APPLYING MULTILEVEL LONGITUDINAL MODELS TO PLANT DEMOGRAPHIC PROCESSES: NOVEL INSIGHTS INTO THE LONG-TERM IMPACTS OF INVASIVE SPECIES AND OVERABUNDANT HERBIVORES

by

Nathan Linn Brouwer

B.S., Seattle Pacific University, 2002

Submitted to the Graduate Faculty of the

Kenneth P. Dietrich School of Arts and Sciences in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy, Biological Sciences

University of Pittsburgh

2015

UNIVERSITY OF PITTSBURGH

KENNETH P. DIETRICH SCHOOL OF ARTS AND SCIENCES

This dissertation was presented

by

Nathan Linn Brouwer

It was defended on

October 29, 2015

and approved by

Dr. Elizabeth Crone, Dept. of Biology, Tufts University

Dr. Nathaniel Morehouse, Dept. of Biological Sciences, University of Pittsburgh

Dr. Stephen Tonsor, Center for Biodiversity & Ecosystems, Carnegie Museum of Nat. History

Dissertation Co-Advisor: Dr. Jonathan Pruitt, Dept. of Biological Sciences, Unv. of Pittsburgh

Dissertation Co-Advisor: Dr. Susan Kalisz, Dept. of Ecology & Evolutionary Biology,

University of Tennessee

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Nathan Linn Brouwer, Ph.D.

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Long-term, multi-factor studies are necessary to understand the population-level impacts and relative importance of species interactions. Such experiments produce data that are rich in detail but challenging to analyse. In my dissertation I have investigated the population-level impacts of two interactions, allelopathy and herbivory, by applying longitudinal statistical models to long-term experimental data. These data were collected during a decade-long investigation of impacts of white-tailed deer (*Odocoileus virginianus*) and an allelopathic invader (*Alliaria petiolata*) on forest herbs and trees.

There is great concern about the impacts of overabundant deer, but little is known about how quickly forests respond when deer abundance is reduced. Using biennial survey data I modeled changes in sapling abundance after deer exclusion. I found that *Acer saccharum* (sugar maple) but not other species exhibited signs of recovery in <7 years, but changes were obscured by density declines near the end of the study, likely due to self-thinning. Using meta-analysis I determined that other studies observed desired changes typically after ~20 years. Few, however, carry out frequent surveys and therefore likely miss important processes such as thinning.

Invasive plants are also widely considered to be an ecological problem. Small-scale experiments have established that allelopathic invaders can negatively impact plant fitness. To determine if an allelopathic plant has population-level effects, I modeled the impacts of *Alliaria* removal on the herb *Maianthemum racemosum*. While *Alliaria* removal benefits *Maianthemum* vital rates, changes take >5 years to appear. Broadening the analysis to compare the effects of deer and *Alliaria* on two additional herbs, I found that *Alliaria* impacts multiples species and vital rates, and that at times its effects can be as detrimental as deer browse.

Combining the power of experiments with sophisticated statistics, I have shown that plant-plant and plant-animal interactions can be similar in magnitude. Without longitudinal data and appropriate models, we would not have been able to characterize the effects of deer on saplings, or *Alliaria* on understory herbs, instead concluding that deer exclusion was not impacting forest regeneration and *Alliaria* removal not improving plant vital rates.

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PREFACE

Numerous people have contributed to the succful completion of my dissertation. My academic committee provide all manner of support. My advisor, Dr. Susan Kalisz, provided a supportive, open environment to develop my ideas and skills. She also concienved and has kept running the Trillium Trail research project that provided that data for most of my work. My interim advisor Dr. Jonathan Pruitt provided much-needed support during the completion of this dissertation and Drs. Nate Morehouse and Steve Tonsor were supportive and helpful committee members throughout the process. I thank my outside committee member, Dr. Elizabeth Crone, for her flexibility in scheduling meetings and her numerous publications that have influenced my ecological and statistical thinking. I'd also like to recognize my two ermitus committee members, Drs. Brian Traw and Mike Grabe.

Other Kalisz lab members have provided tremendous support over the last seven years. Dr. Alison Hale has generously shared input, encouragement, and a passion for *Maianthemum* ecology. Chris Heckel was a comrade in arms as we both honed our skills in *R* and wrestled with the complex – and frusting – ecology of long-lived plants. Dr. Rachel Spigler helped Susan steer the Trillium Trail project for two years and made many important contributions to the project in general as well as providing input on my work. Dr. Mason Heberling provided extremely valuable comments on several chapters and has generously shared an office with me during the final push of writing. Alani Grant and Eden Wellesley both have listened to practice talks and heard me curse R innumerable times, and shared the other adventures of graduate school; I thank them both for their great attitudes and friendship. Fellow graduate students, especially Mike Chips and Eric Griffin, have provided feedback over the years and their friendship is valued immensely.

This dissertation relies on data collected by dozens of undergrads and field technicans since 2003. Technical assistance in the field and at the computer was provided at various key stages by Will Benham, Monica Ruwdowski, Tim Park and Mia Waverk. Monica in particular helped with mounds of data cleaning, and Mia assisted with QA/QC of my meta-analysis.

I can't imagine completely this journey the last two years without the support of Tom and Shirley Wilson, who have provided many home-cooked meals and hours of baby sitting.

My mother-in-law Cindy Wilson has provided laughter, baby-sitting, and much needed encouragement and opportunities to have a life outside of academia. I can't thank you enough.

I owe more than I can imagine to my parents, Bud and Lorraine Brouwer. Thanks so much for setting me loose in the woods, taking me up into the mountains, and supporting me on every journey and adventure. The love of nature that inspires this work and the integrity I try to bring to my work were both learned from you.

Finally, this dissertation is dedicated to April and Zetta Brouwer. This dissertation bears my name but your love, support, kindness and laughter accompanied every thought in its formation and sentence in its writing. Thank you for the life we share. Abaraka baake.

1.0 THE NEED FOR LONG-TERM, LONGITUDINAL, AND DEMOGRAPHIC STUDIES INTO THE IMPORTANCE OF SPECIES INTERACTIONS

1.1 INTRODUCTION

A unifying interest of many ecologists is the role species interactions play in determining the distribution and abundance of organisms (Krebs 1972). Many of ecology's most enduring – and controversial (Peters 1981) – ideas, images, and metaphors involve interactions between species: trophic cascades and the green world hypothesis (Hairston *et al.* 1960, Paine 1980), keystone predators (Paine 1969), and herbivores caught between the "devil" of predation and the "deep blue sea" of plant defenses (Lawton and McNeill 1979).

Beginning with the first *Pisaster* sea star that Paine (1969) tossed into the Pacific, experimentation has been central to demonstrating the validity of these ecological principals. Since Paine (1969), there have been experiments on aquatic and marine trophic cascades from the scale of pitcher plants (Kneitel and Miller 2002) to entire lakes (Carpenter *et al.* 2001). When it was questioned whether the interactions that result in trophic cascades were much stronger in aquatic than terrestrial ecosystems, and therefore the idea was "all wet" (Strong 1992), further experimentation revealed the generality of cascades across biomes (Pace 1999, Estes *et al.* 2011). Questions inspired by the "green world" hypothesis have been addressed by experimentally manipulating herbivores and predators, from aphids and parasitoid wasps (Costamagna et al 2007) to elephants (Ford *et al.* 2014).

While observational approaches remain central to ecological understanding (Sagarin and Pauchard 2010), progress in an ecological sub-discipline is now often marked by transition from initial observational studies to increased experimentation, especially within a null-hypothesis framework (Diamond 1986). For example Williamson (1999) called for increased experimentation in invasive species ecology, which over the last decade has been met with increasingly experimental and mechanistic approaches (Stricker *et al.* 2015; Lowry *et al.* 2013).

Thanks to these experiments, ecologists have been able to confirm the ecological role of species interactions. The question ecologists now frequently face is not whether a given species interaction can be important, but when, where, and how often it is important (Maron and Crone 2006, Bolker 2005, Kikivide *et al.* 2011). That is, how often, when, and where does an interaction affect the distribution and abundance of organisms in the real world. Many experiments on species interactions are conducted at relatively small scales, over short time periods relative to the generation time of the organism, and focus on a subset of fitness components. Additionally, for plants, many experiments are conducted with seedlings grown from seed so that developmental conditions can be controlled. An essential route for understanding how species interactions play out in the real world is to scale experiments up to the messier realm of long-term population dynamics of multiple life stages of an organism (Maron *et al.* 2010, Goldberg and Scheiner 2001).

Similarly, many experiments on species interactions are necessarily focused on a specific interaction and remove the influence of other environmental factors or species interactions. To holistically understand a species interaction it therefore needs to be determined how important the focal interaction is (*sensu* Welden and Slausson 1986) relative to environmental variation and other species interactions (Kikvidze *et al.* 2011; e.g. von Euler *et al.* 2014, Maron *et al.* 2014).

Three interrelated ways to address these questions are population-level experiments that are 1) long-term, 2) longitudinal, and 3) demographic. Such experiments produce larger amounts of nested and correlated data. The analysis of these experiments therefore requires the application of modern methods for handling correlated, nested data, and non-normal data (Bolker *et al.* 2009, Zuur *et al.* 2009, Bolker 2015, Kéry 2010). These approaches allow researchers to observe and assess the impacts of species interactions across life history stages and throughout the literal life history of an organism while accounting for spatial variation and temporal stochasticity.

In my dissertation I have used long-term, longitudinal data and a demographic perspective to address the importance of two negative interactions plant species must contend with: mammalian herbivory and invasive species. Native plant species often must face both of these stresses simultaneously, and I have leveraged the power of contemporary statistical methods to assess the relative importance of these two interactions on plant life histories and population dynamics.

1.2 EXPERIMENTAL DESIGN

Data for most of my dissertation (Chapters 2, 4, and 5) was collected during an ongoing study initiated in 2003 to understand how herbaceous and woody plants are impacted by herbivores and invasive species (Kalisz *et al.* 2014, Brouwer *et al.* 2015). This study is comprised of six pairs of plots; within each pair one plot is fenced to exclude deer while the other is unfenced

(Fig. 26 Appendix D). Half of each plot has had the invasive biennial garlic mustard (*Alliaria petiolata*) removed, resulting in a factorial deer exclusion-invader removal experiment. In these plots >10,000 individuals of six native herb species have been monitored annually since 2003. Additionally, over 400 4m^2 subplots have been surveyed biennially to monitor change in woody and herbaceous vegetation over time. This research has resulted in a rich but complex dataset comprised of longitudinal measurements on individual plants or survey units nested within a complex experimental design (split-split plot) where two dynamic species interactions have been manipulated.

1.3 CHAPTER SUMMARIES

1.3.1 Outline of dissertation

My dissertation is comprised of four data chapters. Three are analyses of long-term data from the experiment detailed in the previous section, and the third is a meta-analysis of deer exclusion experiments from around the globe.

1.3.2 Chapter 2: Impacts of an allelopathic invader on native vital rates

Invasive species are often ranked by ecologists as a principal threat to biodiversity (Young and Larson 2011) and thought to cause considerable economic harm (Pimentel *et al.* 2005). Numerous small-scale experimental studies have confirmed that invasive plants reduce the fitness of native plants (e.g. Gioria and Osborne 2014, Morales and Traveset 2009, Inderjit *et al.*

2011, Liao *et al.* 2008, Enge *et al.* 2013), but long-term and/or demographic field studies are much rarer (Stricker *et al.* 2015; but see e.g. Williams and Crone 2006, Dangremond *et al.* 2010). The lack of solid, long-term evidence makes it difficult to conclusively answer vocal critics who question the conservation threat posed by invasive species and the uniqueness of the ecological and evolutionary situations they create (Rosenzweig 2001, Slobodkin 2001, Davis 2003, Brown and Sax 2004, Thomas and Palmer 2015).

In Chapter 2 of my dissertation (Brouwer *et al.* 2015), I demonstrate the population-level impacts of the invasive plant *Alliaria petiolata* on a common native herb, *Maianthemum racemosum*. There is extensive evidence from small-scale studies that *Alliaria* impacts components of plant fitness (Prati and Bossdorf 2004, Callaway *et al.* 2008, Lankau 2012, Leicht-Young *et al.* 2012), but two recent field experiments have questioned the impacts of invasive species in forests (Davalos *et al.* 2014), particularly *Alliaria* (Waller and Mass 2013). A major limitation of studies indicating either negative or negligible impacts of *Alliaria* is that they have relied almost entirely on assessing the impacts of *Alliaria* on native seeds or seedlings in their experiments (but see Hale *et al.* 2011, Hale *et al.* in press). In Chapter 2, I use long-term, longitudinal data on plant vital rates to demonstrate that *Alliaria* impacts multiple fitness components of *Maianthemum* adults, which are the life history stage of this species that is most important to population growth and persistence (Knight 2004, Franco and Silvertown 2004). Key to this analysis is the use of long-term data and longitudinal analyses to identify increases in vital rates over time when *Alliaria* is removed.

1.3.3 Chapter 3: Meta-analysis of deer impacts in closed canopy forests

Along with invasive plant species, overabundant, feral, invasive, or overstocked mammalian herbivores are considered a major environmental problem (Fleischner 1994, Campbell and Long 2009, Sutherland et al 2006, Cote *et al.* 2004, Flueck 2010). Deer are some of the most frequently problematic mammalian herbivores, especially white-tailed deer (*Odocoileus virginianus*) in their native North American range (Cote *et al.* 2004) and red deer/elk (*Cervus elaphus, C. canadensis*) where they have been introduce in New Zealand (Coomes *et al.* 2003). Deer are generalist foragers and it is thought that their browse preferences can dramatically alter forest community composition (browse preference hypothesis; Waller and Alverson 1997). This has been shown to occur after intense forest management such as clear cuts (e.g. Marquis 1981, Horsley et al 2003, Hidding *et al.* 2013) and it has been assumed that this will also occur in closed-canopy forests where successional processes are much slower. More recently, it has been proposed that instead of changing the species composition of forests, deer can change the structure of the forest to be more open and parkland- or savanna-like (canopy recruitment hypothesis; Tanentzap *et al.* 2011). Because of the long timeframes necessary to test hypotheses about forest succession it is difficult to address the generality of these proposals. In Chapter 3 I have assessed the plausibility of these two hypotheses using a systematic review and meta-analysis of all published deer exclusion studies in closed canopy forests. While both of these models of deer-induced forest change are likely to apply in different situations, across all available studies I found that deer have stronger impacts on the abundance of woody vegetation than on species richness or community diversity. Additionally, non-palatable species often increase in abundance inside deer exclosures. These results imply that in the presence of deer non-palatable species do not replace palatable species 1:1. The canopy-recruitment hypothesis therefore deserves additional attention when researchers consider the impacts of deer on forests.

1.3.4 Chapter 4: Longitudinal analysis of deer impacts

Most studies of the impacts of deer, and mammalian herbivores in general, are not longitudinal. We therefore do not have much information on the temporal dynamics of vegetation change after deer become overabundant, and after they are reduced in density. In Chapter 4**,** I analyzed data from 432 4m^2 woody vegetation plots that have been re-surveyed biennially. This experiment was begun after deer had been overabundant at this site for only ~15 years and so it provides the opportunity to monitor continued vegetation change after deer become problematic, as well as how vegetation responds to deer exclusion over time. Surprisingly, many aspects of the woody vegetation, such as sapling abundance, increased both inside and outside of exclosure plots and were not significantly different between treatments. I demonstrate, though, that deer do slow the rate that saplings grow into the mid-canopy, and that they impact the spatial distribution of stems.

1.3.5 Chapter 5: Are the impacts of invaders as important as herbivores?

North American forests are frequently invaded by non-native plant species and experience browse pressure from high densities of deer (Cote *et al.* 2004, Martin *et al.* 2009). As for almost all species interactions, the impacts of these two negative species interactions have mostly been studied in isolation (but see Eschtruth and Battles 2008a, Christopher *et al.* 2014). This raises the question of whether both of these interactions are important to plant population stability or if one is more important than the other (Kikvidze *et al.* 2011). As noted previously, two studies have recently questioned the relevance of controlling invasive species when deer are overabundant (Davalos *et al.* 2014), specifically calling for de-emphasis on *Alliaria* control (Waller and Maas 2013). Both of these were replicated field experiments, but both used nursery grown seedlings of native species. The vital rates of adult forest plants, however, are generally much more important for population stability (Whigham 2004, Knight 2004). In Chapter 5 of my dissertation I demonstrate that *Alliaria* impacts can be of similar magnitude as deer for adults of three common forests plants. These changes develop gradually over multiple years and are apparent only when annual variation in vital rates is accounted for. Additionally, I show how the effects of deer are highly variable and that native species can temporarily achieve high flowering rates despite heavy browse pressure. This demonstrates that even a strong, well-understood negative species interaction can be highly variable and reinforces the need for statistical models that can account for temporal variation and gradual change over time.

1.3.6 Chapter 6: Conclusions

In chapter six I conclude by summarizing my results and discussing their relevance for plant ecology and demography. I also outline how I think demographic and statistical methods can further our understanding of population ecology.

2.0 MUTUALISM-DISRUPTING ALLELOPATHIC INVADER DRIVES CARBON STRESS AND VITAL RATE DECLINE IN A FOREST PERENNIAL HERB

2.1 INTRODUCTION

The majority of flowering plant species form mutualisms with root fungal symbionts (RFS) such as arbuscular mycorrhizal fungi (AMF; 74% of angiosperms; Brundrett 2009) and dark septate endophytes (DSE; ≥600 species; Jumponnen and Trappe 1998). AMF and DSE live inside plant roots and deploy hyphae outside the root that increase water, nitrogen, phosphorus and other soil nutrients' availability to their plant partner (Smith and Read 2008; Newsham 2011). The RFS receive a substantial fraction of the plant partner's fixed carbon (for AMF up to 20%; Smith and Read 2008).

Recent work highlights how anthropogenic changes in the environment, such as invasion, can negatively affect mutualisms (Tylianakis *et al.* 2008; Kiers *et al.* 2010). Invasive species can impact belowground processes and directly or indirectly alter soil microbial communities, including RFS. Mechanisms through which belowground impacts can occur (summarized in part by Wolfe and Klironomos 2005) include alterations in the quality, quantity, and timing of litter inputs and subsequent changes in soil nutrient status (reviewed by Ehrenfeld 2003), direct changes to soil nutrient status through novel nutrient fixation strategies by the invader (*e.g.* Vitousek and Walker 1989), mutualist degradation (Vogelsang and Bever 2009), and allelopathy (*e.g.* Callaway *et al.* 2008; Grove *et al.* 2012). Specifically, allelochemicals can act as novel weapons that are directly toxic to plants or act indirectly on their associated microbes (Callaway and Ridenour 2004; Weir *et al.* 2004).

The invasion of North American forests by *Alliaria petiolata* (Brassicaceae, garlic mustard) is an emerging model system for investigations of allelopathic effects on belowground processes (Rodgers *et al.* 2008a). This species produces a suite of allelochemicals (Vaughn and Berhow 1999; Cipollini and Gruner 2007) that are toxic to RFS (Roberts and Anderson 2001; Stinson *et al.* 2006; Koch *et al.* 2011) even at low concentrations (Callaway *et al.* 2008; Cantor *et al.* 2011). Field studies document that areas infested with *Alliaria* exhibit shifts in soil fungal community composition with frequent reductions in AMF species richness (Burke *et al.* 2008; Lankau 2011a; Lankau *et al.* 2014), declines in total soil hyphal abundances (Cantor *et al.* 2011; Koch *et al.* 2011), and changes in the within-root community of AMF-dependent plants (Burke 2008; Bongard *et al.* 2013). Together, these studies suggest that within *Alliaria*-invaded ecosystems the function of the mutualistic fungal community can be compromised and that these changes contribute to *Alliaria's* invasive success.

Herbaceous perennials dominate the temperate forest understories that *Alliaria* invades and these species as a group are typically highly- to obligately-dependent on RFS (Brundrett and Kendrick 1988; Whigham 2004). The fact that temperate forest soils are strongly resource limited (Whigham 2004; Gilliam 2015) likely drives the obligate nature of the relationship for many understory herbaceous perennials. Typically these species are slow growing (Gilliam 2015), exhibit high rates of RFS colonization (*e.g.* Brundrett and Kendrick 1988; Boerner 1990; Burke 2008), and have long-lived arbuscules (Brundrett and Kendrick 1990). Many also lack fine roots or root hairs (*e.g.* LaFrankie 1985) perhaps because their associated RFS hyphae fulfill this soil resource-gathering role. Since resources supplied by RFS are intimately tied to many plant metabolic functions (Schweiger *et al.* 2014), disruption of soil mutualisms is expected to severely limit the physiological rates of forest species (Hale *et al.* 2011). In the absence of RFS, plants generally exhibit reduced photosynthetic rates (Allen *et al.* 1981; Wright *et al.* 1998; Zhu *et al.* 2011) and subsequent carbon stress can curb their ability to carry out carbon-demanding functions such as growth (Lu and Koide 1994) and flowering (Koide *et al.* 1994).

Carbon stress is the reduction of a plant's pool of total non-structural carbohydrates (*sensu* Anderegg *et al.* 2012). In herbaceous perennials, chronic carbon stress can alter key vital rates including survival (Gremer and Sala 2013), flowering (Crone *et al.* 2009) and prolonged dormancy (Gremer *et al.* 2012). Invaders like *Alliaria* that alter the soil environment and essential RFS functions could induce carbon stress or "carbon starvation" (*sensu* McDowell *et al.* 2008), ultimately diminishing the stability of populations of RFS-dependent native species.

Our prior experiments on the RFS-dependent understory perennial, *Maianthemum racemosum* (Ruscaceae, false Solomon's seal) confirm the dramatic physiological consequences of short-term RFS disruption by *Alliaria*'s allelochemicals. Key physiological traits including stomatal conductance, which is known to be highly dependent on RFS colonization (Augé *et al.* 2014), and photosynthetic rate both significantly declined in plants exposed to fresh *Alliaria* leaf litter (Hale *et al.* 2011). Soil respiration, to which fungi are the primary contributors (Anderson and Domsch 1975), was also reduced with *Alliaria* treatment. Importantly, in field plots invaded by *Alliaria* and in pot experiments with an *Alliaria* litter treatment, we demonstrated significant declines in the abundance of soil fungal hyphae relative to controls (37% decline, Cantor *et al.* 2011; 29-38% decline, A. Hale *et al.* unpubl. data). Together these data strongly support the idea that the observed physiological declines are driven by the inhibition of the RFS hyphal network in the soil (Hale *et al.* 2011).

Here we explore how the physiological stress of RFS mutualism disruption in *Alliaria*-invaded forests could result in performance declines in an RFS-dependent forest perennial across two time scales. First, we ask: Given that *Alliaria's* allelochemicals cause detectable shifts in the soil fungal community and alter native plant physiological rates, do they also cause declines in carbon storage in plants within a single growing season? In a greenhouse experiment we show that *Alliaria*-treated *Maianthemum* store significantly less carbon in their rhizome over one growing season relative to controls. Second, to determine the potential for short-term effects to scale up over time and affect population processes, we conducted a seven-year field experiment in an *Alliaria*-invaded forest in which *Alliaria* was weeded or left at ambient levels. We test whether *Maianthemum* exhibit lower growth rates consistent with carbon stress in the *Alliaria* ambient plots. We also ask if *Alliaria* reduces size-based vital rates of *Maianthemum* and if so, how quickly these changes occur. We show that where *Alliaria* is present, *Maianthemum* have supressed growth and vital rates relative to adjacent plots where *Alliaria* is removed.

2.2 METHODS

2.2.1 Greenhouse study: Assessing potential for carbon stress

The greenhouse study was conducted during the summer of 2010 in the greenhouse facilities at the University of Pittsburgh. In May, we obtained bare-root adult *Maianthemum* plants (N = 42) from a native plant nursery (Prairie Moon Nursery, Winona, MN, USA). Rhizomes ranged in size from 6.7 to 39.7 g fresh weight. We potted each rhizome in a 3:1 mixture of autoclaved Fafard potting soil and Turface. We inoculated plants with RFS by adding 150 g of field soil collected from areas adjacent to *Maianthemum* plants at our experimental field site (see details below). Pots were then placed in the greenhouse and watered every 2-3 days for one month, allowing the plants to complete stem elongation and establish the RFS mutualism.

In June, we assigned each plant to either an *Alliaria* treatment or a control treatment. To control for potential differences in initial carbohydrate status due to differences in plant age and/or size (e.g. Olano *et al.* 2006), we stratified the randomized assignment of rhizomes into the treatments to ensure that mean rhizome mass was the same in the *Alliaria* and control treatments. Plants in the *Alliaria* treatment were then exposed to *Alliaria* allelochemicals by placing 25 g of fresh *Alliaria* leaf tissue collected from a population with a recent history of invasion (< 20 years) on top of the soil. When these plants were watered, the glucosinolates leached out of the *Alliaria* leaves and into the soil (A. Hale *et al.* unpubl. data). As in previous experiments (Hale *et al.* 2011), plants in the control treatment received 25 g of fresh *Hesperis matronalis* (dame's rocket; Brassicaceae) leaf tissue. Like *Alliaria*, *Hesperis* is an invasive mustard in eastern North America (Leicht-Young *et al.* 2012). While *Hesperis* produces some glucosinolates (Larsen *et al.* 1992), RFS hyphae and vesicles have been observed within its root system (DeMars and Boerner 1995), indicating that *Hesperis* chemicals are less toxic to RFS than *Alliaria*. In the field, the high mortality rates of *Alliaria* seedlings and rosettes throughout the year (Davis *et al.* 2006) and the mortality of adults in the summer (Anderson *et al.* 1996) likely results in a sustained supply of allelochemicals into the soil. Thus, we re-applied fresh leaf tissue in both treatments every two weeks until the end of August to simulate a season-long supply of *Alliaria* allelochemicals.

We destructively harvested plants three times during the growing season (9 July, 6 August, and at senescence) to assess the effect of the treatments on carbohydrate status. For the last time point, we classified plants as being senesced when 40% of the leaf tissue had yellowed and photosynthetic rates were $< 1.0\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Details of the leaf gas exchange protocol for *Maianthemum* can be found in Hale *et al.* (2011). To harvest the plants, we carefully clipped the shoot and roots away from the rhizome. We also stained the roots of a subset of plants per treatment following Brundrett *et al.* (1984) to confirm RFS colonization. We then weighed the rhizome and immediately flash-froze it in liquid nitrogen. We stored samples at -80°C until they could be lyophilized and ground. We followed the protocol of Zuleta and Sambucetti (2001) to analyse rhizome inulin (storage carbohydrate) and sucrose (mobile carbohydrate) content via HPLC. [Note: Starch is not present in the rhizome of *Maianthemum* (A. Hale *et al.*, unpubl. data)]. In brief, a 0.03 g dried sample for each plant is boiled while stirring with a magnetic stir bar. Once samples cool to room temperature, they are filtered through a 0.20 μm filter, and run on HPLC (Aminex HPX-87C anion-exchange column, deionized water at 85°C was set as the mobile phase with a flux rate of 0.6 mL/min). Standards are used (inulin from dahlia tubers, Sigma-Aldrich; sucrose, Sigma-Aldrich) to confirm the identity of the sample peaks and to create standard curves to determine inulin and sucrose concentrations. Here, we express inulin and sucrose concentrations as a % of the HPLC dry sample mass. We also sum each plant's inulin and sucrose content to determine total non-structural carbohydrate (NSC) concentration (%).

To explore the effect of our treatments on rhizome carbohydrate status, we use a multivariate analysis of covariance (MANCOVA). Following a significant MANCOVA, individual ANCOVA tests are conducted for inulin, sucrose, and total NSC. For all models, we include harvest date as a main effect because rhizome carbohydrate concentration varies over the growing season in perennial herbs (e.g. Lapointe 1998; Wyka 1999; Kleijn *et al.* 2005). We also include initial plant mass as a covariate to account for differences in carbohydrate storage that are related to plant size/age (MANCOVA model: Total NSC + Inulin + Sucrose = Treatment + Harvest date + Initial plant mass; ANCOVA models: Carbohydrate = Treatment + Harvest date + Initial plant mass). We calculate least squares means and standard errors for all ANCOVA models with a significant ($P < 0.05$) treatment effect. All analyses were conducted in SAS (v. 9.3, SAS Institute, Cary, NC).

2.2.2 Field study: Measuring impacts on vital rates of native plants

2.2.2.1 Study site

Our experimental plots are located in a beech-maple forest in southwest Pennsylvania (Trillium Trail Nature Reserve (hereafter TT), Allegheny Co. PA, USA: 40° 52' 01.40" N; 79° 90" 10.75" W) with a rich herbaceous perennial understory flora (Knight *et al.* 2009). Based on previous work at TT (Burke 2008) and other temperate deciduous forests (e.g. Brundrett and Kendrick 1988) we estimate that 73% of TT herbaceous perennials are AMF-dependent (Hale *et al.* 2011). We detected *Alliaria* allelochemicals in the soil of TT in concentrations that are toxic to AMF spores in lab assays (Cantor *et al.* 2011). Additionally, we showed that in soils where *Alliaria* occurs at TT, the density of fungal hyphae is lower (Cantor *et al.* 2011) and the fungal community composition shifts (Burke *et al.* 2008) relative to paired, non-invaded areas. *Maianthemum* plants collected at TT are heavily colonized by RFS, but their intra-root AMF community is significantly altered where *Alliaria* is present (Burke 2008). These results motivate further investigation of mutualism disruption by *Alliaria* in understanding mechanisms driving native plant performance declines.

2.2.2.2 Field experiment

We collected data on naturally occurring individuals of *Maianthemum racemosum* within six 14×14m plots in TT from 2003 through 2013. Our six plots are split in half longitudinally so that each contains two experimental treatments: *Alliaria* removal (= low or no allelochemicals) or *Alliaria* present at ambient levels (= allelochemicals present). Annual removal of *Alliaria* from half of each plot (i.e. a 14×7m area) began in spring 2006, ~15 years after *Alliaria* became established at this site (L. Smith pers. comm.) This time frame for TT invasion coincides with the estimated *Alliaria* invasion history in the region that indicates that this invader has been present locally for < 25 years (Lankau *et al.* 2010). We remove *Alliaria* concurrent with the onset of emergence of the perennial herb community. *Alliaria* individuals are removed as tiny seedlings, minimizing disturbance to the soil and other plants. Removed plants are discarded off site. In June of each year prior to *Alliaria* seed dispersal we erect a barrier at the border of the two treatments to block seed dispersal from the ambient into the *Alliaria* removal treatment. All *Maianthemum* plants emerging in the plots are permanently tagged and have annually been scored for individual size, stage (i.e. seedling, non-flowering, flowering, dormant), and deer browse status. Prior to initiation of the *Alliaria* removal treatment in 2006 there was no difference in *Alliaria* percent cover between the plots ($\chi^2 = 0.11$, $P = 0.74$) or total percent cover of all species ($\chi^2 = 0.038$, $P = 0.85$).

2.2.2.3 Plant vital rates

We assess the effect of *Alliaria* removal on *Maianthemum* growth and three vital rates: annual flowering frequency, retrogression of flowering plants to non-flowering the following year, and the frequency of prolonged vegetative dormancy (Shefferson 2009). We test for differences using data collected prior to the implementation of the removal treatment (2003-2006) and after the removal treatment began (2007-2013). All models have the general form: Response variable = Treatment + Year + Treatment*Year. To estimate differences in growth rate, we investigate the differences in average size between treatments for the initial cohort of plants first observed when the experiment began in 2003. Mean size of this cohort is estimated with a linear mixed model for each year since 2006 (Zuur *et al.* 2009). We model log(plant size) to improve normality of the residuals.

Annual flowering frequencies are modeled using a logistic mixed model. Retrogression frequencies were modeled without random effects for the years 2008 to 2013 because of limited sample size. Our retrogression model, stated in terms of probability is:

$\Pr(\text{Not Flowering}_{\text{time } t} | \text{Flowered}_{\text{time } t-1} \text{ \& Not dormant}_{\text{time } t})$.

Our sample for retrogression was therefore set by the number of plants that flowered the previous year (time t-1) that emerged as either flowering or non-flowering the next year (time t).

Growth and vital rate analyses are conducted in *R 3.1.0* (R Core Team 2014) using the *lme4* package (Bates *et al.* 2014). To account for repeated measures and blocking effects, we include random intercepts for individual plants and pairs of treatments within a plot. For each response variable we test for significant differences between annual means using the *multcomp* package in *R* (Bretz *et al.* 2010). We test for the presence of a long-term trend since 2006 in each treatment mean by specifying a trend contrast (Rosenthal and Rosnow 1985, Gurevitch and Chester 1986). All tests are planned contrasts so we do not correct for multiple comparisons. To further investigate trends in flowering frequencies we also analyze these data using a two-level hierarchical model with time as a continuously varying main effect and year as a random effect.

Results of flowering and retrogression analyses are reported as effect sizes using odds ratios (Rita and Komonen 2008). Odds ratios have a lower bound of zero and no upper bound.

Odds ratios of 1 indicate no difference between two treatments in the odds of an event happening. Statistical tests for odds ratios therefore test whether they are different from 1. Odds ratios and their 95% confidence intervals are given in the text on their normal scale but graphed on a log scale to improve interpretation (*sensu* Galbraith 1988).

Mark-recapture models: We use mark-recapture models, a modified logistic regression approach (Kéry *et al.* 2005), to estimate the probability of prolonged vegetative dormancy. To test for pre-existing differences in dormancy rates, we conduct separate mark-recapture analyses of the three years prior to implementation of the removal treatment (2003-2005) and the seven years after the treatment began (2007-2013). Mark-recapture results are assessed using the small sample size corrected information criteria AIC*c* to rank the explanatory ability of different models (Anderson 2010). To summarize the data we also analyse the entire data set (2003-2013) and calculate the mean difference in dormancy rates between treatments. We first calculate dormancy rates for each treatment in each year, calculate the difference between these means, and average the differences for the pre- and post-treatment time periods. We use the delta method (Powell 2007) in the *R* package *msm* to combine multiple standard errors and construct 95% confidence intervals around our final effect size estimates. Mark-recapture models are run in the *R* package *marked* (Laake *et al.* 2013).

