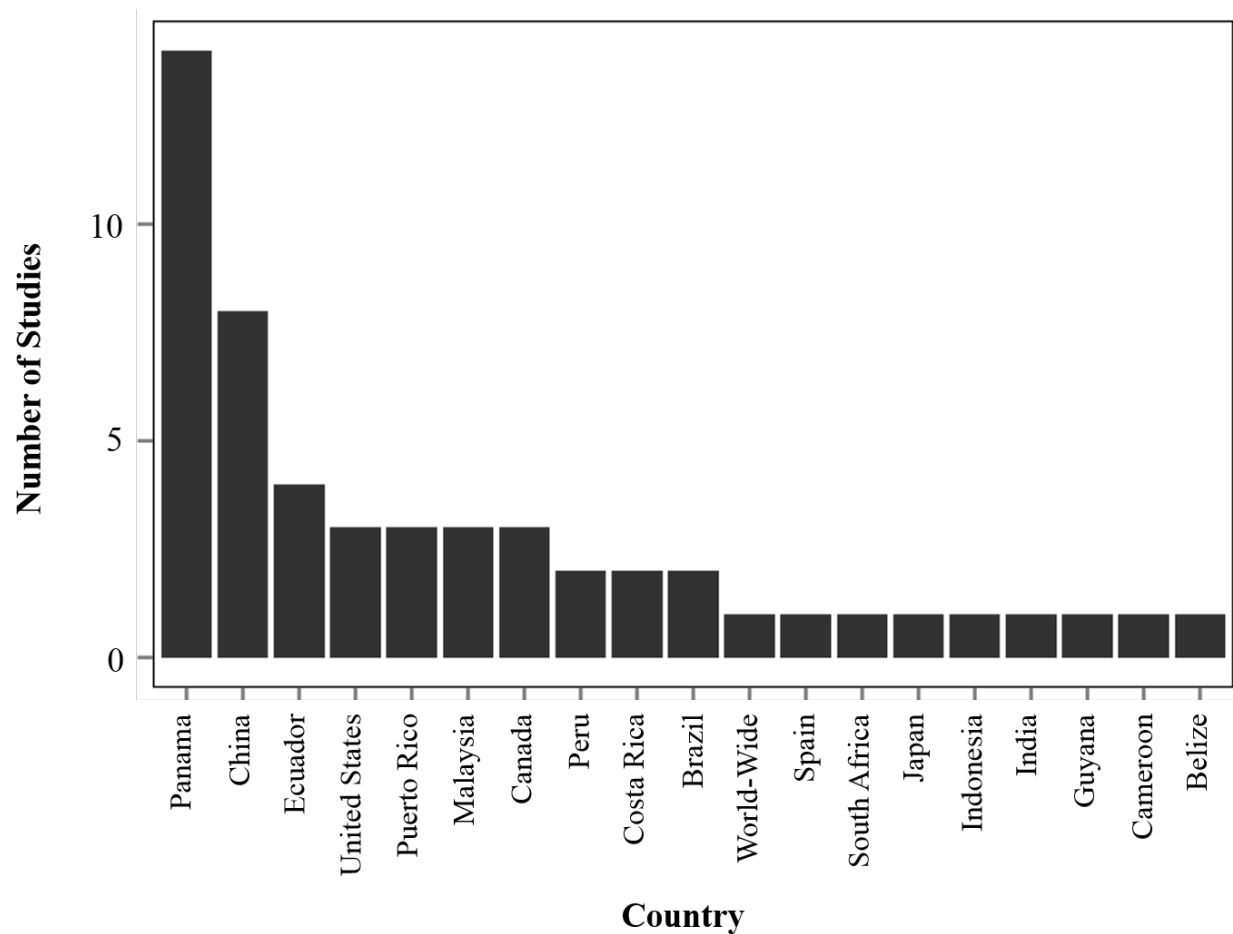


Figure 1.3: Plant group used for testing the four major hypotheses for forest plant diversity maintenance. All but 16 total studies focused on the role of the reported mechanism in maintaining tree diversity. Non-vascular plants were included only in a single study. Studies that reported trends from multiple growth forms were counted in both categories. Data are from a review of 51 studies on the maintenance of diversity published between 2000 and 2015.

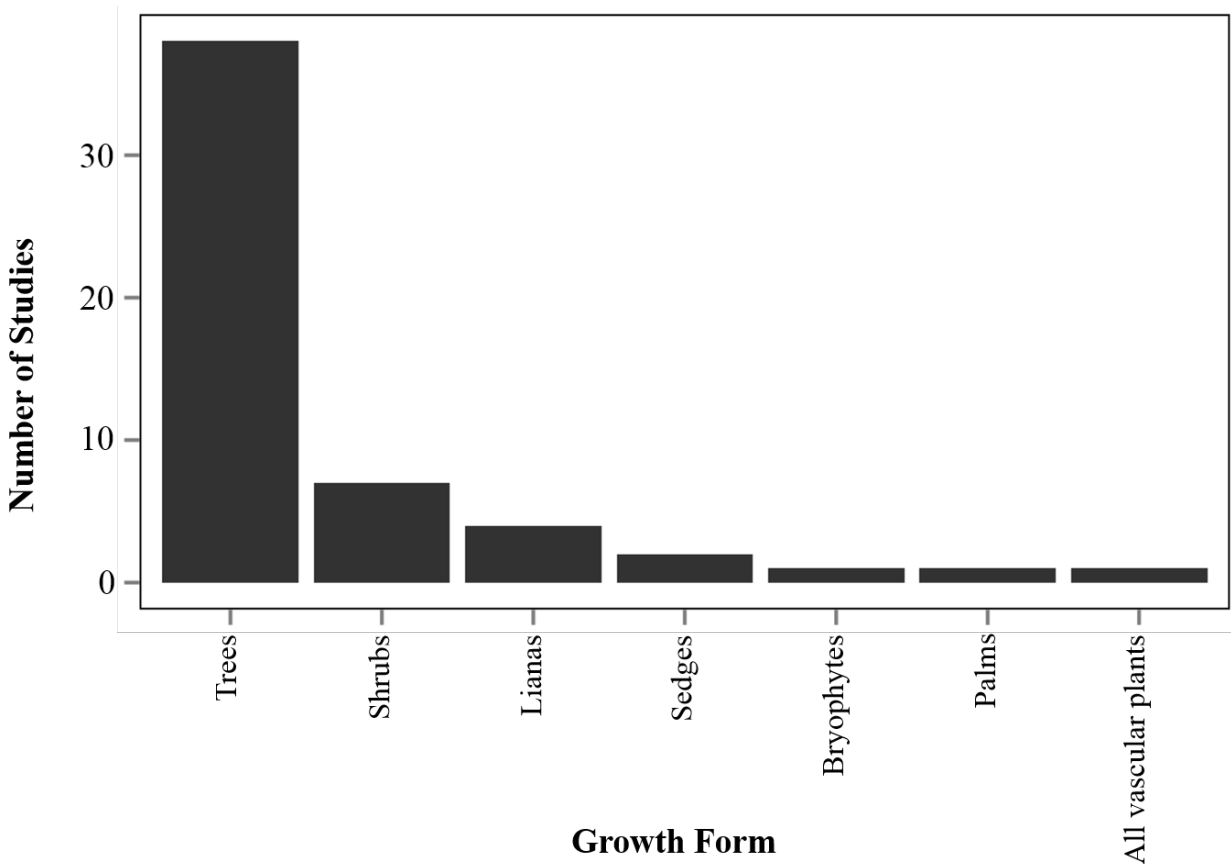
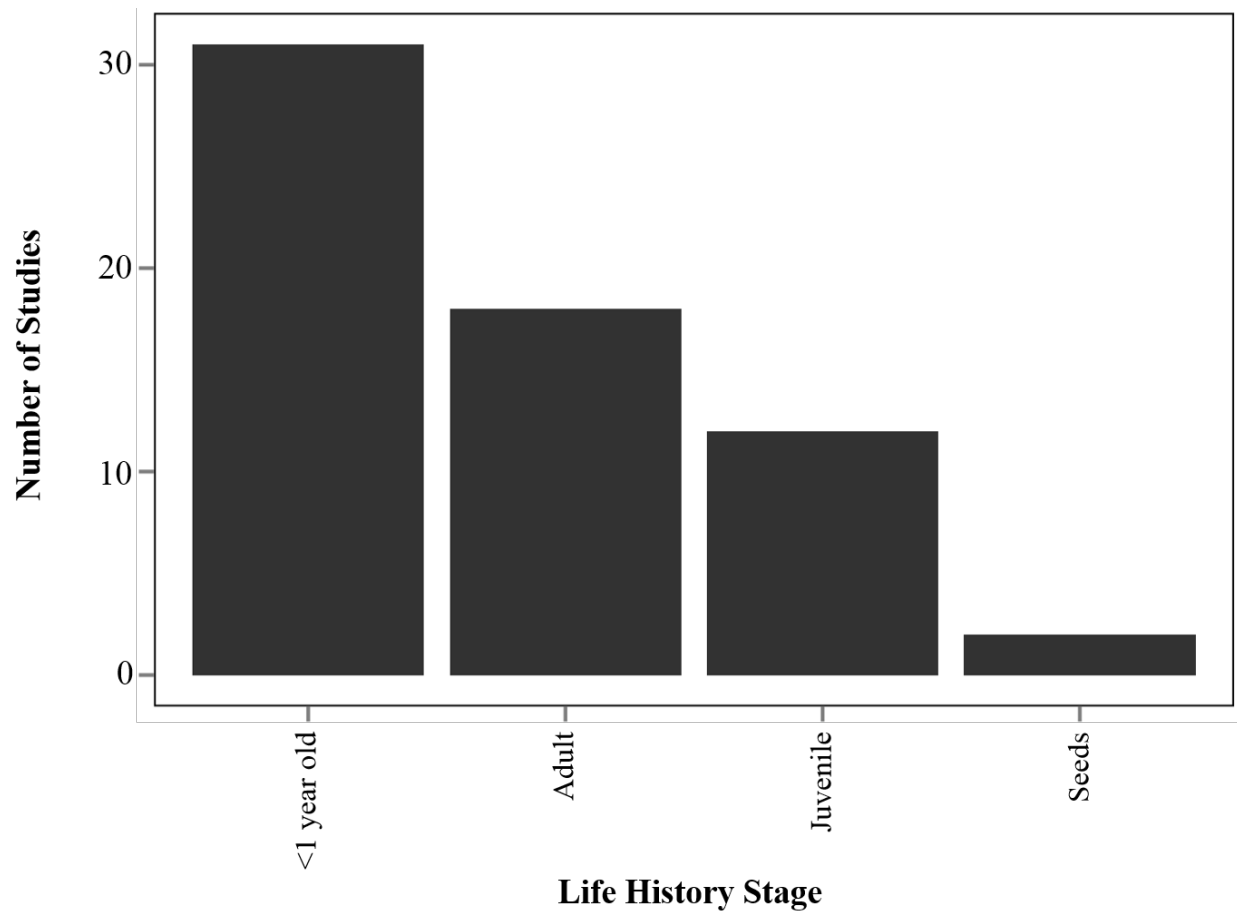


Figure 1.4: Life history stage of individuals included in each of the 51 studies reported on in a review of studies on the 4 major hypotheses for the maintenance of plant species diversity. The majority of studies (60.7%) included seedlings (< 1 year old) in their sample while adults and juveniles (>1 year old but not reproductively mature) were less well represented (24%). Studies that included more than one life history stage were counted in both categories.



Chapter 2: Are we missing the forest for the trees? Negative density dependence in a temperate deciduous forest

Authors: Kathryn E. Barry & Stefan A. Schnitzer

Status: In review, Ecology.

Abstract:

One of the central goals of ecology is to understand the mechanisms that enable coexistence among species. Evidence is accruing that negative density dependence (NDD), the process by which plant seedlings are unable to survive in the area surrounding adults of their same species, is a major contributor to plant species coexistence. However, the extent to which the plant community is maintained by NDD, whether NDD increases in strength with plant size, and whether NDD occurs across life history strategy, three conditions necessary for NDD to maintain diversity, are poorly understood. We examined the extent to which the woody community is overdispersed (a spatial pattern indicative of NDD) across plant life history stages and life history strategies. We found that the majority of the community is overdispersed; however, this pattern is driven by large canopy trees. Understory plants were not overdispersed as adults, suggesting that NDD may not maintain diversity in this plant group. Our results confirm that while NDD may be a viable mechanism for canopy tree diversity, it seems unlikely to maintain the diversity of the woody understory.

Introduction:

One of the central goals of community ecology is to understand the maintenance of species diversity. Negative density dependence (NDD) is one of the most well-supported mechanisms for diversity maintenance. Negative density dependence occurs when individuals have relatively low rates of growth and survival near members of their own species (conspecifics), resulting in a distinct spatial pattern where conspecifics occur further away from each other than would be expected by chance (overdispersion, but see Murrell 2009). Negative density dependence can result in stable species coexistence across the landscape because dominant species cannot displace subordinate ones (Janzen 1970, Connell 1971). Evidence for NDD has been reported in a variety of ecosystems, including lakes, deserts, grasslands, marine ecosystems, and particularly in temperate and tropical forests (Anderson 2001, Goldberg et al. 2001, Lorenzen & Enberg 2002, Petermann et al. 2008, Comita et al. 2010, Mangan et al. 2010, Schnitzer et al. 2011, Johnson et al. 2012, Johnson et al. 2014). For forests, evidence for NDD has been reported over 30 times in 13 countries across five continents over the past ten years alone (Barry & Schnitzer in press).

For negative density dependence to be confirmed as a mechanism that maintains diversity, the following conditions must be met. 1) Individuals of the majority of the species in the community will be overdispersed because of greater mortality near conspecific adults. 2) The degree of overdispersion will increase with life-history stage. The effects of NDD should accumulate over time, and thus larger individuals of a species in the community are likely to be more overdispersed than smaller individuals. 3) NDD will operate across life history strategies, including growth form and dispersal syndrome.

While there is an abundance of evidence for NDD as a diversity maintenance mechanism in vascular plant communities, all three of the above conditions have not yet been demonstrated empirically. First, the vast majority of studies that examined NDD in vascular plant species focused on growth and mortality at the seedling stage (Packer & Clay 2000, 2003, Comita et al. 2010, Mangan et al. 2010, Johnson et al. 2012, Johnson et al. 2014). Dynamics at the seed-to-seedling and seedling-to-sapling transitions do not necessarily translate to overdispersion in the more established size classes. That is, dispersal limitation results in most seeds arriving underneath the parent tree and NDD dynamics at the seed-to-seedling, and seedling-to-sapling transitions must be sufficiently strong to overcome the spatial signature of dispersal limitation. Second, few studies have examined whether overdispersion increased with plant size (e.g., Goldberg et al. 2001, Hille Ris Lambers et al. 2002, Zhu et al. 2013). The negative effects of growing near a conspecific adult should accumulate over time, and thus, the level of overdispersion should increase with plant size. Third, the vast majority of NDD studies focused only on canopy trees, ignoring other important plant growth forms (Ledo & Schnitzer 2014, Barry & Schnitzer in press). The biased selection in growth form is particularly problematic in temperate forests, where canopy tree species represent a small fraction (~20%) of the total vascular plant community (Gilliam 2007). Furthermore, canopy species may be more prone to overdispersion due to their capacity for long distance dispersal (McCarthy-Neumann & Kobe 2008, Kobe & Vriesendorp 2011, DeWalt et al. 2015). Thus, our perception of the prevalence of NDD and overdispersion may be biased by the focus on canopy trees. By contrast, understory plants have a lower capacity for long distance dispersal due to their relatively short stature and position in intact forests, and thus may be less likely to be

overdispersed. Nonetheless, if NDD is the primary mechanism that maintains diversity, we would expect it to operate across life history stage and life history strategy.

We addressed each of these core conditions for NDD to be a general mechanism for the maintenance of plant species diversity by evaluating the spatial patterns of a woody plant community (shrubs, understory trees, midstory trees, canopy trees, and lianas) across life history stages and strategies in a temperate forest in western Pennsylvania, USA. We tested three specific hypotheses: 1) Woody plant diversity in temperate forests is maintained by NDD. 2) The effects of NDD accumulate over time (across plant life-history stage). 3) NDD operates independently of growth form and life history strategy. We tested these hypotheses by examining the degree of overdispersion on a per species basis across the woody plant community and plant life-history stage (i.e., size) and life-history strategy (i.e., growth form and dispersal mechanism).

Materials and Methods:

Study site

We conducted this study at Powdermill Nature Reserve, an 890-hectare reserve located in the Allegheny plateau at the base of the Appalachian Mountains in southwestern Pennsylvania, USA (Westmoreland County; 40°09' N, 79°16' W). This region receives ~1100 mm of precipitation per year and is characterized by mixed mesophytic vegetation that is dominated by maples (*Acer spp.*), tuliptree (*Liriodendron tulipifera*), and oaks (*Quercus spp.*). Elevation at Powdermill Nature Reserve ranges from 392 to 647 m above sea level. Powdermill Nature Reserve contains a matrix of vegetation types consisting primarily of secondary deciduous forest but with several areas of maintained fields and

managed lands. Last known logging occurred in this region in the 19th century, and land was primarily used for agriculture into the early 20th century (see Murphy *et al.* 2015 for more detailed site description).

Plot establishment and plant census

We established sixteen 5-m radius sites in the temperate deciduous forests at Powdermill Nature Reserve. We chose the 5-m radius spatial grain to enable direct comparison at an intermediate spatial scale between canopy species and woody understory species, which likely have different neighborhood sizes. We avoided canopy gaps, and each site had >80% canopy cover. We ensured that these sites were not within 10 m of a waterway and that soil cover was not predominantly rocks. Between June 1st 2014 and June 30th 2014, at each site, we used a Trimble GeoExplorer 6000XH to measure the precise location (up to 10 cm accuracy) of each woody individual >10 cm in height (Trimble Navigation Limited, Westminster, CO). For each individual, we measured height and basal diameter.

To examine how overdispersion changes with plant size, we divided individuals into four height classes (<0.5 m, 0.5-1 m, 1-5 m, and 5-10 m). To understand how overdispersion interacts with life history strategy, we classified each species as either canopy or understory, and as either bird, wind, self, or other animal dispersal (based on species descriptions in the Flora of North America; Flora of North America Editorial Committee eds. 1993+).

Data analysis:

We performed all data analysis in R statistical computing software (v. 3.2.2, R Development Core Team 2015). To measure plant spatial distribution (the degree to which

plants are clustered or overdispersed), we calculated Ripley's K in the package "spatstat" using Ripley's translational border correction at each plot for each species and then converted K to Besag's L (Ripley 1977, Besag 1977, Baddeley & Turner 2005, Baddeley et al. 2015). Several studies have demonstrated that spatial point pattern analysis is capable of detecting spatial patterns that can be attributed to processes (e.g. Ledo & Schnitzer 2014, Brown et al. 2015). To eliminate point patterns based on low replication, we removed species at any plot with fewer than five individuals (resulting in final data from a total of 16 sites). We then calculated a pooled L for each comparison (by species, by species type, by species type/plant size, or by species type/dispersal mechanism) by weighting the individual L estimates by the number of points in a given L-function (methods follow Bagchi & Illian 2015). We bootstrapped these estimates 999 times to create 95% confidence intervals. We then calculated the predicted L for complete spatial random to ensure that reported spatial patterns are significantly different (not overlapping with) complete spatial random. Data manipulation of input to and output from point pattern analysis was done using a combination of the "abind", "gridExtra", and "reshape" packages (Wickham 2007, Aguié 2015, Plate & Heiberger 2015). We constructed all figures in the package "ggplot2" (Wickham 2009).

To allow for easier interpretation of figures, we corrected our measures of L with the distance at which each measure of L is calculated ($L(d)-d$). Besag's L is a measure of spatial aggregation, and when $L(d)-d$ is high, a greater proportion of neighbors are observed within distance d of focal individuals than predicted by a complete spatial random pattern. When $L(d)-d$ is low, a smaller proportion of neighbors are observed within distance d of focal individuals than predicted by a complete spatial random pattern

(Besag 1977). We classify any point pattern where a linear regression slope of $L(d)-d$ is significant and positive (using the command “lm” in R, Table 2.S1, 2.S2) with increasing distance (d) as overdispersed. This designation implies that more individuals are found far away from an individual of a given species than near an individual of that species. We classify any point pattern where a linear regression slope of $L(d)-d$ is significant and negative with increasing distance as clustered. These designations differ from "pure overdispersion" (i.e. regularity or inhibition), which would begin with a significantly negative $L(d)-d$ that indicates fewer individuals close to the parent than would be expected by chance (Dale 1999, Bagchi & Illian 2015, Baddeley et al. 2015). However, natural dispersal typically results in more conspecific seeds and seedlings close to adults than predicted by complete spatial random, and thus we did not expect to find a significant negative $L(d)-d$ close to the parent. Therefore, we account for dispersal limitation by focusing on overdispersion as having a positive slope with regards to distance (d), which indicates a significant increase in individuals with distance from the adult.

We consider any point pattern to be significantly different from complete spatial random if a mixed effect linear model (calculated using the command “lmer” in package “lme4” with plot as a random effect and using the package “lmerTest” to calculate p-values) of the $L(d)-d$ and the distance (Table 2.1). If the total model was considered significant, we did not consider the point pattern to be significantly different from complete spatial random at any distance where the bootstrapped 95% confidence intervals of $L(d)-d$ overlap with complete spatial random. We consider any two point patterns to be significantly different from each other if their bootstrapped 95% confidence intervals do not overlap at a given distance.

Results:

At the community level, all woody plants combined were significantly overdispersed (Figure 2.1a). The largest individuals (>5 m) had a significantly lower $L(d)-d$ at intermediate distances (2-5m), than the two middle height size classes (1m – 5m and 0.5 – 1 m), but $L(d) - d$ did not differ significantly at distances greater than 5 m (Figure 2.1b). By contrast, the smallest individuals (< 0.5 m) had significantly lower $L(d) - d$ than intermediate height individuals (0.5-1m and 1-5 m tall) for all distances greater than 2m (Figure 2.1b) and significantly lower $L(d) - d$ than individuals in all of the larger height categories for all distances greater than 5m.

Both canopy trees and understory plants were significantly overdispersed; canopy trees were more overdispersed (significantly higher $L(d)-d$) for distances greater than 3 m (Fig. 2.2a). The differences in overdispersion between canopy and understory plants become more pronounced with plant life history stage (*i.e.*, plant size). Canopy trees did not differ significantly from complete spatial random when they were small and young, but became significantly overdispersed when they were larger (Figure 2.2b), which is consistent with NDD. Understory plants displayed the opposite pattern: they were overdispersed when small, but larger individuals were indistinguishable from complete spatial random (Figure 2.2c).

Of the four dispersal mechanisms that we examined, wind, bird, and self-dispersed species were all overdispersed and statistically indistinguishable from each other. Species dispersed by animals other than birds (including secondary dispersal via squirrels) were all significantly less overdispersed than the other three dispersal types (Figure 2.3a).

Dispersal syndrome for bird and wind dispersed species did not explain the differences in

spatial pattern between canopy trees and understory plants; canopy trees were always more overdispersed than understory plants regardless of dispersal mechanism (Figure 2.3b), indicating that the height of canopy trees is the most important factor in dispersal distance. We limited this analysis to bird and wind dispersed species because these two groups had sufficient replication for robust comparisons between canopy and understory plants.

Discussion:

We found strong support for NDD for canopy trees. Canopy trees were overdispersed and the strength of overdispersion increased with plant size - two critical conditions that must be met for NDD to be a mechanism that maintains species diversity. Our findings are consistent with a growing number of studies that have reported empirical support for NDD as a putative mechanism to maintain canopy tree diversity in temperate and tropical forests (*e.g.*, Comita *et al.* 2010, Mangan *et al.* 2010, Johnson *et al.* 2012, Zhu *et al.* 2015). Thus, our findings confirm that NDD is a highly supported mechanism for the maintenance of canopy tree species diversity in this temperate forest.

For woody understory plants, NDD does not appear to maintain species diversity at Powdermill Nature Reserve. Understory species were overdispersed, but only at the smallest size classes, and overdispersion did not increase with plant life-history stage. If NDD was operating the way that it is predicted in plant communities, overdispersion would have increased with plant size, as we found for canopy trees. Because we did not find this phenomenon for understory plants, and since overdispersion of understory plants

appeared to be relatively weak at the community level, it is unlikely that NDD is the mechanism that maintains diversity of woody understory plants in this forest.

Similar conclusions that NDD is not a general mechanism for the maintenance of woody plant diversity were reported for tropical forests. For example, Ledo & Schnitzer (2014) found that lianas, which comprised ~35% of the woody species diversity in a Panamanian tropical forest, were underdispersed (clustered) rather than overdispersed. Thus, they concluded that, while there was evidence for NDD for canopy trees, there was little evidence for NDD for lianas, indicating that NDD was not a general mechanism for the maintenance of woody plant species diversity. In a Caribbean tropical forest, DeWalt and colleagues (2015) found that non-canopy tree woody seedlings (lianas and shrubs) were less likely to suffer negative density dependent mortality than canopy trees. In tropical forests, however, trees commonly represent 65% or more of the woody diversity (*e.g.*, Schnitzer *et al.* 2012, 2015), and thus NDD is still a powerful diversity maintenance mechanism. By contrast, NDD may fail to maintain the majority of species diversity in temperate forests, where understory species represent ~80% of the diversity (Gilliam 2014).