Missing data due to herbivory: Deer browse compromised our ability to gain information on some individuals. Deer preferentially browse flowering *Maianthemum* and flowering individuals are of larger size than non-flowering individuals (Brouwer and Kalisz, unpubl. data). Accordingly, in the cases where an individual was browsed before its reproductive status was determined during the ten annual censuses (n = 103 instances across 10 years), we assumed the browsed individual was flowering. Further, if browse occurred before an individual's size data was collected or size was otherwise unavailable, we used linear imputation (Gelman and Hill 2007) to estimate its size (412 instances of size imputation out of 1481 total size records). Including imputed size data for the browsed plants prevents biasing our results against detecting a treatment effect (Nakagawa and Freckleton 2008; Hadfield 2008).

We imputed missing size data using estimates generated from multiple rounds of linear regression based on observed size data from the years prior to and after the missing data. We averaged these multiple estimates to arrive at a final imputed size estimate for each browsed individual. Linear regression models included all available covariates, including previous size, current status, treatment and reproductive output for flowering plants. We validated our imputations by comparing mean plant size and the overall size distribution in the population with and without imputed data (Table 5, Appendix A).

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2.3 RESULTS

2.3.1 Greenhouse study: Assessing potential for carbon stress

All *Maianthemum racemosum* plants examined exhibit colonization by internal RFS structures. However, *Maianthemum*'s rhizome carbohydrates were significantly affected by the *Alliaria* treatment (MANCOVA; Roy's greatest root = 7.57, *P* = 0.002), with plants in the *Alliaria* treatment experiencing a significant reduction in total NSC (Fig. 1; ANCOVA $F_{1,36} = 7.31$, *P* = 0.01). Specifically, plants treated with *Alliaria* stored, on average, 17% less inulin relative to plants in the *Hesperis* treatment (Fig.1; ANCOVA $F_{1,36} = 9.28$, *P* = 0.004). While plants in the

Alliaria treatment had fewer stored sugars, they had higher sucrose concentrations in their rhizomes compared to plants in the *Hesperis* treatment (Fig. 1; ANCOVA $F_{1,36} = 12.88$, $P = 0.001$). The increase in mobile sugars did not compensate for the dramatic difference in stored sugars between treatments as total NSC in the *Alliaria* treated plants was 13% lower than that of *Hesperis*-treated plants. Harvest date was not a significant predictor of total NSC, inulin, or sucrose.

2.3.2 Field study: Impact on vital rates

Growth: Prior to implementation of the removal treatment there was no difference in the mean size of plants in the initial 2003 cohort (Fig. 2; $P = 0.55$). By 2013 plants in the removal treatment are significantly larger than those in the ambient *Alliaria* treatment (mean difference = 6.70 cm, SE = 2.96; $P = 0.02$). There is a significant positive linear trend in size from 2006 to 2013 (trend contrast $P = 0.0056$) in the *Alliaria* removal plots but no trend in the ambient plots ($P = 0.91$).

Flowering: There is no significant difference in flowering probability across treatments for the first six years of the *Alliaria* removal (e.g. Fig. 3; $P_{2006} = 0.65$, $P_{2007} = 0.29$, $P_{2008} = 0.42$). However, by 2012 the flowering probability is “leaning” (*sensu* Tukey 1991) in the predicted direction (Odds ratio (OR) = 1.72, $CI_{95\%} = 0.84\text{-}3.52$, $P = 0.14$) and by 2013 is significantly higher (OR = 1.96 $CI_{95\%} = 1.0\text{-}3.87$, $P = 0.051$) in the removal treatment. Across all years (2006-2013) there is an increasing trend in flowering probability in the removal treatment (trend contrast $P = 0.00008$) but no increase in the ambient treatment ($P_{trend} = 0.57$).

Analyses using time as a continuous variable and year as a random effect confirmed that flowering frequencies diverged between the treatments (treatment*time $\chi^2 = 6.81$, $P = 0.009$)

with a significant positive linear trend in the removal treatment ($\beta_{removal*time}$ = 0.18, SE = 0.069) contrasted with evidence of a decrease in flowering probability in *Alliaria* ambient plots (β_{time} = -0.10, SE = 0.072).

Retrogression: The number of flowering individuals was too low in 2005 and 2006 to accurately estimate retrogression of flowering plants in 2006 and 2007. By 2011, there was evidence that removal-treatment plants were less likely to retrogress (OR = 0.28 $CI_{95\%}$ = 0.052-1.57, *P* = 0.15) and in 2012 they were significantly less likely to retrogress (OR = 0.14 $CI_{95\%}$ = 0.021-0.96, *P* = 0.045). There was a significant decreasing trend in retrogression in the removal treatment from 2008 until 2013 (P_{trend} = 0.011) but no trend in the ambient treatment (P_{trend} = 0.90).

Dormancy: Dormancy rates were highly variable between years, ranging from less than 10% to > 30%, but estimated to be lower in the *Alliaria* removal treatment in six out of seven years (Table 6 Appendix A). For years prior to the implementation of the *Alliaria* removal treatment (2003-2006) the best-ranked model contains only a year effect (Table 1) while for models of post-treatment years (2007-2013) and the entire dataset (2003-2013) the best models contain an effect of *Alliaria* removal, indicating that dormancy rates were typically lower in this treatment. There was an initially large difference in dormancy rates between plots that would be allocated to the two treatments in the first year of the study (Table 6 Appendix A), potentially resulting in the model of the pre-treatment years containing an *Alliaria* removal effect (AICc = 454.6) ranked almost as high as a year-only model (AICc = 452.8). However, since the year-only model has a lower AICc and fewer parameters, the larger model is not considered competitive (Arnold 2010). Moreover, in the other two pre-treatment years (2004 and 2005) there is no difference between dormancy estimates (Table 6 Appendix A). The results of model selection are reinforced by the calculation of average effect sizes for the period prior to *Alliaria* removal and after removal (Fig. 5). Prior to removal there is no significant difference between dormancy rates (ES = -0.05, $CI_{95\%}$ = -0.13 - 0.03) but after removal dormancy rates are ~7% lower than in the *Alliaria* ambient treatments (ES = -0.069, $CI_{95\%}$ = -0.12 - -0.2).

2.4 DISCUSSION

To our knowledge this is the first study to explore the connections between an allelopathic invasive species' impacts on the soil biotic environment and changes in individual plants' carbon status and vital rates. The results presented here in conjunction with prior studies substantiate multiple steps in a physiologically-based causal pathway between invasion and population-level impacts on native plants. Our prior work demonstrates that *Alliaria* treatment of soil around *Maianthemum* reduces the density of soil fungal hyphae; A. Hale *et al.*, unpubl. data) and plant photosynthetic rates (Hale *et al.* 2011). Here, our results demonstrate that treatment with *Alliaria* across the entire growing season results in negative effects on season-long carbon storage (Fig. 1). Relative to control plants, *Maianthemum* exposed to *Alliaria* stored 17% less inulin in their rhizomes and experienced an overall reduction in total non-structural carbohydrates (NSC) at the end of the season. Stomatal conductance modulates carbon fixation and is a key physiological rate affected by *Alliaria* exposure (Hale *et al.* 2011). Interestingly, a recent meta-analysis (Augé *et al.* 2014) comparing the effects of AMF inoculation on stomatal conductance (g_s) in field vs. greenhouse studies indicates that greenhouse experiments have smaller effect sizes than field studies. Thus, our carbon storage results are likely conservative estimates of the carbon impacts of mutualism disruption in the field.

Over time, chronic exposure to *Alliaria* was predicted to compound this carbon deficit and affect plant growth and vital rates. Results from our long-term field study of *Alliaria* removal are consistent with this prediction. Individual aboveground plant size (Fig. 2) and multiple carbon-intensive and size-dependent vital rates (Figs. 3-5) are positively affected in *Alliaria* removal relative to *Alliaria* ambient plots.

Other experimental studies where *Alliaria* and native plants are grown together in pots (Meekins and McCarthy 1999, Wixted and McGraw 2010, Lankau 2012, Smith and Reynolds 2013) or in the field (McCarthy 1997, Carlson and Gorchov 2004, Lankau 2012, Cipollini *et al.* 2008) also find negative effects of *Alliaria* on native species. Competition, direct allelopathic phytotoxicity, and allelopathic RFS mutualism disruption are all mechanisms that could contribute to these results. Our greenhouse experiment adds support to the idea that it is *Alliaria*'s disruption of key belowground mutualists (RFS) rather than competition or direct phytotoxicity that accounts for its success as an invader. Below we discuss the general support or lack thereof for the likelihood of all three mechanisms.

<u>Competition</u>: We are aware of only two studies that have attempted to quantify reciprocal competition between *Alliaria* and focal plants. These pot studies found that *Alliaria* was equal to or weaker in competitive ability than three of four species tested (Meekins and McCarthy 1999, Leicht-Young *et al.* 2012). However, these studies are problematic in that they cannot separate competition from phytotoxicity or mutualism disruption. Bossdorf *et al.* (2004) found that *Alliaria* individuals from the native range outcompete *Alliaria* plants from the invaded range, supporting the hypothesis that invasive *Alliaria* express a different trade-off relative to their source populations. Invasive *Alliaria* are armed with novel allelochemical weapons but have evolved to be less competitive (Bossdorf *et al.* 2008). Further, field experiments demonstrate that

native competitors can suppress *Alliaria* performance and abundance when the natives are not experiencing overabundant herbivore pressure (Eschtruth and Battles 2008b), as deer preferentially consume native plants and facilitate the high population growth and spread of *Alliaria* (Kalisz *et al.* 2014). In experimental studies that exclude deer from invaded sites, *Alliaria* abundance rapidly declines (Knight *et al.* 2009, Eschtruth and Battles 2008b, Kalisz *et al.* 2014). In total, these results underscore the widely held view that *Alliaria* is a relatively poor competitor (Rodgers *et al.* 2008).

<u>Direct phytotoxicity</u>: Glucosinolates are known antimicrobial chemicals produced by members of the mustard family as defenses against pathogens (Tierens *et al.* 2001). While *Alliaria's* allelochemicals can be inhibitory to germinating seeds and inhibit new seedling root growth (lettuce and radish seed experiments: Vaughn and Berhow 1999; Roberts and Anderson 2001; Pisula and Meiners 2010; *Impatiens* and *Viola* seed experiments: Prati and Bossdorf 2004; Barto *et al.* 2010; Cipollini and Flint 2013), to our knowledge direct toxicity of *Alliaria* on mature plant tissues has never been demonstrated. *Alliaria* invades forest understories dominated by adult perennial plants dependent on RFS. The direct effect of allelochemicals is inversely proportional to target plant density or biomass (Weidenhamer 2006). Single-celled fungal spores and thin fungal hyphae should be much more susceptible to *Alliaria* allelochemicals than mature plant tissues. Thus, while we cannot rule out direct phytotoxic effects of *Alliaria* on adult *Maianthemum* performance in our field or greenhouse experiments, a direct allelochemical effect is likely of small magnitude relative to indirect effects on RFS.

<u>RFS-mutualism disruption</u>: Mounting evidence shows that *Alliaria* can exert potent indirect effects on plants by suppressing RFS. Glucosinolates, like those produced by *Alliaria*, have a short half-life in the soil (<15 hrs; Gimsing *et al.* 2006). Yet, native plants grown in soils

conditioned by *Alliaria*, treated with *Alliaria* tissue extracts, or collected from *Alliaria*-invaded sites all express reduced growth (Stinson *et al.* 2006, Callaway *et al.* 2008, Wolfe *et al.* 2008) despite the fact that the volatile allelochemicals were likely no longer present. Importantly, these studies demonstrate that *Alliaria* impacts are similar in magnitude to soil sterilization and that experimental soils result in lower colonization of roots by mycorrhizae (Stinson *et al.* 2006, Callaway *et al.* 2008, Wolfe *et al.* 2008). Finally, *Maianthemum* plants treated with *Alliaria* retain RFS structures internal to their roots, while exhibiting significant declines in soil hyphae (A. Hale *et al.* unpubl. data). Together these experiments provide strong support for RFS mutualism disruption and that its effects are of large magnitude relative to competition or direct phytotoxicity.

Mechanistically, our working model linking RFS mutualism disruption to carbon stress is based on the following premises: If *Alliaria*'s allelochemicals destroy the hyphal network, yet the normally long-lived internal structures (Brundrett and Kendrick 1990) remain intact, then we would predict that the plant would increase carbon allocation to its RFS to provision the regrowth of the soil hyphal network, resulting in significant carbon stress for the plant. Loss of the hyphal network severely limits available soil nutrients and water to the plant (Newsham 2011, Augé *et al.* 2014). As a result, the plants photosynthesize less (Hale *et al.* 2011) and fix less carbon (NSC; Fig. 1). With this limited carbon pool, we suggest that plants may maintain concentrations of mobile sugars in the rhizome and roots to re-establish a functional RFS hyphal network that is repeatedly destroyed by our application of fresh *Alliaria* tissue. While our results are consistent with this working model (e.g. we observe greater sucrose concentrations in the rhizome of *Alliaria* vs. *Hesperis* treated plants (Fig. 1), additional experiments are needed to fully explore this hypothesis.

We note that the effects of allelopathic mutualism disruption by *Alliaria* could be amplified by additional factors. Like other invasive species of deciduous forests (Ehrenfeld *et al.* 2001; Poulette and Arthur 2012; Schuster and Dukes 2014; Kuebbing *et al.* 2014; Smith and Reynolds 2012), *Alliaria* can affect multiple components of the soil environment. *Alliaria* increases soil nutrient availability (Rodgers *et al.* 2008a; 2008b), litter decomposition rates and nitrogen loss (Ashton *et al.* 2005). Since the RFS community in general (Van Diepen et al 2011) and specific RFS-plant interactions (e.g. Klironomos 2002) are sensitive to soil conditions, multiple invader-mediated changes to the soil environment could magnify the impacts of allelopathic RFS mutualism disruption. These diverse and widespread consequences of invasive species for soil environments and RFS communities are alarming given the potentially central role RFS and other microbes play in the diversity, productivity and functioning of plant communities (Van Der Heijden *et al.* 2008).

Our greenhouse study indicates that *Maianthemum* carbon storage declines significantly in response to *Alliaria* treatment in just one growing season. In contrast, we observe a relatively slow recovery of individual size, growth and vital rates following *Alliaria* removal in our field study. The predicted significant trends indicative of recovery (Figs. 2-4) emerged after a few years of *Alliaria* removal while significant differences within the single-year comparisons were not seen until ~6-7 years post removal (2012 or 2013). Two, non-mutually exclusive mechanisms could underlie this lag. First, the lag could be due to *Maianthemum*'s habit (LaFrankie 1985). In general, forest understory herbaceous perennials are light-limited, slow-growing, long-lived species (Whigham 2004) with slow responses to perturbation (Morris *et al.* 2008). Our data are consistent with the idea that following *Alliaria* removal, *Maianthemum* may take multiple years to re-gain sufficient carbon stores to allow size growth, sustain flowering and maintain low dormancy rates. Second, the observed lag in *Maianthemum* vital rate responses may be due to slow recovery of the RFS soil community following *Alliaria* removal, a phenomenon observed by Anderson *et al.* (2010) and Lankau *et al.* (2014). If populations of beneficial RFS have gone locally extinct and low dispersal distance limits RFS re-colonization (Rout and Callaway 2012), then the observed time lag of *Maianthemum* could be due to the low abundance of effective fungal partners. Given the reciprocal obligate dependence of AMF and forest herbaceous perennial plants, declines in the native understory community may drive reciprocal declines in the RFS soil community (Lankau *et al.* 2014).

2.5 CONCLUSIONS

Increases in invasive species are generally correlated with declines in native biodiversity (e.g. Butchart *et al.* 2010). However, the mechanistic underpinnings leading to native population collapse are rarely understood yet are the subject of numerous studies and invasion hypotheses (Levine *et al.* 2003, Hulme *et al.* 2013). The disruption of plant soil feedbacks and root fungal symbioses are common aspects of plant invasions (i.e. Grove *et al.* 2012, Meinhardt and Gehring 2012, Ruckli *et al.* 2014, Shannon *et al.* 2014). As suggested by Hale and Kalisz (2012), chronic RFS mutualism disruption could act as the first step in native plant biodiversity loss. In our system, the disruption of RFS by an allelopathic invader appears to begin a downward spiral in the physiological function (Hale *et al.* 2011), carbon status (Fig. 1) and ultimately vital rates (Fig. 2-5) of a common native forest plant. Loss of these critical belowground mutualisms may be the proximate cause of plant mortality that is instead attributed to second order effects (e.g. drought or herbivory) that are easier to observe (*sensu* McDowell 2011). Additional studies in invaded communities that explore the links between plant physiology, carbon allocation, and population demographic performance are needed to determine the generality of these results. Mutualism disruption may be a widespread mechanism that helps explain how invasive species can cause large-scale changes to forest biodiversity observed in the wake of invasion (e.g. Rodgers *et al.* 2008a).

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Table 1. Ranking of mark-recapture models testing the effects of *Alliaria* removal on prolonged vegetative dormancy. Three sets of models were run over different time periods during the study: Set 1) Years before *Alliaria* removal began (Pre-treatment), Set 2) Years after the annual weeding treatment was initiated (Post-treatment), and Set 3) All years. N is the number of plants tracked over each time period, K is the number of parameters in a model, and Ln(lik) is the log likelihood. To calculate the mean pre-treatment and post-treatment effect size (Fig. 5) we used the parameters from the "Removal*Year" model in the "All years" model Set 3.

Set	Period	Model	N	K	AICc	ΔAICc	Ln(lik)
1)	Pre-*Alliaria*	Year	158	5	452.8	0.00	-216.21
	removal	Removal + Year		6	454.6	1.74	-215.00
	(2003-2006)	Removal * Year		9	466.2	11.59	-214.47
2)	Post-*Alliaria*	Removal + Year	210	9	1166.4	0.00	-564.73
	removal	Year		8	1172.4	6.03	-569.84
	(2007-2013)	Removal * Year		15	1187.2	14.76	-562.34
3)	All years	Removal + Year	236	12	1646.3	0.00	-798.46
	(2003-2013)	Year		11	1652.5	6.23	-803.68
		Removal * Year		21	1680.3	27.74	-795.98

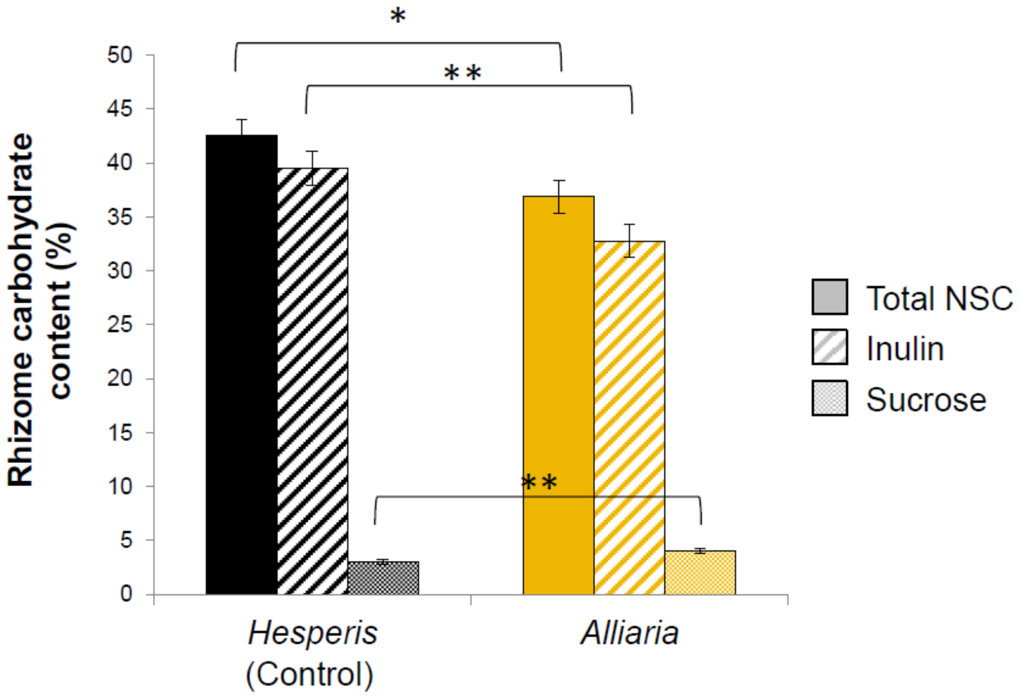

Figure 1. ***Maianthemum racemosum*** **rhizome carbohydrate content (%) from *Alliaria* (yellow) and *Hesperis* (control; black) treatments in the greenhouse experiment. Total non-structural carbohydrate (NSC) content is shown in solid-colored bars. Total NSC is a composite measure of stored sugars (inulin; bars with diagonal shading) and mobile sugars (sucrose; stippled bars). Values are least squares means from ANCOVAs +/- 1 standard error. * indicates $P < 0.05$; ** indicates $P < 0.005$.**

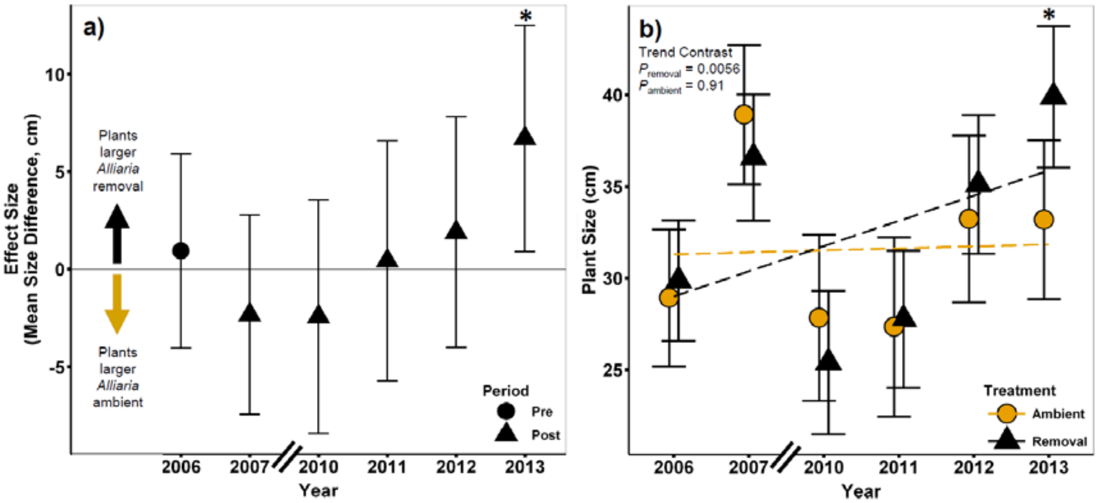

Figure 2. Effect of *Alliaria* on plant size of *Maianthemum* marked in the initial 2003 survey of the field experiment. a) Mean difference (effect size) in plant size between *Alliaria* in ambient and removal treatments. b) Annual mean plant sizes in both treatments and ANOVA trend contrasts. Error bars represent +/- 95% confidence intervals. * indicates a significant difference in plant size between the two treatments (P < 0.05). Size data were not available for 2008 and 2009.

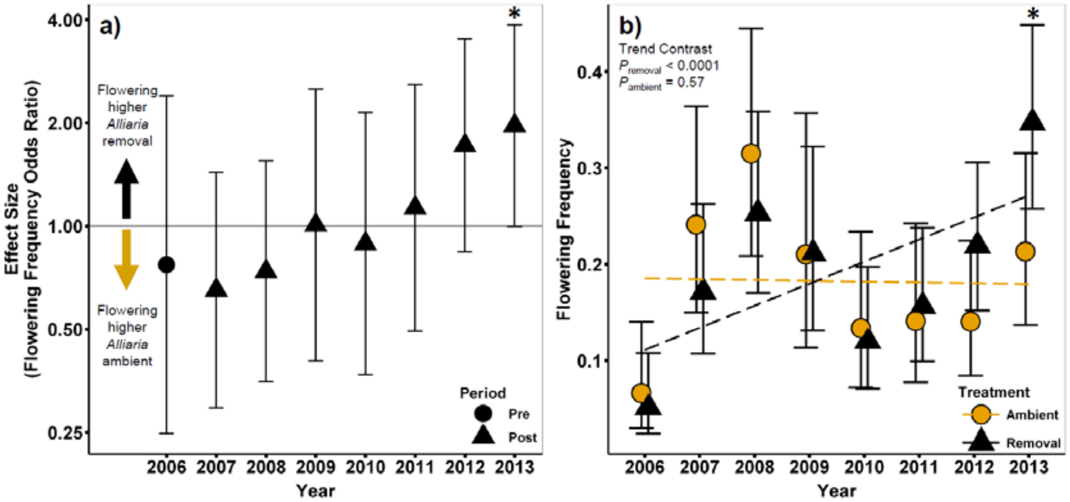

Figure 3. Effect of *Alliaria* on *Maianthemum* flowering frequency. a) Mean difference (Effects size, ES) in flowering frequency in *Alliaria*-ambient and removal plots. ES is expressed as an odds ratio and plotted on the log scale. b) Annual mean flowering frequencies for both treatments and ANOVA trend contrasts. Error bars represent +/- 95% confidence intervals. * indicates a significant effect of *Alliaria* removal (P < 0.05).

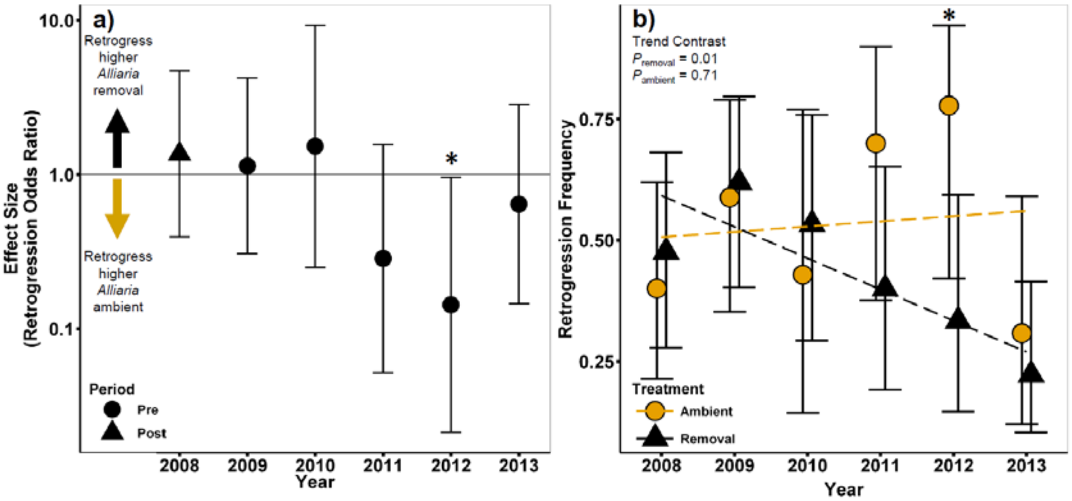

Figure 4. Effect of *Alliaria* on *Maianthemum* retrogression from flowering to non-flowering. a) Annual mean difference in retrogression frequency (Effect size, ES) in *Alliaria*-ambient and removal plot. ES is expressed as an odds ratio and plotted on the log scale. b) Mean retrogression frequencies in both treatments and ANOVA trend contrasts. Error bars represent +/- 95% confidence intervals. * indicates a significant effect of *Alliaria* removal ($P < 0.05$). Retrogression is calculated conditional on a plant being observed above ground and not dormant. Sample sizes for 2006 and 2007 were insufficient for vital rate calculation.

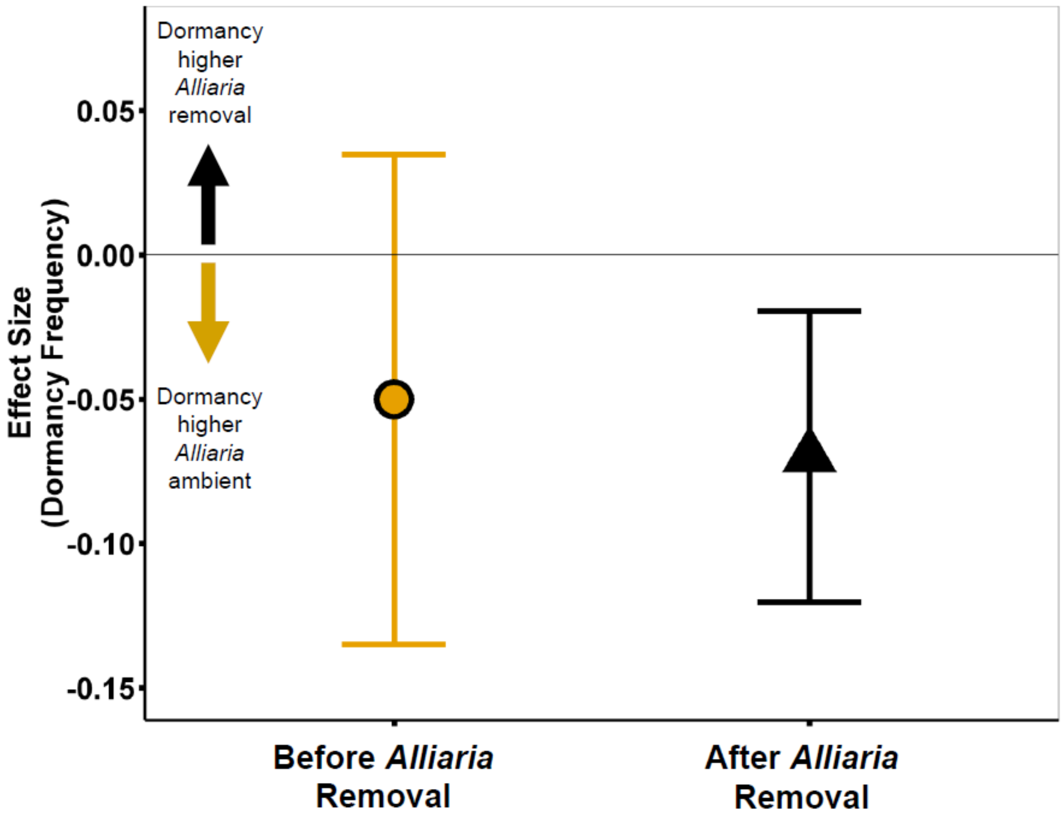

Figure 5. Effect size of *Alliaria*-removal on the frequency of prolonged vegetative dormancy in *Maianthemum* before (2003-2006; yellow) and after the treatment began (2007-2013; black). Calculated with mark-recapture models; error bars represent +/- 95% confidence intervals. * indicates a significant effect of Alliaria removal ($P < 0.05$).

3.0 HOW DO OVERABUNDANT DEER AFFECT LONG-TERM VEGETATION CHANGE IN CLOSED CANOPY FORESTS? USING META-ANALYSIS TO ASSESS THE COMMUNITY COMPOSITION CHANGE AND CANOPY RECRUITMENT FAILURE HYPOTHESES

3.1 INTRODUCTION

Herbivores can have profound impacts on plant populations (Maron & Crone, 2006), communities (Olff & Ritchie, 1998), and ecosystem processes (Bardgett and Wardle 2010, Peltzer *et al.* 2010, Tanentzap and Coomes 2012). While specialist insect herbivores can have large-scale effects on a single species' population (Mattson and Addy 1975), generalist mammalian herbivores appear to more readily exert broad impacts at community, ecosystem, and biogeographic scales (Crawley 1989; Bond 2005). Some mammalian species have been termed keystone herbivores (Owens-Smith 1987) for their apparent ability to structure entire ecosystems through biomass consumption. This is most frequently hypothesized for large grazers and browsers such as bison (Collins *et al.* 1998, Allerd *et al.* 2011), elephants (Owen-Smith 1989), and moose (Molvar *et al.* 1993), but has also been proposed for rodents such as voles (Manson *et al.* 2001, Huitu *et al.* 2012). Similarly, grazers or browsers influence successional processes (Barrette *et al.* 2014; Seabloom and Richards 2003). In particular, livestock, overabundant ungulates and invasive mammalian herbivores are frequently hypothesized to exert keystone-like effects (Waller and Alverson 1997), impact succession (Bakker *et al.* 1993; Fleischner 1994), and permanently degrade ecosystems (Rietkerk *et al.* 1997).

The profound effects of overabundant or invasive mammalian herbivores likely occur most frequently and quickly in systems where plant-animal interactions are trait-structured rather than size structured. In open habitats such as grasslands and savannas, as well as in forests after large disturbances, a large portion of plant biomass is within reach of mammalian herbivores. Most plant life history stages can therefore be impacted by biomass consumption, nutrient deposition (van der Wal *et al.* 2004), trampling, rubbing and debarking (Ihwagi *et al.* 2010, Ramos *et al.* 2006), or even toppling, in the case of elephants (Asner and Levick 2012). The outcomes of plant-herbivory interactions are therefore heavily influenced by plant traits such as specific leaf area, physical defenses and chemical composition (Forsyth *et al.* 2005, Evju *et al.* 2009, Cingolani *et al.* 2005). Under many conditions plant traits that influence palatability allow mammalian herbivores to act as selective filters against the most palatable species of the community (Augustine and McNaughton 1998) and can occur at the rate of plant growth or herbivore feeding. For example, grazer preference for grass can allow open habitats to undergo succession towards brushy or wooded systems, while browser preference for woody species can prevent further succession of savannas (Straver *et al.* 2009). Similarly, after timber harvest, deer browse can bias tree communities towards less-preferred species (Marquis *et al.* 1978).