Canopy trees may be significantly more overdispersed than understory species simply because being tall results in a higher propensity for long distance dispersal. We found higher overdispersion of canopy trees than for understory plants regardless of dispersal mechanism (Figure 2.3b). Thus, plant height rather than dispersal mechanism accounted for greater overdispersion in canopy trees. Understory plants tend to have universally smaller dispersal kernels regardless of dispersal mechanism because of their smaller stature (van der Pijl 1982). Small stature results in fewer seeds dispersed at longer

distances - even for bird-dispersed seeds (Figure 2.3b). The inability to move seeds far away from the parent tree may force understory plants to be better defended against soil pathogens, which appear to be strong agents of NDD (Packer & Clay 2000, Packer & Clay 2003, Mangan *et al.* 2010, reviewed by Bever 2003, Kulmatiski *et al.* 2008). Furthermore, negative feedback from soil pathogens may be inversely related to light availability (Smith & Reynolds 2015). Indeed, many understory plants are naturally well defended because of the importance of preserving plant tissue in a low-light environment (Coley 1983, Coley *et al.* 1985); thus, understory plants may be predisposed to developing greater defenses to pathogens rather than increasing dispersal abilities.

Differences in the level of overdispersion between canopy species and understory species did not appear to be due to the spatial scale of study in spite of our relatively small plot size (5 m). If spatial scale had biased our results, we would expect the spatial point pattern analysis to show little evidence of overdispersion for large canopy trees, but rather a signature indistinguishable from complete spatial random. Our results show a clear spatial signature of overdispersion for our largest individuals and thus it seems unlikely that this difference in pattern is caused by differences in plant scale alone. Furthermore, Bagchi & Illian (2015) demonstrate that replicated point pattern analysis is significantly more robust to problems of small scale than traditional point pattern analysis.

The intense focus on canopy trees, and in particular on canopy tree seedlings, may have biased our current understanding of diversity maintenance in forest ecosystems. If we had restricted our sampling to only the smallest understory individuals, we would have concluded that NDD is a likely diversity maintenance mechanism for the woody understory. The smallest understory individuals (<0.5 m tall) were overdispersed, while the smallest

canopy individuals did not differ significantly from complete spatial random (Figure 2.2). However, examining larger individuals indicated that adult canopy trees were distributed in a density dependent manner, but understory plants were not. Zhu and colleagues (2015) emphasized similar caution in drawing large-scale conclusions from studies of seedling dynamics, arguing that patterns of seedling mortality often have little effect on broader community and demographic patterns.

To fully understand the way mechanisms interact to maintain plant species diversity, it is necessary to examine spatial patterns both across plant size and age, as well as across plant groups that vary in life history characteristics. Spatial patterns may be even more complex when considering species that vary more broadly in their life history characteristics, such as herbaceous species, which comprise the majority of plant diversity in temperate deciduous forests (Gilliam 2007) and are largely neglected with regard to their diversity maintenance. Nevertheless, even by simply dividing the woody plant community into canopy trees and woody understory plants, we demonstrated that NDD, which is thought to maintain canopy tree diversity, fails to maintain understory plant diversity in this temperate forest.

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Table 2.1: Results of mixed effects linear model to calculate L statistic significance at Powdermill Nature Reserve in Southwestern Pennsylvania for all comparisons of all individuals >10 cm height. To calculate significant differences from complete spatial random we used a mixed effects linear model with plot as a random effect to control for between plot differences due to environmental heterogeneity between plots. We report model degrees of freedom based on the number of L estimates (calculated every 10 cm per point pattern per plot).

Model	dF	T Stat	P value	Figure
All individuals	2228	19.37	<0.0001	1a
All individuals, <0.5	781	-4.477	0.6689	1b
All individuals, 0.5-1	889	7.83	<0.0001	1b
All individuals, 1-5	797	8.5828	<0.0001	1b
All individuals, >5	358	-14.97	<0.0001	1b
Understory	1071	10.191	<0.0001	2a
Canopy	1059	5.796	<0.0001	2a
Canopy, <0.5 m tall	380	-7.14	<0.0001	2b
Canopy, 0.5-1 m tall	478	8.67	<0.0001	2b
Canopy, 1-5 m tall	463	9.14	<0.0001	2b
Canopy, >5 m tall	186	-10.71	<0.0001	2b
Understory, <0.5 m tall	397	2.045	0.0415	2c
Understory, 0.5-1 m tall	407	0.3348	0.7379	2c
Understory, 1-5 m tall	381	1.038	0.2998	2c

All individuals, bird dispersed	1159	2.86	0.0042	3a
All individuals, animal dispersed	200	-6.806	<0.0001	3a
All individuals, wind dispersed	803	3.404	<0.0001	3a
Overstory, wind dispersed	601	3.903	<0.0001	3b
Overstory, bird dispersed	250	5.482	<0.0001	3b
Understory, wind dispersed	199	-8.895	<0.0001	3b
Understory, bird dispersed	906	-3.533	0.0004	3b

Figure 2.1. Pooled Besag's L statistic across distance from spatial point pattern analysis for the full community of woody plants >10 cm in height at Powdermill Nature Reserve in Southwestern Pennsylvania. a.) The community of woody plants (all species, $n=62$ point patterns) was significant overdispersed regardless of dispersal mechanism. However, the $L(d)-d$ for the community remains positive across all distances indicating that some individuals occur close to members of their own species. b.) Individuals that were <0.5 m tall were the least overdispersed ($n=25$ point patterns). Individuals that were intermediate in height (0.5m to 5 m tall) were significantly more overdispersed than smaller individuals, though not significantly more or less overdispersed than the largest individuals ($n_{0.5-1m}=26$ point patterns, $n_{1-5m}=27$ point patterns). The largest individuals (> 5 m tall, $n= 13$ point patterns) were not significantly more overdispersed than individuals that were 0.5m to 5m tall; however, the drop in the line below complete spatial random indicates that they had less clumping over small distances. Grey shaded regions represent 95% confidence intervals, darker grey regions represent overlapping confidence intervals.

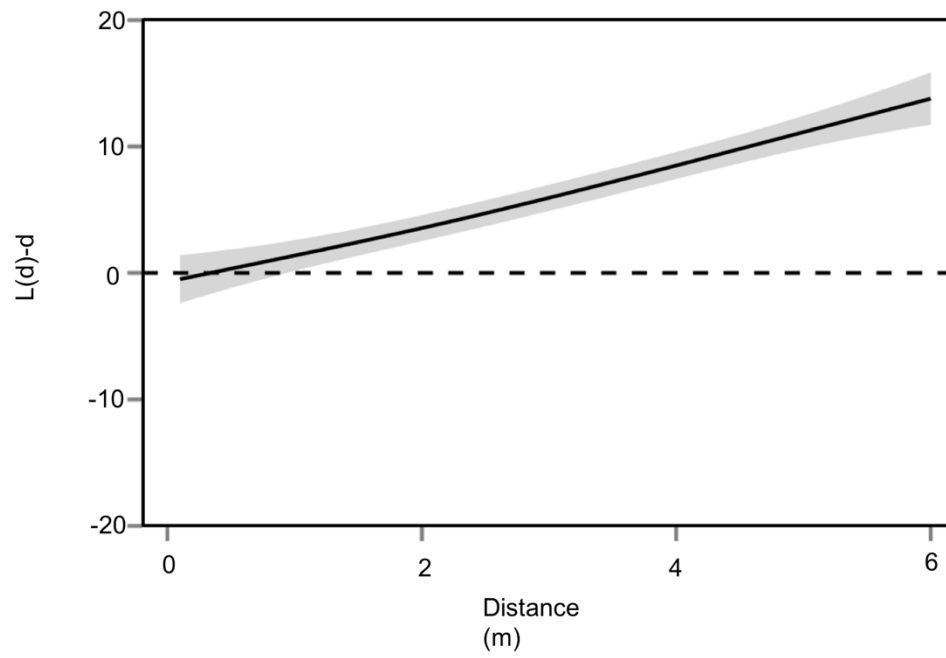
Figure 2.2: Pooled Besag's L statistic across distance from spatial point pattern analysis for woody plants >10 cm in height at Powdermill Nature Reserve in Southwestern Pennsylvania separated by growth form. a.) Canopy($n = 29$ point patterns) and understory plants ($n=33$ point patterns) were both significantly overdispersed, indicative of negative density dependence. Canopy plants were significantly more overdispersed than understory plants. b.) Canopy plants were more overdispersed with increasing life-history stage in accordance with predictions for negative density

dependence ($n_{<0.5}=14$ point patterns, $n_{0.5-1}=48$ point patterns, $n_{1-5}=32$ point patterns, $n_{>5}=15$ point patterns). c.) Understory plants were not more overdispersed with life-history stage ($n_{<0.5}=21$ point patterns, $n_{0.5-1}=22$ point patterns, $n_{1-5}=20$ point patterns). Grey shaded regions represent 95% confidence intervals, darker grey regions represent overlapping confidence intervals.

Figure 2.3. Pooled Besag's L statistic across distance from spatial point pattern analysis of the woody plant community stratified by dispersal mechanism and plant type at Powdermill Nature Reserve in southwestern Pennsylvania. a.) Wind dispersed($n=16$), bird dispersed ($n=23$), and self dispersed($n=2$) species were significantly more overdispersed than species dispersed by animals other than birds($n_{\text{animal}}=6$). b.) Canopy plants were significantly more overdispersed than understory plants regardless of dispersal mechanism($n_{\text{canopy-bird}}=5$, $n_{\text{canopy-wind}}=12$, $n_{\text{understory-bird}}=18$, $n_{\text{understory-wind}}=5$). Bird dispersal was emphasized here; however, plants did not differ significantly from wind dispersed plants either in the canopy and the understory. All reported sample sizes (n) are in number of total point patterns contributing to a pooled L function. Grey shaded regions represent 95% confidence intervals, darker grey regions represent overlapping confidence intervals.

Figure 2.1:

a.)



b.)

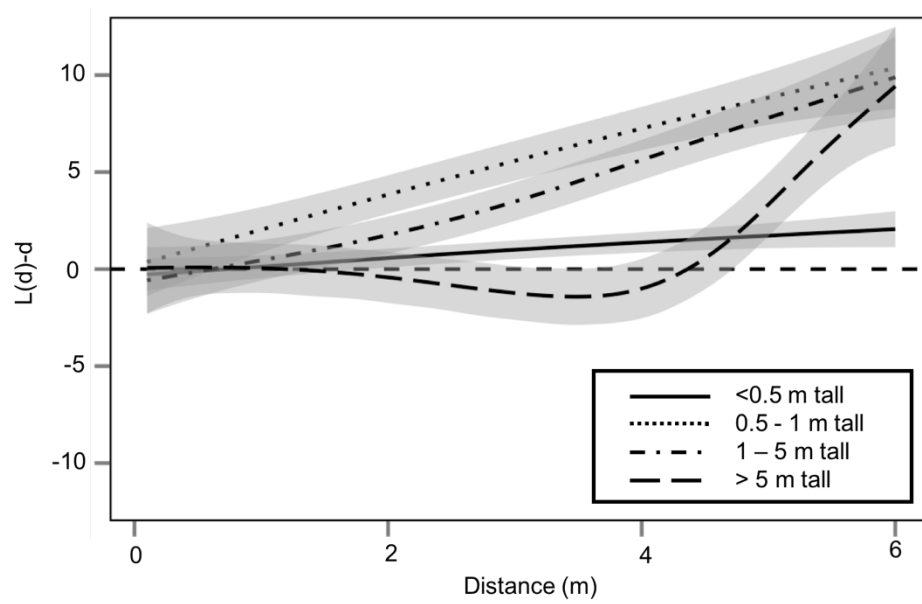
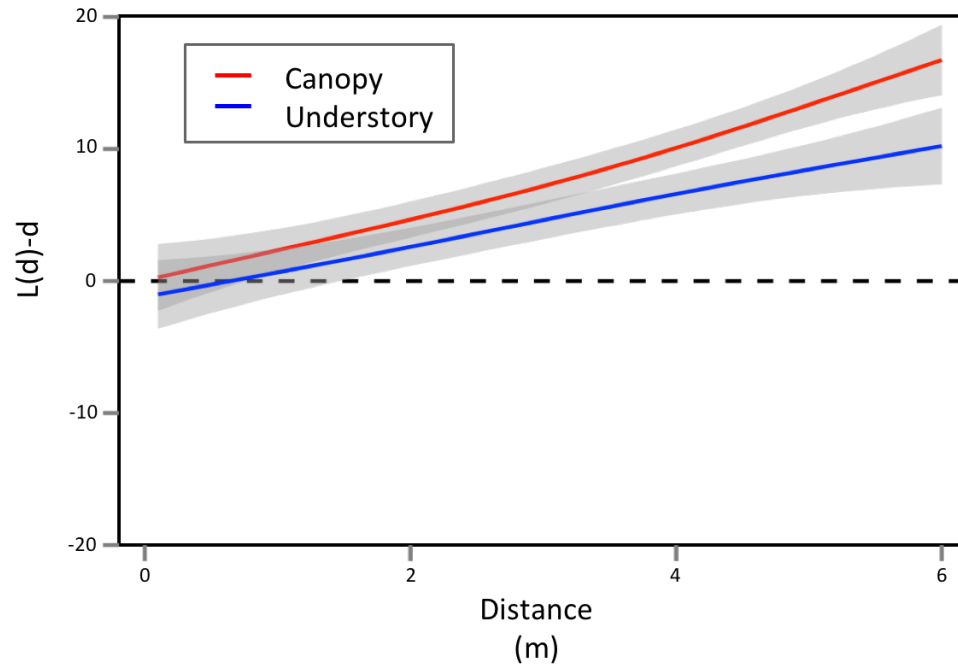
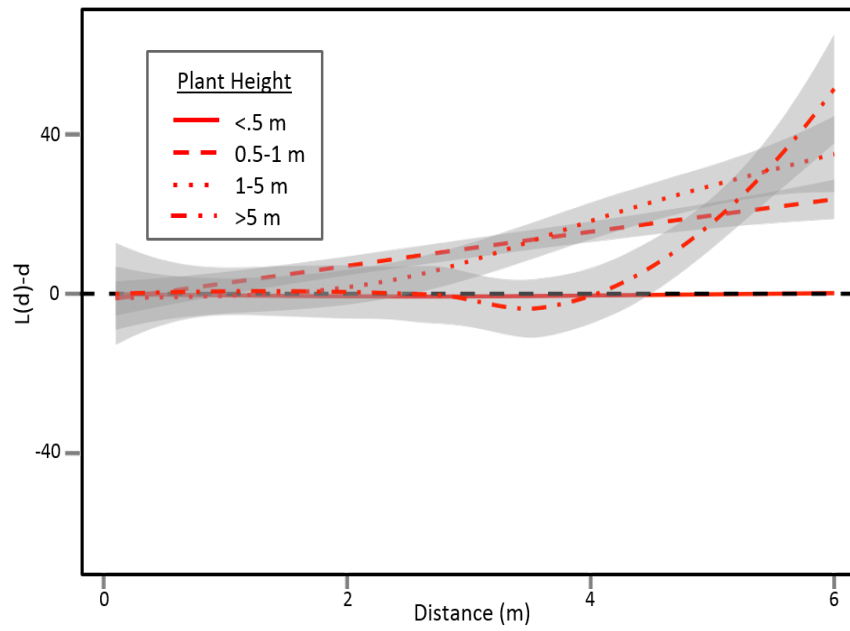


Figure 2.2:

a.)



b.)



c.)

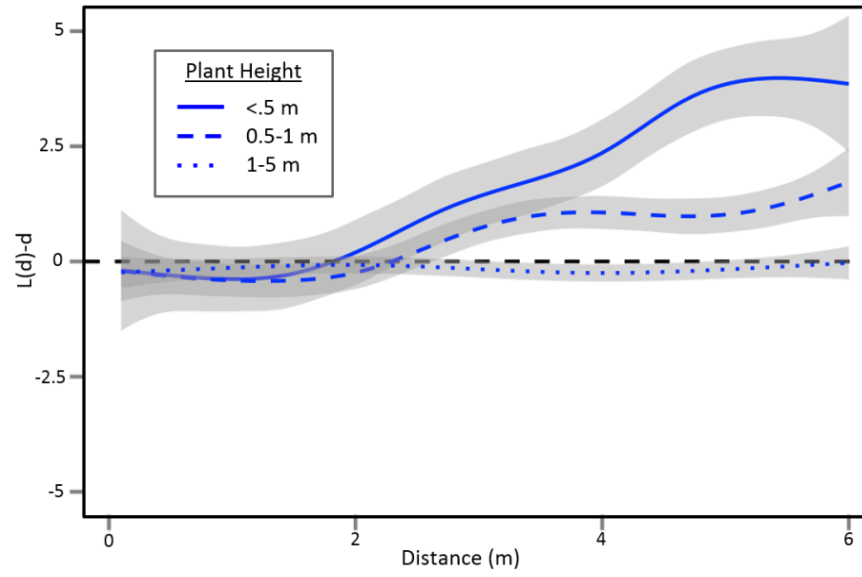
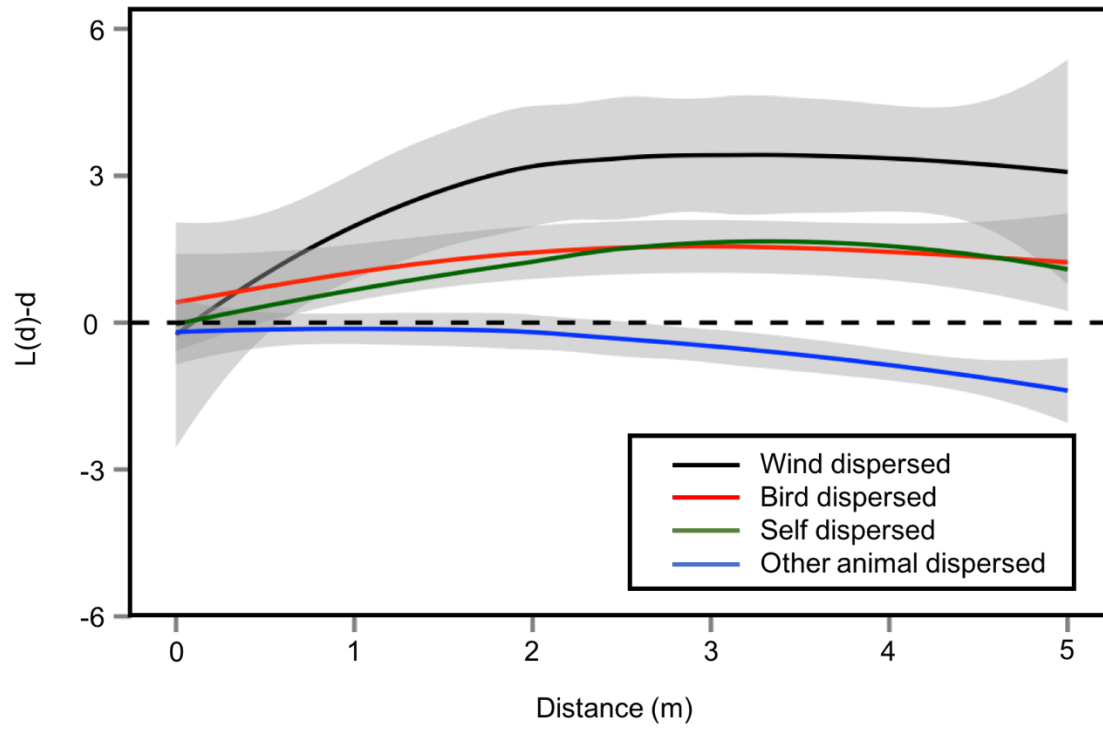
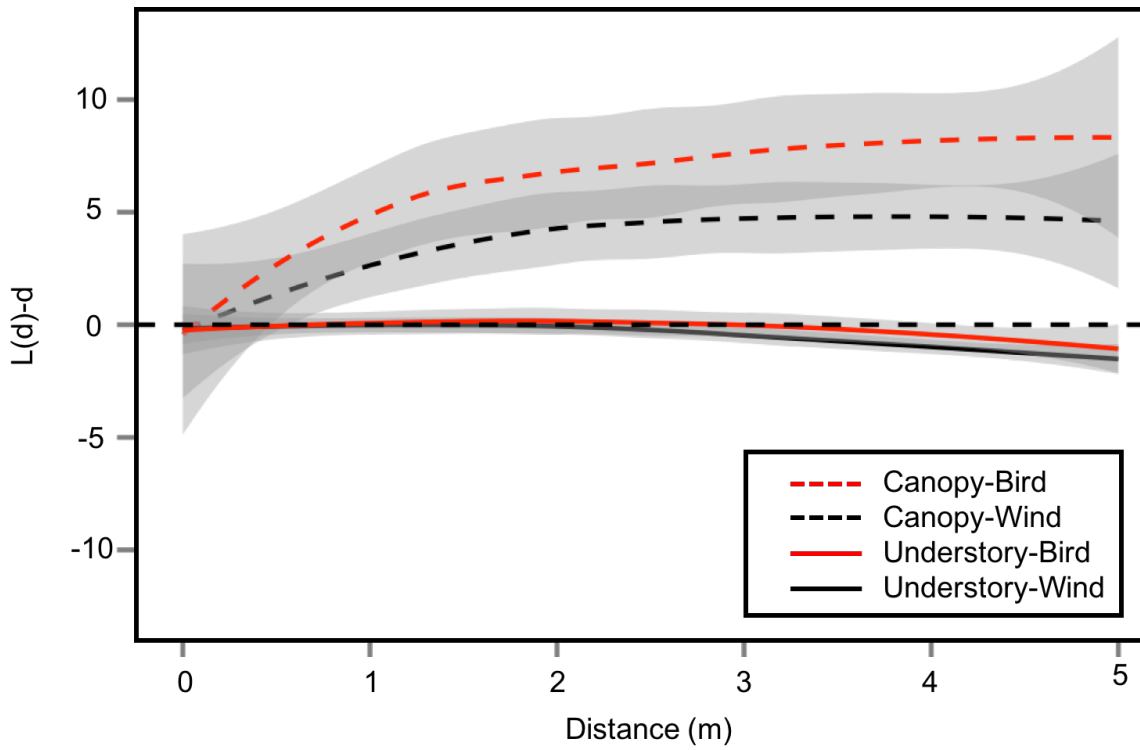


Figure 2.3.



a.)



b.)

Table 2.S1: Linear estimates of the relationship between L and distance for all pooled point patterns at Powdermill Nature Reserve. We report any pooled point pattern as overdispersed if it has a significantly positive slope and any pooled point pattern as clustered if it has a significantly negative slope.

Point pattern	Df	T Stat	P value	Figure
All individuals	2242	11.706	$<2 \times 10^{-16}$	1a
All individuals, <0.5	792	0.07535	0.000145	1b
All individuals , 0.5 - 1m	1238	4.243	2.43×10^{-5}	1b
All individuals, 1-5 m	1133	5.22	2.25×10^{-7}	1b
All individuals, >5 m	441	-5.914	7.65×10^{-9}	1b
Overstory	1069	8.737	$<2 \times 10^{-16}$	2a
Understory	916	10.191	$<2 \times 10^{-16}$	2a
Overstory, <0.5	387	-5.441	9.41×10^{-8}	2b
Overstory, 0.5-1	486	4.82	1.93×10^{-6}	2b
Overstory, 5-1	471	6.14	1.75×10^{-9}	2b
Overstory, >5	190	-3.007	0.003	2b
Understory, <0.5	403	0.422	0.673	2c
Understory, 0.5-1	414	0.529	0.597	2c
Understory, 1-5	386	-1.596	0.111	2c
All individuals, bird dispersed	1171	8.594	$<2 \times 10^{-16}$	3a
All individuals, animal dispersed	202	11.97	$<2 \times 10^{-16}$	3a

All individuals, wind dispersed	814	6.973	$6.43 \times e^{-12}$	3a
Canopy, bird dispersed	253	5.482	$1.02 \times e^{-7}$	3b
Canopy, wind dispersed	610	6.341	$4.40 \times e^{-10}$	3b
Understory, bird dispersed	916	8.12	$1.49 \times e^{-15}$	3b
Understory, wind dispersed	202	10.897	$<2 \times e^{-16}$	3b

Table 2.S2: Linear estimates of the relationship between L and distance for all pooled point patterns utilizing degrees of freedom based on the number of points represented by each point pattern rather than the degrees of freedom based on the number of L estimates. To make a more conservative estimate of significance, we calculated the P value for each pooled point pattern using the standard deviation of the L estimates and the number of points contributing to each point pattern. We used the number of points contributing rather than the number of L estimates because L is calculated 51 times (each 10 cm distance bin) for each individual point pattern resulting in an inflated degrees of freedom for the overall model. We then calculated the t statistic as the slope/standard error and used a T table to find the estimated P value for a two-tailed t test. We report the P value for each T statistic at the closest degrees of freedom on the table to our degrees of freedom that was not greater than the actual degrees of freedom (i.e. for a degrees of freedom of 204, we report the p-value for 200 degrees of freedom). This analysis may be overly conservative because the variance, standard deviation, and standard error are calculated based on the L estimates which have a higher variance (as they are calculated 51 times per point) than the average L estimate for each point.

Point pattern	N	Df	Slope	Standard Error	T Stat	P Value	Figure
All individuals	704	702	1.265	0.580	2.179	<0.05	1a
All individuals, <0.5	206	204	0.467	0.118	3.960	>0.1	1b
All individuals , 0.5 - 1m	181	179	1.490	1.156	1.289	<0.05	1b
All individuals, 1-5 m	171	169	1.039	0.636	1.635	<0.05	1b

All individuals, >5 m	42	40	-0.415	0.320	-	1.296	<0.4	1b
Overstory	338	336	1.740	0.527	3.298	<0.002		2a
Understory	352	350	0.828	0.228	3.629	<0.001		2a
Overstory, <0.5	97	95	-0.140	0.080	-	1.745	<.10	2b
Overstory, 0.5-1	96	94	3.060	2.122	1.442	<.10		2b
Overstory, 5-1	89	87	2.103	1.147	1.833	<.10		2b
Overstory, >5	22	20	-0.348	0.538	-	0.647	<0.4	2b
Understory, <0.5	109	107	0.032 2	0.210	0.154	<0.5		2c
Understory, 0.5-1	85	83	0.020	0.124	0.162	<0.5		2c
Understory, 1-5	97	95	-0.067	0.125	-	0.536	<0.5	2c
All individuals, bird dispersed	312	310	1.160	0.387	3.001	<0.01		3a
All individuals, animal dispersed	53	51	0.760	0.192	3.953	<0.01		3a
All individuals, wind dispersed	316	314	1.541	0.526	2.930	<0.01		3a
Canopy, bird dispersed	50	48	2.342	1.475	1.588	<0.1		3b
Canopy, wind dispersed	245	243	1.822	0.675	2.698	<0.01		3b
Understory, bird dispersed	262	260	0.832	0.284	2.933	<0.01		3b

Understory, wind dispersed	33	31	0.698	0.254	2.748	<0.05	3b
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Table 2.S3. List of species from Powdermill Nature Reserve. We classified species using the Flora of North America species descriptions. If a species had an average height of 5 m or higher, we classified it as a canopy species. If a species had an average height of 5 m or lower, we classified it as an understory species. We based our dispersal syndrome on the description of seed morphology.

Species name	Common name	Growth form	Dispersal syndrome
<i>Acer pensylvanicum</i>	Striped maple	Understory	Wind
<i>Acer rubrum</i>	Red maple	Canopy	Wind
<i>Acer saccharum</i>	Sugar maple	Canopy	Wind
<i>Berberis thunbergii</i>	Japanese barberry	Understory	Bird
<i>Betula lenta</i>	Black birch	Canopy	Wind
<i>Carpinus caroliniana</i>	Musclewood	Understory	Wind
<i>Carya glabra</i>	Mockernut hickory	Canopy	Animal
<i>Carya ovata</i>	Shagbark hickory	Canopy	Animal
<i>Cornus florida</i>	Flowering dogwood	Understory	Bird
<i>Crataegus sp.</i>	Hawthorn	Understory	Bird
<i>Fagus grandifolia</i>	American beech	Canopy	Wind
<i>Fraxinus Americana</i>	Green ash	Canopy	Wind
<i>Hamamelis virginiana</i>	Witch hazel	Understory	Self
<i>Lindera benzoin</i>	Spice bush	Understory	Bird

<i>Liriodendron tulipifera</i>	Tuliptree	Canopy	Wind
<i>Magnolia acuminata</i>	Cucumber magnolia	Canopy	Bird
<i>Nyssa sylvatica</i>	Black gum	Canopy	Bird
<i>Prunus serotina</i>	Black cherry	Canopy	Bird
<i>Prunus virginiana</i>	Bird cherry	Understory	Bird
<i>Quercus alba</i>	White oak	Canopy	Animal
<i>Quercus prinus</i>	Chestnut oak	Canopy	Animal
<i>Quercus rubra</i>	Red oak	Canopy	Animal
<i>Rosa multiflora</i>	Multiflora rose	Understory	Bird
<i>Rubus sp.</i>	Bramble	Understory	Bird
<i>Toxicodendron radicans</i>	Poison Ivy	Understory	Bird
<i>Vaccinium corymbosum</i>	Highbush blueberry	Understory	Bird
<i>Viburnum acerifolium</i>	Maple-leaf viburnum	Understory	Bird
<i>Viburnum prunifolium</i>	Blackhaw viburnum	Understory	Bird

Chapter 3: Disturbance overrides negative density dependence for the maintenance of diversity in a temperate deciduous forest

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Status: In preparation for submission to Ecology.

Abstract:

One of the central goals of community ecology is to understand the mechanisms that maintain diversity. For temperate forests, there is now compelling evidence that negative density dependence (NDD), where individuals of the same species perform poorly near members of their own species, maintains diversity. Negative density dependence may interact with a suite of other mechanisms, such as disturbance and herbivory, which may strengthen or obscure NDD. However, interactions of diversity maintenance mechanisms are poorly understood. We examined the effects of disturbance via canopy gap formation and fire, vertebrate herbivores and seed predators on NDD in a factorial 16-year experiment in an eastern deciduous forest. Specifically, we tested whether negative density dependence maintains diversity, whether disturbance weakens or strengthens NDD, and whether browsing weakens or strengthens NDD.

We found that negative density dependence maintained diversity in the absence of disturbance. Disturbance via canopy gaps obscured negative density dependence. Furthermore, disturbance combined with the removal of large vertebrate herbivores resulted in an 60% increase in species richness. In the absence of vertebrate herbivores, negative density dependence was weakened. Our findings suggest that negative density dependence may maintain diversity in temperate deciduous forests and it is strengthened

by vertebrate herbivores; however, disturbance via canopy gap formation enhanced diversity while obscuring negative density dependence.

Introduction:

One of the central goals of community ecology is to understand the mechanisms that maintain diversity. One of the most compelling diversity maintenance hypotheses in terms of empirical support is negative density dependence. Negative density dependence (NDD) is the process where individuals perform poorly near members of their own species (Janzen 1970, Connell 1971, Connell et al. 1984, Johnson et al. 2012, Zhu et al. 2015). Negative density dependence creates unfavorable conditions for common species thereby limiting the ability of any given species to dominate and creating a pattern of overdispersion (Ledo & Schnitzer 2014). There is now strong empirical support for NDD in many ecosystems (Anderson 2001, Goldberg et al. 2001, Hille Ris Lambers et al. 2002, Lorenzen & Enberg 2002, Petermann et al. 2008, Comita et al. 2010, Mangan et al. 2010, Schnitzer et al. 2011, Johnson et al. 2012, Johnson et al. 2014, Zhu et al. 2015). In forests, NDD is considered pervasive for seedlings, numerous studies now demonstrate unequivocally that seedlings of canopy trees are less likely to survive near conspecifics (reviewed by Comita et al. 2014). In fact, over the past 10 years alone over 70 studies have confirmed the presence of NDD for canopy tree species (reviewed by Barry & Schnitzer in press).

While there is strong evidence for NDD, other putative diversity maintenance mechanisms may alter the strength of NDD; however, these interactions are poorly understood. For example, in temperate forests, disturbance may promote coexistence by reducing the abundance of the most common species (Huston 1979, Pickett 1980) or by creating resource heterogeneity in both space and time (Sousa 1984, Chesson 2000). In a review of more than 450 studies in temperate and boreal forests, Thom and Seidl (2015) concluded that canopy gaps and fire (individually and combined) can increase species

richness by more than 30%. In particular, treefall gaps are critical to the maintenance of diversity for pioneer trees, woody vines, and species that cannot reach the canopy such as understory trees, shrubs, and herbaceous species (Royo et al. 2010, Schnitzer & Carson 2001, Schnitzer & Ledo 2014). Disturbance may obscure NDD if the influx of resources relaxes intraspecific competition or if extra resources permit plant growth even with increasing amounts of disease (Figure 3.1a,b). Alternatively, disturbance may reinforce NDD if the influx of resources following disturbance causes individuals to compete more intensely with conspecifics or if higher densities of recruiting conspecifics increase the prevalence of disease (Figure 3.1c,d).

Vertebrate browsers and seed predators may also interact with NDD. Vertebrate browsers and seed predators can maintain diversity or reduce it, depending on their relative abundance and what they eat (Janzen 1970, Connell 1971, Royo et al. 2010, Sedio 2013). Herbivores may strengthen NDD if they have strong plant preferences and they preferentially prey on common species (Figure 3.1e,f; Janzen 1970, Connell 1971, *sensu* Sedio & Ostling 2013). Alternatively, herbivores may negate NDD if they forage preferentially on rare species (Figure 3.1g,h). Additionally, plants found in canopy gaps may have traits that make them more susceptible to browsing (Coley 1983, Coley & Barone 1996). Thus, vertebrate herbivores may interact with both NDD and disturbance simultaneously. Furthermore, vertebrate herbivores, particularly ungulates, are now abundant in temperate ecosystems and have recently caused significant declines in plant diversity (Cote et al. 2004, McShea & Rappole 1992, Stromayer & Warren 1997, Waller & Alverson 1997, Nuttle et al. 2014).

Interactions among NDD, disturbance, and vertebrate herbivores may be pervasive and occur simultaneously, making them difficult to predict *a priori*. Nonetheless, the degree that these processes interact may underlie patterns of forest regeneration and diversity across landscapes (Royo et al. 2010, Nuttle et al. 2013). We evaluated the degree that vertebrate herbivores and disturbance (by both fire and canopy gap formation) together and alone impact the presence and strength of NDD. Specifically, we tested the following hypotheses:

1. Negative density dependence maintains diversity; diversity will be highest where the spatial signature of NDD is the strongest.
2. Disturbance weakens NDD; disturbance will erase the spatial signature of NDD (Figure 3.1 a, b).
3. Disturbance strengthens NDD: the signature of NDD will be strongest where disturbance is present (Figure 3.1 c,d).
4. Browsing strengthens NDD; the spatial signature of NDD will be strongest where vertebrate herbivores are present (Figure 3.1 e, f).
5. Browsing negates NDD; the signature of NDD will be weakest when browsing is present (Figure 3.1 g,h).

Methods:

Study site

We conducted this study in four sites in the the Eastern Deciduous Forest Biome in central West Virginia, USA. Two sites were in the Monongahela National Forest (39° 06' N, 79° 43' W) and two sites were at the Fernow Experimental Forest (39° 01' N, 79° 42' W).

The sites were located in forest stands that were 10 to 40 ha in size and 670-810 m in elevation (Royo et al. 2010, Thomas-Van Gundy 2014). All sites were located in mature secondary forests that had been logged between 70 and 90 years previously. Mean annual precipitation in all sites was approximately 145 cm per year (Thomas-Van Gundy et al. 2014). Deer populations in this region ranged from 4.6 deer/km² to 7.7 deer/km² (Royo et al. 2010). While this is higher than historical levels, it is modest relative to large portions of Eastern Deciduous Forest Biome (Royo et al. 2010).

We used a split-plot factorial design (Figure 3.2). Each of the four sites was split in half and randomly assigned a fire or no-fire treatment. Control burns were conducted in 2001 in four 5 to 20 ha sections. Sites were almost completely burned nearly completely (mean = 92%) and fire temperature ranged from 245°C ± 15.4 °C near the surface to 91.9 °C ± 1.7 °C 1m above the surface. In each half, eight 20 x 20 m treatment plots were established a minimum of 20 m away from each other, site edges, and fire breaks. These 8 plots were randomly assigned one of four treatments: exclosure fence (2 m woven wire fence), canopy gap (multiple central trees were girdled and killed to form a large canopy gap and allowed to regrow, 284 ± 16 m²), exclosure fence and canopy gap, and no fence/no gap (for full site establishment details see Royo et al. 2010, Thomas-Van Gundy et al. 2014).

Census methods

At each of the 64 individual plots, we identified all woody individuals greater than 20 cm in height in the 10 x 10 m center of the 20 x 20 m plot to species. We mapped the location of each individual to the nearest 10 cm by using triangulation with a laser distance meter. There were 1847 of individuals and 24 species in the study (Table 3.S1). The

dominant species were *Quercus alba* and *Quercus rubra* in the canopy, *Betula lenta* in the midstory, and *Prunus spp.* and *Aralia spinosa*. Additionally, for each treatment we calculated the species richness and standard error to examine how diversity was related to spatial pattern.

Data analysis

To measure plant spatial distribution (the degree to which plants are clustered or overdispersed), we calculated Ripley's K in the package "spatstat" and then converted K to Besag's L (Ripley 1977, Besag 1977, Baddeley & Turner 2005, Baddeley et al. 2015). We did not use a calculated buffer zone or border correction because all plots were surrounded with a physical buffer of 5 m. We eliminated species in any plot with fewer than three individuals because Ripley's K cannot be calculated for fewer than three individuals (Baddeley et al. 2015). This elimination resulted in usable data from a total of 40 out of the 64 possible sites). We then calculated a pooled L for each treatment by weighting the individual L estimates by the number of points in a given L-function (Bagchi & Illian 2015). We bootstrapped these estimates 999 times to create 95% confidence intervals. We then calculated the predicted L for complete spatial random and used the "envelope" function in the package "spatstat" to calculate a bootstrapped 95% acceptance interval around complete spatial random. That is, we bootstrapped each point pattern within a pooled L-function 99 times to create a 95% acceptance interval for our null hypothesis (that individuals were completely spatially randomly distributed). We considered any pooled L-function that was not overlapping with all of the acceptance intervals contained in a given L-function to be significantly different from complete spatial random. We consider any two

point patterns to be significantly different from each other if their bootstrapped 95% confidence intervals did not overlap at a given distance (d). Data manipulation of input to and output from point pattern analysis was done using a combination of the “abind”, “gridExtra”, and “reshape” packages (Wickham 2007, Aguié 2015, Plate & Heiberger 2015). We performed all data analysis in R statistical computing software (v. 3.2.2, R Development Core Team 2015).

To allow for easier interpretation of figures, we corrected our measures of L with the distance at which each measure of L is calculated ($L(d)-d$). Besag’s L is a measure of spatial aggregation, and when $L(d)-d$ is high, more individuals are present than predicted by a complete spatial random pattern. When $L(d)-d$ is low, fewer individuals are present than predicted by a complete spatial random pattern (Besag 1977). We classify any point pattern where a linear regression slope of $L(d)-d$ is positive with increasing distance (d) as overdispersed. This designation implies that more individuals are found far away from an individual of a given species than near an individual of that species. We classify any point pattern where a linear regression slope of $L(d)-d$ is significant and negative with increasing distance as clustered (underdispersed). These designations differ from some literature (i.e. Dale 1999, Bagchi & Illian 2015, Baddeley et al. 2015) because pure overdispersion (i.e. regularity or inhibition) should begin with a significantly negative $L(d)-d$. However, patterns of dispersal in plants are well studied and almost always result in more individuals close by an adult than predicted by complete spatial random (reviewed by Willson & Traveset 2000). Therefore, we account for dispersal by defining overdispersion as having a positive slope with regards to distance (d). This designation implies that the

degree to which plants are more abundant than complete spatial random increases with increasing distance.

Several studies have demonstrated that spatial point pattern analysis is capable of detecting spatial patterns that can be attributed to multiple processes (e.g. Ledo & Schnitzer 2014, Brown et al. 2015). However, one critique of point pattern analysis suggests that results are most valid for a quarter of the shortest dimension of the plot (5 m in this case; Baddeley et al. 2015). We address this critique by replicating point pattern analysis, which dramatically reduces this source of error, and we include results up to 10 m (50% of the shortest dimension of the total plot; for further justification see Bagchi & Illian 2015).

Results:

Plants in control plots (no canopy gap, fire, or exclosure fence) were significantly overdispersed (Fig. 3.3), indicating a strong spatial signature of NDD. By contrast, disturbances (fire or gaps) together or alone created plant spatial patterns that were not significantly different from complete spatial random (Fig. 3.3). Fire and canopy gaps had very similar effects on plant spatial patterns and did not differ significantly from each other. Thus, our results suggest that NDD is common throughout the undisturbed forest and that disturbance weakens or obscures the NDD pattern (Fig. 3.3).

Plants were significantly overdispersed in plots with with large herbivores and no disturbance (i.e. control plots; Fig. 3.3). Plants in fenced plots with disturbance were significantly less overdispersed throughout the plot than when vertebrate herbivores were excluded (Fig. 3.3c). Disturbance overpowered browsing in terms of plant spacing (Fig.

3.3a,b,c). The addition of disturbance to any plot with or without herbivory resulted in significantly less overdispersal than controls and a pattern that overlapped with complete spatial random.

In spite of demonstrating the strongest signature of NDD, control plots at these sites had a slight but significantly lower species richness than treatments that combined deer exclosure with canopy gap formation (Fig. 3.4). Excluding large vertebrates and adding canopy gaps resulted in a >60% increase in species richness (Fig. 3.4). Fire treatments did not result in significantly higher diversity than the control except when fire was combined with canopy gap formation and deer exclosure (Fig. 3.4).

Discussion:

Our results indicate that disturbance in the form of canopy gaps may be a strong mechanism for the maintenance of diversity in temperate forests, and that disturbance may reduce or mask NDD. When plants were growing in undisturbed forest they were significantly overdispersed indicating that NDD is a strong structuring factor in the absence of disturbance (Fig. 3.3). However, the strong signature of NDD was not correlated with relatively high species richness. Evidence for NDD as a structuring force in temperate forests is prevalent for canopy trees. Johnson et al. (2012) demonstrated that 148 out of 151 species of tree seedlings were less likely to establish in the area surrounding a member of their own species indicating strong NDD. There are now many studies that further confirm the presence of the NDD pattern and, in some cases, particularly in the tropics (e.g. Harms et al. 2000), this pattern has been linked to higher recruitment diversity (Hille Ris Lambers et al. 2002, Packer & Clay 2004, Comita et al. 2010, Mangan et al. 2010, Johnson et

al. 2014). Our results may be contrary to these studies because these studies limit their purview of NDD to negative density dependent mortality of seedlings which may not be indicative of broader demographic patterns (Zhu et al. 2015). We analyzed plant distributions across the total community to integrate the effects of negative density dependence over time. We suggest that NDD may be present in the total community but that the degree of disturbance may dictate the importance of NDD (Janzen 1970, Connell 1971).

We found that disturbance causes significant deviation from NDD (Fig. 3.3). In spite of this deviation from NDD, plots with canopy gaps had significantly higher species richness than any other treatment (Fig. 3.4). This higher diversity is a good indicator that canopy gap formation contributes to the maintenance of diversity in these forests. Disturbance is a well recognized diversity maintenance mechanism throughout temperate and tropical forests, particularly for specific groups of species (Thom & Seidl 2015). Schnitzer and Carson (2001) and Ledo and Schnitzer (2014) found that lianas (woody vines) are likely maintained by canopy gaps, while the majority of the tree species are less likely to be maintained by disturbance (see also Schnitzer et al. 2008). Similarly, Royo and colleagues (2010) suggest that complex disturbance results in higher diversity in eastern deciduous forests among understory species, which represent upwards of 80% of diversity in temperate forests (Gilliam 2014).

Disturbance may promote the maintenance of diversity across systems when disturbance provides an influx of resources. Wright et al. (2015) found that disturbance via flooding enhanced diversity while simultaneously reducing stability in a temperate grassland. Fire and canopy gaps add significantly to resource pools in temperate forests

(Ojima et al. 1994, Pickett & White 1985, Thom & Seidl 2015). These resource addition disturbances may momentarily override NDD because species that were previously resource limited can allocate additional resources to defenses against pests and pathogens or avoid strong intraspecific competition, both putative drivers of NDD. This momentary override of NDD may reset the community clock. Over time, NDD may once again dominate community composition in this forest until it is reset by periodic resource addition disturbance once again.

Plants were overdispersed in the presence of vertebrate herbivores and were significantly less overdispersed when herbivores were excluded (Fig. 3.3d). Therefore, vertebrate herbivores may be a contributing factor in NDD (Fig. 3.3d). Both Janzen (1970) and Connell (1971) originally proposed that vertebrate herbivores and seed predators could underlie NDD provided that they are sufficiently species specific (Hammond & Brown 1998, *sensu* Sedio & Ostling 2013). One of the most common vertebrate herbivore groups in the temperate zone are ungulates which are abundant in temperate forests worldwide (Russell et al. 2001, Rooney & Waller 2003, Côté et al. 2004). In the Eastern Deciduous Forest Biome, white-tailed deer are abundant, and they were the most commonly excluded species by our vertebrate herbivore exclosures (Royo et al. 2010, Chips et al. 2015). White-tailed deer forage on a wide variety of plant species; however, they have clear feeding preferences (Russell et al. 2001, Horsley et al. 2003, Côté et al. 2004), which may contribute to a pattern of overdispersion at these sites but did not result in higher species richness. Indeed, excluding vertebrate herbivores doubled species richness (Fig. 3.4) while simultaneously reducing NDD (Fig. 3.3). The removal of vertebrate herbivores resulted in a significant increase in diversity and a significant decrease in overdispersion (from controls,

Figure 4). However, plants in these plots are overdispersed which is consistent with smaller amounts of NDD indicating that other drivers are also present. Our evidence suggests that even NDD from vertebrate herbivores when combined with disturbance may result in diversity maintenance.

Our results demonstrate that canopy gaps promote diversity in this system particularly when vertebrate herbivores are removed. This result is consistent with previous work on browsing and disturbance but suggests that findings of NDD in temperate forests may not be as tightly linked to the maintenance of diversity as previously thought. Indeed, many authors have cautioned that evidence of negative density dependent mortality is not *prima facie* evidence of maintaining diversity (Wright 2002, Carson et al. 2008, Comita et al. 2014, Zhu et al. 2015, Barry et al. in press). We suggest that NDD may contribute to the maintenance of diversity, while resource addition disturbance (such as a canopy gap formation) determines its importance.

Acknowledgements:

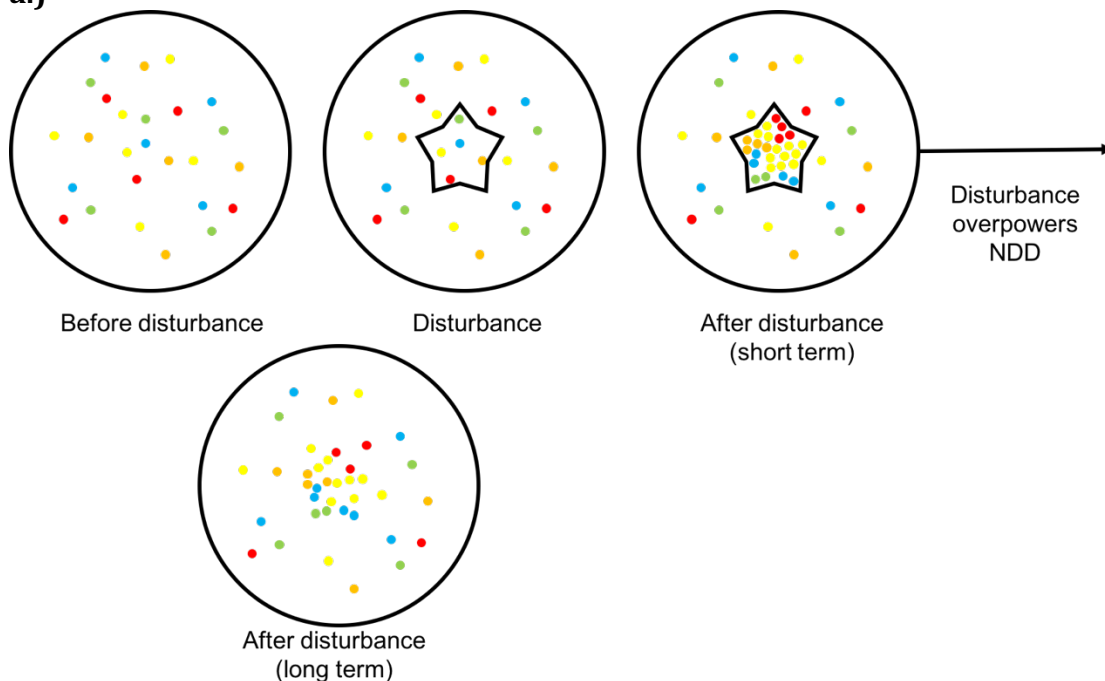
This work was supported by the USDA National Research Initiative Competitive Grant 99-35101-7732 to Walter Carson. Additional support was provided by the USDA Forest Service Northern Research Station. Funding for K.E.B. was provided by the Ivy Balsam-Milwaukee Audobon Society Grant. Travel funding for K.E.B. was provided by the University of Wisconsin Milwaukee Ruth Walker Travel Grant. The authors would like to thank Arie Hunt and Joe Strini for field assistance, Pamela Edwards, Doug and Chris for administrative support and materials provision, and Sergio Estrada Villegas, Maria Elizabeth Rodriguez Ronderos, and Sasha Wright for comments on early drafts of this

manuscript.