In closed canopy forests, mammalian herbivory impacts highly size-structured and are most severe on herbs, shrubs, and the smallest size classes of trees in the understory. While rubbing (e.g. Ramos *et al.* 2006, Boyce and Lubbers 2011), and nutrient deposition (Lucas *et al.* 2013) can affect some larger individuals, most stems > 2 m in height in forests enjoy a size refuge from direct deer impacts. In some cases, the youngest and smallest individuals can also experience low rates of herbivory if in the winter they are buried by snow (Alisson 1990). Interactions between mammalian herbivores and forest trees are therefore size structured, and most impacts on large size classes occur indirectly over time through successional processes at the pace of gap-phase dynamics. Trait-structured interactions in the understory of closed canopy forests will eventually impact overstory tree composition or density, but on a time scale of decades as less preferred species grow towards the overstory and capture gaps created by palatable overstory species. This is known to have happened in locations where deer have been overabundant or invasive for long periods of time, such as the upper Midwest of North America (White 2012) and New Zealand (Wright *et al.* 2012).

Cervids are now overabundant throughout much of North America (Leopold *et al.* 1947, Cote *et al.* 2004), are invasive in temperate forests around the world (Flueck 2010, Spear and Chown 2009), and in some countries are expanding or re-establishing their ranges (Ward 2005, Flueck *et al.* 2003, Carden *et al.* 2011). Many temperate forests are therefore in danger of having the successional dynamics and community composition of their overstories reshaped by persistent deer impacts to forest understories. The long time scales involved, however, make it difficult to characterize how resistant forests are to deer impacts, or how resilient they are if deer abundance can be reduced. Thus far most studies have only characterized deer impacts to forest understories and demonstrated the likelihood of canopy impacts (Bellingham and Lee 2006).

It is generally hypothesized that overabundant deer will prevent their preferred browse species from escaping the understory but that less preferred species will continue to grow, perhaps even benefiting from competitive release (Waller and Alverson 1997, Cote *et al.* 2004). With only a subset of the community growing towards the overstory, deer browse will eventually cause changes to canopy community composition (H_1). An alternative hypothesis that has been proposed is that deer reduce canopy recruitment of all species, resulting eventually in canopy recruitment failure (H_2) and more open woodlands (Tanentzap *et al.* 2012). In some communities all canopy tree species might be relatively palatable to deer. Deer diet preferences are also plastic and at high densities deer switch to less palatable species after their preferred browse is depleted (Coomes *et al.* 2003). Additionally, it is being increasingly recognized that deer can exert negative indirect soil-mediated effects on non-palatable species (Heckel *et al.* 2010, Kardol *et al.* 2014). Finally, deer browse is thought to facilitate the formation of recalcitrant understories by non-palatable herbaceous species such as ferns and grasses (Royo and Carson 2006). These recalcitrant layers reduce germination and seedling growth of all species, eventually preventing canopy recruitment.

In this study, we use data from a systematic review and meta-analysis of deer exclusion studies to test the community composition change (H_1) and community recruitment failure (H_2) hypotheses and characterize how forest midstories and understories respond to overabundant deer and what successional pathways forests are likely following. In particular we investigate how widespread are deer impacts on forest midstories, how quickly they occur, and whether these impacts presage changes in canopy tree composition or canopy recruitment failure. We also assess whether recalcitrant understories (Royo and Carson 2006) are forming in response to deer overabundance and affecting to successional processes. Since most deer exclusion studies are short duration and consider only impacts on stems < 2 m in forested sites (Bellingham and Lee 2006) we also investigate whether forest understories are shifting towards being dominated by non-palatable species or simply being reduced in overall density.

3.2 METHODS

3.2.1 Literature inclusion criteria

We conducted a systematic review and meta-analysis of deer exclusion studies conducted in closed canopy forests. We searched the peer-reviewed literature for deer exclusion studies conducted in both temperate and boreal closed-canopy forests or woodlands that measured responses on multiple naturally occurring woody species. We included studies on any species of deer (Family Cervidae) in either their native or invasive ranges but did not include moose (*Alces alces*) or reindeer (*Rangifer tarandus).* We did not distinguish between North America elk (*Cervus canadensis)* and old-world red deer *(Cervus elaphus).* Much of the literature was published before these species were determined to be distinct (Ludt *et al.* 2004) and we use the nomenclature assigned by the authors of the exclusion studies.

We considered only studies that included experimental treatments with deer access controls and fenced deer exclusion plots. We excluded studies in heavily managed systems such as coppice woods in England (e.g. Morecroft *et al.* 2001). Studies that included other treatments such as gaps (Nuttle *et al.* 2013, Collard *et al.* 2010), clearcuts (e.g. Hidding *et al.* 2013, Beguin *et al.* 2009, Beguin *et al.* 2011, Casabon and Pothier 2007, Kosco and Bartholome 1983) or fire (Nuttle *et al.* 2013, Andruk *et al.* 2014) were included only if we could extract information that concerned only deer access and exclusion plot data under closed canopies without other manipulations. We did not use studies that considered only a single focal plant species (e.g. Simard *et al.* 2013) or used only planted seeds or seedlings. If a study focusing on herbaceous species also presented separate information on woody species it was included in our analyses (e.g. Rooney 2009).

In the spring of 2014 we conducted a systematic literature search in Web of Science using the terms "TS = (deer) AND TS = (exclos* OR exclus* OR exclud* OR fenc*)". We also scanned the bibliographies of previous reviews (e.g. Cote *et al.* 2004, Russel *et al.* 2001). From the resulting >1000 citations we identified 49 papers that met our inclusion criteria.

3.2.2 Data extraction

For each study we identified the response variables (e.g. percent cover, stem density) and size classes (e.g. seedling, sapling, small trees) of woody species the authors considered. For each size class we determined how it was delineated, such as maximum height or minimum diameter at breast height. We recorded two kinds of information about the experimental results from each study. First, for each response we determined whether a nominally significant result ($p < 0.05$) was reported. Second, for responses related to species diversity, species richness, and over-story trees, we then calculated the response ratio (Hedges *et al.* 1999, Gurevitch and Hedges 2001) as $(\text{Response}_{\text{Exclosure}})/(\text{Response}_{\text{Control}})$. Each study was weighted by the samples size as $(N_e*N_c)/(N_e+N_c)$ (Lajeunesse and Forbes 2003). Usually $N_c = N_e$ = the number of pairs of deer exclusion/deer access plots. However, in some cases summary statistics such as total species richness in exclusion plots versus total species in control plots were reported (e.g. Rooney 2009), in which case the number of plot pairs was set as 1. If a study compared exclusion plots to controls in other locations (plots were not paired; Murray *et al.* 2013) or if the study was unbalanced we set N as the number of exclosures or controls, whichever was lower. When responses in a single study were reported for multiple sites or stand types (i.e. Bughalo *et al.* 2013) we calculated the response ratio for each site and then took the average. In most cases the response ratio was calculated from treatment means for the final time point of the study. Some studies (e.g. White 2012) report results in terms of change from baseline condition, such as mean change within exclusion plots versus mean change within control plots. In such cases we calculated the response ratio from these mean change scores.

We chose to use the non-parametric version of the response ratio to broaden the number of studies we could include (Lajeunesse and Forbes 2003). The more familiar Hedge's *d* as well as the parametric response ratio both weight studies using standard errors, which is less frequently available than sample sizes, especially from older publications. Lajeunesse and Forbes (2003) found that the non-parametric response ratio compared favorable to Hedges *d* and the parametric response ratio.

3.2.3 Covariate extraction

We determined the duration of each experiment and, when available, information on local deer density at the time of the study and the duration of deer overabundance prior to fences being built. If studies included exclosures built at different times (e.g. Shelton *et al.* 2014) we used the midpoint between time points to calculate the duration of the experiment. If authors did not report information on ambient deer densities or the duration of overabundance prior to the study we consulted external sources to estimate values as follows. We first determined as much geographic information as possible for a site (name of tract of land, county, nearest city) and then located relevant studies conducted in the same area, historical records of deer irruptions and invasion, and the initiation of controls measures such as culls.

In most cases no localized information could be found for the duration of deer overabundance. For North American estimates of the duration of overabundance we therefore used maps and descriptions from Leopold *et al.* (1947) to determine if deer had become overabundant at a location in the first half of the 20th century. The beginning of overabundance was set at 1947 for sites located in regions delineated as experiencing overabundant deer by Leopold *et al.* (1947), or earlier if Leopold *et al.* (1947) provided more detailed information. For sites with no evidence of deer overabundance by 1947, we examined the maps created by the Southeastern Cooperative Wildlife Disease Study (SCWDS; http://vet.uga.edu/scwds/range-maps), which compiled information on deer abundance in much of the eastern USA for 1970, 1980, 1982 and 1988. The SCWDS also created a map indicating deer re-introductions in the 1950s for the southeast and mid-Atlantic states. We compared these maps and interpolated between dates, or one of these dates and the start of a study, to arrive at an estimate for when deer likely became overabundant at a site.

For New Zealand we used historical information provided by study authors, Clark (1949), and Atkinson (2006) to determine when deer were introduced onto a given island and/or when the expanded their range into a region. We then determined when deer culls first began for that region, assuming this was evidence of negative impacts at a site. We did not locate historical information on deer overabundance for Japan, Europe, or the UK and so only used overabundance information if provided directly by authors of the papers.

3.2.4 Delineating size classes

We encountered a wide variety of definitions of seedlings, saplings, and small trees with respect to the range of height and/or stem diameters included in each stage class. Because of this variation and overlap we assigned studies to several non-exclusive size classes and conducted separate analyses on each class. First, we defined midstory plants as stems in size classes that were either ≥ 2 m in height, defined by a minimum diameter at breast height (DBH), and/or was referred to as a "tree" by the authors of the study. This class was delineated so that most stems would be beyond the typical browse height of deer in during the growing season. Second, we defined understory plants as stems <2 m and/or where not defined by a DBH. This class was delineated so as to include stems that were generally within reach of most species of deer. Third we split the understory class into saplings (≥0.5 m in height or < 2 m in height) and seedlings (<0.5 m in height) because these are generally recognized size classes in the literature.

3.2.5 Meta-regression

We used mixed model meta-regression to determine the relationship between effect sizes and two key predictors: the duration of deer overabundance (DOA), and the duration of deer exclusion (DoEx). We log transformed the response ratio and conducted all analyses in the *lme4* (Bates 2015) package in *R 3.1.2 (R* Core Team 2014*)* using study as a random effect. We conducted separate analyses for our four size classes: midstory trees, all understory stems, saplings, and seedlings. Many studies report both species richness and an index of species diversity (*i.e.* Simpson's diversity *H'*). We included both of these as a community metric and averaged over them via our study-level random effect. We constructed 95% confidence intervals for all effect sizes using the *confint.merMod* function in *lme4* with 500 bootstrap samples.

3.2.6 Time-to-event analysis

To characterize the rate at which changes occur in forests after deer densities are reduced we modeled the detection of significant exclosure effect ($p < 0.05$) using time-to-event analyses (also known as survival analysis; Muenchow 1986, Fox 2015). To conduct this analysis we made two simplifying assumptions. First, we assumed as an experiment progressed response variables such as sapling abundance or species richness would increase in exclosures, while controls remained similar to their original state. Second, we defined an "event" arbitrarily as a statistically significant difference being observed between an exclosure and a control. We therefore defined change between treatments in the limited terms of null hypothesis significance testing.

Our data are all left censored and many are right censored (Hosmer and Lemeshow 1999). Responses are all left censored because the occurrence of an event, such as a statistically significant increase in sapling species richness after deer are excluded, happened at an unknown time between when a deer exclosure experiment began and data were collected. That is, if the study had been conducted after less time had elapsed, a statistically significant difference may still have been reported. Our data are also frequently right censored, like most time to event datasets, because at the time of measurement an event may not have yet occurred. Left-censorship of time-to-event data possess statistical challenges (Klein and Moeschberger 2005) and we chose to treat our data as if they were not left censored. We therefore make the conservative assumption that if an "event" occurred, it happened the year the measurements were taken. A consequence of this assumption is that we will overestimate the time that elapses between when an experiment starts and when a difference is detected between treatments.

We ran two sets of time-to-event analyses. First, we explored the impact of the duration of overabundance (DoA) prior to the start of an experiment on the observation of significant impacts after deer are excluded. Second, we explored the relationship between the duration of deer exclusion and the observation of significant impacts. For both analyses we modeled response for different strata (midstory, saplings, seedlings) and levels of ecological organization (population vs. community). Analyses were conducted in the *R* package *survival*.

3.2.7 Reviewing the nature of community change

To determine the importance of deer preference for different species in determining experimental results we searched all papers for the terms “preference” or “palatable”. We then examined how authors analyzed or discussed their results with regard to preference, such as whether the abundance of non-palatable species was increasing over time in the controls, or whether non-palatable species also benefited from deer exclusion. To determine if deer recalcitrant understories were relevant to the outcomes of exclusion experiments we searched all papers for whether they cited Royo and Carson (2008), used the term “recalcitrant”, or discussed understory taxa associated with these layers, such as ferns and dwarf bamboo in Japan.

3.3 RESULTS

3.3.1 General description of studies in review

General information on the 49 studies that met our broad inclusion criteria are given in Table 2 (See Tables 7, Appendix B for full details). Most studies were conducted in the USA (n = 26) or New Zealand on white-tailed deer (*Odocoileus virginianus*; n = 28) or red deer (*Cervus elaphus*; n = 6). Most studies built <10 exclosures (mean = 22.5, median = 7; Fig. 20, Appendix B), excluded deer for just over 10 years (mean = 13, median 10, range = 1 - 60) and analyzed only two annual time points of data (mean 2.4, median 2, range 1 - 9). Studies in the USA were typically somewhat shorter (mean 12.5 years; Fig. 20) than in New Zealand (15.7 years). Based on our estimates and interpolations, the duration of overabundance prior to exclusion for our studies is about 40 years (range: 1-80). Deer were overabundant for a shorter period of time in North American (mean: ~25 years, range: 1 to 60) than in New Zealand (mean: 75, range: 40-80). Deer density varied widely, from 3 to 4 deer km^{-2} (Husheer *et al.* 2003; Tanentzap *et al.* 2009) to 88.2 km^{-2} (Abrams and Johnson 2012). Most studies report densities of 15-30 deer km^{-2}.

3.3.2 Summary of data

We extracted and summarized 143 responses from these 49 papers. Most studies reported on seedlings (n = 30 studies) and saplings strata (n = 25), but only 18 on mid-canopy or larger trees (Fig. 20, Appendix B). Stems referred to as seedlings were on average less <1 m and saplings < 2 m. There was, however, considerable variation between authors in these definitions. Most studies found some nominally significant impact ($p < 0.05$) on seedlings, shrubs and/or saplings (83% of studies). Mid-story impacts (stems ≥ 2m) were observed less often (45% of studies). Community characteristics (richness, diversity, composition) were investigated in many studies (n = 28; 57%) but impacts where detected only 50% of the time.

3.3.3 Meta regression

We calculated effect sizes for seedling and sapling community-level responses, and all midstory abundance and community-level responses. This resulted in 49 responses from 23 studies for use in our meta-regressions. Log response ratios for individual studies were almost all >0 (response ratio > 1) and the grand mean for all studies was significantly greater than zero (grand mean of all strata = log RR = 0.49, SE = 0.12, 95% $CI_{bootstrap}$ = 0.06-0.93, n = 49 effects from 23 studies) and the effect sizes for all individual strata where greater than zero (Fig. 6). Considering abundance and community-level response separately, abundance effect sizes were always greater than community-level effect sizes, and some community-level effect sizes were near zero (Fig. 7). Pooling seedlings and saplings together into a single understory strata, the community-level effect size was significantly less than zero (logRR = -1.78, $CI_{bootstrap}$ = -3.67 - -0.077; 33 responses from 16 studies). Pooling across strata there was no difference between species richness and species diversity effect sizes.

There was no evidence of an increase in effect sizes with increased duration of overabundance for any strata (DoA). In contrast, there was a strong positive relationship between the duration of exclusion and log response ratios (Fig. 8; $\beta = 0.027$, SE=0.01, $CI_{bootstrap}$ = -0.020-0.078; n = 49 responses from 23 studies). For individual strata there was only sufficient data to assess the relationship for saplings, which showed a stronger response than the pooled data (Fig. 8; $\beta = 0.066$, SE = 0.017, $CI_{bootstrap}$ = -0.053 - 0.19).

3.3.4 Time-to-event analysis

3.3.4.1 Duration of Overabundance (DoA)

Time-to-event models were used to estimate the median duration of overabundance (DoA) when a significant effect is observed. Among the studies that investigated subcanopy effects (stems generally > 2m in height), the median duration of overabundance was estimated as 60 years for abundance effects (11 of 14 effects significant at $p < 0.05$) and 80 years for community-level effects (9 of 12 effects significant). There was no evidence, however, that these median times were different than each other. Among studies that investigated sapling effects (stems generally 50 – 200 cm) the median duration of overabundance was 45.5 years for effects on sapling abundance (17 of 29 results significant) and 80 years for community effects (10 of 20 results significant), though there was no evidence that these medians were different. Among studies that investigated seedling effects (stems generally < 50 cm) the median duration of overabundance before was 40 years (12 of 24 results significant). For community effects four of 13 results were significant, but there was insufficient data to estimate a median time-to-event with survival models.

3.3.4.2 Duration of Exclusion

Time-to-event models were also used to model how much time elapses from the beginning of an experiment to when differences between fenced exclosures and controls are observed. For subcanopy trees the median time for a difference to be observed was 18 years (Fig. 9a; n = 22 of 28 results significant at $p<0.05$). Cox proportional hazard models indicated that there was no difference between abundance and community metrics in the response time, but did provide some evidence that a longer duration of overabundance (DoA) increased the time until a difference was observed ($p = 0.16$). The median time to event for sapling responses was 16 years (n = 35 of 59 results significant). There was no evidence that abundance responses were different than community response or of an effect of duration of overabundance. The median time to event for seedling responses was 13 years for abundance (20 of 33 responses significant) and 18 years for community metrics (6 of 17 responses significant), but there was no evidence that these were statistically different from each other. There was some evidence that an increased duration of overabundance delayed responses after deer exclusion ($p = 0.11$; Fig. 9b).

3.4 DISCUSSION

Ecologists and foresters around the globe are concerned that overabundant and invasive deer are altering the dynamics and structure of forest canopies (North America: Cote *et al.* 2004; Europe: Gill and Beardall 2001; New Zealand: Coomes *et al.* 2003, Tanentzap *et al.* 2012; Japan: Takatsuki 2009). Almost every exclusion study we review reported at least some form of understory (vegetation < 2 m in height) impact, indicating that overabundant and invasive deer consistently act as keystone herbivores (Waller and Alverson 1997) in the understories of forests around the globe (Fig. 6). Studies that are of long enough duration to assess impacts to forest midstories (≥2m in height) report significant changes after deer exclusion, indicating that canopy recruitment dynamics are potentially becoming different where deer are overabundant.

Several long-term studies report changes in community composition of midstory trees after deer exclusion (e.g. Kain *et al.* 2011, White 2012, Wright *et al.* 2012), providing direct support of the canopy composition change hypothesis. In contrast, midstory impacts are stronger for the abundance of trees than for community attributes such as species richness and diversity, though the difference is not significant (Fig. 7). In the understory strata (vegetation generally < 2 m; saplings and seedlings combined), increases in abundance are very strong after deer exclusion, yet community attributes decrease. This is likely occurring because formerly rare palatable species are becoming much more common in exclosures, resulting in a decline in species diversity. Overall, this indicates that non-palatable species are not-replacing palatable species 1:1 when deer become overabundant, and do not suppress palatable species after deer are excluded. This indicates that forests with overabundant deer have relatively low stem densities in their mid- and understories, potentially setting the stage for regeneration failure of both palatable and non-palatable species.

The few studies that attempted to model changes in abundance as a function of deer palatability did find that relative deer preference was an important predictor of responses to exclusion (Tanentazap *et al.* 2009, Wright *et al.* 2012). Both of these studies were conducted in New Zealand, where deer culls in recent decades have reduced deer densities and deer are hypothesized to be at low enough densities that there is not strong competition among the remaining deer for their preferred browse. Under these conditions deer impacts to canopy composition are most likely to occur because the remaining deer are at liberty to eat only their most preferred browse. In contrast, several studies report that species normally considered to be non-palatable increase when deer are excluded (Allen *et al.* 1984). For example, black cherry (*Prunus serotina*) is browsed by deer but is considered much less preferred than other species (Horsley *et al.* 2003, Kruger *et al.* 2008). Surprisingly, black cherry's abundance almost always increases when deer are excluded (Kain *et al.* 2011, Abrams and Johnson 2012, Rossell *et al.* 2005, Rossell *et al.*2007; see also Horsley *et al.* 2003). Low-palatability plants benefiting from exclusion could indicate that deer have undergone a diet switch due to depletion of preferred browse (Hiroshi and Koichi 2001, Coomes et al 2003) or alternatively could result from indirect, soil-mediated effects (Heckel *et al.* 2010, Kardol *et al.* 2014). Under these conditions, it is possible that deer will cause a general failure of canopy regeneration and potentially direct forest succession towards a more open woodland structure (Tanentzap *et al.* 2011).

Surprisingly, our meta-regression indicates that there is not a strong connection between the duration of overabundance and the magnitude or rate of change. This is counter to predication of Tanentazap *et al.* (2011) that recovery time should increase non-linearly with increasing duration of deer impacts. Time lags before recovery might not begin to become substantial until community composition has progressed and substantially changed seed rain. In contrast, time lags might not occur at all if general canopy regeneration failure is occurring because canopy density is changing, not the composition of seed sources. As expected, the effects of deer exclusion tend to increase in magnitude as the duration of overabundance increase (Fig. 8).

Time-to-event analysis indicates that the median duration of overabundance before impacts to this strata was 60 to 80 years. Many stands in North America that first experienced overabundant deer by the middle of the 20th century (Leopold *et al.* 1947) are therefore potentially reaching a critical stage where change in the midstories is occurring. A median time of 60-80 years of deer overabundance until a midstory change occurs agrees with estimates for how long it takes some deciduous trees to approach the canopy. Shade tolerant deciduous trees such as North American sugar maple *(Acer saccharum*) and American beech (*Fagus grandifolia*) can take 60-125 years before being in position to reach the canopy (Canham 1988, 1990). After deer are excluded our time-to-event analysis indicates that it typically takes a median of 13 to 18 years for changes to be detected, with faster changes occurring in seedling and sapling strata. The fact that changes in subcanopy strata can typically be detected in 18 years indicates that deer management will have to be conducted on a decadal scale, but that forests do respond to reduced deer densities.

We found no indication that recalcitrant understories were present in any of the studies we reviewed. Collard *et al.* (2010) specifically monitored ferns and observed no difference in abundance between controls and exclosures. Dwarf bamboos occurred in studies in Japan (Kumar *et al.* 2006, Nomiya and Kanazashi 2011) and form monocultures, but they are browsed by deer, reducing their impact (Kumar *et al.* 2006). Royo and Carson (2006) proposed that recalcitrant understories would be most likely to form in deer impacted stands that have also experienced disturbance such as logging. Many of the stands represented in our studies are young and even-aged and therefore likely have few and relatively small canopy gaps (Yamamoto 2000) and limited opportunities yet for recalcitrant layers to form.

Our meta-analysis confirms that deer impacts to forest understories are pervasive, and the changes to understory populations and communities can be propagated to midstories over the course of stand development and maturation. We find support for both the canopy composition change and canopy regeneration failure hypotheses, which highlights the need to consider both hypotheses when assessing deer impacts. Deer have been overabundant in many places in North America for >50 years (Leopold *et al.* 1947) and New Zealand for >100 years (Clark 1949, Atkinson 2006). The midstories of these forest are now potentially structured in a way that will result in a future canopy community or structure that is different than the original stand. Unless deer densities are reduced soon these stand will likely begin a process of permanent change. In areas where deer have only recently increased in abundance or become invasive it is unlikely that changes have progressed much into forest midstories given the slow rate of tree growth in closed canopy forests (Cowden *et al.* 2014, Rentch *et al.* 2003, Canham 1988, Canham 1988). The prospects for recovery are therefore much higher in these stands.

Table 2. Summary statistics for 49 studies included in review and meta-analysis.

Summary statistic	**Geographic Subset**	**Mean**	**Stand dev.**	**Median**	**Mode**	**Range**	**n**	**%**
Number of vegetation surveys		2.4		2	1.5 a	1-9	49	
Exclosure plot number		22.5	63	7	3 (n=6) b	1-400		
Exclosure plot size (m2)		10180	33150	400	400 (n=11)	1-160000		
Deer density (km^2)		28.8	22.8	23		3.5-88.2	31	63%
Duration of exclusion	**All studies**	13	11.6	10		2 to 60		
	North America	12.5	13	8	4 (n=4)	2 to 60	27	55%
	New Zealand	15.7		14.5		3 to 36.5	10	20%
	Non N. Am/NZ	10.8	9.1	8.5		3 to 30	9	18%
Duration of overabundance prior to exclusion	All	40.8	27.4	30		1 to 80	31	63%
	All studies	26.36	17.1	25.5		1 to 60	27	55%
	New Zealand	74	13.3	80	80	40 to 80	10	20%
Duration of overabundance at time of study	All	53.8	39	40		1 to 80	31	63%
	North America	38.86	30.1	33.5		1 to 60	27	55%
	New Zealand	89.7	13.3	94.5	80	40 to 80	10	20%

Notes:

a 16 studies with 1 survey, 16 studies with 2 surveys

b 5 studies used only 1 fenced/control plot pair

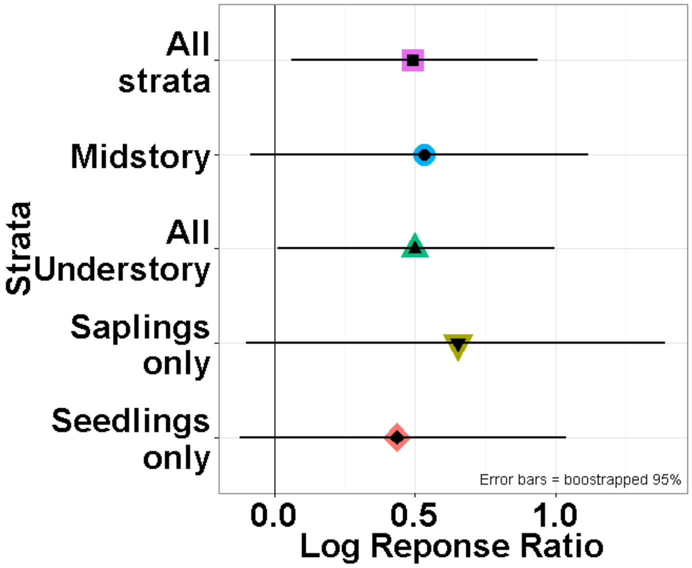

Figure 6. Meta-analytic mean effect of deer exclusion by woody vegetation strata. Effect sizes were calculated as log response ratios with zero indicating no mean difference in responses between fenced deer exclosures and controls. All strata = grand mean effect size across all strata and all responses. Stata are not mutually exclusive due to heterogeneity in how authors of individual studies defined strata. Midstory strata were generally > 200 cm in height and/or > 2 cm DBH. Saplings were generally > 50 cm and < 200 cm. Seedlings were generally <50 cm. Data are pooled across responses related to abundance and community metrics using a mixed model. No covariates (e.g. duration of overabundance) were included in the model. Error bars are +/- bootstrapped 95% confidence intervals.

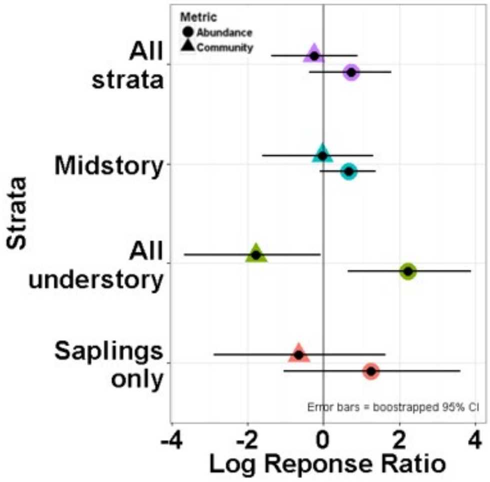

Figure 7. Meta-analytic mean effect of deer exclusion by woody vegetation response type and strata. Abundance metrics were usually counts of stems. Community metrics include species richness and community diversity (e.g. Simpson's diversity). Effect sizes were calculated as log response ratios with zero indicating no mean difference in responses between fenced deer exclosures and controls. All strata = grand mean effect size across all strata and all responses. Stata are not mutually exclusive due to heterogeneity in how authors of individual studies defined strata. Midstory strata were generally > 200 cm in height and/or > 2 cm DBH. Saplings were generally > 50 cm and < 200 cm. Seedlings were generally <50 cm. Data are pooled across responses related to abundance and community metrics using a mixed model. No covariates (e.g. duration of overabundance) were included in the model. Error bars are +/- bootstrapped 95% confidence intervals.

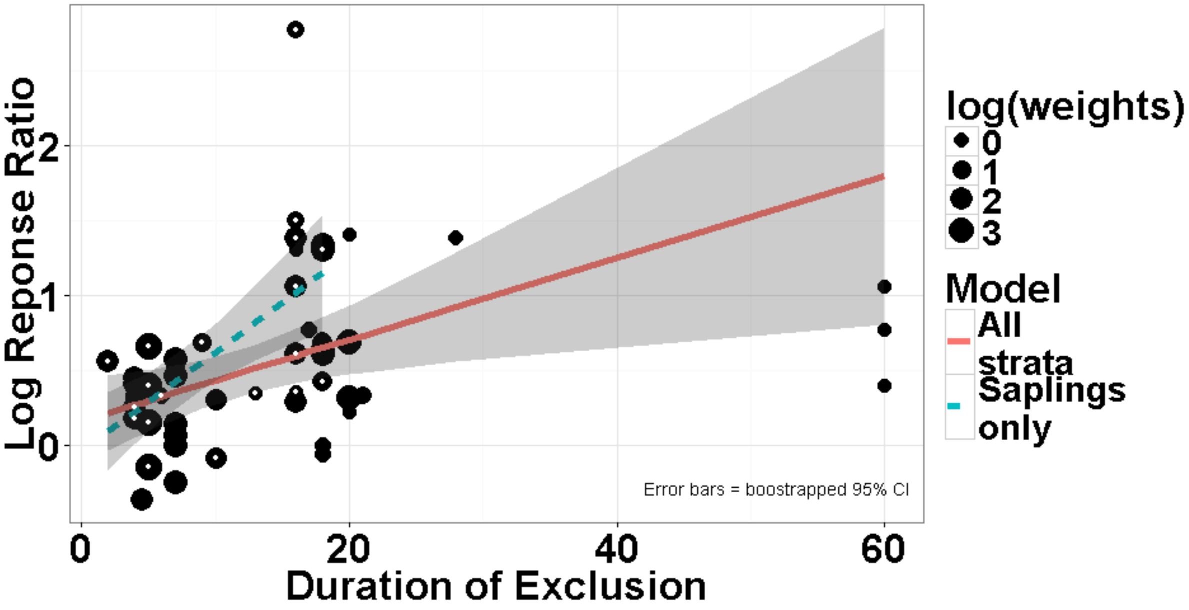

Figure 8. Effect of the duration of deer overabundance on observed effect sizes. Effect sizes (Log response ratios) of all strata (solid red line) and the sapling strata only (dotted blue line) are depicted. Size of points is proportional to the log of the meta-analysis regression weights, with smaller weights contributing less information to the regression. White dots indicate sapling data points. Error band = 95% confidence interval.

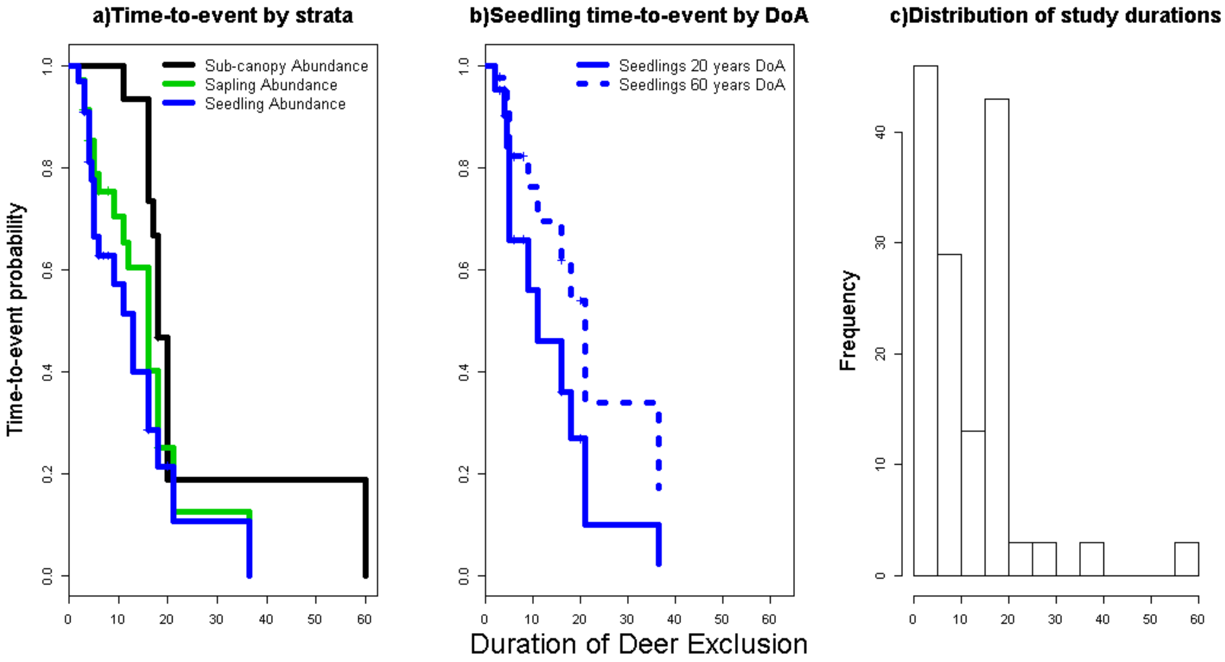

Figure 9. Time to event analysis indicates the relationship between observation of a significant change at $p < 0.05$ between deer exclusion plots and un-fenced controls. a) Variation in time to event by strata. b) Variation in time-to-event for seedlings for 20 versus 60 years of deer overabundance (DoA). c) The distribution of deer exclusion times in the 49 studies used in this meta-analysis.

4.0 COMPLEX TEMPORAL DYNAMICS DISGUISE SIGNIFICANT IMPACTS OF DEER EXCLUSION IN FORESTS.

4.1 INTRODUCTION

Mammalian and insect herbivores have pervasive impacts on plant biomass (Coupe and Cahill 2003, Flower and Gonzalez-Meler 2014), demography (Maron and Crone 2006), and diversity (Olff and Ritchie 1998, Carson and Root 2000; Allan and Crawley 2011). Surprisingly, reduction or removal of herbivores can fail to result in expected changes in plant populations' biomass, demography or communities' diversity (Gibson *et al.* 1990; Carson and Root 2000; Howe and Brown 2001; Simard *et al.* 2013). This lack of response can result from biotic factors such as dispersal limitation of re-colonization (Royo *et al.* 2010). Likewise, abiotic factors such as disturbance or light can be necessary for germination (Baskin and Baskin 1992) or growth (Canham 1988, 1990), even after herbivore removal (Royo *et al.* 2010, Nuttle *et al.* 2013). Mammalian herbivores can also potentially create coupled abiotic-biotic legacy effects through mechanisms such as soil compaction (Persson *et al.* 2000, Heckel *et al.* 2010, Kardol *et al.* 2014) or nutrient enrichment (Jensen *et al.* 2011, Murray *et al.* 2013) that alter both belowground conditions and plant communities (Bardgett and Wardle 2003; Wardle *et al.* 2004)

Factors moderating the responses of vegetation to herbivore removal are of great relevance to the ecological management of mammalian herbivores. Overabundant, invasive or overstocked ungulates and other large mammals have been shown to have especially strong impacts on biodiversity around the globe (Fleischner 1994; Côté *et al.* 2004, 2014; Campbell and Long 2009; Takatsuki 2009; Kuijper 2011). Surprisingly, reduction in the abundance of these large mammals does not always result in the desired vegetation change (Royo *et al.* 2010, Tanentzap *et al.* 2012, Collard *et al.* 2010). Recent experimental studies have investigated how the response of vegetation to the removal of mammalian herbivores can be moderated by abiotic and biotic factors, including competition (Royo and Carson, 2006, 2008), disturbance (Royo *et al.* 2010, Nuttle *et al.* 2013, Collard *et al.* 2010), and animal density (Knight *et al.* 2009, Horsley *et al.* 2003, Tremblay *et al.* 2007). Temporal factors such as the duration of reduced herbivore density (Brouwer 2015 Chapter 3), duration of overabundance prior to management or experimentation (Tanentzap *et al.* 2012, Brouwer 2015 Chapter 3) and the response rates of different metrics of vegetation change (i.e. biodiversity, biomass, density and community composition; Tanentzap *et al.* 2012) are likely to be equally important in understanding diverse vegetation responses**,** but are more difficult to address.

Temporal factors such as the rate at which vegetation changes when mammalian herbivores first become overabundant and the rate it changes when they are subsequently reduced in density are likely to be affected by numerous factors. Understanding these dynamics is an essential area of research since temporal variation in management intensity plays a central role in recent novel approaches for deer management. McShea (2012) asserted that long-term and large-scale reduction of deer herds to historical densities (~4 deer km^{-2}) is not acceptable to many stakeholders (e.g. USA: Frye 2010; New Zealand: Nugent and Fraser 1993). McShea (2012) proposed that localized, temporary, but extreme reductions in deer density could create suitable windows for forest management goals to be achieved. One way to achieve this for white-tailed deer (*Odocoileus virginianus*) could be through strategic doe hunting that removes matrilineal groups because deer have high female philopatry and low female dispersal (Porter *et al.* 1991, Hyngstrom *et al.* 2011; Lutz *et al.* 2015;). Sage *et al.* (2003) concluded that the creation of "windows of opportunity" through deer culls were essential to tree regeneration in their forestry system in central New York. Temporal and spatial variability in browsing pressure is also key to recent proposals to manage herbivores through "hunting for fear" whereby human hunters act more like real predators to induce higher vigilance and lower browse rates by deer (Cromsigt *et al.* 2013). However, a fundamental knowledge of temporal dynamics of vegetation change is essential in order to implement these forms of management. For example, data are needed on how long deer densities have to be reduced to achieve different management goals, or how long abundances can remain high between periods of intensive management.

The duration of herbivore reduction or exclusion will determine the amount of time for deterministic processes to occur, such as the re-growth of vegetation that tolerates browse, and for the chance occurrence of stochastic factors affecting community re-assembly such as seed dispersal and disturbance. Not surprisingly, a recent meta-analysis (Brouwer 2015, Chapter 3) confirmed the importance of the temporal dimension of ungulate management by indicating that effect sizes of deer exclusion increase significantly with time. Empirical explorations of how deer exclusion effects changes over time are uncommon. In fact, conclusions from most exclusion studies are limited by the short duration of the experiment (Bellingham and Lee 2006, Brouwer 2015 Chapter 3) and analyses that either only have available or only use one or two time points of data (Wisdom *et al.* 2006, Brouwer 2015 Chapter 3). These limitations preclude detailed analyses of temporal factors such as the rate and dynamics of vegetation change (but see for example Long *et al.* 2007). Similarly, the duration of overabundance should an important determinant of how vegetation responds; the longer deer have been overabundant, the more severe their impacts and the longer it will take for a forest to recover (Tanentzap *et al.* 2012). Generally, studies that manipulate ungulate densities are conducted at locations with extended histories of overabundance, or where the duration is not known (Brouwer 2015 Chapter 3). We therefore do not know how rapidly mammalian herbivores such as deer can change vegetation, or which components change most quickly.

Finally, there is likely to be a consistent temporal sequence of change during the periods of overabundance or after reductions in ungulate density. Tanentzap *et al.* (2012) hypothesize that when ungulates become overabundant, negative impacts will first occur to plant biomass, then to abundance, and finally to community diversity. Changes to vegetation after ungulate populations are reduced will likely occur in the same order, as tolerant vegetation grows, reproduction results in successful recruitment, and locally extirpated species disperse into a site. This sequence was partially observed by Royo *et al.* (2010) after increased sport hunting reduced deer herds; plant biomass and plant population density increased, but there was no increase in species diversity after six years.

To better understand how forests respond to deer impacts over time we experimentally excluded deer for a decade at a site that recently experienced an increase in white-tailed deer (*Odocoileus virginianus,* hereafter deer). Deer densities four times higher than historic levels (~20-40 deer km^{-1}; Kalisz *et al.* 2014) persisted for ~15 years prior to establishment of pairs of fenced deer exclusion and unfenced deer access (control) plots. Woody vegetation was then surveyed biennially to track changes over time. This unique combination of a recent deer irruption and intensively monitored experimental exclusion allowed us to address five questions: 1) Was the relatively short duration of deer overabundance (~15 years) sufficient to suppress woody plant populations and communities? 2) Has a doubling of the duration of deer overabundance resulted in continued decline in our control plots? 3) Do the effects of deer exclusion on vegentation follow the temporal sequence proposed by Tanentzap *et al.* (2012), with changes occurring first to biomass, then plant populations, then community diversity? 4) Has enough time elapsed for changes in understory vegetation within the browse height of deer (< 2 m) to affect the abundance or diversity of midstory trees? 5) Are vegetation changes driven by the relative palatability of different species as is frequently hypothesized (Waller and Alverson 1997; Knight *et al.* 2009; Tanentzap *et al.* 2012)?

We will address these questions by systematically using two statistical comparisons across the years of the study. First, we compare metrics between the two treatments within each year. Second, we compare metrics over time for each treatment to its initial state when the experiment began. Explicitly conducting within-year comparisons between the treatments as well as between-year comparisons within treatments allows us determine whether differences between treatments are due to recovery in our deer exclusion plots, continued vegetation degradation in our deer access control plots, or both (Fig. 21 a-c, Appendix C). We consider three size classes of woody plants that can be affected by deer, seedlings (stems < 30 cm), saplings within the browse layer (stems 30 cm - 200 cm) and small tress in the sub-canopy (stems ≥200 cm in height), and compare the responses of woody species known to be preferred deer browse versus those of less preferred species.

4.2 METHODS

4.2.1 Deer exclusion experiment

We conducted our study in a beech-maple forest in southwestern Pennsylvania (Fox Chapel Borough, Allegheny County; 40° 52' 01.40" N; 79° 90" 10.75" W). The Trillium Trail, a 16 ha nature reserve along Squaw Run, is embedded within 1450 ha of forests and parklands owned and stewarded by Fox Chapel Borough. This forest contains a diverse array of woody (Table 8 Appendix C) and herbaceous species (Table 9 Appendix C; see also Appendix 1 in Hale *et al.* 2011) growing on moderately sloping (8-15%) silt- loam soils. Increases in deer abundance in this area occurred in the early 1990's (L. Smith, West Penn Conservancy, *personal communication*). Aerial surveys conducted between 1992 and 2002 confirmed high deer abundances (range 20-40 deer/km^2), which is ~2-4 times the historical average in western Pennsylvania (Kalisz *et al.*, 2014).

In the fall of 2002, six 12 m x 12 m paired deer exclusion and deer access treatment plots were established in Trillium Trail. Paired plots were chosen with respect to understory herb diversity but without respect to woody species diversity. In autumn 2002, fences surrounding the deer exclusion plots were built. Fences are 3 m tall and the mesh size (15 cm x 15 cm) effectively excludes deer (Vercauteren *et al.* 2010) but allows most other vertebrates access. Each plot is divided into 36 2m^2 subplots and all data is collected within these subplots. Tree falls were left in place except for sections that breech the deer excluding fences.

4.2.2 Data collection

Since 2003 we have censused seedlings and saplings of all vine, shrub, and tree species (hereafter "woody species") biennially. Seedlings and saplings were defined by height classes (<30cm, 30-200cm, respectively) and all individuals of all woody species within the 36 subplots/plot were counted (Table 8 Appendix C). As an index of biomass (Hermy 1988) we also estimated the percent cover of all woody vegetation ≤ 2 m. Percent cover for an individual species could not exceed 100% but could for the summed cover of multiple species in the same sampling unit.

To determine if understory impacts had propagated beyond the browse layer we collected additional data in 2011 and 2013 on all stems ≥200 cm in height. For these mid- and overstory stems we measured the diameter at breast height (DBH) of all individuals with any portion of their stems rooted in our plots. To determine if deer diet preference (aka "palatability") impacts the magnitude and rate of change of species over time we classified the relative preference of deer for all wood species. Deer preference for each species was qualitatively classified as high or low (Table 8 Appendix C) using peer-reviewed studies (Healy 1971, Heinrich 1983, Krueger *et al.* 2009, Long *et al.* 2007, Wakeland and Swihart 2009, Nuttle *et al.* 2013), and government reports (Latham *et al.* 2005). A species was ranked as high preference if most sources indicate that deer preferred it, low if most studies indicated that they did not, and equivocal if there was no consensus or a lack of information. Overall, our classification was informed by two considerations: deer utilization of or preference for the species, which depends on deer behavior, and the palatability of the species to deer, which is generally a function of leaf traits (Mason *et al.* 2010).

4.2.3 Statistical analyses

Because of the large number of sugar maple stems (*Acer saccharum*), likely due to a mast event in the early 2000s (S. Kalisz, *personal observation*), and the variation in life history among the woody species, we analyzed our seedling and sapling data using two approaches. First, we pooled the abundance of all species and analyzed the total number of woody stems in the seedling and sapling strata. Second, we grouped the data in each based on species identity and life history. These groups were: sugar maple (*A. saccharum*), other canopy tree species (all tree species except sugar maple capable of joining the canopy; e.g. *A. rubrum, Fagus grandifolium, Fraxinus americana, Prunus serotina, Quercus rubra, Q. alba,* and *Tilia americana*) and all small trees, shrubs, and vines that do not enter the canopy (e.g. *Hamamelis virginiana, Lindera benzoin, Parthenocissus quinquefolia* and *Toxicodendron radicans*).

We used two analytical approaches to determine the temporal dynamics of change inside and outside our experimental plots. First, we compared the effects of deer exclusion on the density of woody stems, calculated as the sum of the number of stems in all 36 subplots within each plot (stems 0.0144 ha^{-1}). Second, we characterized the spatial distribution of woody stems by considering their frequency of occupancy in subplots within each plot. We defined occupancy as the presence of ≥ 1 stem in a subplot and calculated percent occupancy for each plot as (# of subplots with ≥ 1 stem)/(36 subplots).

We analyzed the woody stem density across sampling years using repeated-measures Poisson mixed models (Gelman and Hill 2007; Zuur *et al.* 2009). To accommodate overdispersion we included an “observation-level” random effect, resulting in a Poisson-normal mixed model (PNMM; Kéry 2010; Maindonald and Braun 2010). We modeled percent occupancy over time using a logistic-binomial mixed model. Proportional data such as these are typically overdispersed (Gelman and Hill 2007) and we included an observation-level random effect in these models as well, resulting in a logistic-normal model (Warton and Hui 2011; Kéry 2010). To determine the influence of overdispersion we calculated a variance inflation factor and tested whether it was different from zero (Gelman and Hill 2007).

To estimate the impact of deer on the biomass of woody species, we averaged the percent cover estimates of species in each 2 m^2 subplot across all 36 subplots/plot. To investigate the effect of deer browse on the abundance of palatable versus non-palatable species we used two separate methods. First, we calculated the percentage of plants classified as palatable (e.g. # of stems in "palatable category/all stems; Table 8 Appenbdix C) in each plot to look for overall changes in relative abundance of palatable stems. We similarly calculated the palatable biomass using our percent cover data. Second, we modeled the abundance of each species in each plot using a mixed effects model with partially crossed random effects (Baayen *et al.* 2008) for plot and species. We only included species that occurred in at least one of the treatments within a pair of plots at some time during the experiment.

To determine the effect of exclusion on the density of subcanopy trees moving beyond the browse line, we modeled the number of stems ≥ 2 m in height but ≤ 10 cm DBH in each plot with a PNMM. Since larger trees (i.e. > 10 cm DBH in 2011) were likely to have already reached a size refuge from deer browse at the time our experiment began, we did not include them in our analyses.

For each treatment in each plot we determined species richness and calculated inverse Simpson's diversity using the *vegan* package in *R* (Oksanen *et al.* 2013). Species richness was analyzed with a Poisson-normal model and diversity with a linear model.

We tested for treatment differences with yearly pairwise contrasts (e.g. Exclosure_{2013} versus Control_{2013}). We also used linear trend contrasts (Bretz *et al.* 2010; Rosenthal and Rosnow 1985; Gurevtich and Chester 1986; Day and Quinn 1989) to determine if there were the linear trends within treatments. Additionally, if trends in control and exclosure plots where both significant we tested if the trends had similar patterns of change (Gurevitch and Chester 1986). Finally, we tested for evidence of curved or asymptotic dynamics over time using quadratic trend contrasts. Curved patterns over time could potentially be indicative of feedbacks due to inter- or intra-specific competition or self-thinning (Coomes and Allen 2007), or plants growing out of a size class. Contrast analyses were conducted using the *multcomp* package in *R* (Hothorn *et al.* 2010). To compare the size distributions of small subcanopy trees (≥ 2 m height, ≤ 10 cm DBH) between treatments and years we used a Kolmogorov-Smirnov test (Sokal and Rolf 2011; Tanentzap *et al.* 2011).

For within-year contrasts we calculated effect sizes to permit comparisons between different types of response variables (i.e. seedling number, sapling number, species richness). For Poisson regression we calculated the log incidence rate ratio (log IRR; Hilbe 2007) and for logistic regression the log odds ratio (Rita and Komonen 2008). Both effect sizes indicate the magnitude of difference between treatments. For example, if the log IRR for the density of saplings in the deer excluded versus the deer access control plot is 0.4, the IRR is exp(0.4) = 1.5. This means that there are 1.5 times as many seedlings in the absence of deer as in the control. We report IRR and OR but plot log IRR and log OR to improve interpretability as recommended by Galbraith (1988). Raw means are reported in appendices.

For all analyses we used mixed models with plots (n=12) nested within pairs of plots (pairs = 6) with treatment and year as fixed effects. Percentage data (cover, palatable stems) were logit transformed (Warton and Hui 2011). All analyses were conducted in *R 3.1.0* (R Core Team 2014) using the *lme4* 1.1-6 mixed modeling package (Bates *et al.* 2014).

4.3 RESULTS

4.3.1 Summary of results

Changes within our seedling size class (< 30 cm) were similar between treatments (Figs. 22 and 23, Appendix C) and we therefore focus mostly on dynamics of our sapling (30 cm – 200 cm height) and subcanopy (> 200 cm height) size classes.

To understand the rate at which different aspects of forest vegetation change, we focus our attention on five different comparisons (Table 3). First, we consider the first year that a significant difference occurred between the fenced exclusion plots “E” and the control plots “C” (Table 3, column ("$C_{\text{year t}} \neq E_{\text{year t}}$"). Second, we check if in the final year of the experiment there were differences between the control and exclusion plots (“$C_{2013} \neq E_{2013}$”). Third, we determined the first year that a treatment was different from its initial condition in (2003; Table 3 columns "$E_{\text{year t}} \neq E_{2003}$" and "$C_{\text{year t}} \neq C_{2003}$"). Fourth, we tested whether either treatment exhibited a linear change over time, and whether there was evidence that the dynamics of their trends was similar ("$C_{\text{trend}} \neq E_{\text{trend}}$"). Fifth, we tested whether either there was any curvature in the response of treatment, as indicated by a significant quadratic trend contrast, and whether these curves were similar. Significant curvature could be an indication of self-thinning or competition in exclusion plots and/or increased browsed rates in access plots.

4.3.2 Total woody biomass (percent cover)

There was a significant positive trend in woody percent cover in the exclusion plots (Fig. 10; linear trend contrast $z = 1.15$, $p = 0.01$) but no change in the control plots ($z = 0.3$, $p = 0.8$). This resulted in subplots in fenced exclusion plots having ~2 times as much cover of woody species as the controls by 2013 (Control cover = 10.23% ± 2.5, Exclusion cover = 20.1% ±/-3.5). Increases in percent cover in the exclusion plots where not completely linear; percent cover increased initially through 2009 but then decreased slightly but significantly by 2013 (Fig. 10; Quadratic trend contrast: $p=0.032$). Percent cover responded fairly quickly to deer exclusion. After four years,, percent cover in the deer exclusion plots exceeded its initial values ($p_{2007}=0.04$), and by 2009 was significantly denser than controls ($p_{2009} = 0.053$, $p_{2011} = 0.017$, $p_{2013} =0.026$).

4.3.3 Seedling dynamics (stems < 30 cm height)

Seedlings dynamics were similar in the control and exclusion plots for all metrics. Seedling abundance (Fig. 22 a-c) and occupancy (Fig. 23 a-c) both declined over time, primarily due to declines in sugar maple in both treatment plots (Figs. 22a, 23a). There were no significant differences between treatments in seedling species richness or diversity.

4.3.4 Sapling dynamics (stems 30 cm to 200 cm)

4.3.4.1 Sapling density

Sapling density in both treatments increased over time (Fig. 11c,d, Fig. 22). In the fenced exclusion plots both sugar maple (Fig. 11c; linear trend contrast $z = 2.6$, $p = 0.008$) and other canopy tree species increased (Fig. 11d, trend contrast $p < 0.001$). In the control plots, sugar maple exhibited a net, but non-significant, decline (linear contrast $z = 0.8$, $p = 0.4$) while other canopy tree species increased (Table 3). While there were never significant differences in sapling density between treatments at the $p < 0.05$ level, both sugar maple and all other species increased in the deer exclusion plots above their starting abundance in 2003 (Table 3; Fig. 11a,b). Both sugar maple and other canopy tree species exhibited significant curvature to their abundance trends (sugar maple: quadratic trend contrast $z = 3.03$, $p = 0.002$; other canopy trees species; $p = 0.003$), due to slight declines in abundance by 2013 relative to 2011. Increases in the control were slow but large enough that the abundance of non-sugar maple stems exceeded initial abundances 2011 ($p=0.04$) and remained high in 2013.

4.3.4.2 Sapling cccupancy

Occupancy rates for saplings of sugar maple and all other species increased in both treatments, though the rate of change was different between treatments (difference between trends contrast $p = 0.02$). Both treatments also exhibited quadratic trends (exclusion plots $p = 0.03$; Control plots $p = 0.06$. Occupancy in the fenced deer exclusion plots responded quickly and exceeded its initial values for sugar maple by 2005 ($p = 0.03$). Overall, sugar maple occupancy in the exclusion plots doubled from 35% (±16% SE) in 2003 to 75% (±7% SE) in 2013. Occupancy in the control plots for sugar maple (Fig. 11c) and all other canopy tree species (Fig.11d) exceeded their initial states, but changed more slowly than the deer exclusion plots.

4.3.4.3 Sapling community metrics

Sapling species richness exhibited a significant positive trend in both treatments (Table 3). Sapling richness was marginally higher in the deer exclusion plots from 2007-2011 ($p_{2007} = 0.13$,

$p_{2009} = 0.23$, $p_{2011} = 0.17$), but exhibited a decline by 2013 (quadratic trend contrast $p = 0.002$). Sapling-layer Shannon diversity decreased over time in both treatments (Table 3, $p < 0.001$).

4.3.4.4 Sapling palatability

Sugar maple (*Acer saccharum*) is a moderately preferred forage for deer in this region and was the most abundant seedling, sapling, subcanopy and overstory in both treatments. Black cherry (*Prunus serotina*) was the most abundant low-preference species, but was relatively rare in the understory of this closed canopy site. We observed no differences between the treatments in the percentage (palatable stems/total stems), relative percent cover, or density (stems / plot) of palatable species (data not shown).

4.3.5 Subcanopy tree dynamics (stems > 200 cm height)

4.3.5.1 Subcanopy tree abundance

Surveys in 2011 and 2013 indicated that 10 years of deer exclusion marginally increased the density of small sugar maple trees (≥ 200 cm height, ≤ 10 cm DBH) relative to the controls. Densities of subcanopy sugar maple were higher in fenced enclosures in 2011 ($\chi^2_{treatment} = 2.57$, $p = 0.11$, incidence rate ratio IRR =1.57). The abundance of sugar maple doubled on average in both treatments from 2011 to 2013 ($\chi^2_{year}=3.8$, $p = 0.052$, IRR = 1.72) but there were no significant treatment by time interactions. The abundance of subcanopy trees, however, was highly variably between plots. There were 151 stems in 2011 > 200 cm, ranging from one to 99 per plot in 2011, and seven to 194 in 2013.

4.3.5.2 Small tree size distribution

In 2011, the first year we took data on stems > 2 m in height, the distribution of diameter at breast height (DBH) measurements of all species combined was significantly different between treatments (Fig. 13; Kolmogorov Smirnov test: $D_{2011} = 0.4$, $p = 0.001$; $D_{2013} = 0.3$, $p = 0.001$). Within each treatment, the DBH distributions changed from 2011 to 2013 ($D_{\text{deer access}} = 0.48$, $p < 0.0001$; $D_{\text{deer exclusion}} = 0.69$, $p < 0.0001$). Considering just sugar maple, there was no difference in the DBH distribution between treatments in 2011 ($D_{2011} = 0.26$, $p = 0.2$, $N_E = 58$, $N_C = 24$) but the distribution was different in 2013 ($D_{2013} = 0.27$, $p = 0.01$, $N_E = 101$, $N_C = 54$). The distribution of non-sugar maple subcanopy trees differed in both years ($D_{2011} = 0.39$, $p = 0.037$, $N_E = 28$, $N_C = 24$; $D_{2013} = 0.35$, $p = 0.012$, $N_E =52$, $N_C = 35$).

4.4 DISCUSSION

Our experiment compared deer access plots that had experienced ~25 years of deer overabundance to exclusion plots that experienced ~15 years deer browse followed by a decade of recovery. Woody vegetation was dynamic regardless of treatment, with increases in sapling density and occupancy through time (Figs. 11, 12). These results indicate that even in at high deer densities (20-40 deer/km^2, Kalisz *et al.* 2014) some woody species can continue to grow and enter the forest midstory. However, changes were always larger and occurred faster in deer exclusion plots than in deer access plots (Table 3). Differences in population dynamics were most obvious in terms of percent cover (Fig. 10), sapling occupancy (Fig. 12) and the size distribution of subcanopy stems (Fig. 13). Difference in sapling abundance were more subtle and most evident when we compared stem densities against their initial levels in 2003, and by considering long-term trends using longitudinal statistical methods. For example, even though comparisons within years implied that saplings in exclusion plots were not more dense than in controls, saplings increased above their initial density generally by 2005 in exclusion plots but not until 2011 in control plots (Table 3). Similarly, by considering all seven sampling periods, we detected significant upward trends in the abundance of sugar maple in our fenced exclusion plots, but there was no such trend in controls.

Almost all of the increases in sapling abundance and occupancy displayed some curvature by 2013, as indicated by significant quadratic trends (Table 3). This implies that after initial increase, sapling abundance began to attenuate. This result could occur due to competition within or between species, or stems were growing out of the size class into our subcanopy strata. Occupancy is bounded at 100% of the total subplots or subplots with suitable habitat (e.g., not obstructed by rocks, treefall, stumps, etc) and it is therefore not surprising that it asymptotes.

4.4.1 Seedling and sapling dynamics

When the experiment began in 2003 sugar maple (*Acer saccharum*) seedlings (stem < 30 cm) were extremely dense (Fig. 22a) and quickly declined from 2003 to 2005, consistent with mortality of seedlings following a masting event. Other studies have found that a sugar maple mast year can result in >100 seedlings m^{-2} directly under maternal canopies, with 90% mortality within the first several years (Hett 1971, Cleavitt *et al.* 2014). Our results indicate that regeneration conditions for sugar maple remained high at our study site, despite the elevated deer abundance. We saw no evidence of differences in mortality between treatments, and other studies have reported no deer-associated mortality with sugar maple seedlings in their first seven years (Cleavitt *et al.* 2014).

Interestingly, seedlings of other tree species also declined significantly in both treatments (both $p_{trend} < 0.001$) and by 2011 were significantly lower in density than when the experiment began (deer access control plots: $z_{2011} = -2.37$, $p = 0.02$; deer exclusion plots $z_{2011} = -3.5$, $p < 0.001$). We found no evidence that the rate of decline differed between treatments ($p_{trend\ comparison} = 0.5$). Interspecific competition between similarly sized seedlings, especially the cohort of sugar maple mast seedlings, shading by larger saplings (Graignic *et al.* 2014; Hane 2003), and some growth into the sapling size class likely account for this.

In contrast to declines in seedling abundance, saplings (30 – 200 cm) consistently increased in occupancy and abundance in both treatments. For sugar maple, we observed marginal but consistently increases in abundance in our fenced exclusion plots (Fig. 22d) and consistent increases in occupancy (Fig. 23d) in both treatments. Increases in occupancy were significantly larger and faster in our fenced plots, indicating that deer exclusion increased the rate that sugar maple entered this size class.

Though they exhibited overall increases, most sapling metrics declined somewhat between 2011 and 2013. Attenuation of abundance is consistent with continued thinning due to competition (Coomes and Allen 2007). Declines in abundance overtime within a large size class (e.g. 30 cm – 200 cm) are inevitable consequences of imposing size classes when in fact size is continuously distributed. In our study, sugar maple sapling abundance increased in the exclusion plots, but quadratic dynamics and modest increases in the controls mask the ecological magnitude of this change (Fig. 11). It is possible that ecologically relevant changes in saplings will not appear statistically significant if sapling density declines due to successional processes such as self-thinning within exclusion treatments.

We observed no evidence of masting or high germination rates among any species other than sugar maple; moreover, non-sugar maple seedlings declined overall. The increase in the sapling abundance and occupancy of non-sugar maple saplings is therefore likely due to suppressed stems increasing in size. On both large (Miller *et al.* 2009, Crimmins *et al.* 2010) and small spatial scales (Jarnemow *et al.* 2014, Moser *et al.* 2006) the availability of alternative browse can increase the growth of tree seedlings. Since the increase in non-sugar maple stems occurred in both treatments, it is possible that the abundance of highly palatable sugar maple stems reduced browse pressure on other species, allowing them to increase in height and transition from our seedling to our sapling size class.

4.4.2 Small tree dynamics

Some movement of sugar maple saplings into the midstory occurred in both treatments as evidenced by marginally significant increases in the abundance of stems > 200 cm between 2011 and 2013. Abundance was higher both years in the deer exclusion plots, indicating that release from deer browse was beginning to affect midstory transition dynamics. Additionally, the size distribution of sugar maple and other species differed between treatments (Fig. 13). This study therefore provides evidence that the effects of 15 years of overabundance can potentially be reversed by a decade of deer exclusion.

Subcanopy sugar maple exhibited different size dynamics relative to the other tree species. Sugar maple was more abundant both years we surveyed stems > 200 cm in height (2011, 2013), but its DBH size distribution was different between treatments only in 2013. We suspect that in our controls abiotic factors allowed some saplings to grow larger despite high browse pressure, which resulted in an increase in small sugar maple trees between 2011 and

2013. Other studies have also reported the growth of some stems into larger size classes despite deer browse, though exclusion always increases this rate. Stems that grow in the presence of browsers are usually less preferred browse species (White 2012, Husheer 2007), but not always (Bellingham and Allen 2003). It is generally assumed that high deer densities in closed canopy forest will result in changes to the overstory in terms of density and species composition. Such changes are common in stands that have been thinned or cut (Horsley *et al.* 2003, Beguin *et al.* 2009), but are not yet common in un-managed forests because of the slow rate of canopy turnover. Unfortunately, long-term studies in closed canopy forests that could confirm that deer effects result in changes in canopy composition are rare (Brouwer 2015 Chapter 3), but are clearly needed. Our study demonstrates that it is possible for a palatable tree species (sugar maple) to survive high deer densities and progress towards the midstory. Masting likely played a role in this response and the importance of other stochastic events and disturbance needs more study. A combination of changes in deer density and disturbance appears to be essential for regeneration in some closed canopy forests (Collard *et al.* 2010, Nuttle *et al.* 2013; Fig. 21f,g, Appendix C). The effects of masting could be studied using seed addition experiments in smaller deer exclusion plots.

4.4.3 Woody cover

Despite increases in the abundance and occupancy of most sapling species in the controls, percent cover did not increase where deer had access; in contrast, it increased by 50% in the fenced exclusion plots (Fig. 10). Tanentzap *et al.* (2012) propose that plant biomass, which can be approximated using cover (Hermy 1988), should be the first vegetation characteristic to respond to deer overabundance, and therefore should be the first to respond to deer exclusion. In our study, percent cover and stem density appear to be somewhat uncoupled. In the exclusion plots, increases in cover match increases in abundance and occupancy, while in the controls increase in abundance and occupancy occur without significant changes to cover (likely due to browse). Our data suggest that seedlings and saplings can persist in the understory for prolonged periods, and are likely changing little in biomass across long periods of time.

4.4.4 Sapling community

We expected that there would be no changes in community-level metrics in the exclusion plots due to the short duration of overabundance (Tanentzap *et al.* 2012) and that community composition would potentially change in the controls due to the doubling of the duration of overabundance. However, sapling species richness increased in both of our treatments and the spike in sugar maple abundance likely drives these dynamics. Our occupancy data indicate that sugar maple appeared in locations where it had previously been absent, thereby increasing species richness, but also dominated numerically, decreasing diversity.

4.4.5 Sapling palatability

Most species at this site were relatively palatable to deer and the only non-palatable tree capable of entering the canopy is black cherry (*Prunus serotina*), but is it not common in the canopy of our study site. Given the numeric dominance of sugar maple, the paucity of low palatability species, and the generally high rate of canopy closure (N Brouwer, *personal obs*.) it is not surprising that differences in deer preference did not affect dynamics in this forest.

Changes in sapling dynamics generally followed predictions of Tanentzap *et al.* (2012) with increases in biomass and abundance but no significant changes in richness or diversity. However, our fastest responding metric was occupancy. We suggest that occupancy is a metric that possibly integrates the net effects of growth, recruitment, and competition by focusing on the occurrence of stems throughout a plot rather than their abundance, which will necessarily decline as plants released from browse begin to grow. To our knowledge we are one of the first studies to use this metric. Changes in occupancy indicate that the horizontal distribution of plant occurrence and biomass is changing throughout our plot. It also indicates and that plants, either from seed or the seedling bank, are successfully colonizing and growing up into the formerly depauperate sapling layer. Thus not only is the vertical structure of the forest responding to deer exclusion as trees grow from seedlings to saplings and from saplings to midstory trees, but also the horizontal structure is changing as well. We note that the use of occupancy as a metric will likely be highly dependent on the size of subplot that is considered.

4.4.6 Relevance for management

Our study provides information relevant to the proposal of McShea (2012) that a shifting landscape of deer management could be used to achieve forestry and biodiversity goals. At our site, ten years of deer exclusion achieved measurable increases in the movement of saplings into the overstory (> 200 cm) after a relatively short duration of deer overabundance. The rate at which our system responded could be considered an optimistic maximum rate of recovery since our site had not experienced overabundant deer previously and deer density was reduced to zero through fencing. Sites that have experienced longer durations of deer overabundance or that cannot reduce deer through exclusion should expect to control deer for a minimum of ten years.

A decade of deer exclusion has been proposed in other studies as a minimum for achieving forest management goals (Tanentzap *et al.* 2012; Collard *et al.* 2010).