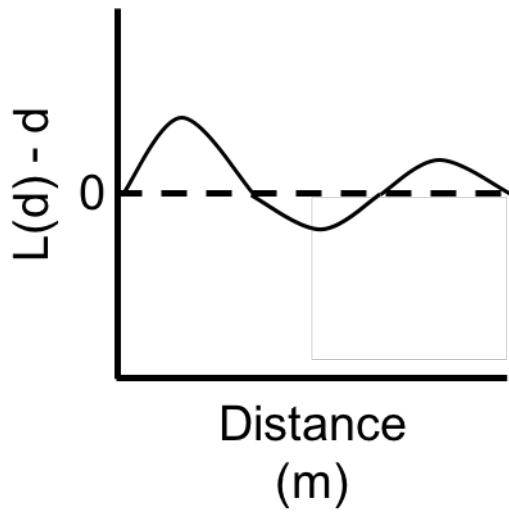
Figure 3.1: Corresponding conceptual models and predictions for four hypotheses for how disturbance and herbivory interact with negative density dependence.

Hypothesis 1 (a,b): Disturbance weakens NDD (a). If this model is accurate disturbance will result in an an L function where the L for the distance ($L(d) - d$) is not significantly different from complete spatial random (b). Hypothesis 2 (c,d): Disturbance strengthens NDD (c). If this model is correct, this will result in an L function ($L(d)-d$) that is significantly negative at near distances and increases with distance(d). Hypothesis 3: Browsing strengthens NDD (e). If this model is correct, this will result in an L function ($L(d)-d$) that is significantly negative at near distances and increases with distance(f). Hypothesis 4: Browsing negates NDD (g). If this model is accurate disturbance will result in an an L function where the L for the distance ($L(d) - d$) is not significantly different from complete spatial random (h).

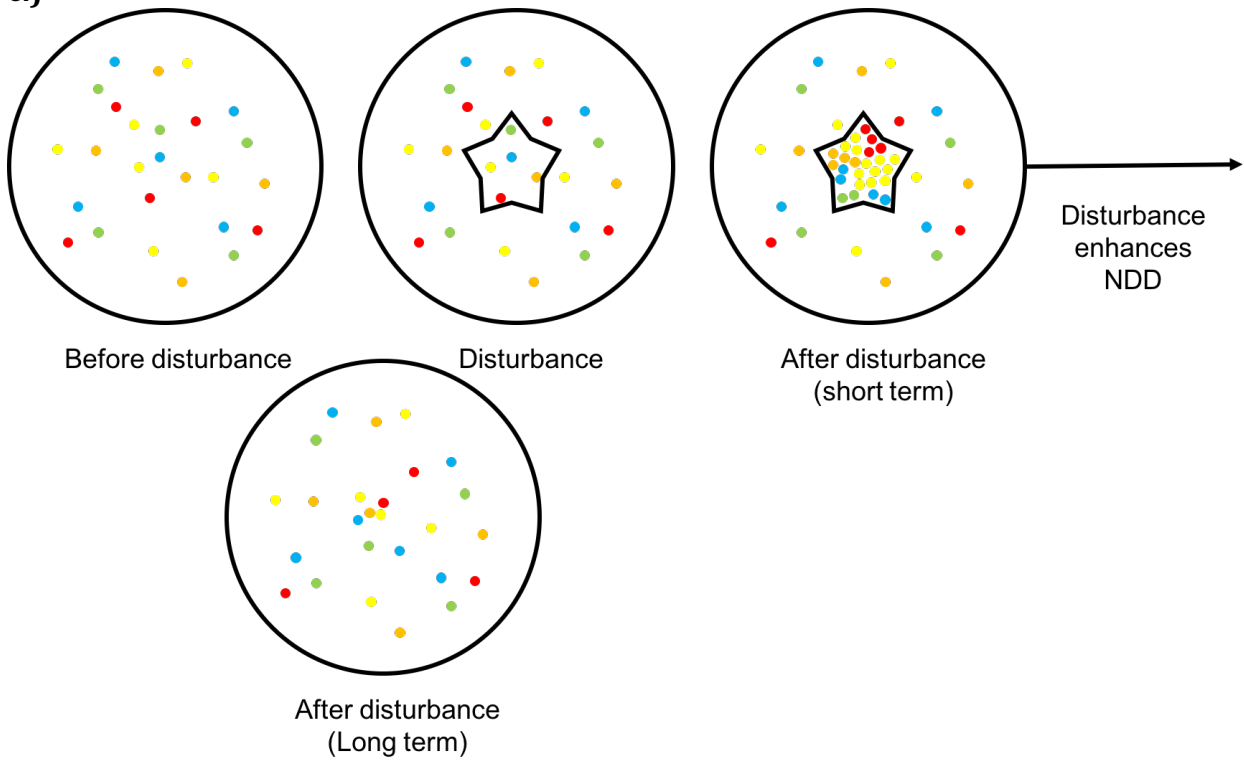
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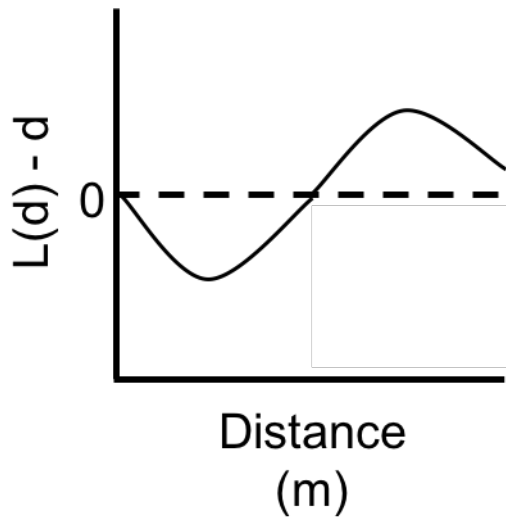
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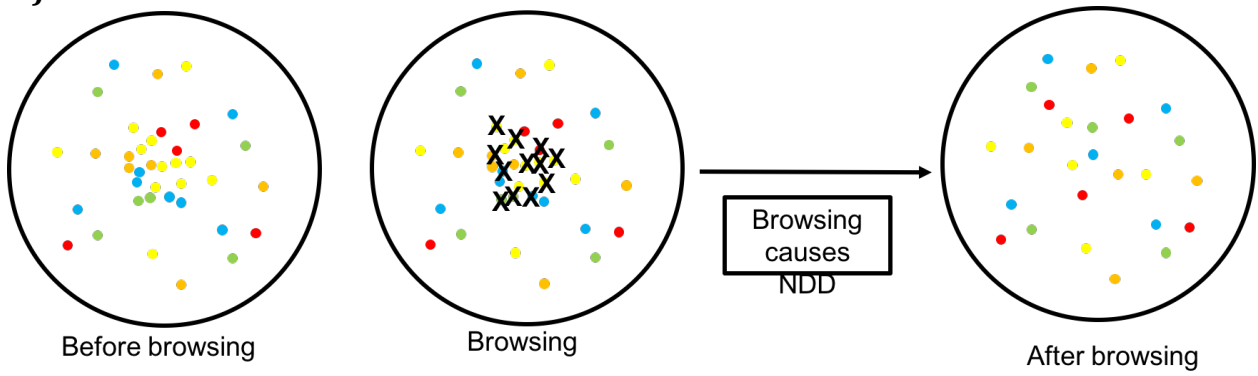
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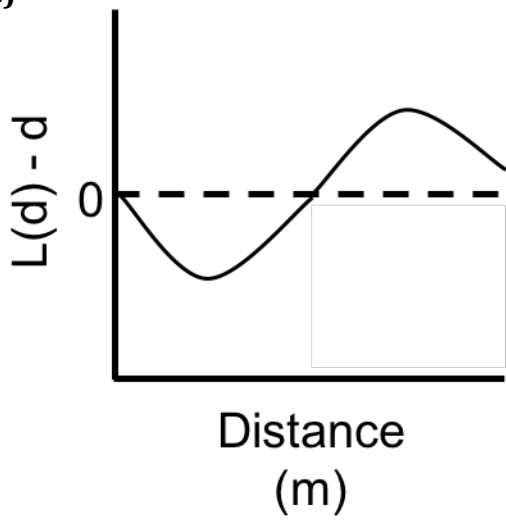
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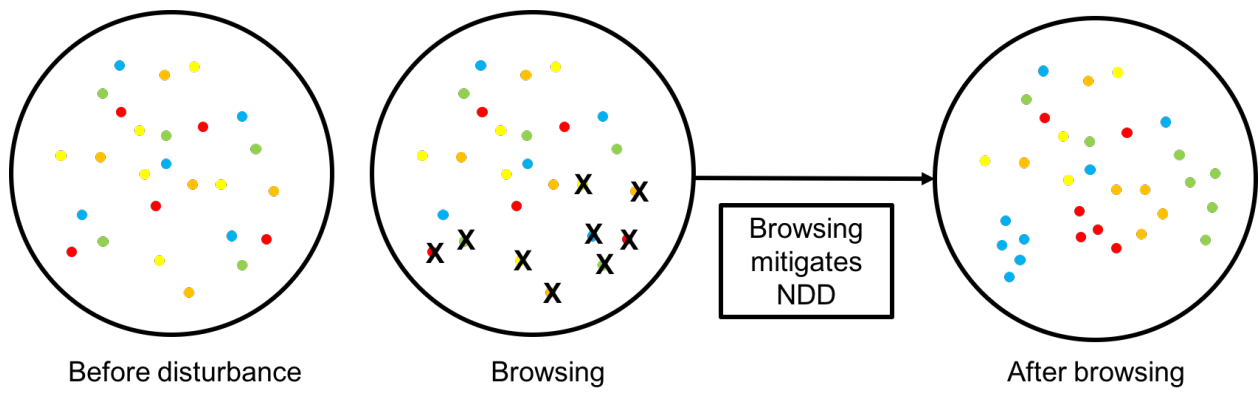
e.)



f.)



g.)



h.)

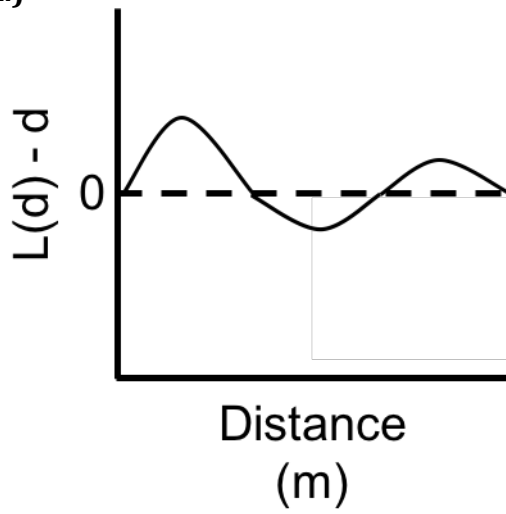


Figure 3.2. Schematic of single replicate of split plot factorial experimental design at the Fernow Experimental Forest and the Monongahela National Forest reproduced with permission from Nuttle et al. 2013. At each of four replicate sites, half of the site was burned. On each half, eight 20 x 20 m plots were established. Four of these plots were randomly selected and surrounded with 2m tall wire large vertebrate exclosure fences. Four plots (two fenced, two unfenced) were selected for a canopy gap. In these plots, large central trees were girdled and allowed to fall out of the canopy naturally over 5 years.

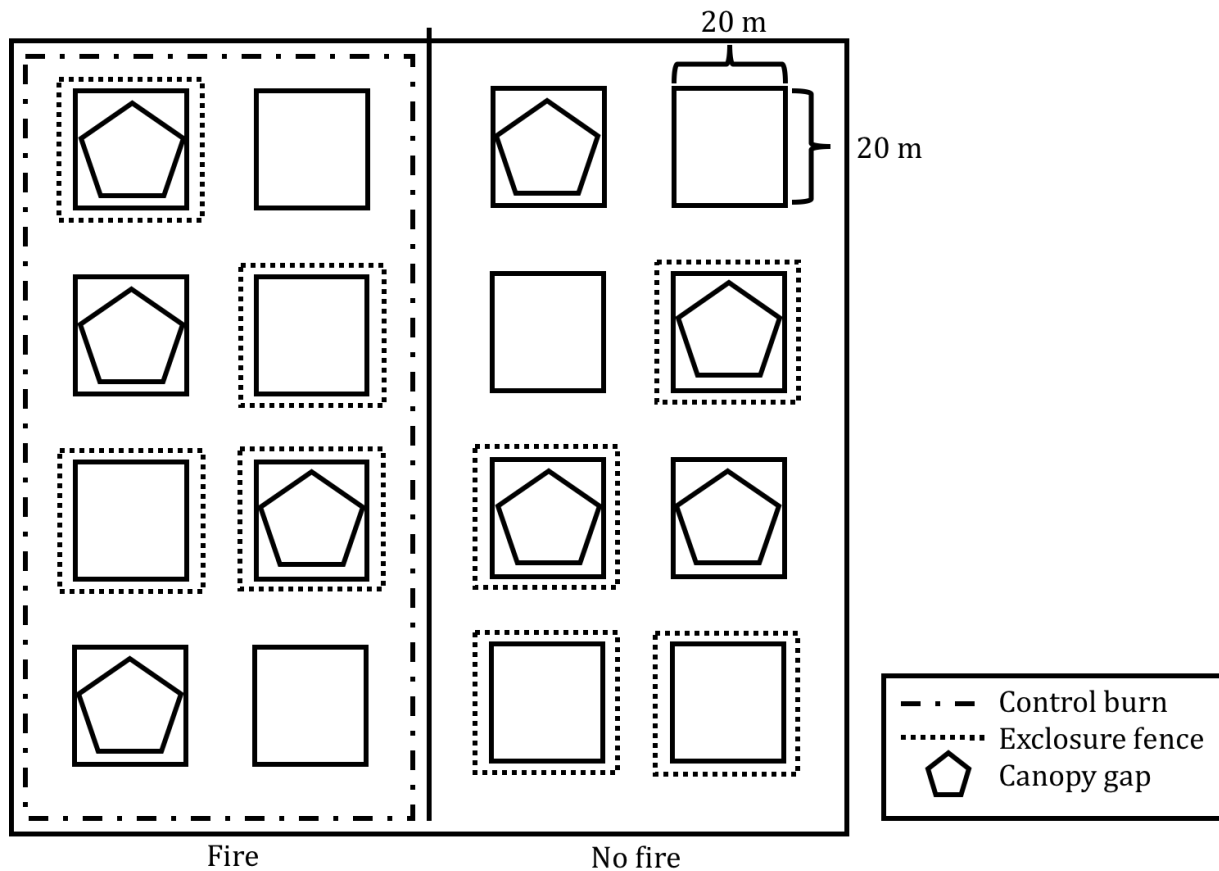
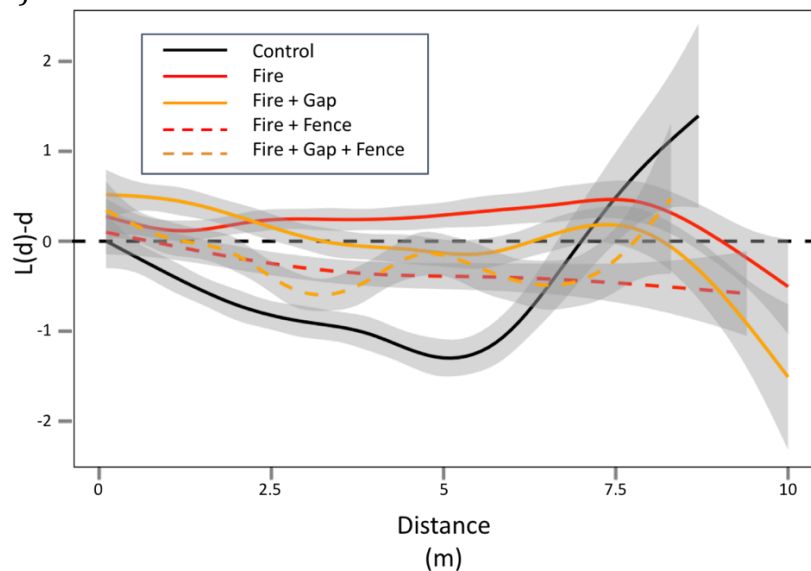
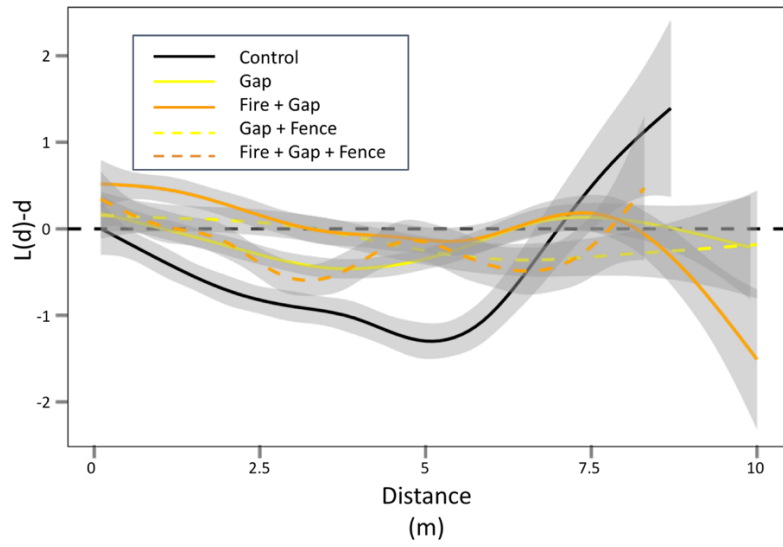


Figure 3.3: Results of pooled L analysis for all burned sites, sites with added canopy gaps, and herbivore exclosures at the Fernow Experimental Forest and Monongahela National Forest in central West Virginia. A.) All plots that were burned demonstrated spatial patterns that are significantly different from the control (black line) but did not significantly differ from complete spatial random (black dotted line). B.) All plots with added canopy gaps demonstrated spatial patterns that are significantly different from the control but did not significantly differ from complete spatial random. When large vertebrates are excluded spatial patterns depart significantly from the control. When the exclosure is combined with disturbance (c) spatial patterns overlap with complete spatial random. When herbivore exclusion is not combined with disturbance (d) spatial patterns are significantly different from the control and demonstrate a weaker signal of NDD, and are closer to complete spatial random.

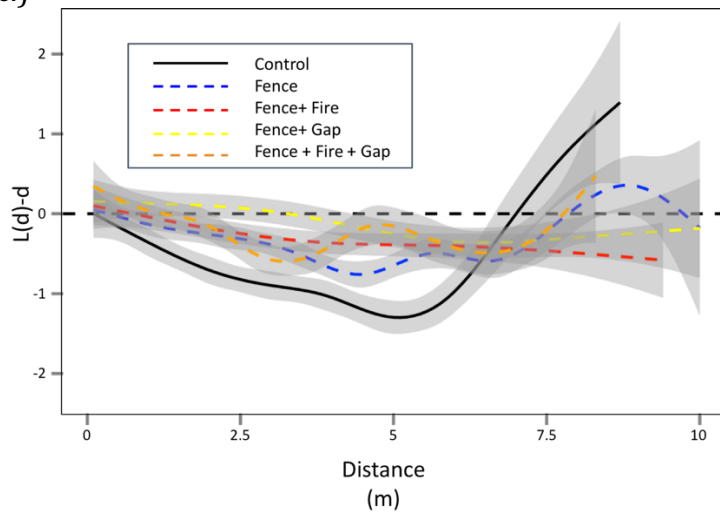
a.)



b.)



c.)



d.)

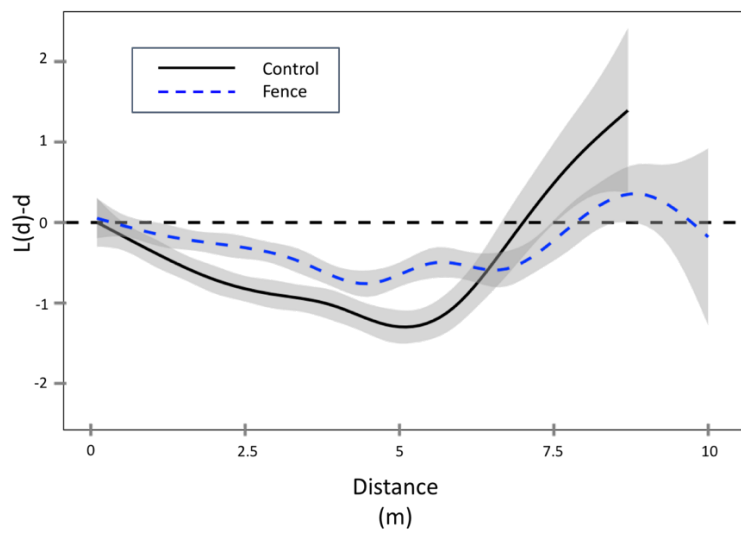


Figure 3.4: Plot level species richness for all treatments at the Fernow Experimental Forest and Monongahela National Forest in central West Virginia. Neither deer

exclosure (n=425) nor canopy gaps (n=527) alone significantly increased species richness from controls (n=139) but when combined deer exclosure and canopy gaps increases

species richness (Fence + Gap = 8.5 ± 0.5 species, n=138, Fire, Fence, + Gap = 10 ± 1 species,

n=79). Unless combined with deer exclosure and canopy gap formation, fire did not

increase diversity (Fire= 5.667 ± 1.202 species, n=179, Fire + Fence = 6 ± 1.155 species,

n=89, Fire + Gap = 5.75 ± 1.93 species, n=270).

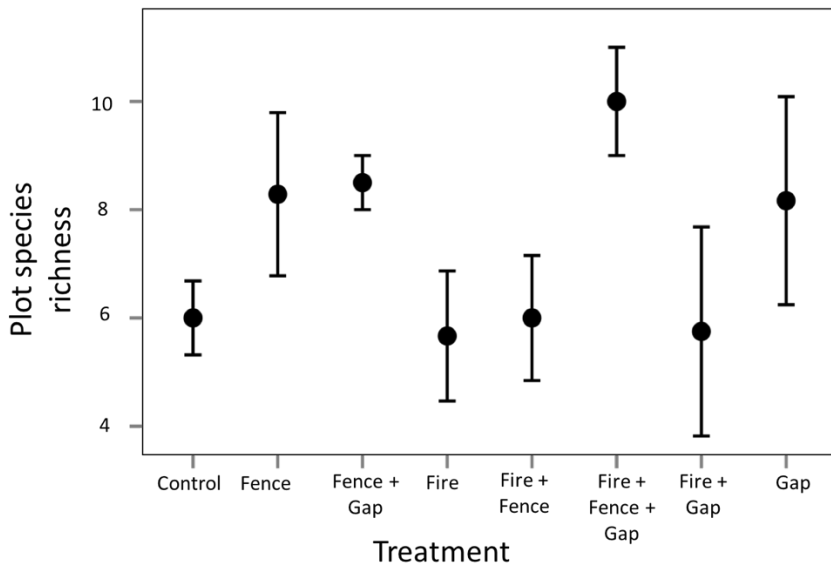


Table 3.S1: List of species included in point pattern analysis with sample size included.

Species name	Common name	N
<i>Acer pensylvanicum</i>	Striped maple	448
<i>Acer rubrum</i>	Red maple	156
<i>Acer saccharum</i>	Sugar maple	94
<i>Amelanchier sp.</i>	Serviceberry	5
<i>Aralia spinosa</i>	Devil's walking stick	26
<i>Betula lenta</i>	Black birch	405
<i>Carya ovata</i>	Shagbark hickory	10
<i>Castanea dentata</i>	American chestnut	7
<i>Fagus grandifolia</i>	American beech	38
<i>Fraxinus americana</i>	Green ash	5
<i>Hamamelis virginiana</i>	Witch hazel	22
<i>Liriodendron tulipifera</i>	Tuliptree	174
<i>Magnolia acuminata</i>	Cucumber magnolia	10
<i>Magnolia fraseri</i>	Fraser magnolia	30
<i>Nyssa sylvatica</i>	Black gum	32
<i>Pinus strobus</i>	White pine	4
<i>Prunus serotina</i>	Black cherry	47
<i>Quercus alba</i>	White oak	10
<i>Quercus prinus</i>	Chestnut oak	32
<i>Quercus rubra</i>	Red oak	156
<i>Sassafras albidum</i>	Sassafras	98
<i>Viburnum acerifolium</i>	Maple-leaf viburnum	29

Chapter 4: What determines the mechanisms that maintain diversity in temperate forests?

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Abstract:

One of the central goals of community ecology is to understand the mechanisms that maintain diversity. There is now compelling evidence that negative density dependence, where small individuals grow poorly near members of their own species is pervasive among canopy species in the temperate zone, this results in a pattern of overdispersal. Disturbance and consumers can also maintain plant species diversity. However, these three factors are all likely to interact with key plant tradeoffs, such as the trade-off between high-light growth and low-light survivorship and the trade-off between competition and dispersal. We used spatial point pattern analysis in two disturbance regimes (fire and canopy-gap formation) and vertebrate herbivore removal to test two hypotheses: 1) The relative strength of disturbance, NDD, and herbivory in terms of the maintenance of species diversity varies with plant shade tolerance. 2) Plant growth form with respect to being a canopy or the understory species determines the strength of negative density dependence, disturbance and herbivory in terms of the maintenance of species diversity.

We found that coarse distinctions between growth forms (canopy plant vs. understory plant) were a stronger determinant of spatial pattern than simple a trade-off between shade tolerance and shade intolerance. Also, negative density dependence was likely to occur in canopy species and not in understory species, but did not result in significantly higher species richness for either canopy or understory species. The

contribution of shade-intolerant species was significantly higher in three out of the four fire treatments than in controls, suggesting that fire is uniquely important for the maintenance of diversity in these species. Furthermore, species richness was significantly higher for both species groups when disturbance by canopy gaps was present. These findings suggest that canopy gap formation contributes to the diversity of both understory and canopy plants.

Introduction:

In forests, multiple processes likely operate concurrently to maintain plant species diversity and promote coexistence (Ledo & Schnitzer 2014, DeWalt et al. 2015, Barry 2016). One of these processes is negative density dependence, where conspecific individuals perform poorly near other conspecifics (Janzen 1970, Connell 1971). Negative density dependence maintains diversity by preventing the dominance of common species allowing more relatively rare species to establish in a community (Janzen 1970, Connell 1971). There is now compelling evidence that negative density dependence operates in ecosystems worldwide (Anderson 2001, Goldberg et al. 2001, Lorenzen & Enberg 2002, Petermann et al. 2008, Mangan et al. 2010, Schnitzer et al. 2011, Johnson et al. 2014, Zhu et al. 2015). In fact, over 30 studies across five continents report that negative density-dependent mortality of seedlings in forest ecosystems maintains plant species diversity (reviewed by Barry & Schnitzer 2016).

Other processes, such as disturbance and herbivory, may also contribute to the maintenance of plant species diversity (Coley 1983, Denslow 1987, Sedio 2013, Ledo & Schnitzer 2014). Disturbance can promote coexistence by creating resource heterogeneity in both space and time (Sousa 1984, Chesson 2000, Schnitzer et al. 2008). Disturbance may also maintain diversity ephemerally because a higher density of stems can grow in a disturbed area. Higher stem number results in higher species number (Denslow 1995). Many studies now confirm that disturbance maintains diversity in many ecosystems including coral reefs (Connell 1978), grasslands (White 1979, Uys et al. 2003, Wright et al. 2015), rocky intertidal zones (Connell 1978, reviewed by Underwood 2000, Bertness et al. 2002), and forests (Brokaw 1985, Denslow 1987, Schnitzer et al. 2008, Ledo & Schnitzer

2014, Barry 2016). In forests, evidence that disturbance maintains diversity is particularly strong. A recent meta-analysis of 478 studies by Thom and Seidl (2015) demonstrated that disturbance by canopy gap formation, fire, or bark beetle infestation increased species richness in temperate and boreal forests by more than a third. Furthermore, in tropical forests, several studies confirmed that lianas and some early successional tree species are maintained by canopy gap formation (Schnitzer & Carson 2000, 2001, Dalling et al. 2012, Schnitzer & Ledo 2014, DeWalt et al. 2015).

Consumers can also maintain diversity by preying differentially on individuals across a community. Consumer-mediated diversity maintenance is common in grasslands (Dupre & Diekman 2001) and is well studied in marine ecosystems where consumers function as keystone species (Paine 1969, Lubchenco et al. 1984, Menge et al. 1985, reviewed by Piraino et al. 2002). In plant communities, herbivores differentially prey on species causing them to diverge along an axis of seed size and chemical defense (Coley & Barone 1997, Sedio 2013). Herbivory can determine competitive outcomes and allocation of resources to reproduction both of which influence community composition (Coley 1983, Marquis 1984, Coley et al. 1985, Marquis 1992, Strauss & Conner 1996, Mothershead & Marquis 2000, Hochwender et al. 2003). Vertebrate herbivores and seed predators can also promote coexistence if they reduce the abundance of common species (Janzen 1970, Connell 1971, Royo et al. 2010, Sedio 2013). If herbivores preferentially forage on common species, these preferences may underlie a pattern of negative density dependence (Janzen 1970, Connell 1971, Hammond & Brown 1998, Sedio & Ostling 2013). Furthermore, vertebrate herbivores are common worldwide and are known to drive community composition (Waller & Alverson 1997, Cote et al. 2004).

The degree to which negative density dependence, herbivory, and disturbance maintain diversity may depend entirely on plant life history strategy (Schnitzer & Carson 2001, McCarthy-Neumann & Kobe 2008, Ledo & Schnitzer 2014, DeWalt et al. 2015, Barry & Schnitzer in review). For forest plants, one of the most important life history tradeoffs is the tradeoff between high light growth and low light survivorship (Kitajima 1994, Kobe 1995, 1999). Species that are shade intolerant invest heavily in quick growth but little in defense. Conversely, species that are shade tolerant grow slowly and invest in defenses against pathogens and herbivory (Coley 1983, Asner & Martin 2015). Indeed, this trade-off determines seedling survivorship and life history (Denslow 1980, 1987; Chazdon 1988; Caldwell & Pearcy 1994, Kobe 1999). Even fine-scale heterogeneity in the light environment of low-light (<2% light penetration) tropical forest floors significantly alters local seedling abundance (Montgomery & Chazdon 2002). This trade-off also determines the degree to which tree seedlings experience negative density dependence (McCarthy-Neumann & Kobe 2008, McCarthy-Neumann & Ibanez 2011, DeWalt et al. 2015, Barry & Schnitzer in review). Additionally, disturbances such as canopy gap formation and fire significantly increase light availability and favor seedling establishment, recruitment and growth of shade intolerant species (Runkle 1981, 1982, Canham & Marks 1985, Collins & Pickett 1988, Clebsch & Busing 1989).

Alternatively, the degree to which negative density dependence, disturbance, and herbivory alter community composition, and spatial distributions may depend upon the collective result of many life history trade-offs. One of the outcomes of many life-history trade-offs is plant location in the vertical structure of a forest at reproductive maturity, i.e.

in the canopy vs. the understory. Plants that complete their life cycle in the understory tend to be shade tolerant, while canopy species have a variety of tolerances across forest age (McCarthy-Neumann & Ibanez 2011). Whether a plant reproduces in the understory or canopy will also determine its ability to disperse its seeds (Howe & Smallwood 1982). Canopy plants are tall and able to disperse their seeds longer distances regardless of their seed dispersal mechanism (Barry & Schnitzer in review). Understory species are small-statured and thus less able to disperse their seeds long distances (Willson & Traveset 2011). Furthermore, understory species may invest heavily in defenses against herbivory and pathogens, which may make them less susceptible to diversity maintaining mechanisms such as negative density dependence. These coarse distinctions between plant groups that incorporate many different life history tradeoffs is thought to be influential for many factors including diversity maintenance (Sedio 2013, Schnitzer & Ledo 2014, DeWalt et al. 2015, Barry & Schnitzer in review).

While negative density dependence, disturbance, and browsing via vertebrate herbivores all contribute to the maintenance of diversity in temperate forests, their interactions remain poorly understood. Here we examine the interactions of these three processes for woody plants in an temperate forest and how they vary with shade tolerance and whether the species are canopy vs. understory plants. We manipulated canopy gap formation, fire, and vertebrate herbivore exposure as part of a 16-year split plot factorial experiment to test the following two hypotheses:

1. The relative strength of disturbance, NDD, and herbivory in terms of the maintenance of species diversity varies with plant shade tolerance.

2. Plant growth form with respect to being a canopy or the understory species determines the strength of negative density dependence, disturbance and herbivory in terms of the maintenance of species diversity.

Methods:

Study site

We performed this study across four sites in central West Virginia, USA (For site establishment details see Royo et al. 2010, Thomas-Van Gundy et al. 2014). Two sites were in the Monongahela National Forest (39° 06' N, 79° 43' W) and two sites were at the Fernow Experimental Forest (39° 01' N, 79° 42' W). The sites were located in forest stands that were 10 to 40 ha in size and 670-810 m in elevation (Royo et al. 2010). All sites were located in mature secondary forests that had been logged between 70 and 90 years ago. The total community consisted of 1847 woody plants comprising 22 species (Table 4.S1). The dominant species were *Quercus alba* and *Quercus rubra* in the canopy, *Betula lenta* in the midstory, and *Prunus spp.* and *Aralia spinosa* in the understory. Mean annual precipitation is 145 cm per year. Deer populations in this region ranged from 4.6 deer/km² to 7.7 deer/km² (Royo et al. 2010, Thomas-Van Gundy et al. 2014). While this is higher than historical levels, it is modest relative to large portions of the Eastern Deciduous Forest Biome.

We used a split-plot factorial design. Each of the four sites was split in half and randomly assigned a fire or no-fire treatment. In each half, eight 20 x 20 m treatment plots were established a minimum of 20 m away from each other, site edges, and fire breaks. These 8 plots were randomly assigned one of four treatments: exclosure fence (2 m woven

wire fence), canopy gap (multiple central trees were girdled and killed to form a large canopy gap, $284 \pm 16 \text{ m}^2$), exclosure fence and canopy gap, and no fence/no gap (for full site establishment details see Royo et al. 2010; Figure 4.2).

Census methods

At each of the 64 individual plots, we identified all woody individuals greater than 20 cm in height. We mapped the location of each individual to the nearest 10 cm by using triangulation with a laser distance meter. We then used the United States Department of Agriculture PLANTS Database to classify all species as: 1. Shade tolerant, 2. Shade intolerant, or 3. Intermediately tolerant (USDA Plants). We also used the Flora of North America (Flora of North America Eds.) to classify all plants as either canopy (reaching an average height of $> 5\text{m}$) or understory (all other species). See Table 4.S1 for full list of species and their classifications.

Data analysis

To measure the clustering or overdispersal of plants, we calculated Ripley's K with an isotropic border correction in the package "spatstat" and then converted K to Besag's L (Ripley 1977, Besag 1977, Baddeley & Turner 2005, Baddeley et al. 2015). To eliminate under-replicated point patterns, we removed species at any plot with fewer than three individuals from our results (resulting in final data from a total of 40 out of the 64 possible sites). We then calculated a pooled L for each treatment by pooling the individual L estimates in a given L-function for each comparison: by shade tolerance (intolerant, intermediate, or tolerant) and plant group (canopy or understory; methods follow Bagchi &

Illian 2015). We bootstrapped these estimates 999 times to create 95% confidence intervals. We then calculated the predicted L for complete spatial random and used the “envelope” function in the package “spatstat” to calculate a bootstrapped 95% acceptance interval around complete spatial random. That is, we bootstrapped each point pattern within a pooled L-function 99 times to create a 95% acceptance interval for our null hypothesis (that individuals were completely spatially randomly distributed). We considered any pooled L-function that was not overlapping with all of the acceptance intervals contained in a given L-function to be significantly different from complete spatial random. Data manipulation of input to and output from point pattern analysis was done using a combination of the “abind”, “gridExtra”, and “reshape” packages (Wickham 2007, Aguié 2015, Plate & Heiberger 2015). We performed all data analysis in R statistical computing software (v. 3.2.2, R Development Core Team 2015).

To allow for easier interpretation of figures, we present a centered L-function ($L(\text{distance}) - \text{distance}$). Besag’s L is a measure of spatial aggregation, and when $L(d) - d$ greater than 0, more individuals are present than predicted by a complete spatial random pattern. When $L(d) - d$ is less than zero, fewer individuals are present than predicted by a complete spatial random pattern (Besag 1977). We classify any point pattern where a linear regression slope of $L(d) - d$ is significant and positive (using the command “lm” in R, Table S1) with increasing distance (d) as overdispersed. This designation implies that more individuals are found far away from an individual of a given species than near an individual of that species. We classify any point pattern where a linear regression slope of $L(d) - d$ is significant and negative with increasing distance as clustered. These designations differ from some literature (i.e. Dale 1999, Bagchi & Illian 2015, Baddeley et al. 2015) because

pure overdispersion (i.e. regularity or inhibition) should begin with a significantly negative $L(d)-d$. However, because dispersal should always result in more individuals close by an adult than predicted by complete spatial random, we account for dispersal by defining overdispersion as having a positive slope with regards to distance (d). Thus, in addition to these characterizations, we consider any point pattern where all points fall significantly below predictions for complete spatial random to be "inhibited." Furthermore, we consider any two point patterns to be significantly different from each other if their bootstrapped 95% confidence intervals did not overlap at a given distance (d).

Several studies have demonstrated that spatial point pattern analysis is capable of detecting spatial patterns that can be attributed to processes (e.g. Ledo & Schnitzer 2014, Brown et al. 2015). Furthermore, spatial point pattern analysis integrates the effects of these mechanisms over time resulting in an image of community patterns rather than simply the effect on seedling recruitment which may or may not result in a community level pattern (Baddeley et al. 2015, Zhu et al. 2015, Barry & Schnitzer in review). However, several criticisms of point pattern analysis suggest that results are most valid for a quarter of the shortest dimension of the plot (5 m in this case). Replicating point pattern analysis, as we have done, reduces this source of error thus we include results up to 10 m (50% of the shortest dimension of the total plot; see Bagchi & Illian 2015 for further justification).

We also performed an Analysis of Variance with treatment as the independent variable to determine the effect of each of our treatments on the following variables: 1. Total number of stems, 2. Relative density of intermediately shade tolerant species (number of stems of intermediately tolerant species/total number of stems), 3. Relative density of shade tolerant species (number of stems of shade tolerant species/total number

of stems), 4. Relative density of shade intolerant species (number of stems of shade intolerant species/total number of stems), 5. Relative density of canopy species (number of stems of canopy species/ total number of stems), 6. Relative density of understory species (number of stems of understory species/total number of stems), 7. Proportion of species richness contributed by canopy species (number of canopy species/total species richness), 8. Proportion of species richness contributed by understory species (number of understory species/total number of stems), and 9. Number of instances where a species was the only member of that species in a plot (called number of singletons). We performed this analysis in two ways: as a fixed effect analysis of variance with treatment as the independent variable and as a mixed effects analysis of variance with treatment as the independent variable and site as a random effect to control for between site variation as plots were located in 4 distinct clusters (Table 4.1, Table 4.2).

Results:

Hypothesis 1: The relative strength of disturbance, NDD, and herbivory in terms of the maintenance of species diversity varies with plant shade tolerance.

Shade tolerant species were significantly overdispersed while shade intolerant and intermediately tolerant species were significantly inhibited (Figure 4.2a). Both of these patterns indicate strong negative density dependence. Furthermore, the three functional groups were not significantly different from each other.

Disturbance in the form of fire negated negative density dependence for all three functional groups (Figure 4.2c). However, fire resulted in significant clustering only for shade tolerant species (Figure 4.2c). Canopy gaps negated negative density dependence for

shade intolerant species (Figure 4.2d) and significantly reduced negative density dependence for shade tolerant and intermediately tolerant species (Figure 4.2d). The removal of vertebrate herbivores significantly reduced negative density dependence for all three functional groups (Figure 4.2b).

When vertebrate herbivores were excluded but fire was added, shade tolerant species were negative density dependent while shade intolerant species were significantly clustered (Figure 4.2e). Conversely, when vertebrate herbivores were excluded but canopy gaps were added both shade intolerant and shade tolerant species were significantly clustered (Figure 4.2f). When fire and canopy gap formation were combined both shade intolerant and tolerant species were clustered (and not significantly different from each other) while intermediately tolerant species were inhibited, demonstrating negative density dependence (Figure 4.2g). However, when both disturbances were present but vertebrate herbivores were excluded shade intolerant and tolerant species were overdispersed and not significantly different from each other while intermediately tolerant species were inhibited (Figure 4.2h).

Total stem density, relative density of intermediately tolerant species, relative density of shade tolerant species, and number of singletons were not significantly correlated with treatment. However, in our mixed effect model total stem density was significantly higher in gap plots. Alternatively, the relative density of shade intolerant individuals was significantly related to treatment (Table 4.1). According to our mixed effects model, the relative density of shade intolerant individuals was significantly higher in three out of the four fire treatments (fire plots, fire + fence + gap plots, and fire + gap plots; Table 4.2).

Hypothesis 2: Plant growth form with respect to being a canopy or the understory species determines the strength of negative density dependence, disturbance and herbivory in terms of the maintenance of species diversity.

Canopy plants in control plots were significantly inhibited while understory plants were significantly clustered though largely overlapping with complete spatial random (Figure 4.3a). Disturbance, however, whether by canopy gap or fire, resulted in canopy and understory plants that were completely spatially randomly distributed (Figure 4.3b,c). Excluding large vertebrate herbivores caused canopy plants to be significantly less overdispersed but had little effect on understory plants suggesting that vertebrate herbivores are a likely mechanism for negative density dependence in canopy species but have little effect on understory woody plants (Figure 4.3d).

The relative density of canopy individuals, relative density of understory individuals, relative proportion of species richness contributed by the canopy, and relative proportion of species richness contributed by the understory were not significantly influenced by treatment (Table 4.1). However, a higher proportion of species were contributed by understory species in plots with both disturbance types and no vertebrate herbivores (Table 4.2).

Discussion:

We found that negative density dependence, disturbance, and herbivory appear to interact across coarse plant groups but that this pattern was not driven by shade tolerance. Whether a plant was a canopy or understory woody species, determined the likelihood that a plant would be negative density dependent. Furthermore, canopy tree species were

significantly released from inhibition with disturbance while woody understory species were significantly less clustered. Shade tolerance, however, did not determine the significance of negative density dependence or the effect of disturbance. Plants that are shade tolerant did not significantly differ from those that are shade intolerant in control plots though all three tolerance levels were negative density dependent. Species that were shade tolerant continued to be overdispersed after the addition of a canopy gap while shade intolerant species did not. Alternatively, both shade intolerant and tolerant species were significantly clustered in plots that were burned. Interestingly, both shade tolerant and intolerant species were clustered in plots with canopy gaps when vertebrate herbivores were excluded or fire was added but not when all three treatment types were combined. In plots where both a canopy gaps and fire were added and vertebrate herbivores were excluded both shade tolerant and intolerant species overlapped with complete spatial random.

As predicted, we found that the location of a plant within the vertical structure of the forest at reproductive maturity had a significant influence on whether or not species were overdispersed/inhibited and thus negative density dependent. Canopy tree species were significantly inhibited, less likely to be found near a member of their own species, in control plots. Understory woody species, however, were significantly clustered in control plots, suggesting that negative density dependence does not structure the understory community (Figure 4.2). This pattern confirms findings from temperate and tropical forests alike: understory species are less likely to be maintained by negative density dependence than canopy tree species (DeWalt et al. 2015, Barry & Schnitzer in review).

Interestingly, disturbance uniformly resulted in a completely spatially random pattern for both canopy and understory individuals. Canopy species experienced a release from inhibition in disturbed sites while understory species were significantly less clustered. The release from clustering in understory plants suggests that, rather than being dispersal limited in the understory, understory plants may demonstrate niche differentiation along light gradients in the absence of disturbance (*sensu* Vriesendorp & Kobe 2011, McCarthy-Neumann & Ibanez 2013). Disturbance may release understory plants from light limitation and release canopy species from negative density dependence. Disturbance did not, however, result in an increase in the proportion of the community contributed by either plant group as would be expected if disturbance maintained diversity differentially for either group (Table 4.2). Disturbance does however increase total diversity at these sites (Barry et al. in prep).

Contrary to our predictions, we did not find that the difference between canopy and understory plants was due to the well-documented shade tolerance tradeoff. Shade tolerance determined neither the strength or presence of negative density dependence nor the effect of disturbance. McCarthy-Neumann and Kobe (2008) suggest that there is a negative correlation between negative density-dependent mortality and shade tolerance (common in understory species). Because negative density dependence does not operate in shade tolerant species, it may exaggerate differences in shade tolerance (McCarthy-Neumann & Kobe 2008, McCarthy-Neumann & Ibanez 2013). This exaggerated shade-tolerance spectrum may maintain diversity as no species is competitively dominant in shifting light conditions (Denslow 1980, Kobe 1999, Clark et al. 2003, Kobe & Vriesendorp 2011, McCarthy-Neumann & Ibanez 2013). We, however, found strong evidence for

negative density dependence in shade tolerant species unless those species were in the understory suggesting that temperate understory species do not adhere to this pattern.

Our results may differ from other studies on the decrease in negative density dependence with increasing shade tolerance for several reasons. First, only McCarthy-Neumann & Ibanez (2011) report results from temperate tree species. While negative density dependence is well documented in the temperate zone, little evidence suggests that it results in diversity maintenance (Barry & Schnitzer 2016, Barry & Schnitzer in review, Barry et al. in prep). In fact, in the temperate zone disturbance may be more compelling as a hypothesis for the maintenance of woody plant species diversity (Royo et al. 2010, Nuttle et al. 2013, Thom & Seidl 2015, Barry et al. in prep). Furthermore, McCarthy-Neumann and Ibanez (2011) used tree species alone which demonstrate a wide variety of shade tolerances but did not include understory species which are almost entirely shade tolerant. Second, no study to date in the temperate zone has examined the differences in negative density dependence with shade tolerance at the community level. Indeed, few studies in temperate species examined negative density dependent mortality outside of seedling mortality dynamics (but see Hille Ris Lambers et al. 2002, Zhu et al. 2015, Barry & Schnitzer in review). Negative density dependent mortality at the seedling level may only influence juvenile community composition and have little effect at broader demographic scales (Zhu et al. 2015). By using spatial point pattern analysis, we integrate negative density dependence across life history. Integrating the effects of this mechanism across the life history of individuals in the community provides new insight into whether this process drives total community composition.

In spite of their differences with regards to negative density dependence, canopy plants and understory plants experienced similar effects whether disturbance was from canopy gap formation or fire. Both canopy gap formation and fire resulted in a random distribution of plants throughout plots. Conversely, shade tolerant species were overdispersed in canopy gaps and were clustered when burned unless vertebrate herbivores were excluded (Figure 4.2c, d, e, f, g). Shade intolerant species were clustered in both disturbance regimes (Figure 4.2c, d, e, f, g). Furthermore, the relative density of shade intolerant species was significantly higher in 3 out of 4 fire treatments (Table 4.2). These findings suggest that fire interacts in a unique manner with the shade tolerance spectrum. Royo et al. (2010) found that shrub richness (and indeed total diversity) was increased significantly by burning and only marginally by the addition of canopy gaps. Nowacki and Abrams (2008) suggest that fire may be unique in its effects on forests particularly in forests where fire was suppressed for several generations. Nowacki and Abrams (2008) suggest that without fire, shade tolerant species proliferate in spite of the continued presence of canopy gaps while shade intolerant species are outcompeted. This pattern of reduced competitive ability for shade-intolerant species begins a cycle of fire deterrence through ecosystem change by shade-tolerant species. In our forests, where fire was suppressed for 80-100 years prior to the establishment of this experiment, the reintroduction of fire for shade tolerant species resulted in reestablishment as predicted by Nowacki and Abrams (2008, see also Abrams 1992). These results indicate that fire may provide unique diversity maintenance services for shade intolerant plants.

How negative density dependence, disturbance, and herbivory interact with life history strategy is crucial to our understanding of the maintenance of diversity in

temperate species. Our study provides evidence that a single life-history trade off (shade tolerance) is not as important for plant diversity maintenance as a suite of interacting trade-offs that result in the location within the vertical structure of a forest at maturity. Shade tolerance may determine interactions within these coarse groups but not between. Furthermore, there is now overwhelming evidence that disturbance is crucial for maintaining temperate woody plant diversity. Additionally, fire may be critical for the maintenance of diversity of shade-intolerant species. The sum-total of these results suggest that focusing on a single mechanism within a life history group or even a single type of disturbance is insufficient for understanding the maintenance of diversity in temperate forests.

Table 4.1: Total model results for Analysis of Variance of each of the dependent variables against treatment. Individual treatment results presented in Table 2. Statistically significant results ($p < 0.05$) presented in italics.

Dependent variable	Degrees of Freedom	Adjusted R²	F Stat	P value
Relative density of intermediately tolerant species	7,25	0.1472	1.789	0.134
Relative density of shade tolerant species	7,25	0.0039	1.018	0.4431
<i>Relative density of shade intolerant species</i>	<i>7,25</i>	<i>0.3718</i>	<i>3.706</i>	<i>0.0070</i>
Relative density of canopy individuals	7, 25	-0.1138	0.5331	0.8011
Relative density of understory individuals	7,25	-0.1138	0.5331	0.8011
Relative proportion of species richness contributed by understory	7,25	-0.0069	0.9684	0.475
Relative proportion of species richness contributed by overstory	7,25	-0.0079	0.9639	0.478
Total stem density	7, 25	0.0613	1.299	0.2915
Number of singletons (only member of the species in a plot)	7, 25	-0.1099	0.5475	0.7903

Table 4.2: Results from mixed effects analysis of variance using “Site” as a random effect for each individual treatment with each of the dependent variables. Significant interactions presented in italics.