Table 3. Summary of effects of deer exclusion on sapling responses. The years in the table indicate the first year during biennial surveys that a statistically significant ($p < 0.05$) difference was observed for a specified comparison. Different types of comparisons are in columns, and different response variables (eg abundance, occupancy) and groups of species (all species, sugar maple, canopy trees) are in rows. Positive (+) signs indicate that responses were larger in fenced exclosures versus controls, e.g., abundance of saplings was higher. Negative (-) signs indicate that responses were larger in controls. All results are for our sapling size class (stems 30 cm - 200 cm in height). Tests were conducted for all woody species together, for sugar maple (*Acer saccharum*), and all canopy tree species other than sugar maple. Canopy species are those capable of entering the canopy. The 1st column ("$C_{year\ t} \neq E_{year\ t}$") indicates the 1st year that a within-year ANOVA contrast shows that the exclosure was not equal to the control. The 2nd ("$E_{year\ t} \neq E_{2003}$") and 3rd columns ("$C_{year\ t} \neq C_{2003}$") indicate the 1st year that conditions within a treatment were not equal to its initial state in 2003 when the experiment began. The 4th and 5th columns indicate the significance and direction of any linear trends. If trends were significant, the 6th column ("$C_{trend} \neq E_{trend}$") indicates whether there is any indication that they changed at unequal rate. The 7th and 8th columns indicate the significance and direction of any significant curvature to the trend (quadratic effect). The final column ("$C_{2013} \neq E_{2013}$") indicate whether curvature to the trend resulted in a non-significant different between the exclosure and control by the final year of the study, 2013.

		Pairwise comparisons				Linear trend			Quadratic Trends	
Strata & Response	**Species Group**	$C_{year\ t} \neq E_{year\ t}$	$C_{2013} \neq E_{2013}$	$E_{year\ t} \neq E_{2003}$	$C_{year\ t} \neq C_{2003}$	**E**	**C**	$C_{trend} \neq E_{trend}$	**Exclosure**	**Control**
Percent Cover	**All species**	2009(+)	(+)	2007(+)		(+)		d	(+)	
Saplings Abundance	**All species**			2005(+)		(+)	(+)		(-)	
	Sugar maple		e	2005(+)		(+)		NA	(-)	
	Canopy trees			2007(+)	2011(+)	(+)	(+)		(-)	
Sapling Occupancy	**All species**	2005(+)	(+)	2005(+)	2007(+)	(+)	(+)		(+)	
	Sugar maple	2005(+)	(+)	2005(+)	2007(+)	(+)	(+)		(+)a	(+)a
	Canopy Trees	2009(+)		2007(+)	2009(+)	(+)	(+)		(+)b	
Sapling Species Richness	**All species**			2007(+)	2011(+)	(+)	2007(+)		(+)	
	Canopy Trees			2007(+)	2013(+)	(+)	(+)		(+)	
Sapling Species Diversity	**All species**			2013(+)	2011(+)	(+)	(+)			
	Canopy Trees			2011(+)	2013(+)	(-)	(-)			(-)

a Quad trend likely occurs due to saturation of available habitat

b p=0.06

c p=0.08

d For % cover the trend within the exclosure is significant while the control trend is not. However, the difference between the trends is only marginally significant. This is likely due to the significant quadratic effect within the exclosure attenuating the linear trend.

e p=0.16

f percent cover includes stems in both the seedling and sapling size classes.

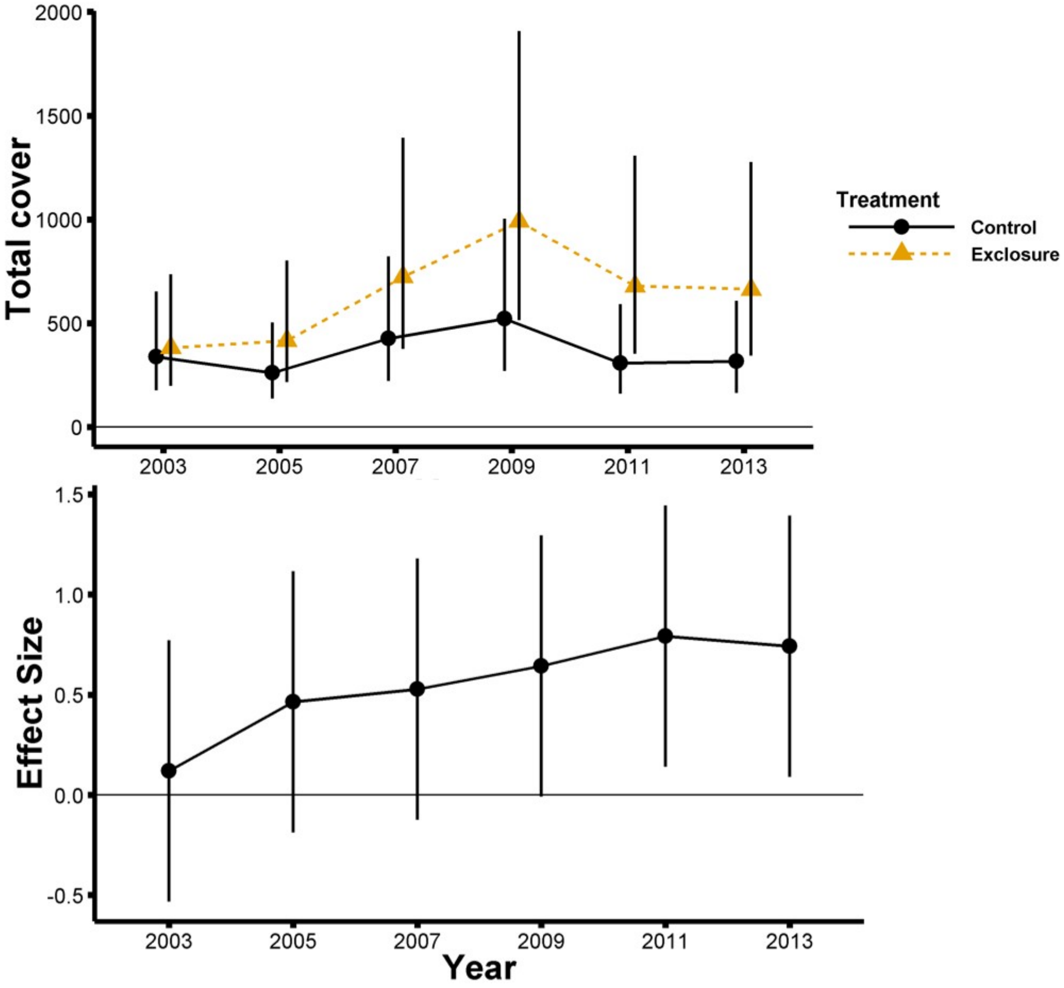

Figure 10. Effect size and annual means of total percent cover from five pairs of fenced deer-exclsoures/deer access plots at Trillium Trail, PA. Effect sizes (upper panel) are on the untransformed logit scale. Our index of biomass (lower panel) is the total cover of all woody species within a plot, summed across all 36 subplots. Error bars are 95% confidence intervals.

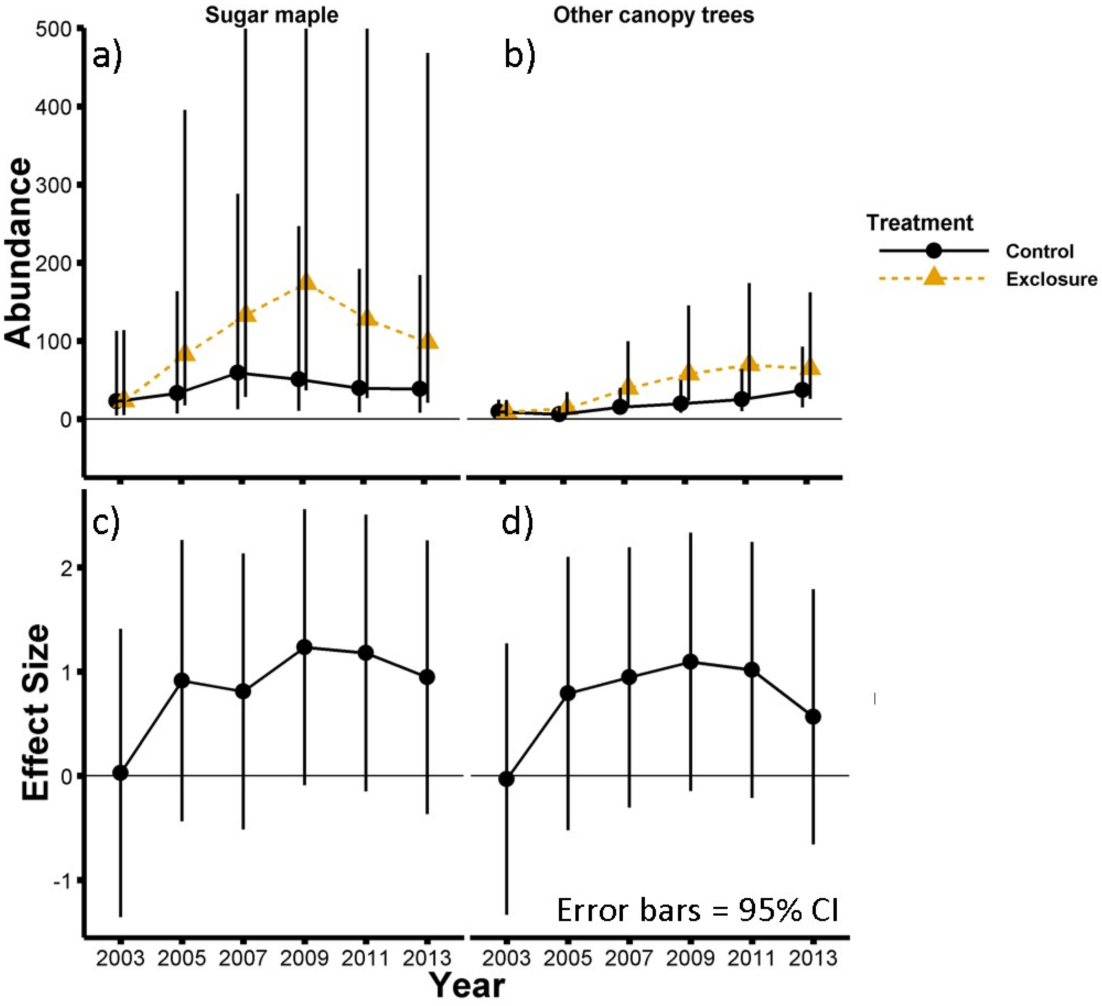

Figure 11. Effects of deer exclusion on sapling abundance of sugar maple (a,c; *Acer saccharum*) and all other species that can reach the canopy (b, d) from 2003 to 2013 at Trillium Trail Nature Reserve. Top panels are predictions from a generalized linear mixed model. Arrows indicate significant trends in mean abundance over time. Lower panels are average annual differences between deer exclosures and access plots. N = 6 plots. Error parts are 95% confidence intervals.

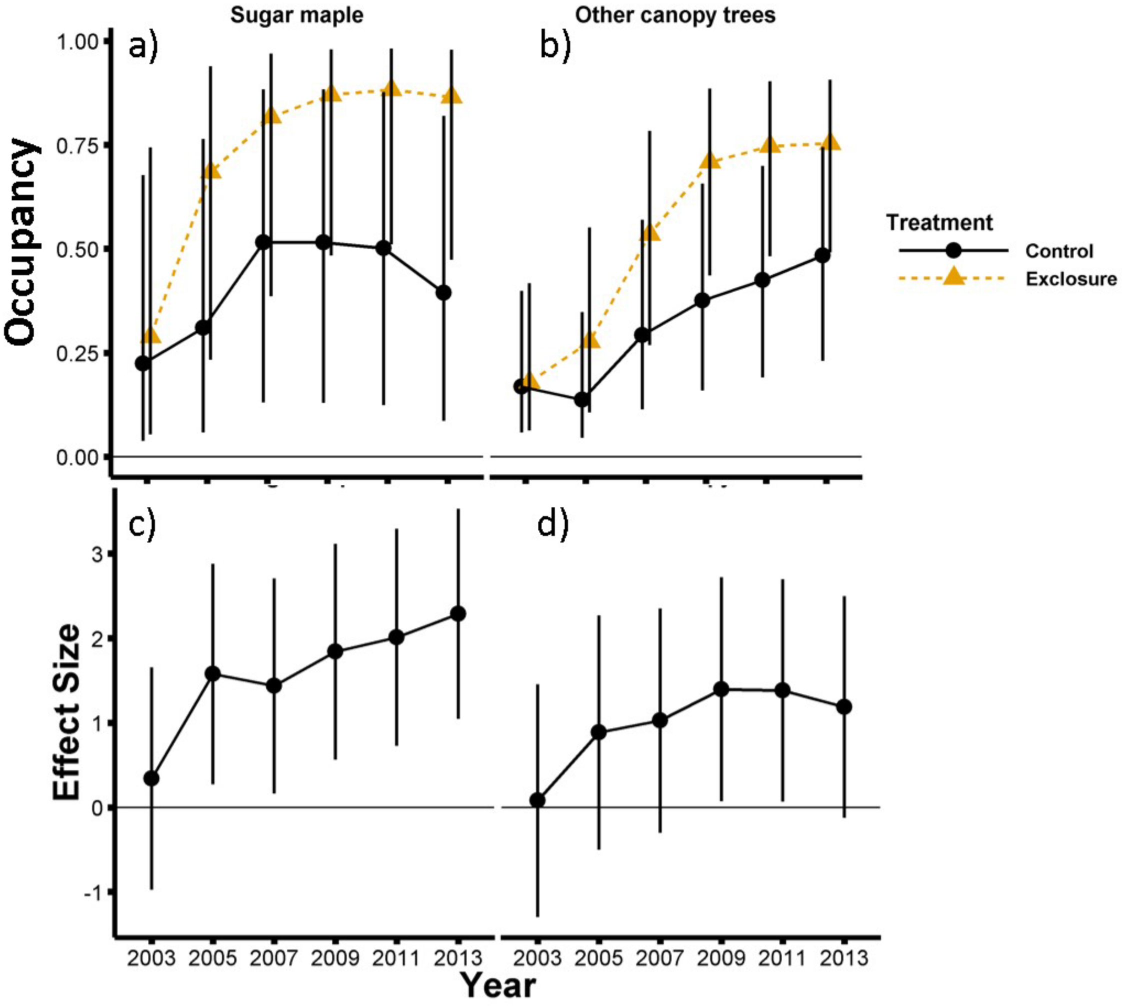

Figure 12. Effects of deer exclusion on occupancy of sugar maple (a,c; *Acer saccharum*) and all other species that can reach the canopy (b, d) from 2003 to 2013 at Trillium Trail Nature Reserve. Top panels are predictions from a generalized linear mixed model. Lower panels are average annual differences between deer exclosures and access plots. N = 6 plots. Error parts are 95% confidence intervals.

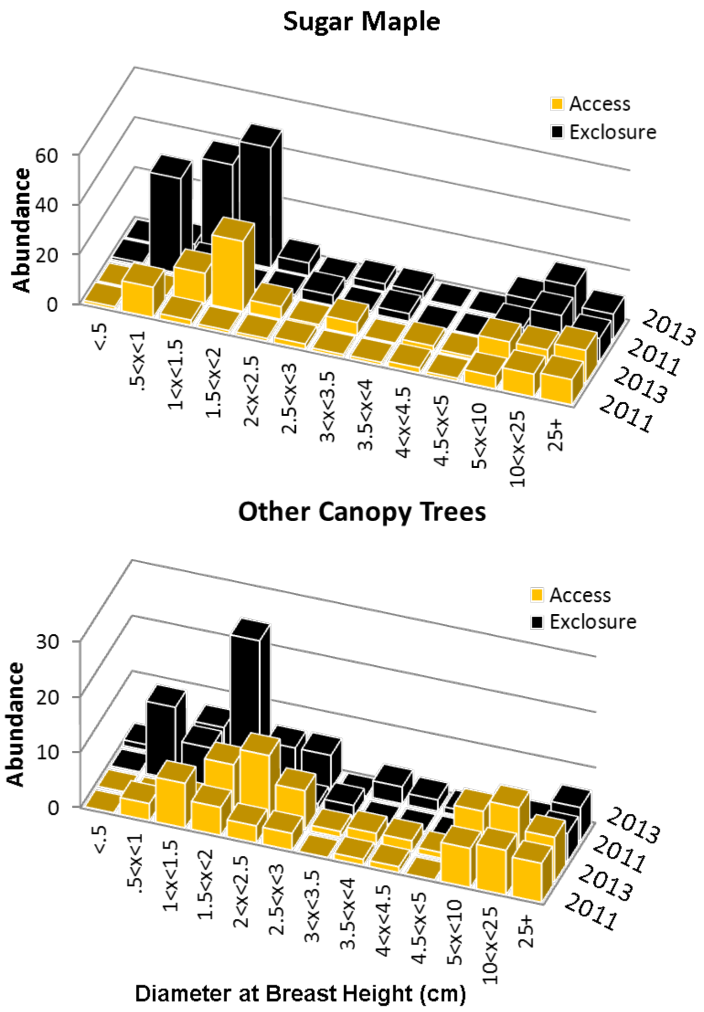

Figure 13. Size distribution of subcanopy trees (stems >2m in height) in permanent deer access plots vs. plots where deer were excluded since 2003. By 2011 size distributions were significantly different between treatments (KS-test, p=0.0011). Size distributions within treatments diverged further between 2011 and 2013 (p<0.01) due to continued recruitment and growth in deer exclusion plots (i.e. compare distribution of plants <3 cm DBH). Note: Large trees (i.e. diameter> 5cm) in both plot types had reached deer browse size refuge prior to start of the experiment and were not expected to differ for sugar maple or other canopy-forming trees. N= 6 plots per treatment.

5.0 LONG-TERM DEMOGRAPHIC RESEARCH REVEALS PERVASIVE EFFECTS OF AN ALLELOPATHIC INVASIVE SPECIES ON VITAL RATES AND POPULATION DYNAMICS OF COMMON FOREST PLANTS

5.1 INTRODUCTION

The increasing use of experiments in invasion ecology (Stricker *et al.* 2015) is revealing the causal links between invasive plants and reduced fitness in native species. Invasive plants have been shown experimentally to impact natives through numerous direct and indirect mechanism, including resource competition (Vila and Weiner 2004; Gioria and Osborne 2014), pollinator interference (Morales and Traveset 2009, Reid *et al.* 2009), pathogen spillover (Beckstead *et al.* 2010), direct allelopathy (Inderjit *et al.* 2011, Svensson *et al.* 2013), allelopathic mutualism disruption (Hale *et al.* 2011, 2015), soil nutrient enrichment from litter and nitrogen fixation (Vitousek and Walker 1989; Liao *et al.* 2008), and apparent competition (Enge *et al.* 2013). Given these experimental advances in our understanding of native-invader interactions it is now incontrovertible that invasive plants can exert intense effects on natives and severely reduce their fitness. However, intense species interactions identified in experiments might be attenuated or change under field conditions or when scaled up to the population level (e.g. Brown *et al.* 2011).

A disconnect between lab and field population studies has recently been identified with one of the most well-known invasive animals, the cane toad in Australia (*Rhinella marina*). Lab feeding trials have shown that most Australian lizards and amphibians are harmed when they consume cane toads (reviewed in Shine 2010). However, long-term population monitoring of these species in the field has indicated that cane toads impact only a subset of the herpetological community (Brown *et al.* 2011, 2013; Somaweera and Shine 2012, Somaweera *et al.* 2013). The lack of impact by cane toads on the native herpetofauna is partially attributed to behavioral adjustment by some native species after initial exposure (O'Donnel *et al.* 2010).

A disconnect between experimental results and population studies has also been identified in situations when invasive plants disrupt pollination. Many experimental studies have shown that invaders can reduce pollinator visitation and seed set (Brown *et al.* 2002, King and Sargent 2012; reviewed in Morales and Traveset 2009). However, the magnitude of invader impacts on pollinator services varies between experiments (Bjerknes et al 2007), can be spatially variable and context-specific (Cariveau and Norton 2009), and native plants may not be pollen or seed limited (Palladini and Maron 2013). Though not specifically investigating the impacts of invaders, several demographic experiments have disrupted plant reproductive mutualisms and found no impact on recruitment or population growth (Geib and Galen 2012, Ford *et al.* 2014, Lundgren *et al.* 2015).

Similarly, even though invaders can exert intense negative effects on natives through multiple mechanisms under experimental conditions, one mechanism may be much more important (*sensu* Welden and Salussen 1986, Kikvidze *et al.* 2011) than another in the field. For example, Palladini and Maron (2013) have shown that direct resource competition by an invasive plant has much stronger impacts on plant fitness than pollinator competition.

A second issue is that even if invader-native interactions are indeed important at population scales, they may be difficult to isolate in observational field studies because of noisy ecological dynamics. For example, there is ambiguity about cane toad impacts on some native amphibian species due to the highly variable population dynamics of these natives (Brown *et al.* 2011). This could be evidence that external environmental forcing is more important than toad impacts, or there may be insufficient statistical power to isolate a real toad effect.

In order to overcome the limits of small-scale experiments and noisy population-level observational data it is essential to conduct long-term demographic experiments on the impacts of invaders. However, to determine whether the experiment has the power to detect significant population-level change and whether the impacts of the invader are truly ecologically important relative to other processes, experiments should be designed to manipulate invader density and other drivers of native plant population dynamics that are known to have major effect. This approach allows the impacts of the invader to be compared to a factor that is already well understood in the community and provides a “positive control”. It also makes it possible to determine how much the effect of a known driver of plant population dynamics can vary in intensity due to temporal or spatial variation. Such information can then be used to gauge how much inferential interference is caused by noisy ecological dynamics, which can obscure the signal of the factors being investigated.

Forests of eastern North American are frequently invaded by exotic plant species including shade-tolerant herbs, shrubs, and trees (Martin *et al.* 2009). Additionally, these forests commonly experience high densities of white-tailed deer (*Odocoileus virginianus*), which are known to reduce population growth rates of forest understory plant on average by 5% (Maron and Crone 2006; Fig. 24 Appendix D). The co-occurrence of invasive plants and overabundance deer provides the opportunity to explore the relative impacts of putatively important invasive species against a powerful “keystone herbivore” (Waller and Alverson 1997). In this study we test whether an invasive allelopathic herb, *Alliaria petiolata* (garlic mustard) has widespread impacts on the population dynamics of multiple understory herb species, and compare its impacts to white-tailed deer (hereafter "deer"). We use a comparative modeling approach that allows us to determine the extent to which the previously demonstrated intense impacts of *Alliaria* at individual (Hale *et al.* 2011, Hale *et al.* 2015) and population (Brouwer *et al.* 2015) scales significantly alter demographic rates and characterize their importance relative to the known strong impacts of deer.

Deer impacts on herbaceous plants are highly stage-structured because deer generally target large flowering plants (Knight 2004, Kalisz *et al.* 2014) and thereby prevent reproduction, cause plants to shrink in size because of lost photosynthetic capacity and resources (e.g. Lapointe *et al.* 2010), and increase mortality (Rooney and Gross 2003). Non-flowering plants, however, are typically browsed at lower rates (Rooney and Gross 2003, Knight 2004). Stage-based consumer-resource interactions can stabilize predator-prey dynamics (Miller and Rudolf 2011) and could slow population declines of plants. In contrast, *Alliaria* impacts have been shown to affect multiple life stages, vital rates, and species. *Alliaria* has been shown to impact seed germination of several species and life forms (Prati and Bossdorf 2004, Callaway *et al.* 2008), tree seedling growth and survival (Lankau 2012, Callaway *et al.* 2008, Stinson *et al.* 2006), herb growth (Wixted and McGraw 2010) and adult herb physiological rates (Hale *et al.* 2011) and resource allocation patterns (Brouwer *et al.* 2015; Hale *et al. in press*). *Alliaria's* broad array of impacts are likely due to the antimicrobial allelochemicals it produces, which disrupt the arbuscular (Cantor *et al.* 2011, Callaway *et al.* 2008, Stinson *et al.* 2006) and ecto-mycorrhizal fungal mutualisms that most forest plants rely on for nutrient capture (Whigham 2004; Courtney *et al.* 2010).

Given consistent experimental demonstration of *Alliaria's* ability to reduce the fitness of multiple plant species and life stages, and previous demonstration of its population-level impacts at this site on one species (Brouwer *et al.* 2015), we make two predictions. First, we expect that *Alliaria* will have pervasive impacts on many herbaceous native perennial species, vital rates and population processes in our study community. Second, because the native species have no size refuge from *Alliaria's* allelochemicals and basic physiological functions can be suppressed, we predict that these impacts can be large and even comparable to the effects of deer browse. To test these predictions we analyze 11 years of field data on the population dynamics of three native herb species from a crossed deer exclusion/*Alliaria* removal experiment. We analyze the data from this experiment with multi-level generalized linear models (West *et al.* 2006, Bolker *et al.* 2009) that allow us to determine if and how our treatments cause plant vital rates to diverge over time. We can therefore determine if *Alliaria* impacts are important relative to deer browse while accounting for native species differences and temporal variability.

5.2 METHODS

5.2.1 Study species

5.2.1.1 Study species: Natives

Our focal native herbs in this study are *Trillium erectum* (Melanthiaceae), *Maianthemum racemosum* (Asparagaceae), and *Polygonatum biflorum* (Asparagaceae). All are long-lived geophytes common throughout forest understories in much of the USA, especially in eastern deciduous forests (LaFrankie 1985, Brundrett and Kendrick 1988, 1990). All three species are browsed by deer (Kirschbaum and Anaker 2005; Fig. 25 Appendix D) and like most forest herbaceous perennials they do not re-sprout until the spring following an episode of browsing by herbivores (Whigham 2004). We found that in some years of our study, flowering *Trillium* and *Maianthemum* can experience almost 100% herbivory, while *Polygonatum* is less frequently browsed Fig. 25 Appendix D). Browse is highly stage-based, with deer showing strong preference for flowering individuals. All three species exhibit high colonization rates by arbuscular mycorrhizal fungi (AMF) (Brundrett and Kendrick 1988, 1990; Burke 2008) and disruption of the AMF mutualism by *Alliaria's* allellochemicals reduces physiological rates in *Maianthemum* (Hale *et al.* 2011), carbon storage (Brouwer *et al.* 2015) and changes resource allocation patterns (Hale *et al.* 2015).

5.2.1.2 Study species: *Alliaria petiolata*

Alliaria petiolata (garlic mustard; Brassicaceae), is a shade-tolerant Eurasian biennial that frequently invades forest understories throughout northeastern North America (Rodgers *et al.* 2008) and more recently in the western United States (USDA NRCS 2015). Each spring, *Alliaria* seeds germinate from both the previous year's seed crop and from a long-lived seed bank (reviewed in Evans *et al.* 2012; pers. obs.). Seedlings grow over the course of the summer and overwinter as rosettes. *Alliaria* bolts in the early summer (May-June) and begins producing seeds in June and July (Rodgers *et al.* 2008). At our study site, adult senescence and seedling mortality coincide with flowering and fruiting of many forest perennial herbs, including our focal species (*Trillium*, *Maianthemum* and *Polygonatum*). *Alliaria* produces a broad suite of allelochemicals, which enter the soil through root exudates (Cippollini and Gruner 2007) and leaf litter (Hale *et al.* 2015). *Alliaria* has been the focus of substantial research effort and become a model for investigations of the novel weapons (*sensu* Callaway and Ridenour 2004) and mutualism disruption hypotheses for the success of invasive plant (Stinson *et al.* 2006; Hale *et al.* 2011, Hale *et al.* 2015; reviewed in Brouwer *et al.* 2015). Previous work in our study plots has shown that *Alliaria* abundance declines when deer are excluded (Kalisz *et al.* 2014). This was also observed occurring adjacent to our study plots in a nearby large fenced area (Knight *et al.* 2009) and in other experiments (Eschtruth and Battles 2008b). Importantly, we have never observed deer browse of *Alliaria*.

5.2.2 Study site: Trillium Trail

This study was conducted at Trillium Trail Nature Reserve (hereafter, TT) in Fox Chapel, PA (40^0 52’ 01.40” N; 70^0 90’ 10.75” W). TT is a mature second-growth mixed-mesophytic forest typical of southwestern PA, West Virginia and parts of Ohio (Braun 1950). The TT overstory contains a high percentage of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), but also oaks (*Quercus rubra* and *Q. alba*), black cherry (*Prunus serotina*), and tulip poplar (*Liriodendron tulipifera*). The herbaceous community is diverse with over 60 native species (Brouwer 2015, Chapter 4). *Alliaria* is the most abundant invader but Japanese stiltgrass (*Microstegium vimeum*), lesser celandine (*Ranunculus ficaria*), various honeysuckle species (*Lonicera* spp.) and other woody invaders are also present.

5.2.3 Experimental design

In the fall of 2002 five study locations were established and a pair of 16 m x 16 plots demarcated at each location. Plot pairs are all located on similar mid- to lower slope positions in closed canopy forests (*Kalisz et al.* 2014). One plot within each pair was designated as a deer access plot (Deer+) and the other as a fenced exclosure (Deer-). Each plot was divided into 36 4m^2 subplots in a 6 x 6 grid with 0.5 wide pathways every four meters (Fig. 26 Appendix D). A 1 m wide buffer surrounds exclosure plots from a 3 m tall fence of 15 cm x 15 cm steel mesh. Trees that fall on the fence are cut so as not to allow deer to breach the fences but otherwise left in place if they fall in the plots. To prevent soil compaction and disturbance to the plant community all work in the subplots is conducted while standing in the buffers or pathways.

5.2.3.1 *Alliaria petiolata* removal

Beginning in 2006 all *Alliaria* have been removed from the left half of each plot, resulting in 18 subplots receiving the removal treatment (Fig. 26 Appendix D). *Alliaria* on the right half of the plot is left un-manipulated and allowed to undergo normal population dynamics. We refer to this as the "ambient" *Alliaria* treatment (*Alli*+). All *Alliaria* rosettes and adults were removed in 2006 after the native community emerged, and since then *Alliaria* have been removed at the seedling stage each year in early spring. *Alliaria* is also removed from the buffer and paths surrounding the subplots receiving the removal treatment. To prevent seed dispersal between the removal and ambient treatments a 1.5 m tall plastic barrier is erected each summer just before *Alliaria* fruit maturation. The barrier is left in place for approximately three weeks, typically from mid-June to early July. In all plots the barrier runs down the slope and so does not affect runoff or the downslope movement of litter.

5.2.3.2 Field methods & data collection

In the spring of 2003 the locations of all *Trillium*, *Maianthemum* and *Polygonatum* individuals were marked by inserting an aluminum tag into the soil near the base of each plant. Plant status each year is recorded as flowering or non-flowering and plant leaf or stem length measured (see

Table 10, Appendix D for species-specific details). Plants are resurveyed later in the spring and summer to determine which plants were browsed, as well as those that achieved successful flower and fruit production. Each year plants that emerge from prolonged vegetative dormancy (*sensu* Shefferson 2009) for the first time or that recruit into the population as multi-leaved individuals from seed are tagged. During their first two years after germinating all three native species only have one leaf (LaFrankie 1985; Rhodes and Block 2007); the location of these one-leaved individuals are recorded, and the number of seedlings counted, but they are not individually tagged. For this study we only consider plants that have recruited to the multi-leafed life history stage. Our 4m^2 subplots (Fig. 26 Appendix D) are divided into four 1 m x 1m quadrats to aid with locating plants and individual location notes are recorded.

5.2.4 Data analysis

5.2.4.1 Response variables

To gain a holistic understanding of deer impacts on plant vital rates and population processes we consider five different response variables at two levels of ecological organization. At the level of individual plants' vital rates, we assessed how our treatments affected flowering frequencies and above-ground plant size. For these analyses we considered only plants that had occurred in the study prior to implementation of the *Alliaria* removal treatment; we therefore considered plants first tagged between 2003 and 2006. At the population level, we considered the overall abundance of plants, spatial occupancy throughout our plots, and the number of young plants recruiting into the multi-leaved stage each year. For these population-level patterns we included all plants in the analysis regardless of when they were first observed.

5.2.4.2 Missing data due to herbivory

Occasionally deer browsed plants before some data could be collected. Typically this resulted in only missing size data. Occasionally, browse occurred before a plant's flowering status could be determined. Stems of all focal species can remain erect for up to one month after being browsed (N Brouwer, *pers. obs.*) and so we are confident that all plants that emerge each year are located, even if some details of their status are not know. Because deer preferentially browse flowering plants we assume that the small subset of browsed plants for which we were unable to determine their status before deer browse were flowering.

5.2.4.3 General vital rate summaries

To summarize how much each species changed over the course of the entire experiment we modeled the relative change in our five response variables from the beginning of the experiment to 2013. Though the methods and metrics varied, our calculations all yielded the relative change, the ratio $(\text{value}_{2013})/(\text{value}_{2003})$, with a value of 1 indicating that no change occurred. We used Poisson mixed models to calculate the mean relative change in abundance over time. We used logit mixed models to calculate changes in flowering probability between 2003 and 2013, yielding an odds ratio. We used linear mixed models to calculate the change in log plant size. For flowering and plant size we calculated these effect sizes just for the group of plants first observed in 2003 and which therefore had similar histories and initial sizes. We analyzed all three species in the same model to allow results to be compared between species.

5.2.5 Statistical analyses: General approach

Previous work with a subset of these data (*Maianthemum* in Deer access plots; Brouwer *et al.* 2015) and graphical analyses indicated that vital rates and abundances varied markedly over time (Fig. 27-29 Appendix D). To assess the effects of deer exclusion and *Alliaria* removal we therefore needed to test for changes in population processes due to our treatments while accounting for considerable variation due to unknown external forcing and random variation.

We accomplished this by using multi-level longitudinal mixed effects models (Fitzmaurice and Ravichandran 2008, Fitzmaurice and Laird 2004; West *et al.* 2006; Kéry 2010). These models allow us to separate both directional changes over time and divergence in responses due to our treatments from annual stochastic variation (Fig. 14). We modeled annual variation in vital rates from 2006 through 2013 with random "year" effects, and directional change over time using elapsed time in years as a continuous predictor variable. We coded deer access plots where *Alliaria* was present (Deer+/Alli+) as our baseline and then modeled divergence in vital rates due to deer exclusion (Deer-) and *Alliaria* removal (*Alli*-) as treatment-by-time interactions ($\beta_{\text{treatment}*time}$). Under this modeling approach, if all time coefficients and time-by-treatment interactions are not significantly different from zero then there is no net increase over time (Fig. 14a). A significant baseline time effect would indicate directional change in vital rates over time for all treatments (Fig. 14b). A significant time*Deer- interaction would indicate divergence over time in a vital rate between the baseline Deer+/*Alli*+ trend and the deer exclusion (Deer-) treatment (Fig. 14c) and so forth.