Dependent Variable	Treatment	Standard Error	Degrees of Freedom	T value	P value
Total stem density	Fence	22.96	22.56	1.704	0.102
Total stem density	Fence + Gap	55.36	22.79	1.636	0.116
Total stem density	Fire	29.07	22.13	1.341	0.193
Total stem density	Fire + Fence	29.48	23.2	0.541	0.594
Total stem density	Fire + Fence + Gap	29.48	23.2	0.541	0.594
Total stem density	Fire + Gap	27	23.58	1.792	0.086
<i>Total stem density</i>	<i>Gap</i>	<i>23.9</i>	<i>22.8</i>	<i>2.81</i>	<i>0.01</i>
Relative density of intermediately shade tolerant individuals	Fence	0.09518	17.408	1.127	0.27486
Relative density of intermediately shade tolerant individuals	Fence + Gap	0.14007	18.644	-0.523	0.6074
Relative density of intermediately shade tolerant individuals	Fire	0.12074	16.26	-1.839	0.08421
Relative density of intermediately shade tolerant individuals	Fire + Fence	0.12172	20.343	-0.534	0.59891
Relative density of intermediately shade tolerant individuals	Fire + Fence + Gap	0.14157	24.146	-0.798	0.43284
Relative density of intermediately shade tolerant individuals	Fire + Gap	0.11128	21.314	-1.793	0.08716
Relative density of intermediately shade tolerant individuals	Gap	0.09	18.206	-0.809	0.429

Relative density of shade intolerant individuals	Fence	0.132516	22.496	-0.071	0.94403
Relative density of shade intolerant individuals	Fence + Gap	0.195439	22.578	1.335	0.19516
<i>Relative density of shade intolerant individuals</i>	<i>Fire</i>	<i>0.167478</i>	<i>22.131</i>	<i>3.527</i>	<i>0.00188</i>
Relative density of shade intolerant individuals	Fire + Fence	0.17051	22.847	1.409	0.17237
<i>Relative density of shade intolerant individuals</i>	<i>Fire + Fence + Gap</i>	<i>0.2014</i>	<i>24.135</i>	<i>2.799</i>	<i>0.00993</i>
<i>Relative density of shade intolerant individuals</i>	<i>Fire + Gap</i>	<i>0.156487</i>	<i>23.243</i>	<i>3.626</i>	<i>0.0014</i>
Relative density of shade intolerant individuals	Gap	0.138015	22.667	1.779	0.08867
Relative density of shade tolerant individuals	Fence	0.1575	23.086	-0.659	0.4162
Relative density of shade tolerant individuals	Fence + Gap	0.232	23.353	-0.777	0.4451
Relative density of shade tolerant individuals	Fire	0.1996	22.706	-1.842	0.0786
Relative density of shade tolerant individuals	Fire + Fence	0.2019	23.743	-0.914	0.3699
Relative density of shade tolerant individuals	Fire + Fence + Gap	0.2359	24.727	-1.769	0.0892
Relative density of shade tolerant individuals	Fire + Gap	0.1848	24.031	-1.974	0.0599
Relative density of shade tolerant individuals	Gap	0.1638	23.303	-0.962	0.3462
Relative density of canopy individuals	Fence	0.152	23.094	-0.225	0.824

Relative density of canopy individuals	Fence + Gap	0.2240	23.324	0.045	0.965
Relative density of canopy individuals	Fire	0.1925	22.725	-0.554	0.585
Relative density of canopy individuals	Fire + Fence	0.1950	23.686	1.309	0.2032
Relative density of canopy individuals	Fire + Fence + Gap	0.2281	24.687	0.127	0.9000
Relative density of canopy individuals	Fire + Gap	0.1784	23.982	0.284	0.778
Relative density of canopy individuals	Gap	0.158	23.298	-0.142	0.888
Relative density of understory individuals	Fence	0.1520	23.094	0.225	0.824
Relative density of understory individuals	Fence + Gap	0.2240	23.324	-0.045	0.965
Relative density of understory individuals	Fire	0.1925	22.725	0.554	0.585
Relative density of understory individuals	Fire + Fence	0.1950	23.686	-1.309	0.203
Relative density of understory individuals	Fire + Fence + Gap	0.2281	24.687	-0.127	0.900
Relative density of understory individuals	Fire + Gap	0.1784	23.982	-0.284	0.779
Relative density of understory individuals	Gap	0.158	23.298	0.142	0.888
Proportion of species richness contributed by canopy species	Fence	0.09132	25.000	-0.294	0.771
Proportion of species richness contributed by canopy species	Fence + Gap	0.13402	25.000	-0.701	0.490
Proportion of species richness contributed by canopy species	Fire	0.11606	25.000	-0.247	0.807

Proportion of species richness contributed by canopy species	Fire + Fence	0.11606	25.000	-0.271	0.788
<i>Proportion of species richness contributed by canopy species</i>	<i>Fire + Fence + Gap</i>	<i>0.13402</i>	<i>25.000</i>	<i>-2.166</i>	<i>0.040</i>
Proportion of species richness contributed by canopy species	Fire + Gap	0.1060	25.000	-1.501	0.146
Proportion of species richness contributed by canopy species	Gap	0.095	25.000	-0.787	0.439
Proportion of species richness contributed by understory species	Fence	0.0768	25.000	1.143	0.264
Proportion of species richness contributed by understory species	Fence + Gap	0.1128	25.000	0.842	0.408
Proportion of species richness contributed by understory species	Fire	0.0977	25.000	0.290	0.774
Proportion of species richness contributed by understory species	Fire + Fence	0.0977	25.000	0.324	0.748
<i>Proportion of species richness contributed by understory species</i>	<i>Fire + Fence + Gap</i>	<i>0.1128</i>	<i>25.000</i>	<i>2.127</i>	<i>0.043</i>
Proportion of species richness contributed by understory species	Fire + Gap	0.08920	25.000	1.766	0.089
Proportion of species richness contributed by understory species	Gap	0.079	25.000	0.919	0.366

Number of singletons (only member of the species in a plot)	Fence	0.7541	25	-0.505	0.618
Number of singletons (only member of the species in a plot)	Fence + Gap	1.1067	25	-1.506	0.145
Number of singletons (only member of the species in a plot)	Fire	0.9584	25	-1.043	0.307
Number of singletons (only member of the species in a plot)	Fire + Fence	0.9584	25	-1.043	0.307
Number of singletons (only member of the species in a plot)	Fire + Fence + Gap	1.1067	25	-0.602	0.552
Number of singletons (only member of the species in a plot)	Fire + Gap	0.8749	25	-1.333	0.194
Number of singletons (only member of the species in a plot)	Gap	0.7825	25	-1.065	0.297

Figure 4.1: Design schematic of one replicate of the “Fire, Fence, Gap” Experiment at the Fernow Experimental Forest and Monongahela National Forest reproduced with permission from Nuttle et al. 2013. At each of four replicate sites, half of the site was burned. On each half, eight 20 x 20 m plots were established. Four of these plots were randomly selected and surrounded with 2m tall wire large vertebrate exclosure fences. Four plots (two fenced, two unfenced) were selected for a canopy gap. In these plots, large central trees were girdled and allowed to fall out of the canopy naturally over 5 years.

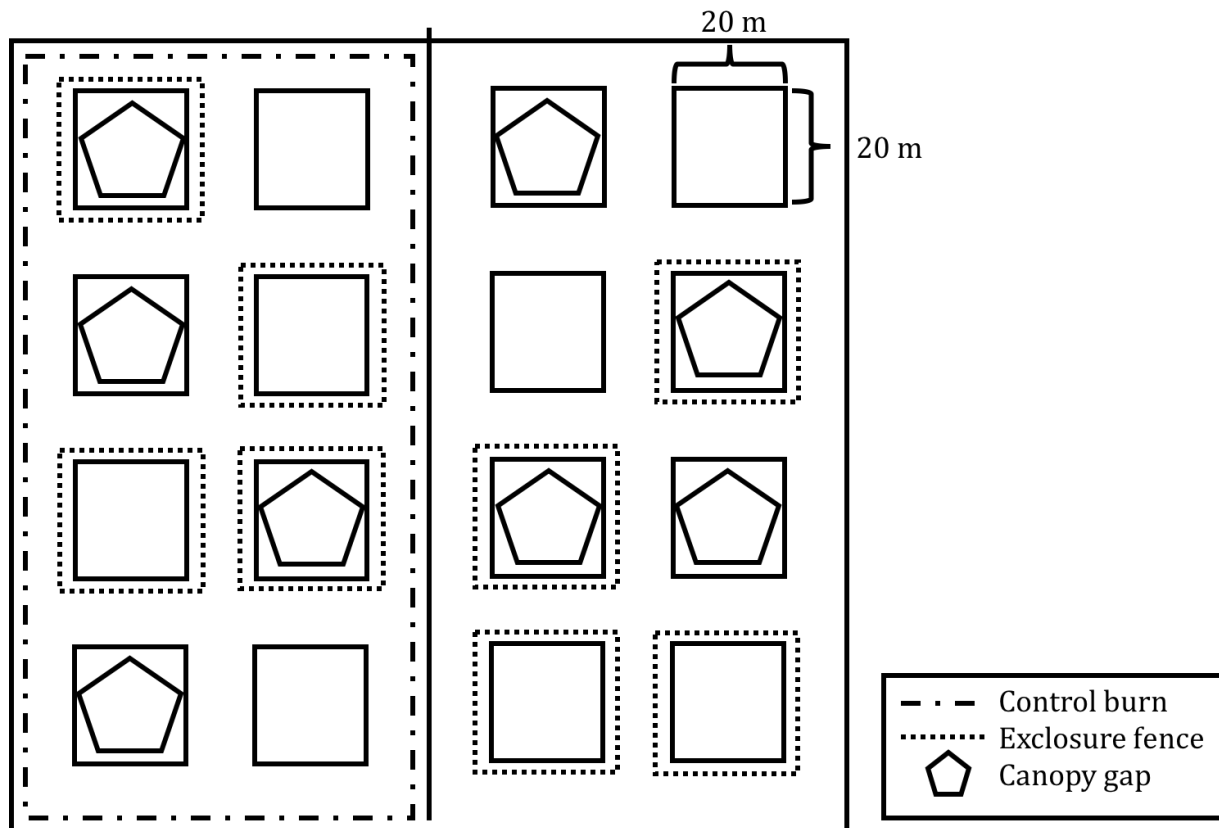
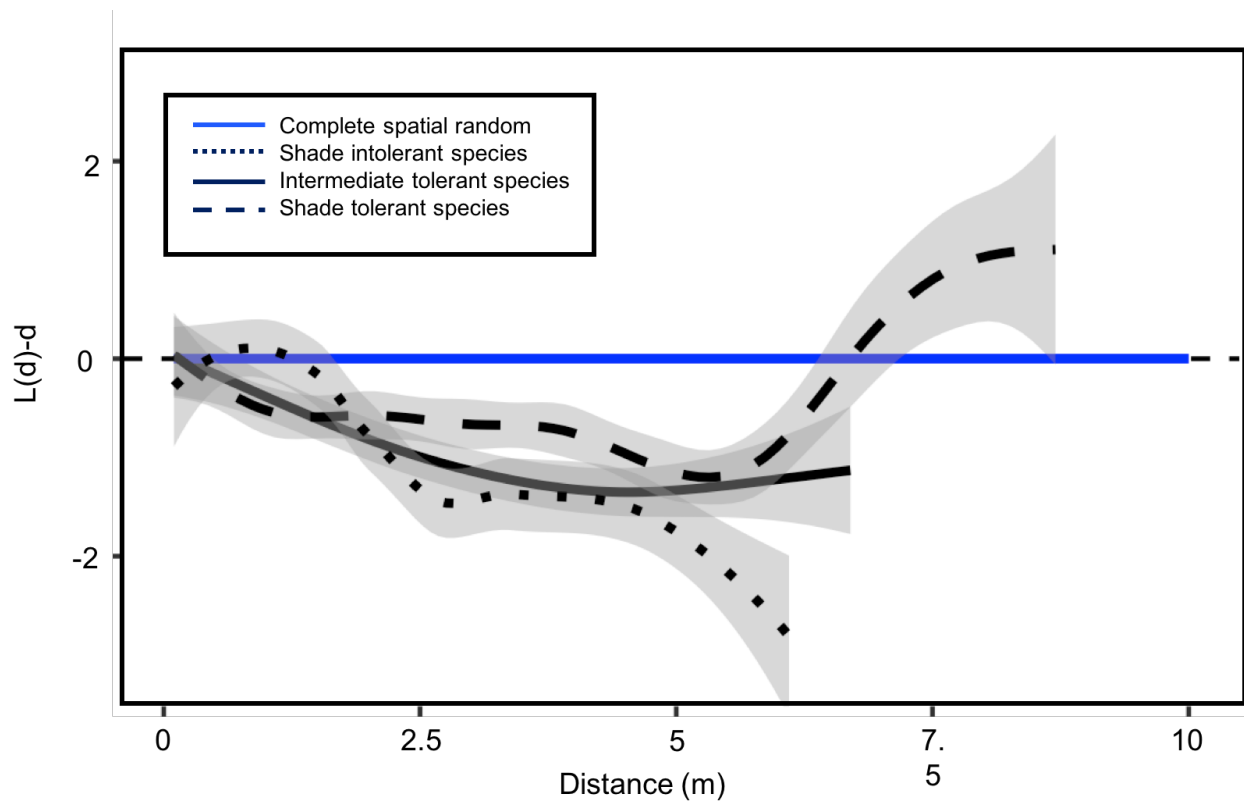
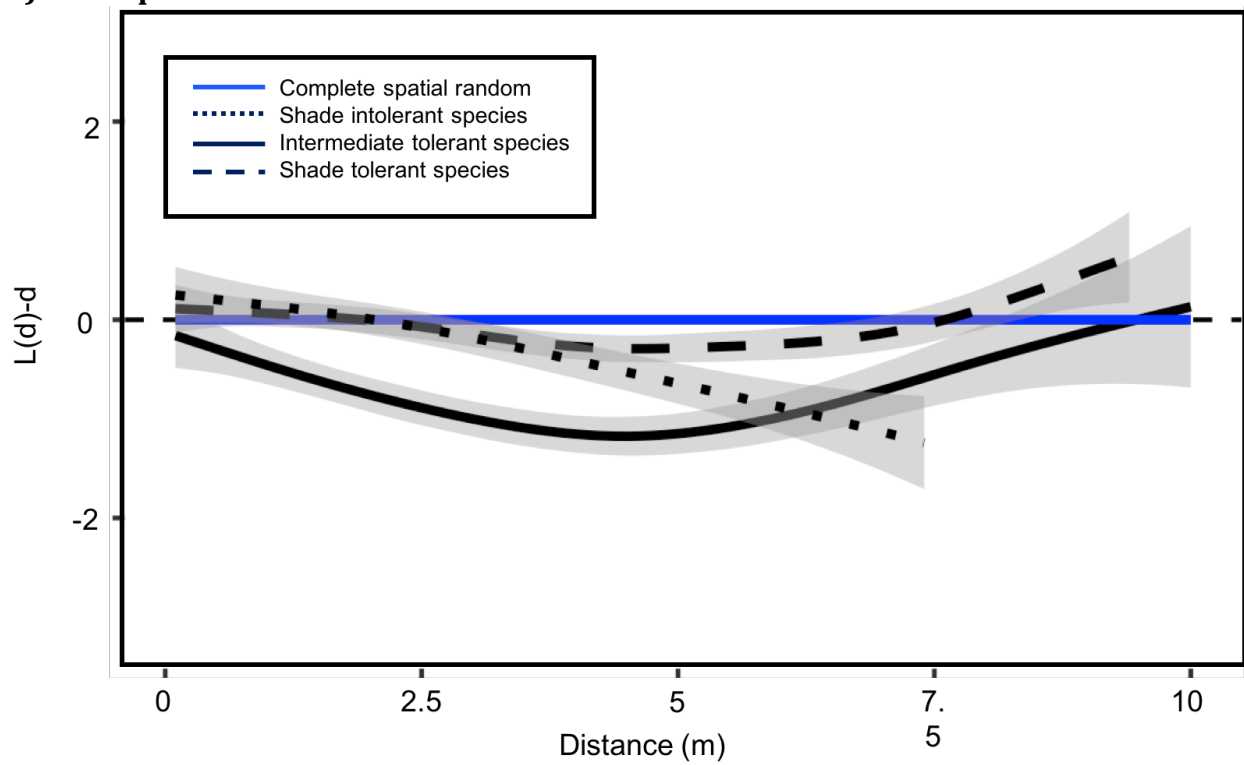


Figure 4.2: Comparison of pooled L functions for overstory and understory woody plants in the “Fire, Fence, Gap” Experiment at the Fernow Experimental Forest and Monongahela National Forest in central West Virginia.. a.) Overstory individuals were significantly inhibited in control plots but did not differ significantly from complete spatial random for the majority of distances. Understory plants were significantly clustered in control plots and overlapped significantly with complete spatial random for most distances in all fire plots with either an added canopy gap or deer exclosure fence. b.) Overstory individuals overlapped significantly with complete spatial random in all plots with added canopy gaps except when canopy gaps were combined with deer exclosure fences. Similarly, understory plants were clustered in control plots but their spatial patterns significantly overlapped with complete spatial random in plots with added canopy gaps with the exception of an added canopy gap with a deer exclosure fence. c.) Removing vertebrate herbivores resulted in canopy species that were significantly more clustered but did not have a significant effect on understory species. Gray shaded regions represent bootstrapped 95% confidence intervals. Blue shaded regions represent bootstrapped 95% acceptance intervals for complete spatial random.

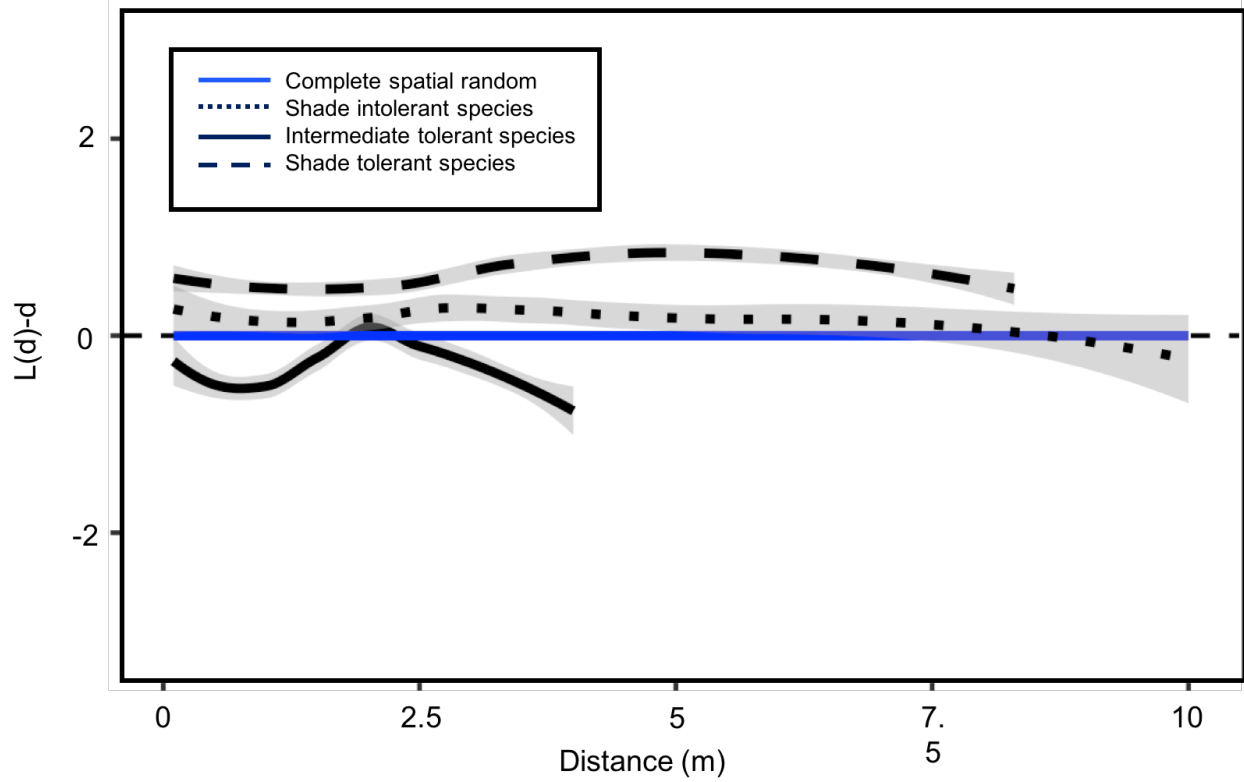
a.) Control plots



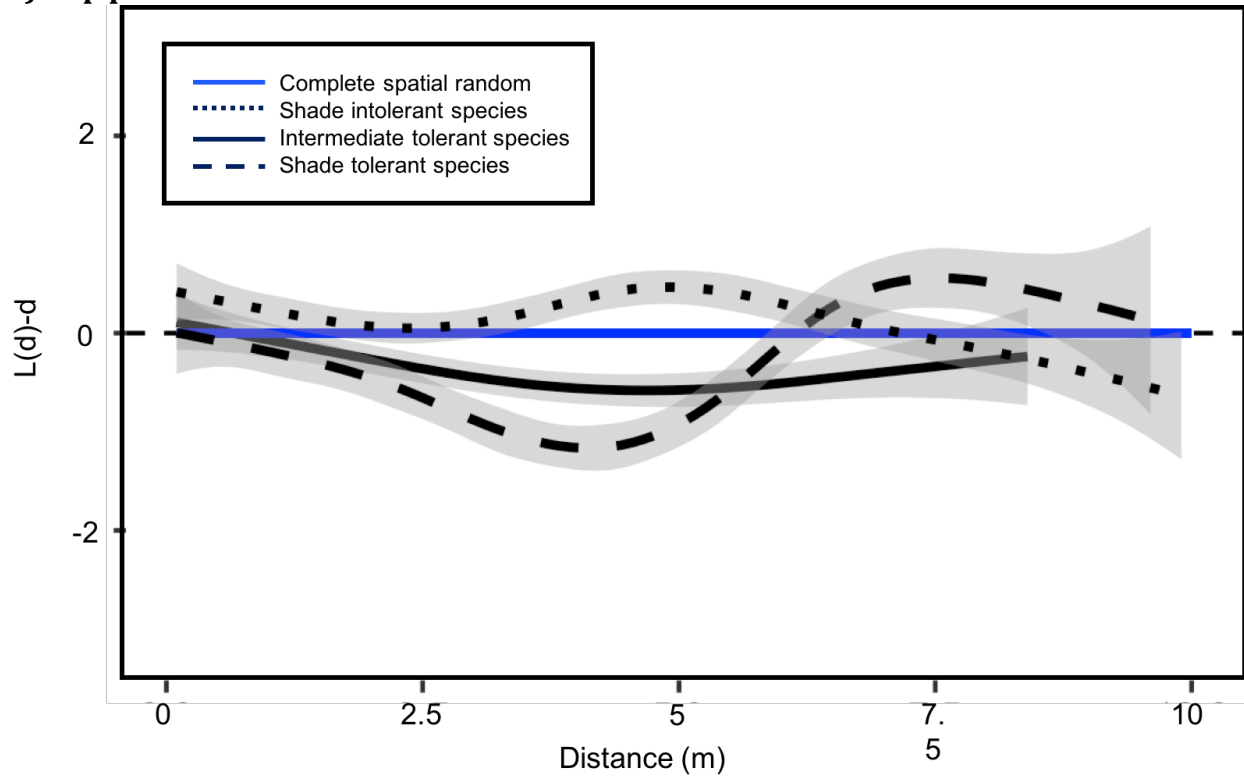
b.) Fence plots



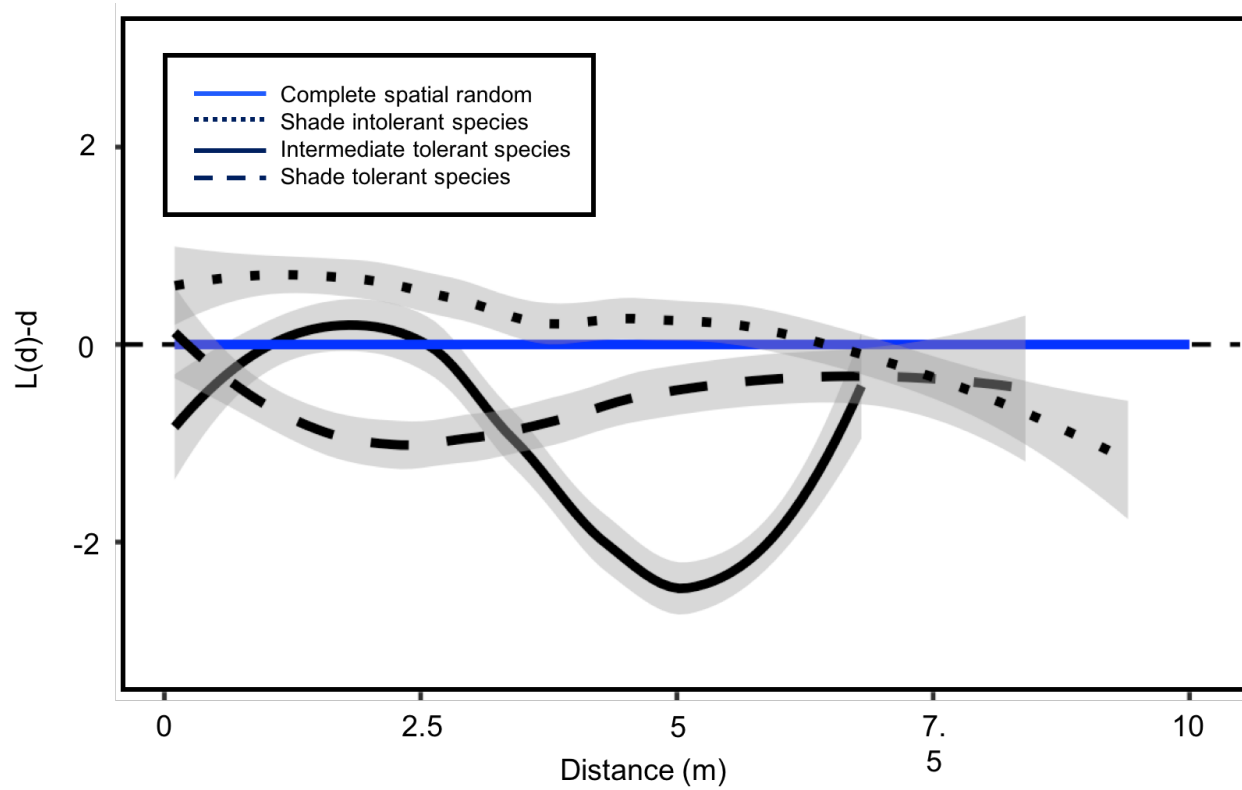
c.) Fire plots



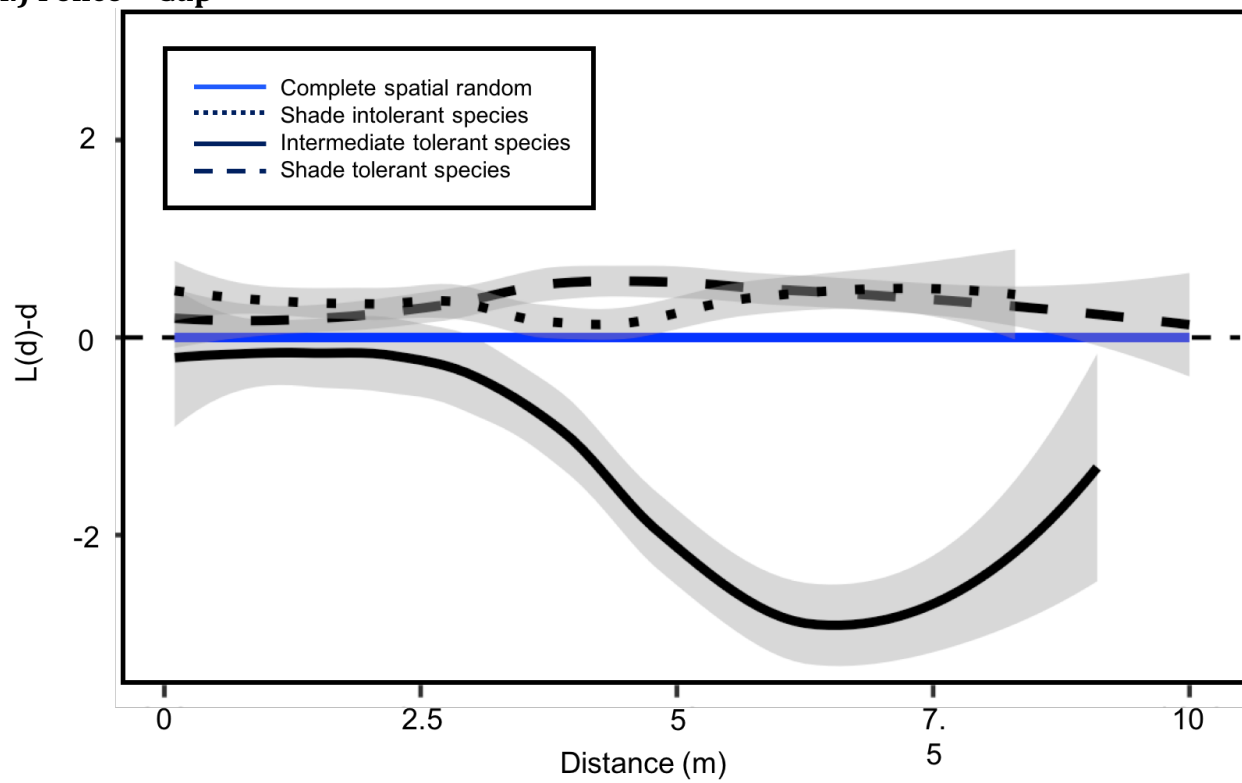
d.) Gap plots



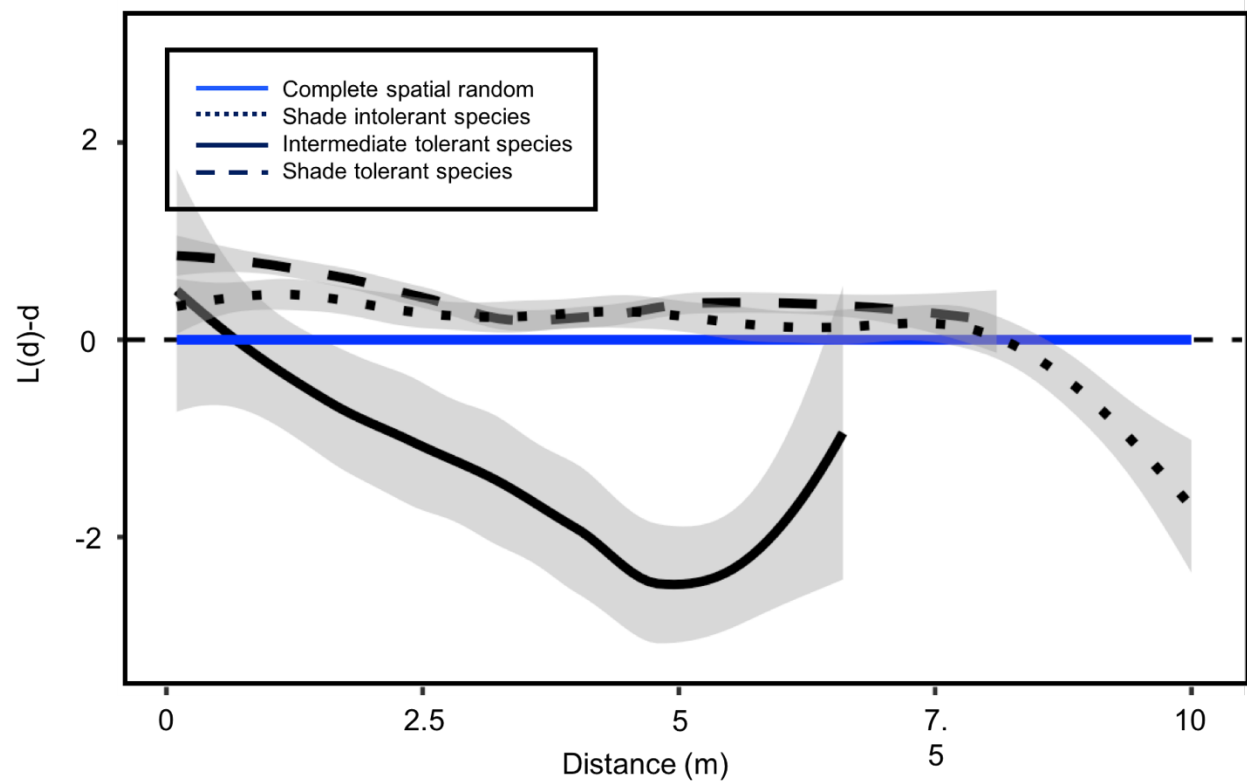
e.) Fence + Fire



f.) Fence + Gap



g.) Fire + Gap



h.) Fire + Fence + Gap

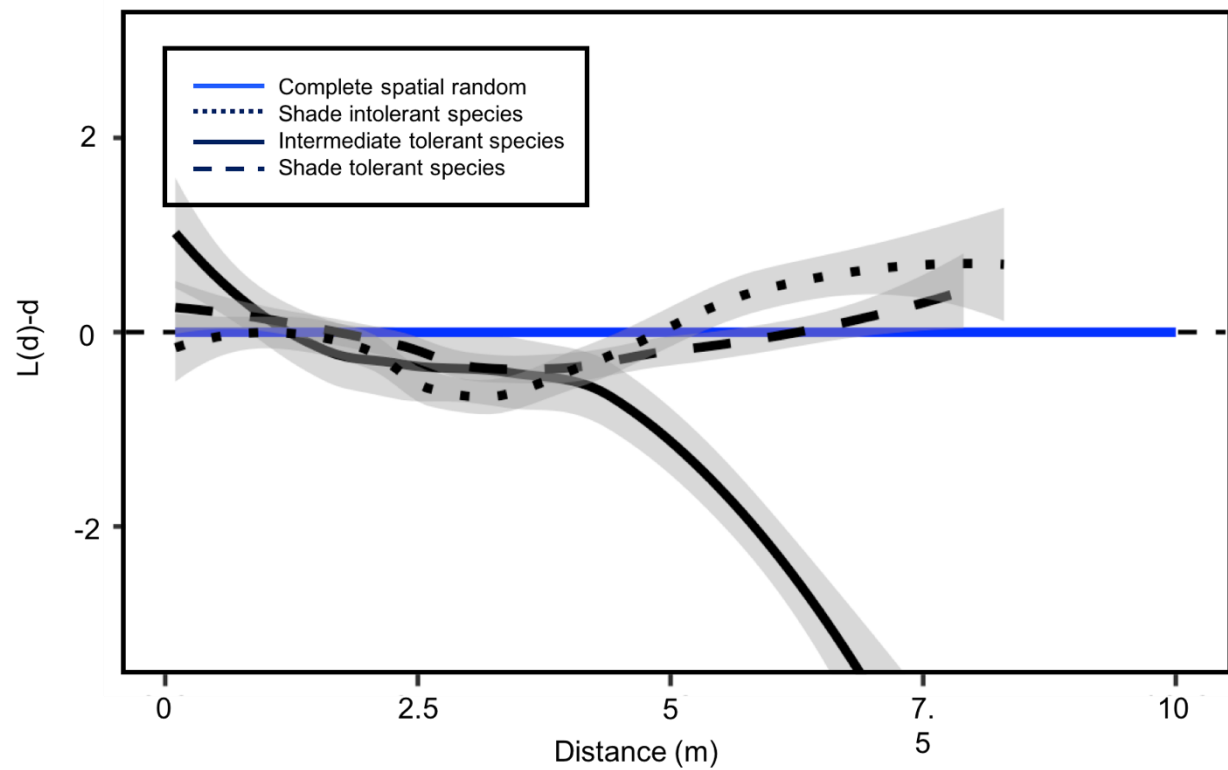
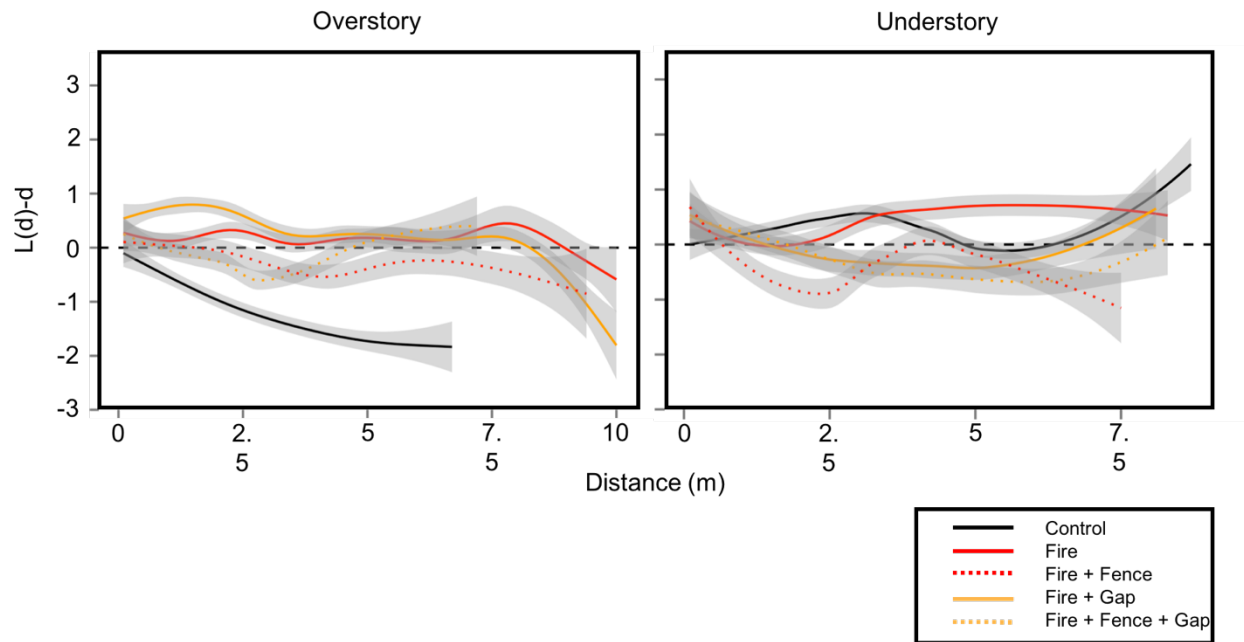
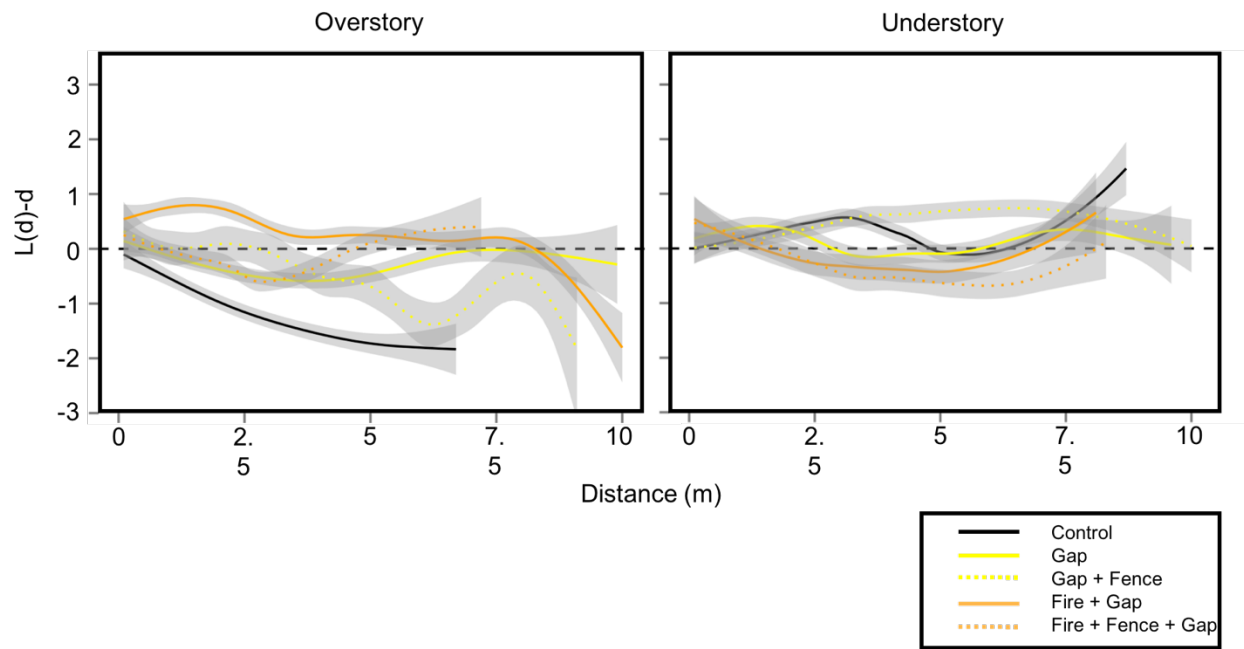


Figure 4.3. Comparison of pooled L functions for overstory and understory woody plants in the “Fire, Fence, Gap” Experiment at the Fernow Experimental Forest and Monongahela National Forest in central West Virginia.. a.) Overstory individuals were significantly inhibited in control plots but did not differ significantly from complete spatial random for the majority of distances. Understory plants were significantly clustered in control plots and overlapped significantly with complete spatial random for most distances in all fire plots with either an added canopy gap or deer exclosure fence. b.) Overstory individuals overlapped significantly with complete spatial random in all plots with added canopy gaps except when canopy gaps were combined with deer exclosure fences. Similarly, understory plants were clustered in control plots but their spatial patterns significantly overlapped with complete spatial random in plots with added canopy gaps with the exception of an added canopy gap with a deer exclosure fence. c.) Removing vertebrate herbivores resulted in canopy species that were significantly more clustered but did not have a significant effect on understory species. Gray shaded regions represent bootstrapped 95% confidence intervals. Blue shaded regions represent bootstrapped 95% acceptance intervals for complete spatial random.

a.)



b.)



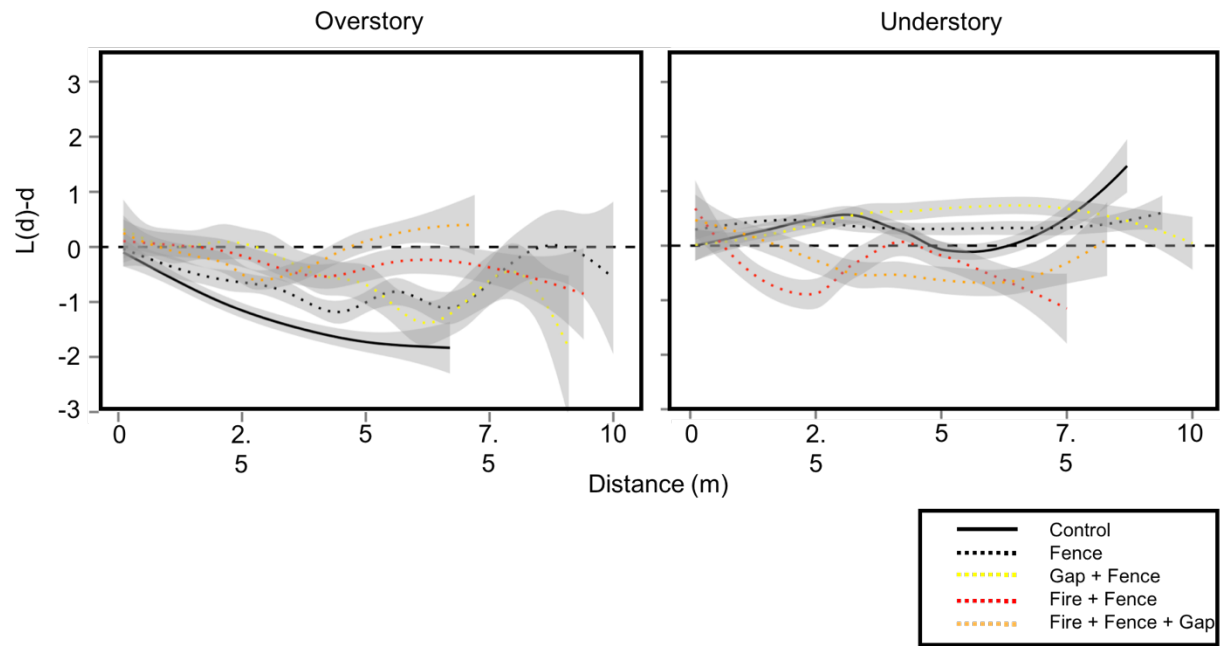
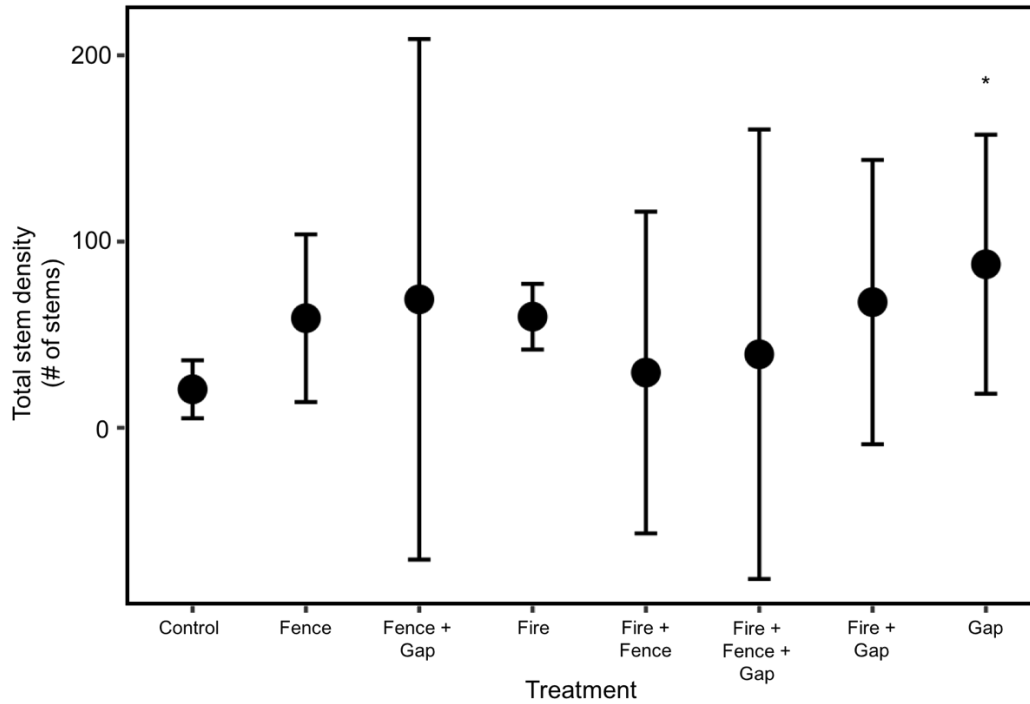


Table 4.S1: List of all species used in all analyses and their classifications and sample sizes.

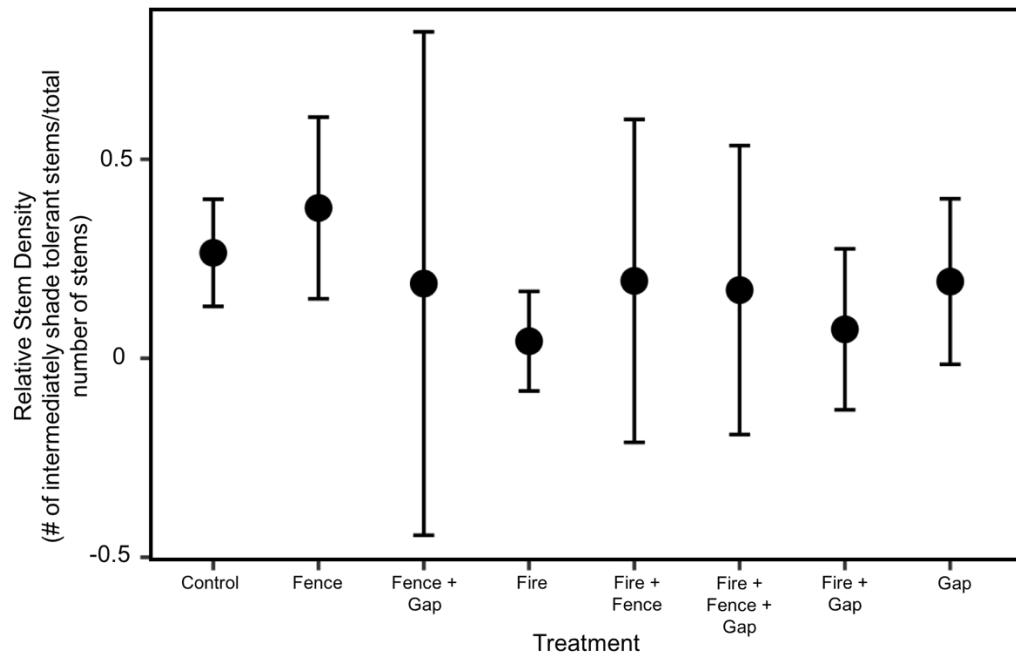
Species name	Common name	Growth form	Tolerance level	N
<i>Acer pensylvanicum</i>	Striped maple	Understory	Tolerant	448
<i>Acer rubrum</i>	Red maple	Canopy	Intermediate	156
<i>Acer saccharum</i>	Sugar maple	Canopy	Tolerant	94
<i>Aralia spinosa</i>	Devil's walking stick	Understory	Intolerant	5
<i>Betula lenta</i>	Black birch	Canopy	Intolerant	26
<i>Carya glabra</i>	Mockernut hickory	Canopy	Intermediate	405
<i>Carya ovata</i>	Shagbark hickory	Canopy	Intermediate	10
<i>Castanea dentata</i>	American chestnut	Canopy	Intolerant	7
<i>Fagus grandifolia</i>	American beech	Canopy	Tolerant	38
<i>Fraxinus americana</i>	Green ash	Canopy	Intolerant	5
<i>Hamamelis virginiana</i>	Witch hazel	Understory	Intermediate	22
<i>Liriodendron tulipifera</i>	Tuliptree	Canopy	Intolerant	174
<i>Magnolia acuminata</i>	Cucumber magnolia	Canopy	Intermediate	10
<i>Magnolia fraseri</i>	Fraser magnolia	Understory	Intermediate	30
<i>Nyssa sylvatica</i>	Black gum	Canopy	Tolerant	32
<i>Pinus strobus</i>	White pine	Canopy	Intermediate	4
<i>Prunus serotina</i>	Black cherry	Canopy	Intolerant	47
<i>Quercus alba</i>	White oak	Canopy	Intermediate	10
<i>Quercus prinus</i>	Chestnut oak	Canopy	NA	32
<i>Quercus rubra</i>	Red oak	Canopy	Intermediate	156
<i>Sassafras albidum</i>	Sassafras	Understory	Intolerant	98
<i>Viburnum acerifolium</i>	Maple-leaf viburnum	Understory	Tolerant	29

Figure 4.S1: Means of dependent variables plotted against treatment for all plots at the Monongahela National Forest and the Fernow Experimental Forest. All error bars represent 95% confidence intervals. Asterisks indicate results that are significantly different from the control.