Details of our modeling approach are provided below. In brief, all models contained a random intercept for each year (2006-2013) and initially random intercepts to represent the full split-split-plot design of the experiment (i.e. *Alliaria* treatment nested within deer exclusion treatment, nested within plot pair). Our plot-pair term (n = 5 plot pairs; equivalent to a complete block) often accounted for little variance but was left in the model (as recommended by Barr *et al.* (2013)) because it was part of the design of the experiment. When we found evidence of convergence problems or over-fitting we simplified the structure of our random effects by removing the plot-pair term, resulting in a split-plot incomplete block design (n = 10 plot-treatment combinations). We also fit individual random slopes whenever it was computationally possible and biologically relevant. Random slopes were removed if there were problems with over-fitting or convergence.

Our fixed effects were i.) elapsed time since 2006, ii.) deer exclusion treatment, iii.) *Alliaria* removal treatment, and iv.) time by treatment interactions. Three-way interactions were tested and dropped if not significant. Time was centered to improve model convergence (Gelman and Hill 2007). We used linear, logistic, and Poisson linear mixed models as appropriate for our different response variables. The corresponding link functions, final random effects structures, and *R* packages used for each model are given in Table 11 (Appendix D). Plant size data were not available for 2008 and 2009 so our size analysis used data from 2007 and 2010-2013. All analyses were conducted in *R 3.1.2* (R Core Team 2014) using the package *lme4 1.1-7* (Bates *et al.* 2014).

5.2.5.1 Modeling details

Individual-level vital rate data: flowering & size

To assess the impact of our treatments between 2006 and 2013 on individual-level flowering probabilities, we fit logistic generalized linear mixed models with random slopes for each individual plant. In these flowering models a significant time*Deer- or time**Alliaria*- effect would indicate that over time individual plants are diverging from the baseline Deer+/*Alliaria*+ treatment in their propensity to flower. To determine the impact of the treatments on plant size, we fit linear mixed models to the log of individual plant size, but did not include individual random slopes. Size in *Maianthemum* and *Polygonatum* appears to have an upper limit due to stem and reproductive architectural constraints (Brouwer and Kalisz, *unpub data*; N Brouwer *pers. obs*). Also, large, healthy individuals of all three species frequently shrink in size when they produce new clonal stems. Individual random slopes would therefore model unrealistic linear growth on these species. In our size analyses, significant time-by-treatment interactions would indicate that the mean size of individuals in different treatment groups was tending to diverge over time.

Population level data: abundance, recruitment & occupancy

We modeled change in the abundance of plants at the plot level. For each pair of plots we summed the number of plants in all $4m^2$ subplots allocated to a combination of treatment (18 subplots per treatment combination per pair of plots). Plots varied in the number of plants they contained when the study began (Table 10 Appendix D) and we therefore used the log of the initial abundance of plants as a covariate. By 2006 all plots had at least one plant in them so we attempted to fit truncated-*Poisson* mixed models to these data using *glmmADMB* in *R* (Skuag *et al.* 2014) but had difficulties with convergence. We therefore approximated a zero-truncated Poisson model by subtracting 1 from the observed abundance. Due to issues with model convergence we dropped the random effect for plot pair and fit the model as an incomplete block design rather than a split-split plot (5 plot pairs x 2 main treatments = 10 incomplete blocks).

We also modeled the number of new multi-leaved individuals tagged for the first time each year at the plot scale. New individuals could appear due to emergence from prolonged dormancy (*sensu* Shefferson 2009), recruitment from seed, or clonal propagation. This metric therefore integrates across several sub-processes that can be affected by both deer browse and *Alliaria* exposure. Plots varied widely in the number of plants present when the study began, so we controlled for the log-transformed initial abundance of plants in each plot. The model was fit with a Poisson mixed model without random intercepts.

To investigate if plants were dispersing to new microsites within our plots we determined for each year whether each of our 4m^2 subplots had ≥1 plant of a given species in them. Subplots could become occupied if dormant plants emerged into that subplot, seeds dispersed and young plants survived and recruited to the multi-leaved stage, or if a plant's rhizome grew horizontally into the subplot. We modeled these data using logistic mixed models with individual random slopes for each subplot.

5.3 RESULTS

5.3.1 Overall Population dynamics 2003-2013

By the end of the study period in 2013 all species in all treatments had increased significantly in abundance relative to 2003 (Fig. 15a). *Trillium* began at the highest initial density (Table 10, Appendix D) and exhibited the smallest relative increase from 2003 to 2013 (1.3 times larger in Deer+/*Alli*+ to 1.6 time larger Deer-/*Alli*-). *Polygonatum* was 1.5 to 2.5 times more abundant by 2013 (Deer+/*Alli*- and Deer-/*Alli*- treatments, respectively). *Maianthemum* exhibited the largest increase in relative abundance over the course of the experiment, becoming three times more abundant in the Deer+/*Alli*- treatment by 2013.

Similarly, from 2003 to 2013 all species in all treatments experienced overall increases in flowering rates (Fig. 15b), though rates varied considerably year to year (Fig. 28, Appendix D). Plants that were first observed in 2003 were also generally larger by 2013 (Fig. 16a). Occupancy rates, however, did not increase significantly over the course of the study (Fig. 16b).

5.3.2 *Alliaria* removal effects 2006-2013

5.3.2.1 *Alliaria* effects on abundance

From 2006 to 2013, deer exclusion had effects on the abundance of all three species, and *Alliaria* removal had effects on the *Polygonatum* and *Trillium* (Fig. 17a). Deer exclusion had a positive effect on *Maianthemum* abundance relative to deer access plots (Fig. 17a; $\beta_{Deer\text{-}*time}$=0.054, SE= 0.014, p<0.001). *Alliaria* removal from 2006 onward did not have any effect on *Maianthemum* abundance ($\beta_{Alli\text{-}*time}$=0.01, SE=0.01, p=0.4). For *Polygonatum*, both deer exclusion ($\beta_{Deer\text{-}*time}$=0.02, SE=0.01, p=0.12) and *Alliaria* removal ($\beta_{Alli\text{-}*time}$=0.024, SE=0.013, p=0.054) had positive effects on abundance. *Trillium* decreased in abundance in exclosures relative to controls ($\beta_{Deer\text{-}*time}$=-0.019, SE=0.007, p=0.01), while abundance tended to increase when *Alliaria* was removed ($\beta_{Alli\text{-}*time}$=0.011, SE=0.007, p=0.14).

5.3.2.2 *Alliaria* effects on recruitment of 3-leaved plants

From 2006-2013 recruitment to the three-leaved life history phase by *Maianthemum* seedlings was not impacted by either treatment (Fig. 17b). *Polygonatum* recruitment did exhibit a marginal positive response due to *Alliaria* removal ($\beta_{Alli\text{-}*time}$ =0.17, SE=0.11, p=0.15). *Trillium* recruitment responded to both treatments and exhibited a Deer-**Alli*- interaction. From 2006 to

2010 deer exclusion had a negative effect on *Trillium* recruitment relative to deer access plots ($\beta_{\text{Deer-}*time}=-0.15$, SE=0.065, p=0.024). *Alliaria* removal in deer access plots had a positive effect on *Trillium* recruitment where deer had access ($\beta_{Alli\text{-}*time}=0.17$, SE=0.07, p=0.009) but a negative effect in deer exclusion treatment ($\beta_{\text{Deer-}*Alli\text{-}*time} = 0.19$, SE=0.09, p=0.041)

5.3.2.3 *Alliaria* effects on flowering

From 2006 to 2013, deer exclusion impacted flowering rates of all species, and *Alliaria* removal impacted *Maianthemum* and Trillium *flowering*. Deer exclusion had a positive effect on *Maianthemum* flowering rates relative to access plots (Fig. 18a; $\beta_{\text{Deer-}*time}=0.14$, SE=0.059, p=0.015). *Alliaria* removal also had a positive effect on *Maianthemum* flowering rates over time relative to the ambient *Alliaria* treatment. This occurred in both the deer access and deer exclosure plots ($\beta_{Alli\text{-}*time}=0.17$, SE=0.055, p=0.0016) and there was no evidence of a three-way Deer-**Alli*-**time* interaction. Deer exclusion had a positive effect over time on *Polygonatum* flowering ($\beta_{\text{Deer-}*time}=0.19$, SE= 0.056, p=0.0005) but unlike *Maianthemum,* there was no effect of *Alliaria* removal on *Polygonatum* flowering ($\beta_{Alli\text{-}*time}=-0.06$, SE=0.06,p=0.3). Deer exclusion had a positive effect over time on *Trillium* flowering ($\beta_{Deer\text{-}*time}=0.07$, SE=0.03, p=0.04). Surprisingly, removal of *Alliaria* resulted in a trend towards lower flowering rates ($\beta_{Alli\text{-}*time} = -0.15$, SE=0.034, p<0.0001).

5.3.2.4 *Alliaria* effects on plant size

Both deer exclusion and *Alliaria* removal impacted the size of all three species, though the impacts of *Alli-* were negative for two of the three species. (Fig. 18b). Deer exclusion had a positive effect over time on mean size of *Maianthemum* (Fig. 18b; $\beta_{Deer\text{-}*time} = 0.045$, SE=0.005, p<0.001), *Polygonatum* ($\beta_{Deer\text{-}*time} =0.016$, SE=0.004, p=0.0002), and *Trillium* ($\beta_{Deer\text{-}*time} =0.01$, SE=0.002, $p<0.001$) relative to deer access plots. *Alliaria* removal had a positive effect over time on *Maianthemum* size ($\beta_{Alli\text{-}*\mathrm{time}}=0.014$, SE=0.0048, p =0.003). However, the mean size of both *Polygonatum* ($\beta_{Alli\text{-}*\mathrm{time}}=-0.016$, SE=0.004, $p<0.001$) and *Trillium* ($\beta_{Alli\text{-}*\mathrm{time}}=-0.009$, SE=0.0024, $p<0.001$) were negatively impacted over time by *Alliaria* removal.

5.3.2.5 *Alliaria* effects on plant occupancy

From 2006 to 2013 deer exclusion had a marginal positive effect on *Maianthemum* occupancy (Fig. 19; $\beta_{\mathrm{Deer}\text{-}*time}=0.12$, SE=0.08, p=0.13) but there was no effect of *Alliaria* removal ($\beta_{\mathrm{Deer}\text{-}*time}$ =-0.05, SE=0.08, p=0.5). For *Polygonatum*, both deer exclusion and *Alliaria* removal had marginal positive effects on occupancy (Deer-: $\beta_{Deer\text{-}*time}$ =0.11, SE=0.071, p = 0.11; *Alliaria*-: $\beta_{Alli\text{-}*time}=0.12$, SE=0.07, p=0.097). There was no overall change in *Trillium* occupancy (β_{time} =0.08, SE=0.09, p=0.4), and no effect of either treatment.

5.4 DISCUSSION

5.4.1 Overall results

In this study we tested two hypotheses. First, that the negative effects of an allelopathic invasive plant, *Alliaria petiolata* are pervasive across species, vital rates, and population processes. Second, that *Alliaria* impacts can be comparable in importance to other antagonistic species interactions that native plants must contend with, specifically herbivory. We addressed these hypotheses by comparing the impact of *Alliaria* removal to deer exclusion while accounting for annual variability over a decade-long experiment; our results support both of our hypotheses (Figs. 17-19; Table 4). We detected significant effects of *Alliaria* removal on three common forest herbs, *Maianthemum racemosum* (see also Brouwer *et al.* 2015), *Trillium erectum*, and *Polygonatum biflorum*. The type and magnitude of responses varied among the species, but each exhibited some form of increased individual or population-level performance after *Alliaria* was removed. The effects of *Alliaria* removal did not occur immediately, but were manifested as steady divergences over time in annual vital rates between treatments.

As predicted, the effects of *Alliaria* removal can be similar in magnitude to deer exclusion effects over the same time period. The abundance and occupancy of *Polygonatum* was increased by *Alliaria* removal, and the effect of removing the invader was of similar magnitude to continued deer exclusion (Fig. 17a, 19). Increases in *Polygonatum* abundance were likely due the effect of *Alliaria* removal on recruitment of multi-leaved plants (Fig. 17b). Similarly, the effect of *Alliaria* removal on *Maianthemum* flowering was of similar magnitude as the effect of deer exclusion (Fig. 18a). Increases in *Maianthemum* flowering were likely due to the significant effect of *Alliaria* removal on *Maianthemum* size (Fig. 18b). *Trillium* recruitment increased when *Alliaria* was removed, but only outside of the deer exclosures (Fig. 17b). When deer were excluded and *Alliaria* removed we observed negative effects on recruitment.

5.4.2 ***Trillium* declines and other negative dynamics**

Over the course of the experiment (2006-2013) *Trillium's* responses to *Alliaria* removal and continued deer exclusion were frequently different from the other two species. While deer exclusion had a positive effect on *Trillium* size and flowering, *Alliaria* removal in both controls and exclosures had a negative impact on these vital rates (Figs. 18a,b). Deer exclusion also had a negative impact on *Trillium* abundance and recruitment of multi-leaved plants (Fig. 17a,b). These declines in the exclosures and the negative deer x *Alliaria* interaction are possibly accounted for by intra- and inter-specific interactions. As *Trillium* continue to get larger in the deer exclusion plots (Fig. 18b), large individuals may be outcompeting smaller individuals and inhibiting their recruitment. Since *Alliaria* removal has positive effects on *Maianthemum* and *Polygonatum*, *Trillium* may be facing increased competition from these and other co-occurring native plants in our plots, resulting in negative effects of *Alliaria* removal on *Trillium*. *Polygonatum* size is also negatively affected by *Alliaria* removal (Fig. 18b). This could potentially also be accounted for by competition between *Polygonatum* and other natives. Alternatively, *Polygonatum* can produce multiple clonal stems from the same rhizome (N Brouwer, *pers. obs.*) so a decrease in average individual size could be due to changes in resource allocation towards increased clonal growth. This would be consistent with increases in *Polygonatum* abundance and multi-leaved recruitment (Fig. 17).

5.4.3 *Maianthemum* and *Polygonatum* dynamics

In general *Maianthemum* and *Polygonatum* are more positively impacted by *Alliaria* removal over the course of the experiment (2006-2013). These two species have a later phenology than *Trillium* that could increase their exposure to *Alliaria* allellochemicals. All three genera are highly mycorrhizal (Brundrett and Kendrick 1988, 1990) and this had been confirmed for *Maianthemum* and *Trillium* at this site (Burke 2008). Of the three species, *Trillium's* phenology overlaps the least with periods of *Alliaria* senescence and seedling death, when its myco-toxic allelochemicals are most likely to be detected in the soil (Cantor *et al.* 2011). Negative species interactions with other natives might therefore be more important for *Trillium* than exposure to

Alliaria. *Trillium* three-leaved recruitment does benefit from *Alliaria* removal, but only when deer are at ambient densities and *Maianthemum* and *Polygonatum* are therefore being suppressed by deer browse.

5.4.4 Emergence of trends over time

Alliaria removal did not result in immediate changes in the vital rates of any of our species. Instead, *Alliaria* removal caused vital rates to diverge positively from rates where *Alliaria* was ambient. This gradual response can be accounted for by two factors: legacy effects of *Alliaria* allelochemicals on the soil fungal community, and the slow life history of forest herbs. *Alliaria* has pervasive effects on soil microorganisms (AMF: Cantor *et al.* 2011, Callaway *et al.* 2008, Stinson *et al.* 2006; EMF: Wolfe *et al.* 2008) and recovery of mycorrhizal community diversity can take years to occur after *Alliaria* removal (Lankau *et al.* 2014). Invaders that modify soil conditions frequently establish legacies that persist long after their removal (Marchante *et al.* 2009, Rodriguez-Echeverria *et al.* 2013, Grove *et al.* 2012, Grove *et al.* 2015, Perkins and Hatfield 2014). Time lags should therefore be accommodated in the design of field experiments testing the impacts of invasive plants. An alternative but not mutually exclusive explanation is that forest herbs generally have slow life histories and may take several years to respond to *Alliaria* removal (Whigham 2004).

5.4.4.1 Annual variation and deer as a positive control

Almost all vital rates increased over the course of the experiment, even where deer had access (Figs. 17-19), and vital rates varied substantially year to year in all treatments (Figs. 27-29

Appendix D). This was especially pronounced from 2008-2009 when almost all of the vital rates and population processes we examined declined, perhaps due to environmental forcing. Some year's vital rates were similar between deer exclusion and deer access treatments. While flowering rates after 2003 were always lower outside of our exclosures, in 2008 *Maianthemum* and *Polygonatum* flowering rates were nearly identical in both treatments; this was true for *Trillium* in 2009. This result indicates that plant populations can remain dynamic even in the face of powerful stressors such as mammalian herbivores.

The ability for plants in the deer access plot to temporarily attain high flowering rates could occur for several reasons. First, non-flowering plants enjoy a size and stage refuge, which potentially allows them to acquire nutrients with which to flower again. Second, plants under stress often alter their resource allocation patterns and life history schedules (Bonser and Aaarssen 2009, Santos-del-Blanco *et al.* 2013). For example, Heckel (2015) found that *Arisaema triphyllum* from sites with high deer densities had a lower threshold size for flowering than plants from sites with low deer densities. Preliminary analyses indicate that *Maianthemum* and *Polygonatum* have a lower threshold size for flowering when deer are present (*Maianthemum* $p = 0.1$, *Polygonatum* $p = 0.12$).

5.4.5 Relative importance of herbivores and invaders

All three species in our study increased considerably in abundance, flowering, and size due to deer exclusion over the 10 years of the study but more slowly and subtly to *Alliaria* removal. Large browsers and grazers frequently reduce population growth rates of the plants they eat (Maron and Crone 2006) and deer have been shown to frequently reduce population growth rates <1 for *Trillium* (Kalisz *et al.* 2014, Knight 2004, Rooney and Gross 2006) and other forest herbs

(Maron and Crone 2006; Fig. 24 Appendix D). Deer impacts are therefore likely to be of principal importance for population growth and stability for forest species.

Our results indicate that *Alliaira* also plays an important role in plant population dynamics, perhaps because it affects all life history stages of native plants and has the ability to exert long-term effects on forest soils (Lankau *et al.* 2014) and create negative plant-soil feedbacks. Deer browse on herbaceous plants at our and other sites is often biased towards large flowering plants (Fig. 25 Appendix D). Deer-plant interactions are therefore highly stage and size structured, providing a refuge for smaller, non-flowering plants that have regressed in size after being browsed. This size/stage refuge likely accounts for the persistence of *Trillium* populations despite high browse rates on flowering plants. In contrast, *Alliaria* impacts are not size structured and affect all plants life history stages from seeds (Pratti and Bossdorf 2006) to adult flowering plants (Fig. 17-19; Hale *et al.* 2011, Brouwer *et al.* 2015, Hale *et al.* 2015). Plants in forests with overabundant deer and *Alliaria* might therefore face a demographic squeeze where deer impact the largest individuals and *Alliaria* reduces seed germination (Prati and Bossdorf 2004, Callaway *et al.* 2008) and growth of all individuals (Fig. 18b). While *Alliaria* and deer effects are additive for individual vital rates, they may have synergistic effects on population growth due to this demographic squeeze.

Community ecologists studying plant competition first promoted consideration of the relative importance of species interactions (Weldon and Slausson 1986). Attempts to develop definitive quantitative indices of the importance of competition have generated considerable debate (Freckleton *et al.* 2009, Kikvidze *et al.* 2010, Rees *et al.* 2012); however, the concept appears useful as a general framework when considering multiple ecological interactions (Kikvidze *et al.* 2011), especially when operationalized in terms of demography (Freckleton *et* *al.* 2009, Goldberg and Scheiner, 2001). One limitation of this framework is that questions of importance often seek to rank the relative importance of different interactions and determine the most important one. We believe this is a key idea for evolutionary, ecological, and conservation understanding. However, populations experiencing reduced vital rates and population growth due to one stressor could potentially be pushed further towards decline or become more susceptible to stochastic events due to what are considered relatively less "important" but still significant stressors.

5.4.6 Conclusions

Using a long-term experimental demographic approach, we have shown that common native species are detrimentally impacted by an invasive species that occurs frequently in eastern North American forests, *Alliaria petiolata*. Our data indicate that numerous factors can affect vital rates, including deer browse, length of *Alliaria* exposure, and environmental variation, but that *Alliaria* exposure can affect vital rates and population processes to the same degree as deer effects. When vital rates declined synchronously across treatment groups, *Alliaria* removal reduced the amount of decline, and when vital rates increased synchronously, *Alliaria* removal amplified the increase. Because *Alliaria* removal benefited vital rates both within and outside of our exclosures, *Alliaria* removal should benefit native plants both when deer densities have been reduced and when they remain high.

Several experimental studies using transplanted seedlings have identified deer as exerting stronger effects on native plants than invasive plants (Davalos *et al.* 2014), particularly garlic mustard (Waller and Maas 2013). It has also been argued that *Alliaria*'s production of allelochemicals declines with time since the invader population is established (Lankau *et al.*

2010). Some authors have therefore advocated that control of *Alliaria* and other invaders are less of a priority than deer, especially since deer control can reduce the abundance of invaders (*Alliaria*: Knight *et al.* 2009, Eschtruth and Battles 2008b, Kalisz *et al.* 2014). More generally, the need to control invaders is hotly debated by some ecologists (Rozenweig 2001, Slobodkin 2001, Davis 2003, Brown and Sax 2004, Thomas and Palmer 2015). Our long-term demographic study indicates that *Alliaria petiolata* is indeed suppressing vital rates of forest herbaceous perennial plants. Much of the information on invasive species in general and *Alliaria* in particular comes from either observational studies or short-term experiments (e.g. Hulme *et al.* 2013, Stricker *et al.* 2015). While short-term studies play a central role in evaluating the impact of species interactions such as invasion, long-term experimental demographic studies are essential for determining the overall importance of invaders because they allow legacy effects to disappear, species with slow life histories to respond to treatments, and environmental stochasticity to be accommodated. Moreover, comparison of invader impacts to other key species interactions or ecological processes allows the putative harm of invaders to be gauged against a positive ecological control.

Table 4. Summary of results of deer exclusion (Deer-) and *Alliaria* removal (*Alli*-) experiment. Analyses were run on either all multi-leaved plants (2003-2013) or just those observed prior to the *Alliaria* removal treatment (2003-2006). ↑= positive effects of treatment (βtreatment*time > 0). ↓ = negative effect of treatment (βtreatment*time < 0). "(=)" indicates that the effect of *Alli*- and Deer- were similar. Deer-*Alli*- = a three way interaction between the treatments and time (βDeer-*Alli*-*time ≠ 0). Empty cells indicate that there was no significant effect.

Ecological Level	Vital rate / Population Characteristic	Cohorts	*Maianthemum racemosum*	*Polygonatum biflorum*	*Trilium erectrum*
Individual	Reproduction (successful flowering)	2003-2006	Deer - ↑ *Alli* - ↑ (=)	Deer - ↑	Deer - ↑ Alli - ↓
	Size / Growth	2003-2006	Deer - ↑ Alli - ↑	Deer - ↑	Deer - ↑ Alli - ↓
Population	Abundance	2003-2013	Deer - ↑	Deer - ↑ Alli - ↑ (=)	Deer - ↓ Alli - ↑
	Occupancy	2003-2013	Deer - ↑	Alli - ↑	
	3-leaved recruitment	2003-2013		Alli - ↑	Deer - ↓ Alli - ↑ Deer-*Alli- ↓

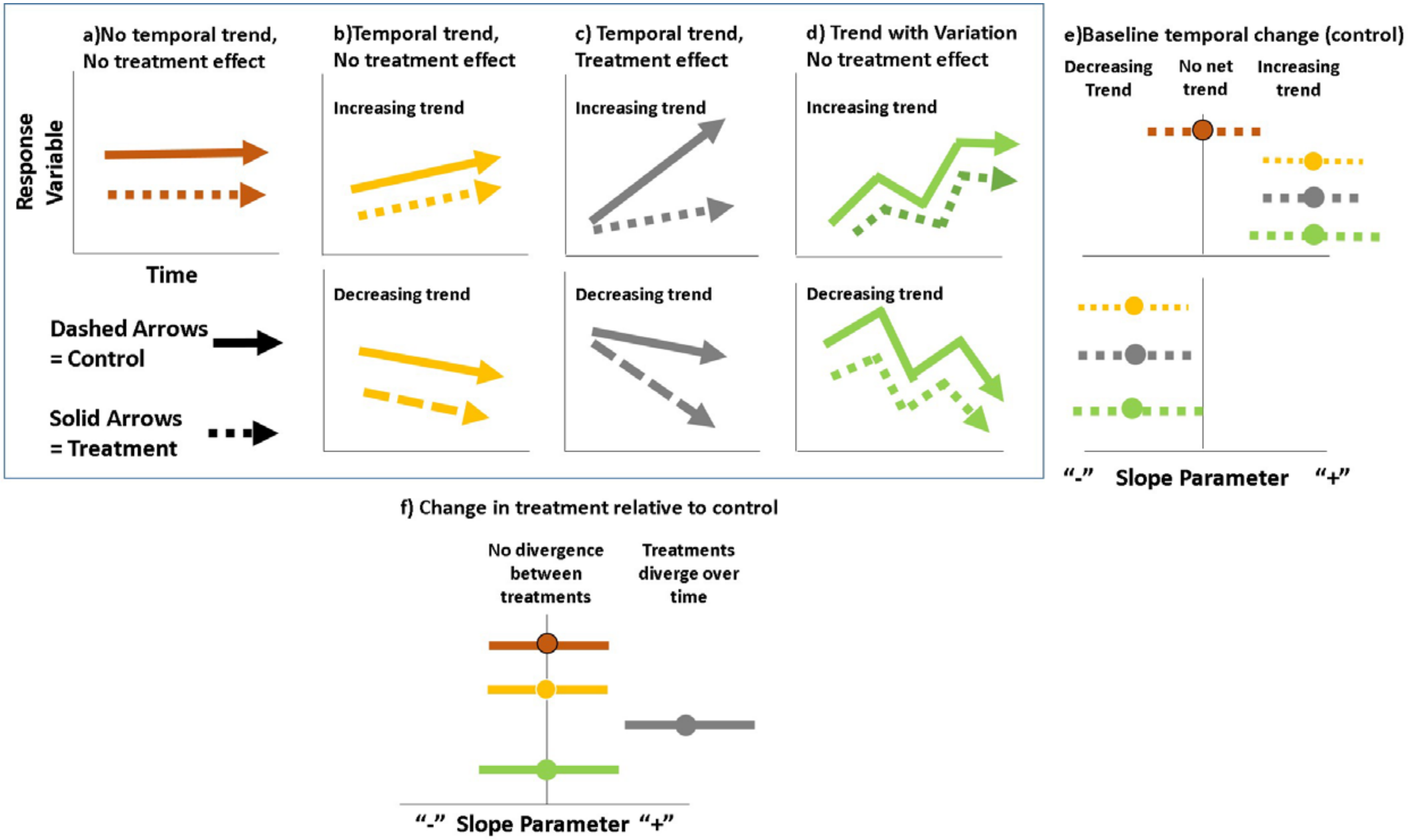

Figure 14. Schematic illustrating how longitudinal multi-level models are interpreted. Panels a through d represent trends in data from a control and experimental treatment. Panels e) shows the magnitude of the regression coefficient for the dotted control line ($\beta_{control}$) while panel f) shows the regression coefficient for the solid treatment arrow ($\beta_{treatment}$), which is modeled in terms of its divergence from the control. The actual slope of the treatment line would be $\beta_{control} + \beta_{treatment}$. When control and treatment lines are parallel (top row in a,b,d) $\beta_{treatmen} = 0$ in panel f.

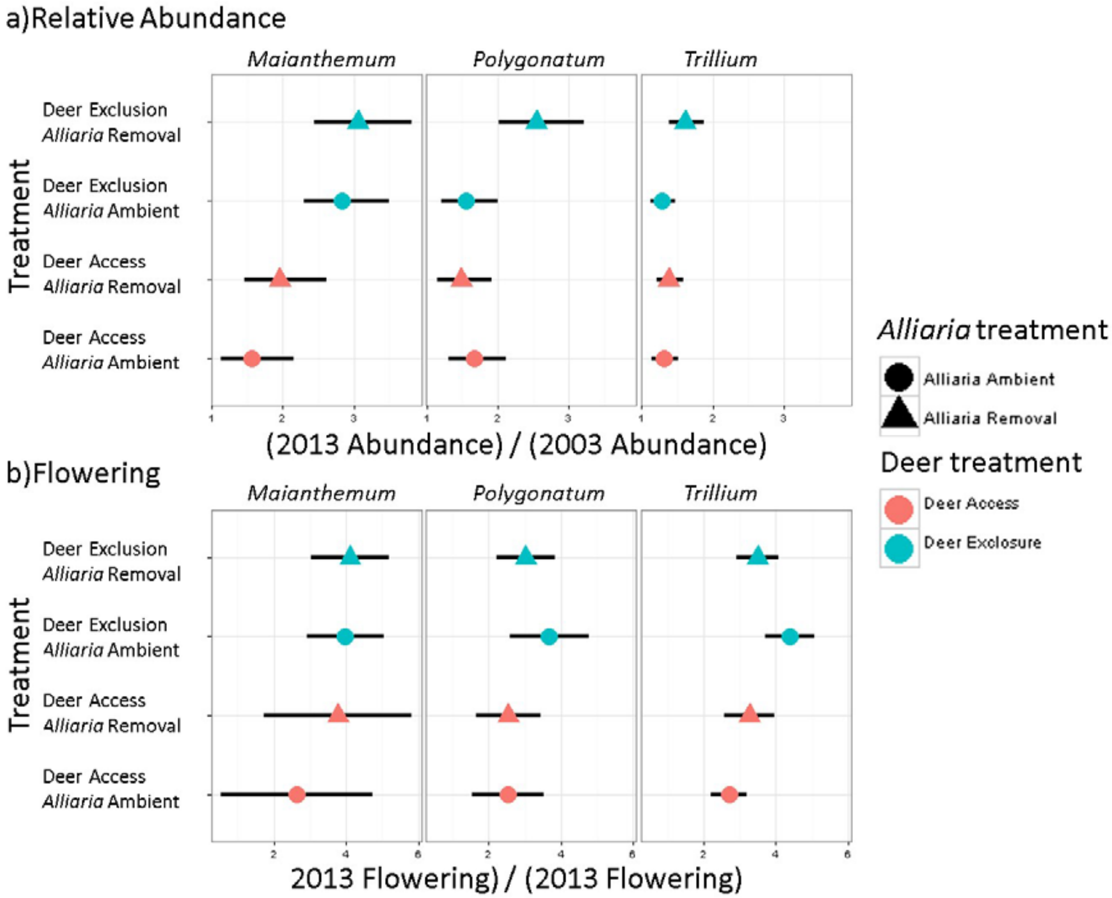

Figure 15. Relative increase from 2003 to 2013 in plant abundance (a) and flowering rates (b) for three species of native plants after deer exclusion and *Alliaria petiolata* removal. A value of one would indicate no change. Error bars are 95% confidence intervals.

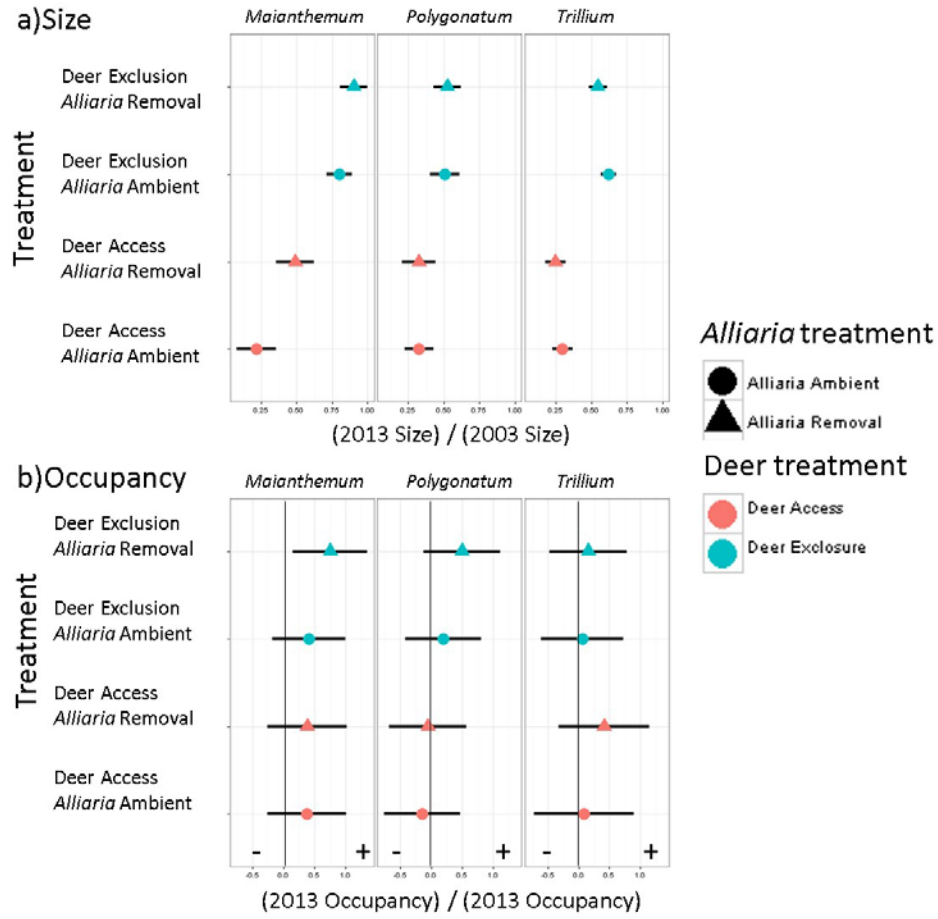

Figure 16. Relative increase in plant size (a) and subplot occupancy rates (b) for three species of native plants after deer exclusion and *Alliaria petiolata* removal. A value of one would indicate no change. Error bars are 95% confidence intervals.

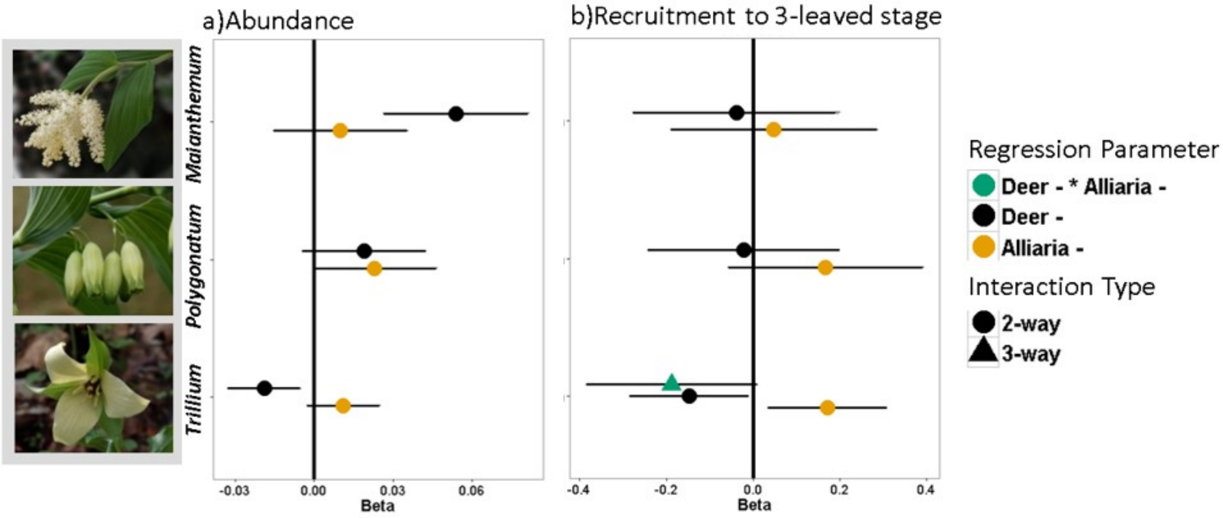

Figure 17. Effects of deer exclusion and Alliaria petiolata removal on changes in a) abundance and b) recruitment to 3-leaved life stage. Changes are from 2006-2013 for three species of perennial plant, Maianthemum racemosum, Polygonatum biflorum, and Trillium erectum. All effects are slope parameter from mixed regression models that represented changes in temporal trends relative to rates in deer access plots where Alliaria was at ambient density. Effect sizes are slope parameters from regression models. For Deer exclusion effects, this is the time*deer exclusion parameter from the regression, and for Alliaria removal this is time*Alliaria removal parameter. No three-way interactions (time*deer exclusion*Alliaria removal) were significant except for 3-leaved recruitment in Trillium.

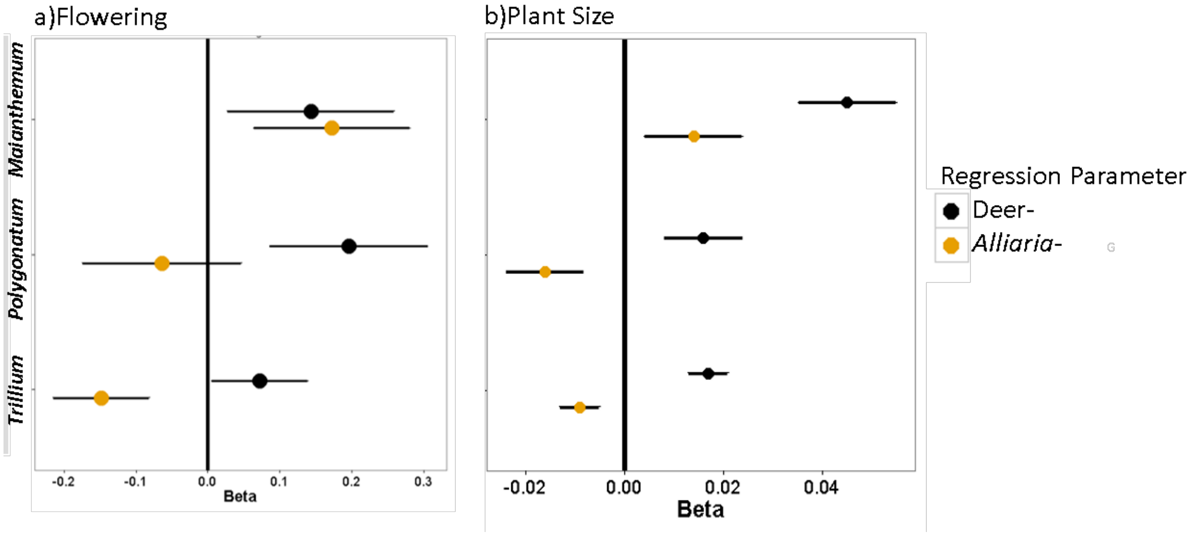

Figure 18. Effects of deer exclusion and *Alliaria petiolata* removal on changes in a) flowering rates, b) plant size. All effects are slope parameter from mixed regression models are represented changes in temporal trends relative to rates in deer access plots where Alliaria was at ambient density. Effect sizes are slope parameters from regression models. For Deer exclusion effects, this is the time*deer exclusion parameter from the regression, and for *Alliaria* removal this is timeAlliaria* removal parameter. No three-way interactions (time*deer exclusion**Alliaria* removal) were significant and effects of deer exclusion and *Alliaria* removal are additive.**

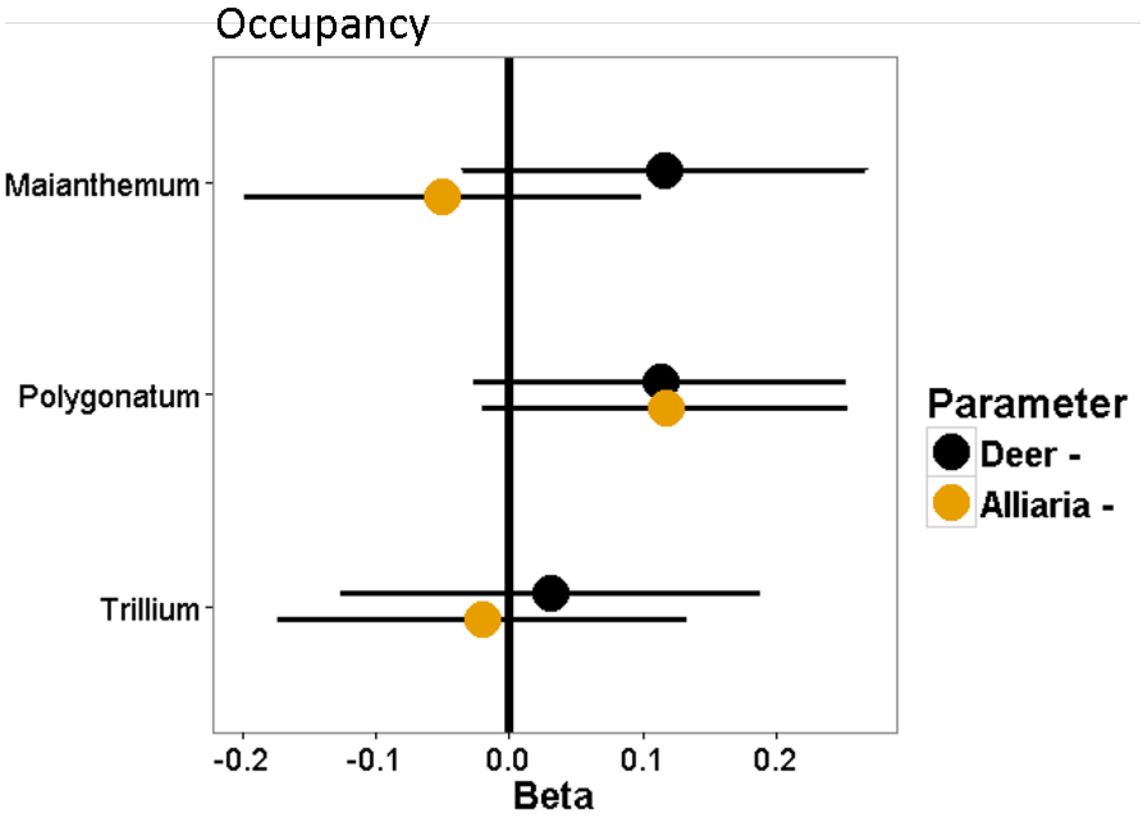

Figure 19. Effects of Deer exclusion and *Alliaria petiolata* removal on spatial occupancy. We defined occupancy as one or more stems of a given species present in a subplot.

6.0 CONCLUSIONS

Species interactions play out over time and over the course of the life histories of the participating organisms. In my dissertation I have analyzed long-term, longitudinal data on plant-plant and plant-herbivore interactions to understand the importance of this temporal dimension for judging the intensity and importance (*sensu* Welden and Slaussen 1986) of putatively strong interactions. This has required applying generalized linear mixed models (Bolker *et al.* 2009) to longitudinal data embedded in a complex experimental design.

Using this approach, I confirmed that the strong individual-level impacts of *Alliaria petiolate*, a common invasive species in the forests of North America (Hale *et al.* 2011, Hale *et al.* 2015), scale up to the population level to impact plant vital rates (Brouwer *et al.* 2015; Chapter 2). The importance of the impacts of this invader has recently been questioned using field-based but short term studies on seedlings (Davalos *et al.* 2014, Waller and Maas 2013). My results demonstrate the central of importance of considering which life history stages most influence population dynamics when conducting species interaction research (Goldberg and Scheiner 2001) and assessing impact over a suitable time scale. In this experiment, *Alliaria* removal did not result in an immediate change to plant vital rates, but this is consistent with evidence of soil legacy effects of *Alliaria* (Lankau *et al.* 2014), and the slow life history of forest plants (Whigham 2004). Additionally, field-based research is subject to significant variation over time and initially small effects can easily be swamped out by noise.

In Chapter 3 I used meta-analytic techniques to understand the temporal aspects of vegetation change when mammalian herbivores are overabundant. Successional processes and canopy turnover takes decades in closed canopy forest, so I used a comparative approach across studies to understand how the ubiquitous problem of overabundant herbivores affects forest canopies. I also utilized a life history perspective, considering different forest strata that interact directly (seedlings, saplings) and indirectly (subcanopy trees) with deer. I found evidence that different forests are moving towards canopies dominated by non-palatable species, as it typically assumed (Waller and Alverson 1997, Cote *et. al* 2004), while others are potentially progressing towards a more open, woodland structure. This latter process has only recently been proposed (Tanentzap *et al.* 2011) and deserves more attention. Meta-analysis has exploded in popularity among ecologists (Koricheva *et al.* 2013) and meta-regression in particular holds great promise for understanding how species interactions vary in intensity and importance under different conditions. In my case, it also allowed me to explore ecological questions not proposed by the original authors of the studies.

In Chapter 4 I explored how deer-tree interactions play out over time using a decade of empirical data. As in my other analyzes I found that there was considerable variation between life history stages and over time. Again, a longitudinal approach allowed me to understand how vegetation in both deer exclosures and deer access controls where changing dynamically. Contrary to our expectations, the abundance and occupancy of saplings increased in both treatments, and the impact of deer was most evident in terms of a difference in the rate of change.

Finally, in Chapter 5 I used data on three native species to test the generality of the effects of *Alliaria petiolata* on native plants, and to compare its impacts to deer. Each species responded differently, but all experienced benefits when *Alliaria* was removed. This study demonstrates not only that *Alliaria* can impact native plants at the population level, but its impacts are pervasive across multiple species and can be comparable in some cases to those of deer.

A key question of my study of vital rates in Chapter 5 was whether *Alliaria* impacts could be similar to deer. This approach was inspired by discussions among ecologists studying competition about how the importance of competition varies along environmental gradients (Kikvidvize *et al.* 2011). It is my view that the most holistic way to address questions about the importance of ecological interactions requires demographic modeling. My work in Chapter 2 and Chapter 5 focused on vital rates of adult perennial plants, which are the most important life history stage with regard to population growth and stability for these plants. Strong impacts on factors such as adult size and flowering forebode strong impacts on fitness and population growth, but full demographic models are needed to confirm this. It is possible that *Alliaria's* impacts are not consistent enough across adult life history transitions to match the known strong impact of deer on population growth rate (Maron and Crone 2006). Since deer impacts are stage-structured and *Alliaria's* are not, it is possible that *Alliaria* could strongly impact population growth rate, and that populations contending with deer and *Alliaira* could experience considerably lower vital rates. It will be especially important to extend population models of deer and *Alliaria* impacts using stochastic and periodic demographic approaches because we observed considerable temporal variability and cyclic patterns in vital rates as the experiment progressed.

A final question that should be addressed when considering the importance of species interactions is how the impact of the interaction compares to the effects of temporal and spatial variability. The development of variance decomposition techniques for generalized linear models, such as Bayesian ANOVA (BANOVA; Gelman 2005, Qian and Shen 2007), holds great promise for partitioning the effects of species interactions, spatial variability, and temporal stochasticity on fitness components of organism.

APPENDIX A

CHAPTER 2 SUPPLEMENTARY MATERIALS

Table 5. Validation of imputed *Maianthemum racemosum* size data. Imputation was done for plants with missing size data due to deer browse (primarily on flowering individuals) and for plants from the two years (2008-2009) when sizes could not be collected (n=412 intances). T-tests were conducted on log-transformed data. Kolmogorov-Smirnov (KS) test indicates whether two samples come from the same distribution. Imputation of size data increases the sample size of flowering plants by 319, which increases the overall mean plants size by 2.2 cm. Within life history stages (non-flowering and flowering) there are no significant differences between the original and imputed data.

Plant	Original Data		Imputed Data		t-test		KS-test	
Status	Mean (SE)	N	Mean (SE)	N	t	p	D	p
All plants	28.8 (0.5)	963	31.0 (0.4)	1481	3.9	<0.001	0.07	0.004
Non-flowering	24.5 (0.3)	808	24.8 (0.3)	1127	1.4	0.2	0.06	0.1
Flowering	51.5 (1.2)	155	51.0 (0.7)	354	0.01	1	0.07	0.7

Table 6. Estimated frequency of prolonged vegetative dormancy in plots allocated to Alliaria Ambient and Removal treatments, in years prior to (2004-2006) and after (2007-2013) implementation of the treatment. Estimate are from a mark-recapture model using all years of data and a Removal*Year interaction (Model set 3, Table 1). Period indicates years before or after implementation of the Alliaria removal treatment.

		***Alliaria* Ambient Plots**		***Alliaria* Removal Plots**	
Period	**Year**	**Frequency**	**SE**	**Frequency**	**SE**
Pre-*Alliaria* Removal	2004	0.31	0.078	0.18	0.061
	2005	0.11	0.052	0.10	0.040
	2006	0.08	0.039	0.07	0.032
Post-*Alliaria* Removal	2007	0.14	0.046	0.09	0.035
	2008	0.18	0.051	0.09	0.034
	2009	0.51	0.065	0.38	0.055
	2010	0.25	0.054	0.13	0.035
	2011	0.25	0.056	0.12	0.035
	2012	0.15	0.047	0.13	0.036
	2013	0.09	0.049	0.13	0.043

APPENDIX B

CHAPTER 3 SUPPLEMENTARY MATERIALS

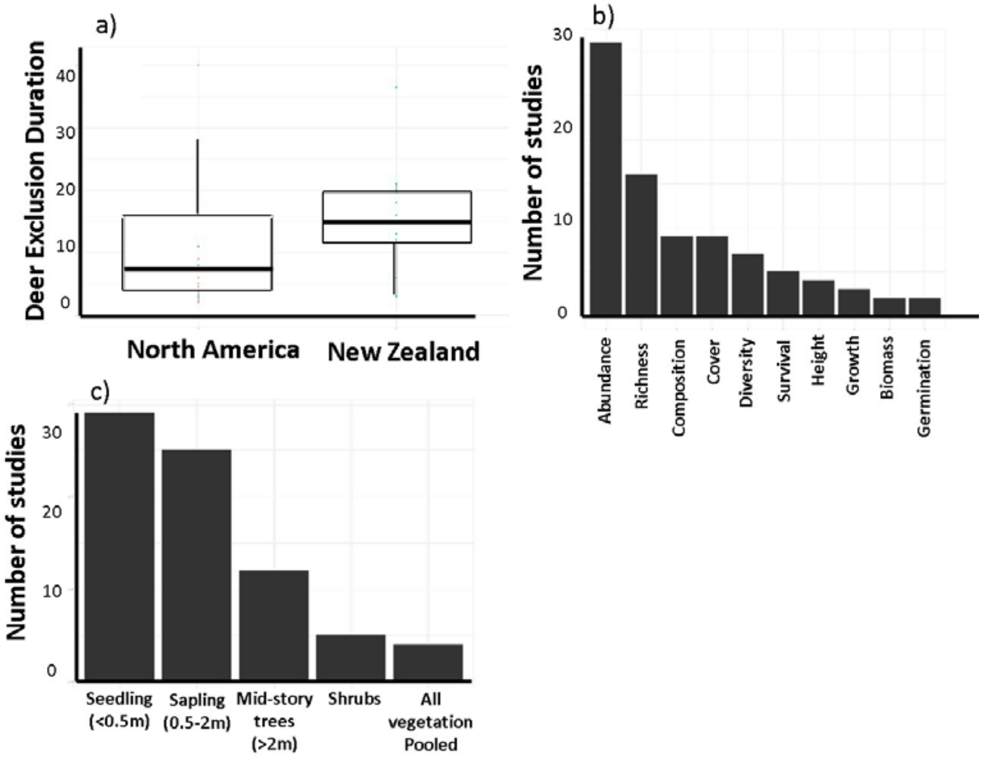

Figure 20. Characteristics of 49 deer exclusion studies in closed canopy forest from around the globe. Duration of overabundance extracted from original studies, or assigned using information from Leopold *et al.* 1947 and Southeastern Cooperative Wildlife Disease Study http://vet.uga.edu/scwds/range-maps. a)The distribution of deer exclusion times in North America and New Zealand. b)The distribution of different response variables reported in studies. c)The distribution of different strata reported.

Table 7. Duration of deeer exclusion, duration of overabundance (DOA), and other details for studies included in the meta-analysis. See methods for information regarding determination of DOA.

Authors	Duration Exclusion (years)	DOA When expt. began	DOA When expt. ended	State / Geographic Location	Deer density (km-2)	Primary deer species
Abrams & Johnson 2012	18	7	25	PA	83.5	ODOVIR
Aldous 1952	6	NA	NA	MI	NA	ODOVIR
Allen et al 1984	16	80	96	NZ	NA	CERELA
Anderson & Loucks 1979	5	35	40	WI	75	ODOVIR
Aronson & Handel 2011	2	22	23	NJ	67.5	ODOVIR
Barrett & Stiling 2006	4	30	34	FL	21.59	ODOVIR
Bellingham & Allan 2003	21	80	101	NZ	NA	ODOVIR
Bresette et al 2012	18	15	33	VA	33	ODOVIR
Bughalo et al 2013	4	30	33	NC	7	ODOVIR
Castleberry et al 2000	3	13	15	SC	5	ODOVIR
Collard et al 2010	8	30	38	QU	16	ODOVIR
Eschtruth & Battles 2008	4	NA	NA	PA	15.1	ODOVIR
Fox et al 2014	4	11	16	IN	56	ODOVIR
Hegland et al 2013	10	0	0	Nor	5.5	CERELA
Husheer et al 2003	13	54	67	NZ	NA	CERNIP
Husheer et al 2005	20	86	104	NZ	NA	CERELA
Husheer 2007	18	19	37	NZ	3.5	CERELA
Kain et al 2011	60	1	63	PA	12.5	ODOVIR
Kay & Bartos 2000	40	NA	NA	UT	NA	ODOHEM
Kraft et al 2004	**5**	47	53	MI	12.5	ODOVIR
Krueger et al 2009	2	NA	NA	PA	4.9	ODOVIR
Kuijper et al 2010	7	0	NA	Pol	4.7	Multiple
Kumar et al 2006	13	0	13	Japan	31	CERNIP
Lessard et al 2012	11	17	28	TN	35	ODOVIR
Levine et al 2012	16	27.5	39.5	NY	12	ODOVIR
Long et al 2007	9	31.5	40.5	PA	12	ODOVIR
Martin & Baltzinger 2010	1	NA	NA	BC	50	ODOVIR
Mason et al 2010	11.5	80	91.5	NZ	NA	Multiple
McGarvey et al 2013	20	14	35	VA	35	ODOVIR

Merganic et al 2009	30	NA	NA	Czech	NA	Multiple
Murata et al 2009	3	NA	NA	Japan	NA	CERNIP
Murray et al 2013	6	58	64	MI	NA	ODOVIR
Nomiya et al 2002	3	NA	NA	Japan	30	CERNIP
Nuttle et al 2013	5	14	19	WV	14.75	ODOVIR
Nuttle et al 2014	15	NA	NA	PA	11	ODOVIR
Perrin et al 2006	16	NA	NA	Ire	32	Multiple
Relva et al 2010	4	41.25	45.25	Arg	36	Multiple
Riemenschneider et al 1995	5	12.5	16.5	IN	88.2	ODOVIR
Rooney 2009	16	60	76	WI	16	ODOVIR
Ross et al 1970	16	1927	NA	MN	28.5	ODOVIR
Rossell et al 2007	2	NA	NA	WADC	23	ODOVIR
Rossell et al 2005	5	NA	NA	VA	67	ODOVIR
Shelton et al 2014	4.5	25.5	30	IN	NA	ODOVIR
Stewart & Burrows 1989	6	NA	NA	NZ	NA	ODOVIR
Tanentzap et al 2009	36.5	40	76.5	NZ	4.64	CERELA
Tanentzap et al 2011	28	28	56	Ont	31	ODOVIR
White 2012	17	60	77	MN	44.5	ODOVIR
Willms et al 1979	2.5	NA	NA	BC	NA	ODOHEM
Wilson et al 2006	3	80	83	NZ	NA	CERELA
Wright et al 2012	12	80	92	NZ	NA	Multiple
Smale et al 1995	NA	NA	NA	NZ	10.5	NA
Andruk et al 2014	3	45.5	48.5	TX	8.83	ODOVIR
Thomas-Van Gundy 2014	9	14	23	WV	14.75	ODOVIR

APPENDIX C

CHAPTER 4 SUPPLEMENTARY MATERIALS

C.1 CONCEPTUALIZING POTENTIAL RESPONSE TO DEER EXCLUSION

Deer exclusion experiments in forests usually test the general hypothesis that deer exclusion will result in differences between fenced and unfenced sampling unit. Over time there are numerous patterns of change by which these differences could develop (Fig. 21). In most experiments there will be at least a short time lag before any change is observed (Fig. 21b-d, short green arrows), though response variables such as growth (e.g. RGR), height or biomass might respond almost immediately (Tanentzap *et al.* 2011). It is possible that deer exclusion will halt changes to vegetation while continued deer browse further degrade the forest. This is most likely to occur if exclusion occurs shortly after deer become overabundant. Most deer exclusion studies appear to implicitly assume that deer exclusion causes conditions sush as sapling density to increase while control plots remain in a degraded state (Fig. 21b). It is also possible that deer exclusion improves conditions while in the control conditions continue to degrade, resulting in divergence between treatments and a very large effect size (Fig. 21c). This potentially occurs when deer densities are very high and all vegetation, including non-palatable species, are being consumed in control plots. It is also possible that increases in state variable could occur in both treatments, but deer exclusion allows them to occur faster (Fig. 21d). This will potentially occur in younger, successional stands or if there has been a recent disturbance before the study began. For example, if a mast event results in more stems than deer can browse, some will escape above browse height, but more will escape in the exclosure.

In some cases, there could be substantial time lags before change can be observed between treatments. For example, in mature stands with low light conditions saplings may grow slowly (Fig 21e). This is hypothesized by Tanentzap *et al.* (2012) to be a common response. For gap or fire dependent species there might be a time lag after exclusion until a necessary stochastic event occurs (Fig. 21f). It is also possible that disturbances could improve growth conditions in both treatments, but that change occur more quickly in exclosures (Fig. 21g). Conversely, the effects of a stochastic event such as ice damage, an insect outbreak or drought could cause declines in both treatments, but decline in controls are more severe (Fig. 21h).

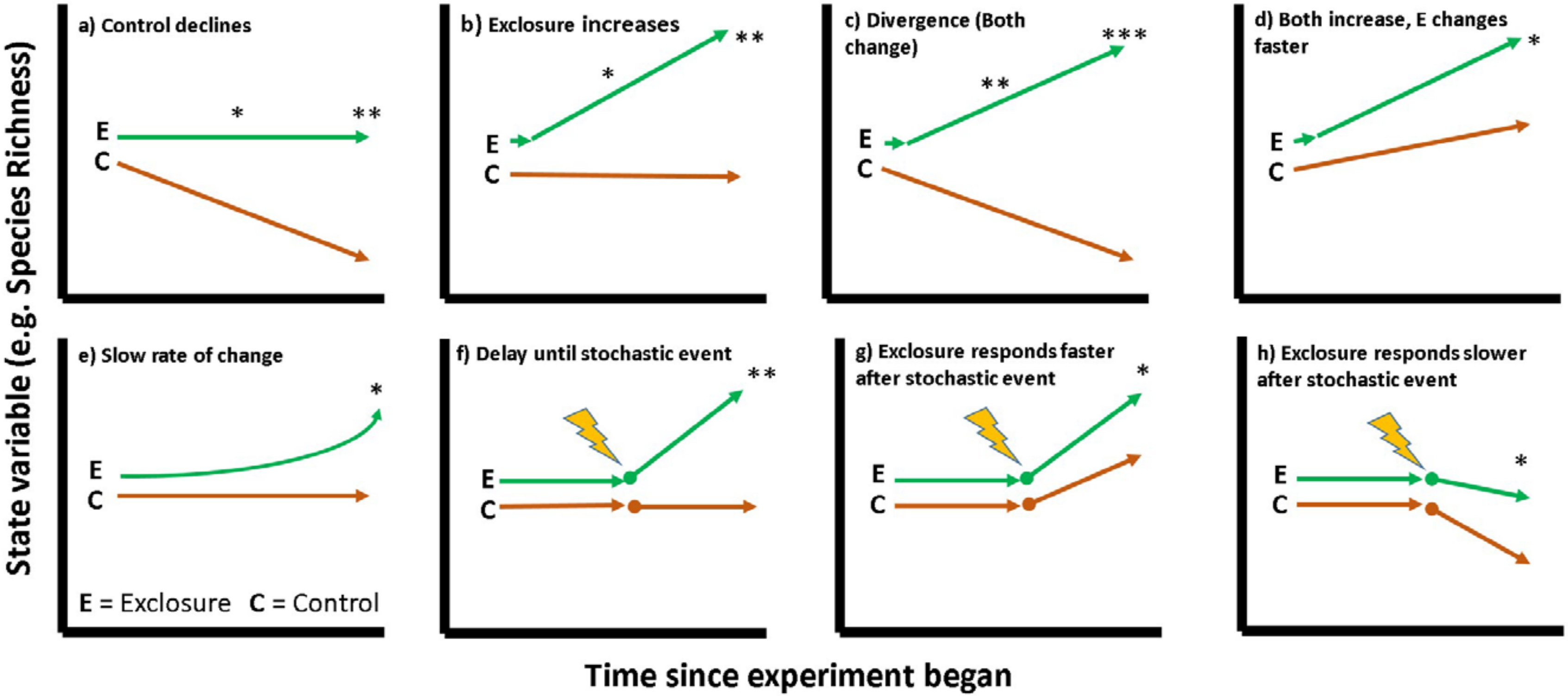

Figure 21. Possible responses to deer exclusion over time (E) relative to controls (C). Asterisks indicate the relative likelihood of detecting a significant effect between treatments by given time. Arrows with balls on their left end indicate changes possibly affected by stochastic events. Stochastic events, such as fire, treefall, insect outbreaks, ice storms or mast seeding, are represented by lightning bolts.

C.2 SUPPLEMENTARY FIGURES AND TABLES

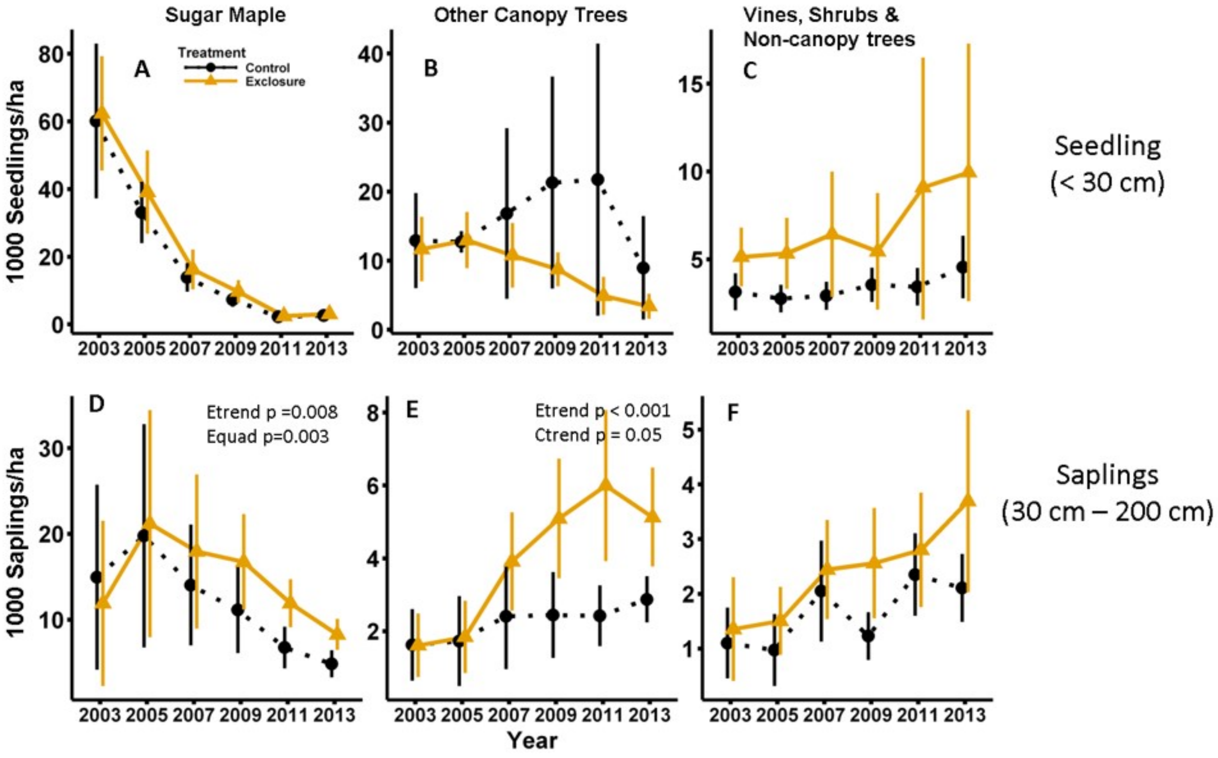

Figure 22. Understory density of woody seedlings <30cm tall (A-C) and saplings 30-200cm tall (D-F) in deer access and deer exclusion plots. Woody species are grouped into 3 categories: sugar maple, (A,D) canopy-forming trees excluding sugar maple (B,E), and non-canopy forming trees (C,F), shrubs and vines. N= 6 plots per treatment and error bars are +/1 SE.

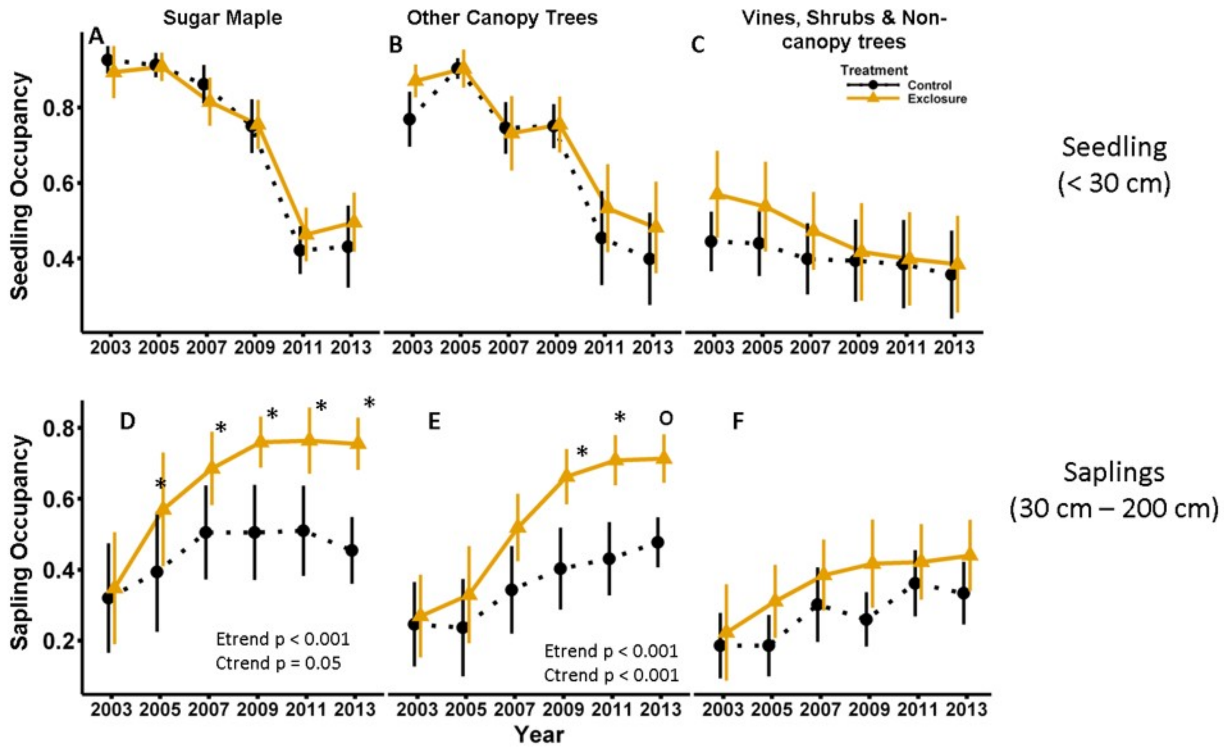

Figure 23. Occupancy of woody seedlings <30cm tall (A-C) and saplings 30-200cm tall (D-F) in deer access and exclusion plots. Trees were grouped into 3 categories: sugar maple, canopy trees (tree species that can reach the canopy excluding sugar maple), and shrubs and vines (small trees that do not reach the canopy). N= 6 plots per treatment and error bars are +/1 standard error. Occupancy was defined as the number of 2m2 subplots with ≥1 stem/36 total subplots per plot.