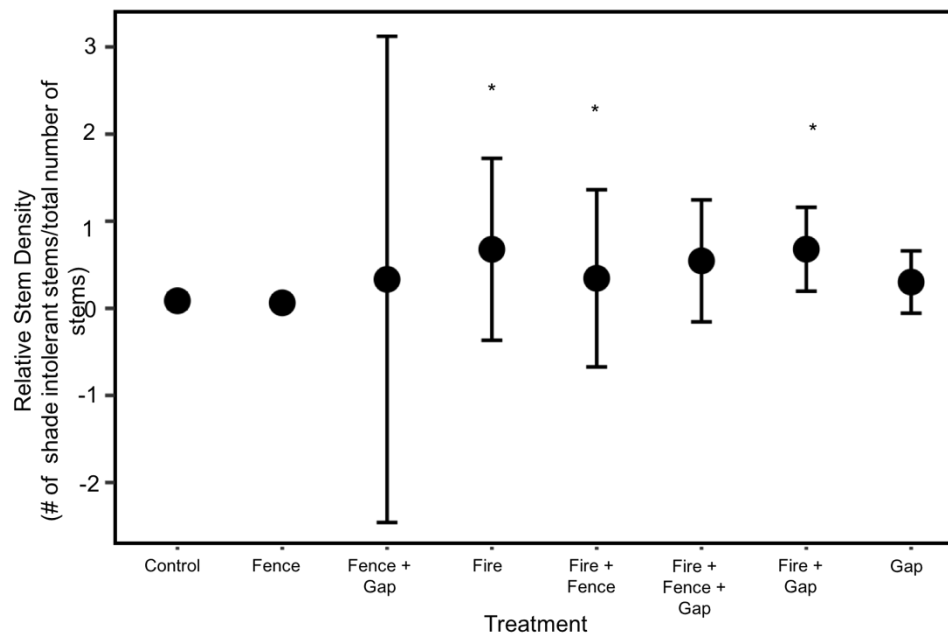
a.) Total stem density



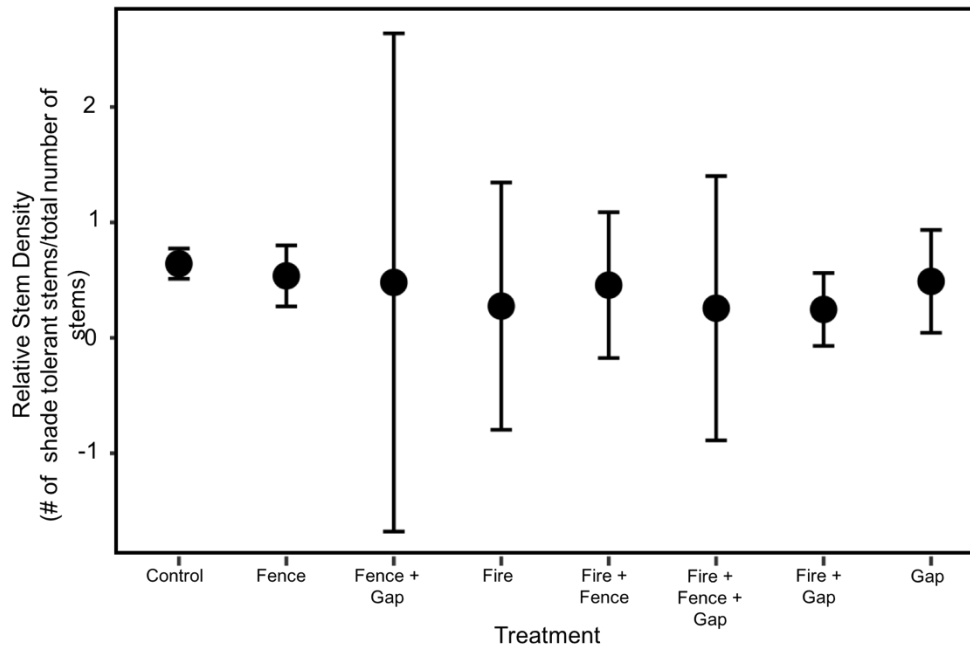
b.) Relative density of intermediately shade tolerant individuals



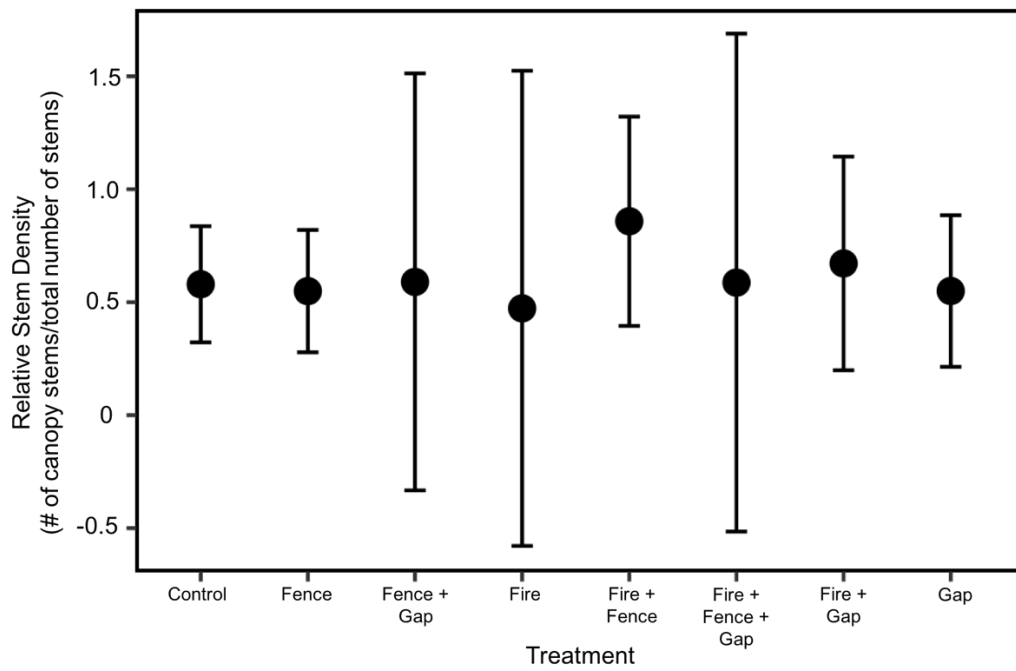
c.) Relative density of shade intolerant individuals



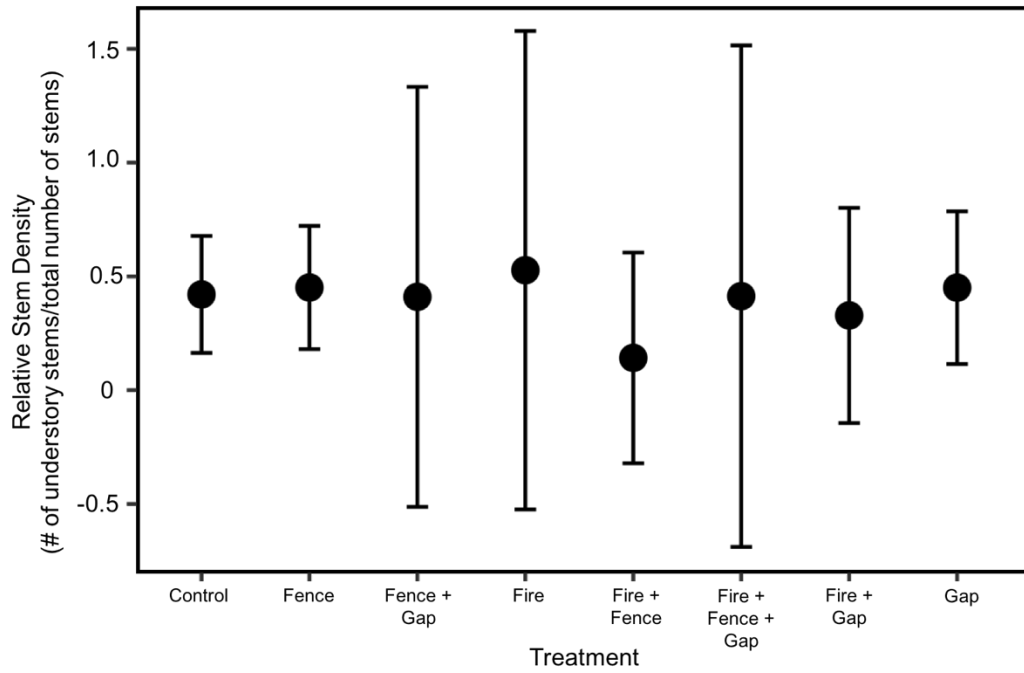
d.) Relative density of shade tolerant individuals



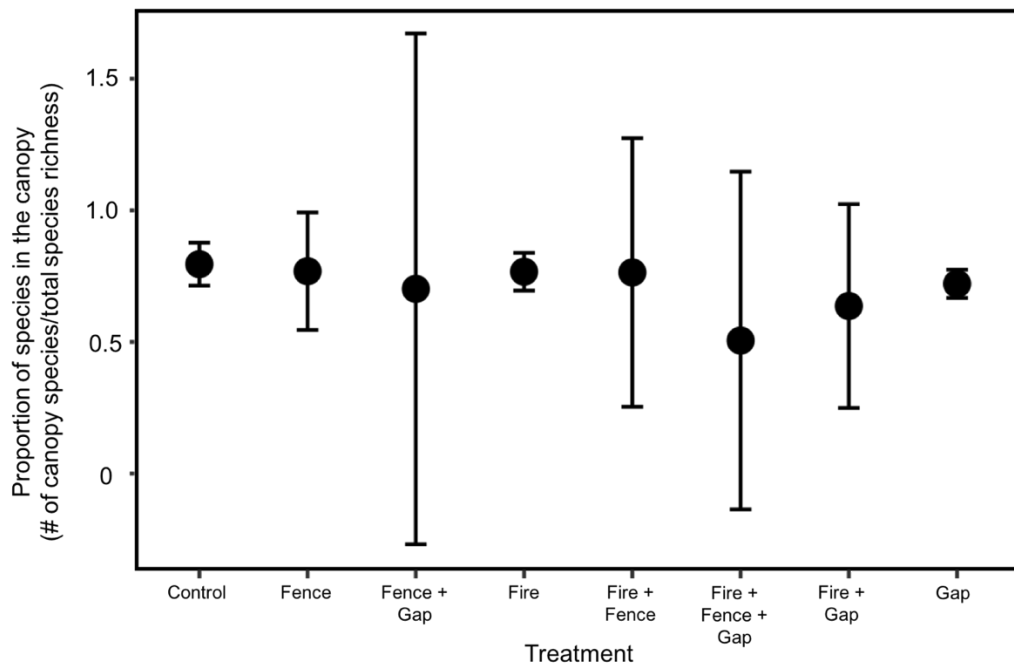
e.) Relative density of canopy individuals



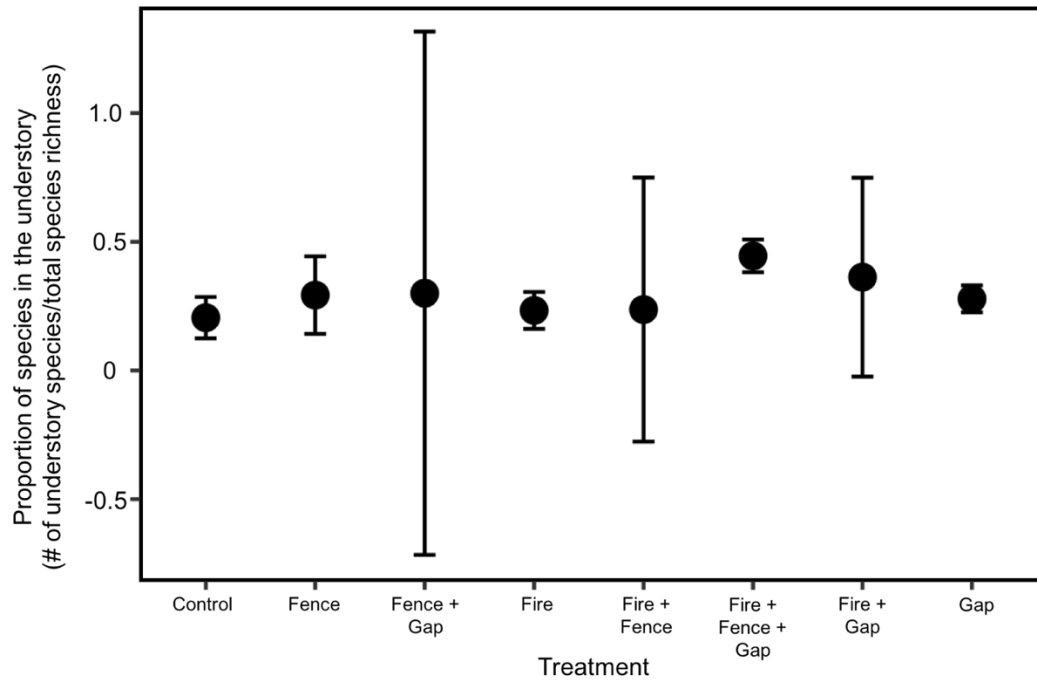
f.) Relative density of understory individuals



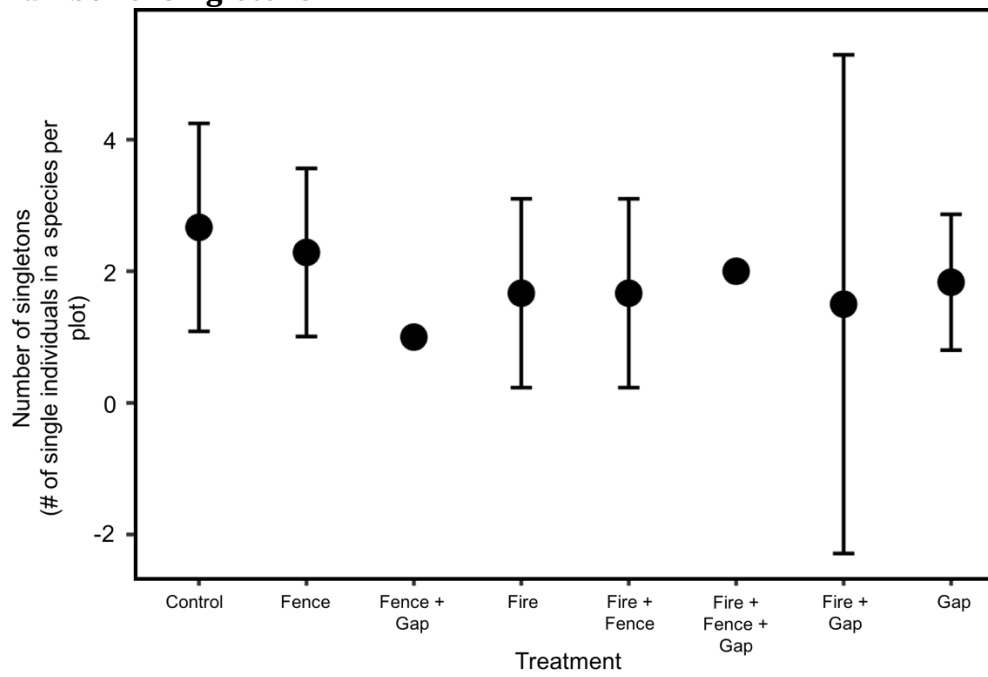
g.) Proportion of species in the canopy



h.) Proportion of species in the understory



i.) Number of singletons



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EDUCATION.

University of Wisconsin-Milwaukee	Milwaukee, WI	09/2010-Present
Ph.D. Candidate		Biological Sciences

Dissertation Title: "Are we missing the forest for the trees? Quantifying the maintenance of diversity in temperate deciduous forests"

Rutgers, the State University of NJ	New Brunswick, NJ	09/2005 – 05/2009
Cook College		
B.S.	Environmental Policy, Institutions and Behavior – U.S. Natural Resources	

AWARDS RECEIVED.

Riveredge Nature Center Student Research Symposium – Best Graduate Oral Presentation	2015
Carnegie Museum of Natural History – Rea Fellowship for Graduate Student Research	2014 & 2015
University of Wisconsin-Milwaukee Biological Sciences Symposium - Outstanding Graduate Student Presentation – Ecology	2014
Ivy Balsam-Milwaukee Audubon Society Award	2014
Sci-fund crowdfunding	2012
University of Wisconsin-Milwaukee – Department of Biological Sciences Ruth Walker Travel Award	2011
Smithsonian Tropical Research Institute – Short Term Fellowship	2011
University of Wisconsin-Milwaukee – Center for Latin American and Caribbean Studies Travel Award	2011
University of Wisconsin-Milwaukee – Chancellor's Graduate Student Award	2010-present
Rutgers University - George F. Clark Academic Excellence and Service Award	2009
Rutgers University – Alpha Zeta/School of Environmental and Biological Sciences Student of the Year Award	2006-2008
Rutgers University – Merit Award for Excellence in Academics	2007-2009
Edward J. Bloustein Distinguished Scholar Award	2006

PUBLICATIONS.

- Barry, K.E., & Schnitzer, S.A.** Maintenance of plant species diversity in forest ecosystems. In: *Plant Biodiversity: Present Situation and Future Scenario*. Editors: A.A. Ansari & S. S. Gill. CAB International. Expected publication date: April, 2016.
- Young, A.M., **Barry, K.E., & Schnitzer, S.A.** Top-down versus bottom up control of *Theobroma cacao*. In press. *Tropical Agriculture*.
- Barry, K.E., Schnitzer, S.A., van Breugel, M. & Hall, J.S.** (2015). Rapid liana colonization and community development along a secondary forest chronosequence. *Biotropica*. 47(6): 672–680.
- Waring, B., Alvarez-Cansino, L., **Barry, K.E.,** Becklund, K., Dale, S., Gei, M., Keller, A., Lopez, O., Markesteijn, L., Mangan, S., Riggs, C., Rodriguez-Ronderos, M.E., Segnitz, M., Schnitzer, S.A., & Powers, J. (2015). Pervasive and strong effects of plants on soil chemistry: a meta-analysis of individual plant ‘Zinke’ effects. *Proceedings of the Royal Society B*. 282: 20151001.

In review:

- Barry, K.E., & Schnitzer, S.A.** Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests. Submitted: 11/4/15. *Ecology*.

In preparation:

- Barry, K.E., Schnitzer, S.A., & Carson, W.P.** Impacts of disturbance on patterns of diversity maintenance in temperate deciduous forest plant communities.
- Barry, K.E., Schnitzer, S.A., & Carson, W.P.** Functional diversity and functional trait shift as a result of complex disturbance in eastern deciduous forests.
- Barry, K.E., Wright, A.J., Strini, J.W., Yang, K.A., Lauko, I.G., Schnitzer, S.A., Reich, P.B., & Pinter, G.A.** The effects of spatial scale on the plant diversity-productivity relationship.
- Barry, K.E., Schnitzer, S.A., & Carson, W.P.** Differential effects of disturbance on overstory and understory plants in temperate deciduous forest plant communities.
- Wright, A.J., **Barry, K.E.,** Pinter, G.A., Schnitzer, S.A., & Eisenhauer, N. Biomass sampling in biodiversity experiments.

PRESENTATIONS.

- Barry, K.E. & Schnitzer, S.A.** *Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests.* 11/14/15. Student Research Symposium. Riveredge Nature Center. Saukville, WI.
- Barry, K.E. & Schnitzer, S.A.** *Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests.* **Invited.** 11/10/15. University of Pittsburgh. Advanced Ecology Seminar Series.
- Barry, K.E. & Schnitzer, S.A.** *Are we missing the forests for the trees? Spatial trends in diversity of overstory and understory temperate vascular plants.* 8/13/15. Contributed Oral Session, Ecological Society of America Annual Meeting. Baltimore, MD.

- Barry, K.E.** *Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests.* 4/24/15. University of Wisconsin-Milwaukee - Department of Biological Sciences Colloquium. Milwaukee, WI.
- Barry, K.E.** & Schnitzer, S.A. *Are we missing the forests for the trees? Quantifying the strength of negative density dependence in an understory plant community.* 4/25/14. University of Wisconsin-Milwaukee – Biological Sciences Symposium. Milwaukee, WI.
- Barry, K.E.** & Schnitzer, S.A. *Negative density dependence and the maintenance of temperate understory species diversity.* 11/9/2013. Riveredge Symposium. Riveredge Nature Center. Saukville, WI.
- Strini, J.W., Yang, K.A., Kruse, H., **Barry, K.E.**, Wright, A.J., Schnitzer, S.A., & Pinter, G.A. *The effects of spatial scale on the biodiversity-productivity relationship in a savannah ecosystem.* 11/18/2012. NIMBioS Annual Conference. Knoxville, TN.
- Hunt, A.A. **Barry, K.E.**, Carson, W.P., & Schnitzer, S.A. *The shift of plant characteristics in response to disturbance in a temperate deciduous forest.* 4/24/2015. University of Wisconsin-Milwaukee Undergraduate Research Symposium.
- Barry, K.E.**, Schnitzer, S.A., Van Breugel, M., & Hall, J.S. *Liana colonization and community development along a Neotropical secondary forest chronosequence.* 4/26/2011. University of Wisconsin-Milwaukee, Annual Biological Sciences Research Symposium.
- Baumhofer, E., Stunteback, J., **Barry, K.E.**, Meyer, G., & Pinter, G.A. *Patterns of bat emergence in a Southeastern Wisconsin hibernaculum.* 11/18/2012. NIMBioS Annual Conference. Knoxville, TN.
- Baumhofer, E., Stunteback, J., **Barry, K.E.**, Meyer, G., Pinter, G.A., & Lauko, I. *Patterns of bat emergence in a Southeastern Wisconsin hibernaculum.* 4/26/2011. University of Wisconsin-Milwaukee, Annual Biological Sciences Research Symposium.
- Tartaglia, E., **Barry, K.E.**, & Handel, S. *Strangers in the Night: Hawkmoth pollination in urban and less urban areas.* 2/19/10. Society for Ecological Restoration: Mid-atlantic Region, Annual conference.

Workshops:

- Barry, K.E.** *Spatial statistics in R. Invited.* 11/10/15. University of Pittsburgh.

TEACHING EXPERIENCE.

Teaching assistant, Department of Biological Sciences	University of Wisconsin-Milwaukee	09/2010-Present
Biological Sciences Mentor, Undergraduate Biological Mathematics Program	University of Wisconsin Milwaukee	09/2011-Present
Associate Ecologist, Center for Urban Restoration Ecology	Rutgers, the State University of NJ	05/2009-08/2010

Teaching assistant, Department
of Ecology, Evolution, and
Natural Resources

Rutgers, the State
University of NJ

09/2007-12/2009

Research assistant, Department
of Human Ecology

Rutgers, the State
University of NJ

02/2009-05/2009

SYNERGISTIC EXPERIENCE.

Reviewer:

Biotropica

Ecology

Journal of Ecology

Oecologia

Canadian Journal of Forest Research

Proceedings from the National Conference for Undergraduate Research

Membership in Professional Societies:

American Association of University Women

Torrey Botanical Society

Ecological Society of America – Early Career Ecologists & Statistical Ecology Sections

Graduate Women in Science – Omega Chapter