Table 8. Woody species at Trillium Trail Nature Reserve, Fox Chapel Borough, Allegheny County, PA. Native species are coded as "N" and exotic invaders are "E".

Genus species	Common name	Family	Exotic?	Palatability
Acer nigrum	black maple	Aceraceae	N	Preferred
Acer rubrum	red maple	Aceraceae	N	Preferred
Acer saccharum	sugar maple	Aceraceae	N	Preferred
Ailanthus altissima	tree of heaven	Simaroubaceae	E	Not Preferred
Aralia spinosa	devil's walking stick	Araliaceae	N	Not Preferred
Berberis thunbergii	Japanese barberry	Berberidaceae	E	Not Preferred
Betula nigra	black (river) birch	Betulaceae	N	Not Preferred
Carya tomentosa	mockernut hickory	Juglandaceae	N	Equivocal
Castanea spp.	chestnut	Fagaceae	N	Preferred
Celastrus orbiculatus	oriental bittersweet	Celastraceae	E	Not Preferred
Cornus spp.	dogwood	Cornaceae	N	Preferred
Craetagus spp.	hawthorn	Rosaceae	N	Equivocal
Fagus grandifolia	American beech	Fagaceae	N	Not Preferred
Frangula alnus	alder buckthorn	Rhamnaceae	E	Not Preferred
Fraxinus americana	white ash	Oleaceae	N	Preferred
Hamamelis virginiana	witchhazel	Hamamelidaceae	N	Preferred
Hydrangea arborescens	hydrangea	Hydrangeaceae	N	Not Preferred
Juglans nigra	black walnut	Juglandaceae	N	Not Preferred
Ligustrum vulgare	privet	Oleaceae	E	Not Preferred
Lindera benzoin	spicebush	Lauraceae	N	Not Preferred
Liriodendron tulipifera	tulip poplar	Magnoliaceae	N	Equivocal
Lonicera spp.	honeysuckle	Loniceraceae	E	Preferred
Magnolia acuminata	cucumber magnolia	Magnoliaceae	N	Equivocal
Morus spp.	mulberry	Moraceae	E	Not Preferred
Ostrya carpinus	eastern hophornbeam	Betulaceae	N	Preferred
Parthencissus quinquefolia	Virginia creeper	Vitaceae	N	Equivocal

Platanus occidentalis	American sycamore	Plantanaceae	N	Not Preferred
Prunus serotina	black cherry	Rosaceae	N	Not Preferred
Prunus virginiana	chokecherry	Rosaceae	N	Preferred
Quercus alba	white oak	Fagaceae	N	Preferred
Quercus rubra	northern red oak	Fagaceae	N	Preferred
Rhododendron	rhododendron	Ericaeae	E	Preferred
Rubus spp.	blackberry	Rosaceae	N	Preferred
Sambuccus canadensis	elderberry	Caprifoliaceae	N	Preferred
Smilax spp.	greenbriar	Similicaceae	N	Preferred
Staphylea trifoliata	American bladdernut	Staphyleaceae	N	Not Preferred
Tilia americana	basswood	Tiliaceae	N	Preferred
Toxicodendron radicans	poison ivy	Anacardiaceae	N	Not Preferred
Tsuga canadensis	eastern hemlock	Pinaceae	N	Not Preferred
Ulmus rubra	slippery elm	Ulmaceae	N	Equivocal
Viburnum acerifolium	maple-leaved viburnum	Adoxaceae	N	Preferred
Viburnum dentatum	arrowwood	Adoxaceae	N	Preferred
Vitus spp.	grape	Vitaceae	N	Preferred

Table 9. Herbaceous species at Trillium Trail Nature Reserve, Fox Chapel Borough, Allegheny County, PA.

Scientific Name	Common Name	Family	Exotic?
Actea pachipoda	white baneberry	Ranunculaceae	N
Alliaria petiolata	garlic mustard	Brassicaeae	E
Anemone quinquefolia	wood anemone	Ranunculaceae	N
Aquilegia canadensis	wild columbine	Ranunculaceae	N
Aralia nudicaulis	sarsaparilla	Araliaceae	N
Arasum canadense	wild ginger	Aristolochiaceae	N
Arisaema triphyllum	Jack-in-the-pulpit	Araceae	N
Aster divaricatus	white wood aster	Asteraceae	N
Aster pilosus	heath aster	Asteraceae	N
Campanula americana	American bellflower	Campanulaceae	N
Cardamine concatenata	cut-leaved toothwort	Brassicaceae	N
Cardamine concatenata	cut-leaved toothwort	Brassicaeae	N
Cardamine diphylla	broad-leaved toothwort	Brassicaceae	N
Cimicifuga racemosa	black cohosh	Ranunculaceae	N
Circaea quadrisulcata	enchanter's nightshade	Onagraceae	N
Claytonia virginica	spring beauty	Portulaceae	N
Clintonia umbellata	white clintonia	Liliaceae	N
Corydalis sempervirens	pale corydalis	Papaveraceae (Fumariaceae)	N
Dicentra canadensis	squirrel corn	Papaveraceae (Fumariaceae)	N
Dicentra cucullaria	dutchman's breeches	Papaveraceae (Fumariaceae)	N
Epifagus virginiana	beech drops	Orobanchaceae	N
Erigeron annuus	daisy fleabane	Asteraceae	N
Eupatorium purpureum	joe-pye weed	Asteraceae	N
Eupatorium rugosum	white snakeroot	Asteraceae	N
Eyrithronium americanum	yellow trout lily	Liliaceae	N
Floerkia proserpinacoides	false mermaid	Limnanthaceaea	N
Gallium odorutum	woodruff	Rubiaceae	E

Gallium spp.	bedstraw	Rubiaceae	N
Gaultheria procumbens	wintergreen	Ericaeae	N
Geranium maculatum	wild geranium	Geranaceae	N
Glechoma hederacea	ground ivy	Lamiaceae	E
Helianthus divaricatus	woodland sunflower	Asteraceae	N
Hepatica nobilis	round-lobed hepatica	Ranunculaceae	N
Houstonia caerulea	bluet	Rubiaceae	N
Hydrophyllum virgianum	Virginia Waterleaf	Hydrophyllaceae	N
Impatiens capensis	spotted touch-me-not	Balsaminaceae	N
Impatiens pallida	pale touch-me-not	Balsaminaceae	N
Laportea canadensis	wood nettle	Urticaceae	N
Maianthemum canadensis	canada mayflower	Liliaceae	N
Medeola virginiana	indian cucumber root	Liliaceae	N
Mertensia virginica	Virginia bluebell	Boraginaceae	E
Microstegium vimenium	Asian stilt grass	Poaceae	E
Mitella diphylla	mitrewort	Saxifragaceae	N
Monotropa uniflora	indian pipe	Monotropaceae	N
Osmorhiza claytonii	hairy sweet cicely	Apiaceae	N
Osmorhiza longistylus	aniseroot	Apiaceae	N
Panax tripholius	dwarf ginseng	Araliaceae	N
Phlox divaricata	blue phlox	Polemoniaceae	N
Phlox stolonifera	creeping phlox	Polemoniaceae	N
Phytolacca americana	pokeweed	Phytolaccaeae	N
Pilea pumila	clearweed	Urticaceae	N
Podophyllum peltatum	mayapple	Berberidaceae	N
Polygala paucifolia	fringed polygala	Polygalaceae	N
Polygonatum biflorum	smooth solomon's seal	Liliaceae	N
Polygonum cuspidatum	Japanese knotweed	Polygonaceae	E
Polygonum persicarium	spotted lady's thumb	Polygonaceae	E
Ranunculus arbortivus	kidney-leaved buttercup	Ranunculaceae	N
Ranunculus ficaria	lesser celandine	Ranunculaceae	E

Sanguinaria canadensis	bloodroot	Papaveraceae	N
Sanicula marilandica	black snakeroot/sanicle	Apiaceae	N
Saxifraga virginiensis	early saxifrage	Saxifragaceae	N
Sedum ternatum	stonecrop	Crassulaceae	N
Silene virginica	fire pink	Caryophyllaceae	N
Silene vulgars	bladder campion	Caryophyllaceae	E
Smilacena racemosa	false solomon's seal	Liliaceae	N
Stellaria media	common chickweed	Caryophyllaceae	E
Symplocarpus foetidus	skunk cabbage	Araceae	N
Thalicrum dioicum	meadow rue	Ranunculaceae	N
Thalictrum thalictroides	rue anemone	Ranunculaceae	N
Tiarella cordifola	foamflower	Saxifragaceae	N
Trillium erectum	red trillium	Liliaceae	N
Trillium grandiflorum	large-flowered trillium	Liliaceae	N
Trillium sessile	toadshade trillium	Liliaceae	N
Tussilago farfara	coltsfoot	Asteraceae	E
Urtica dioica	stinging nettle	Urticaceae	N
Uvularia perfoliata	bellwort	Liliaceae	N
Viola blanda	sweet white violet	Violaceae	N
Viola canadensis	canada violet	Violaceae	N
Viola eriocarpa	smooth yellow violet	Violaceae	N

APPENDIX D

CHAPTER 5 SUPPLEMENTARY MATERIALS

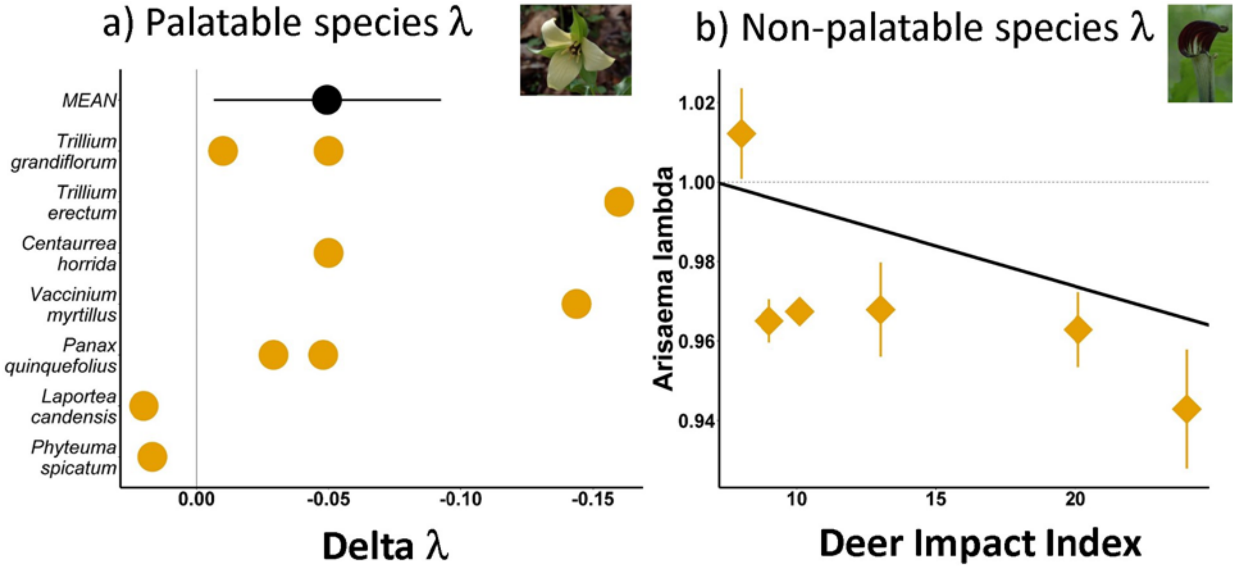

Figure 24. Deer reduce λ of palatable and non-palatable forest plants. a) Deer reduce λ of palatable specices by ~5%. Species that have been studied include including *Trillium erectum* (Kalisz *et al.* 2014), *T. grandiflora* (Knight 2004, Rooney and Gross 2003), *Panax quinquefolius* (Farrington *et al.*2009, McGraw and Furedi 2005), *Centaurea horrida* (Pisanu *et al.* 2012), and *Vaccinium myrtillus* (Hegland *et al.* 2010). Positive effects on λ have been documented in just two species, *Laportea Canadensis* (Augustine *et al.* 1998) and *Phyteuma spicatum* (Kolb 2012). Data extracted from Maron and Crone (2006) and primary literature. b) Across a natural gradient of browse pressure, deer also negatively impact the non-palatable species *Arisaema*

***triphylllum* (Heckel 2015), probably through soil-mediated mechanisms (e.g. compaction; Heckel *et al.* 2010). Indirect soil-mediated effects of deer have also been observed in other species (e.g Kardol *et al.* 2014).**

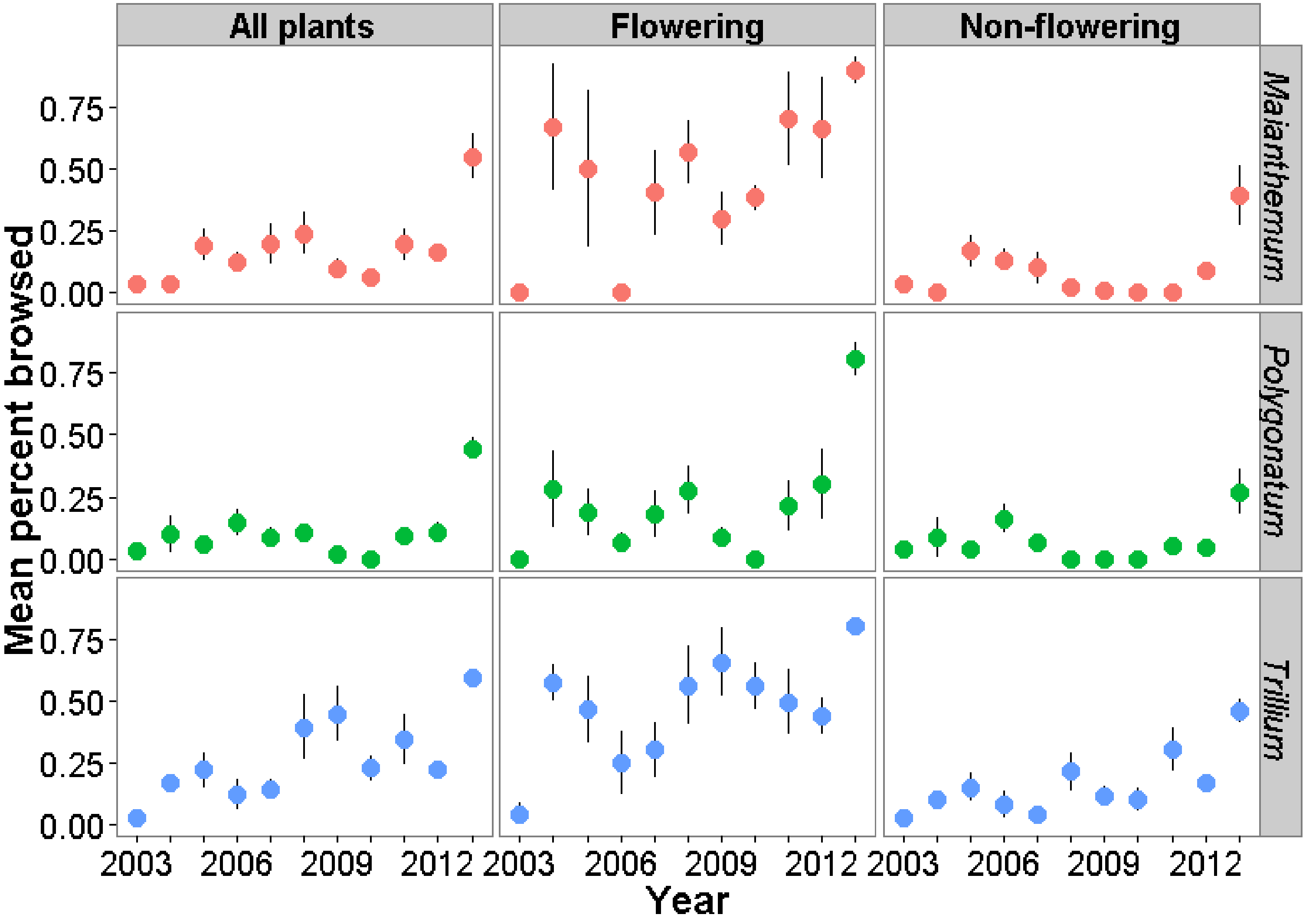

Figure 25. Mean percentage of *Maianthemum racemosum*, *Trillium erectum* and *Polygonatum biflorum* browsed by deer in deer access plots at Trillium Trail Nature Reserve, Fox Chapel, PA, 2003-2013. Error bars are +/- 1 SE. N = 5 plots per combination of treatments.

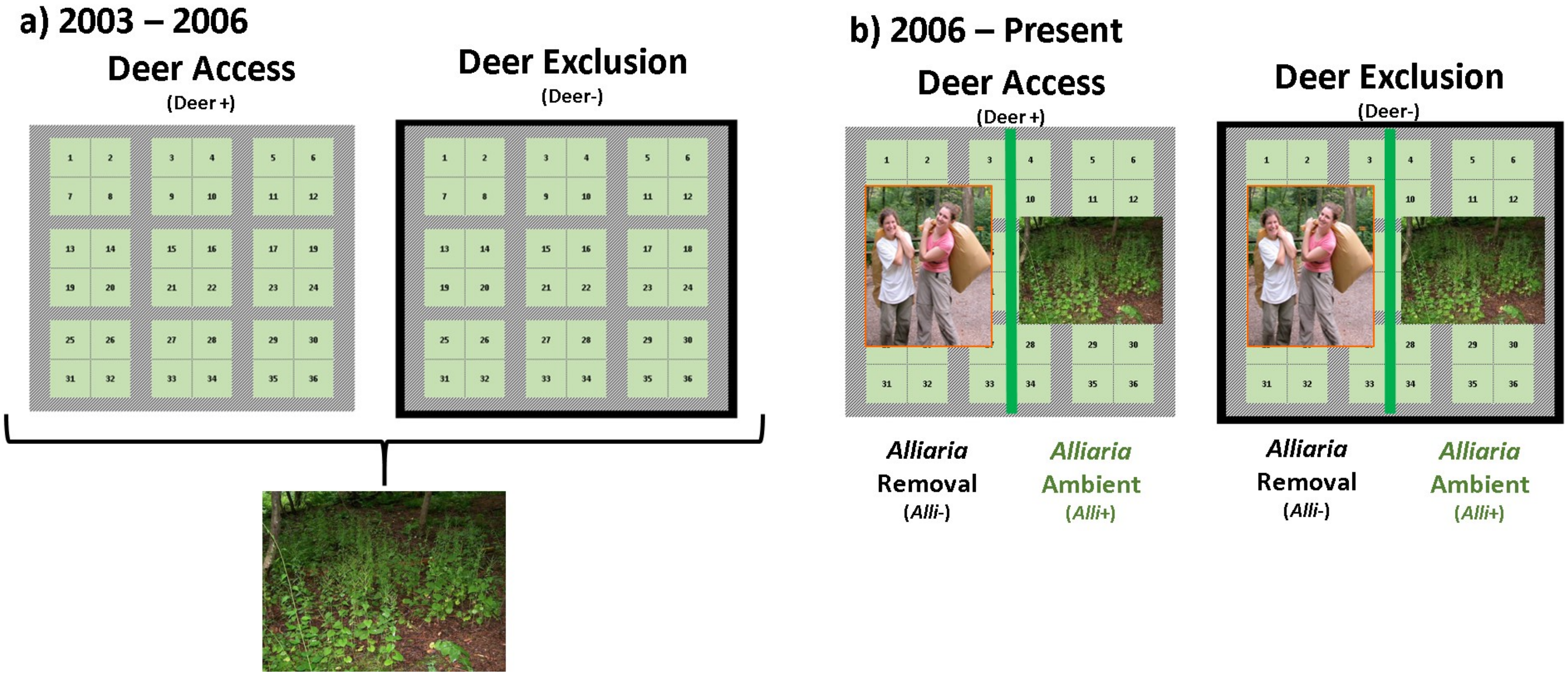

Figure 26. Layout of crossed deer exclusion and *Alliaria petiolata* removal experiment at Trillium Trail Nature Reserve, Fox Chapel, PA. a) Five study sites were sited and a pair of plots designated at each site. One of each pair was fenced to exclude deer (Deer-). Each subplot is divided into 36 2 m x 2 m subplots, and each subplot is approximately divided into 1m2 quadrats. Alliaria was not manipulated but declined in abundance in fenced exclosures from 2003-2006. b) In late spring of 2006 all *Alliaria* were removed (Alli-) from half of each plot (18 subplots per plot) while it remained at ambient densities in the other half of the plot (*Alli*+). Seed dispersal barriers are erected each year when Alliaria fruits become mature. Each year all *Alliaria* seedlings that emerge from the seedbank in Alli- plots are removed.

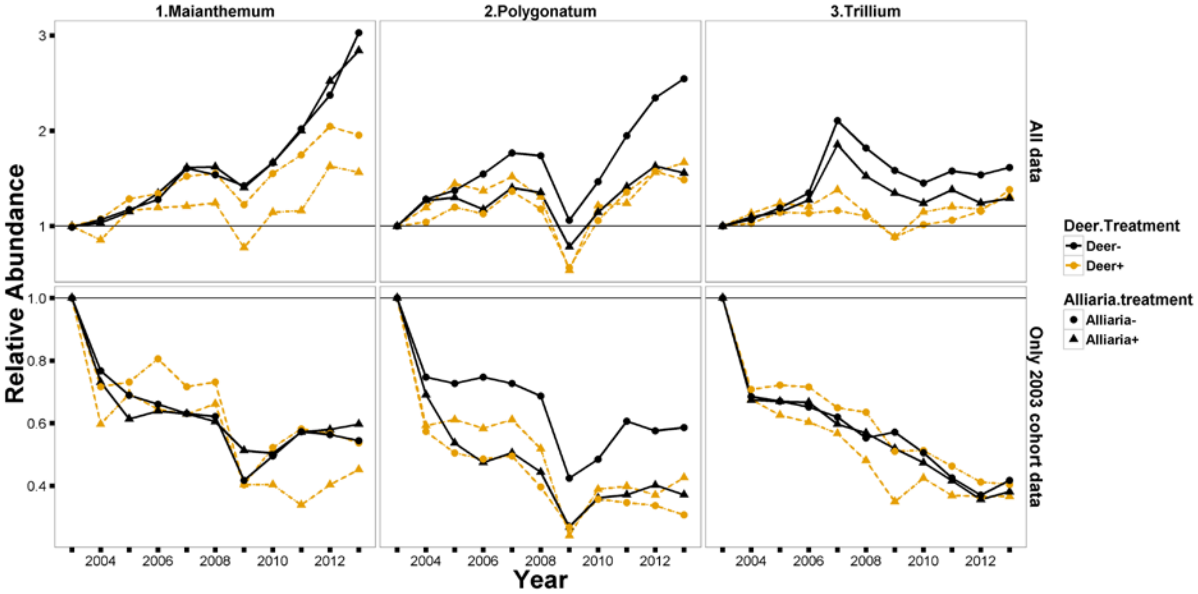

Figure 27. Changes in relative abundance of multi-leaved plants from 2003 to 2013 for all plants (a-c) and plants first observed in 2003 (d-e). A value of 1 indicates no change from the initial abundance in 2003. Means are calculated from N = 5 plots per treatment and weighted by the initial abundance in each plot. Changes in abundance occur due to mortality, prolonged dormancy, and recruitment of seedlings to the multi-leaved stage.

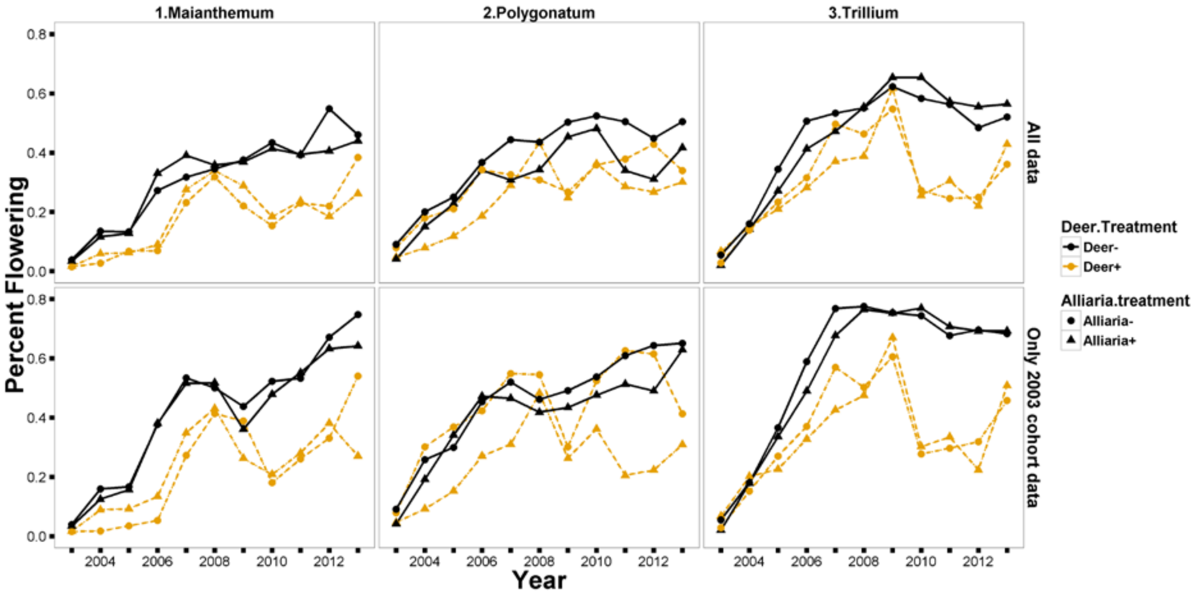

Figure 28. Changes in flowering frequencies from 2003 to 2013 for all plants (a-c) and plants first observed in 2003 (d-e). Means are calculated from N = 5 plots per treatment and weighted by the initial abundance in each plot. Plants that were browsed before being observed were assumed to be flowering.

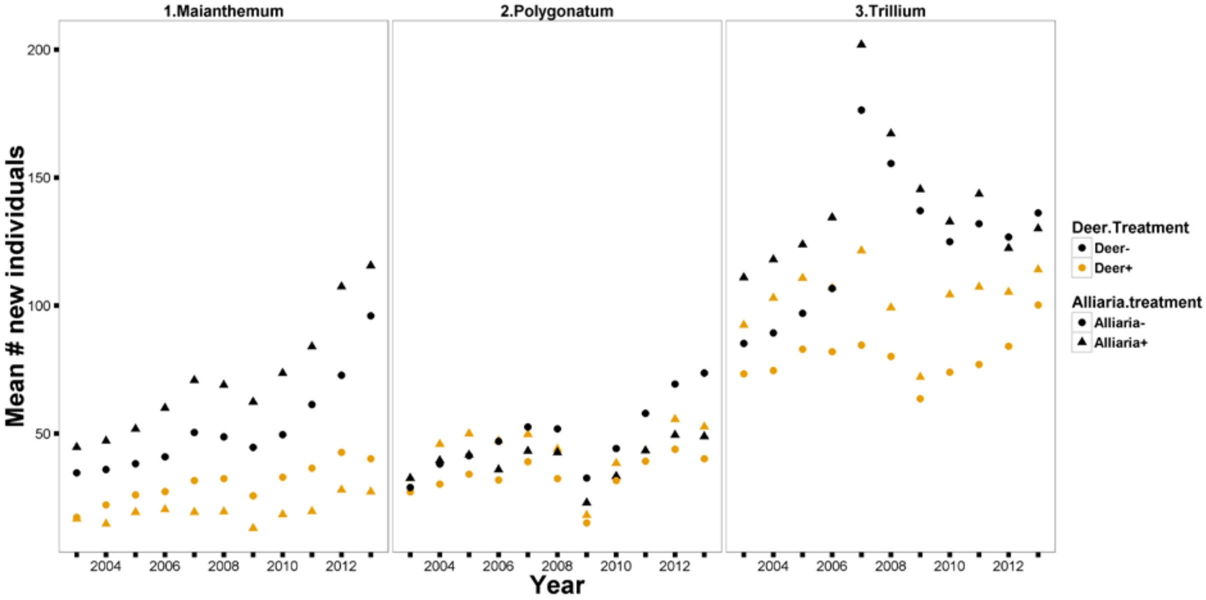

Figure 29. Changes in mean number of newly tagged multi-leaved plants from 2003 to 2013. Means are calculated from N = 5 plots per treatment. New multi-leaved plants can appear through recruitment from seed and survival of seedlings, emerge from prolonged vegetative dormancy, production of multiple clonal stems from a single rhizome, and clonal fragmentation.

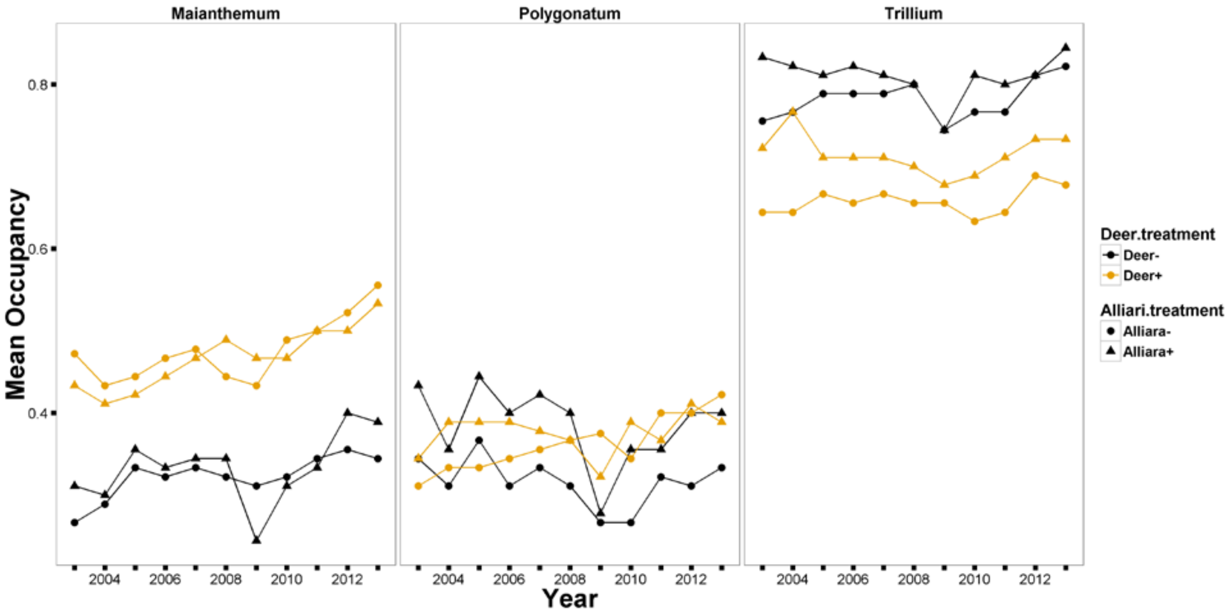

Figure 30. Changes in mean rate of occupancy of eight 4m2 subplots/treatment over time. Means are from N = 5 plots per treatment combination, with 18 subplots per plot per treatment.

Table 10. Plant taxonomic information, species-specific measurement details, and population summaries. The number of plants list is the total summed across the entire experiment.

Species information	**Species**	***Polygonatum biflorum***	***Maianthemum racemosum***	***Trillium erectum***	***Alliaria petiolata***
	Family	Asparagacea	Asparagacea	Melanthiaceae	Brassicaceae
	Authority	Walter (Elliott)	L.	L.	(M. Bieb.) Cavara & Grande
	Common Name	Solomon's seal	false Solomon's seal	Red Trillium	Garlic Mustard
	Size measurement	Stem + terminal leaf	Stem + terminal leaf*	Longest leaf	
Descriptive stats	**N 2003**	405	351	1389	
	N 2006	529	457	1715	
	N 2013	733	881	1923	
	N min	296	351	1389	
	N Max	733	881	2227	

*Stem + terminal leaf, excluding raceme

Table 11. Summary of response variables, data subsets, and random effects structure.

Ecological Level	Vital rate / Population Characteristic	Cohorts	Measurement Unit	Type of regression model	R Package	Split-split-plot	Split-plot	Random slope	Covariate
Individual	**Reproduction (successful flowering)**	**2003-2006**	**Plant**	logistic	*glmer*	✓		✓	
	Size / Growth	**2003-2006**	**Plant**	linear	*lmer*	✓		✓	
Population	**Abundance**	**2003-2013**	**plot**	negative binomial	*glmm ADMB*	*glmer*	✓	✓	2003 abundance +
	Occupancy	**2003-2013**	**subplot**	logistic	*glmer*	*glmer*	✓	✓	
	3-leaved recruitment	**2003-2013**	**subplot**	logistic	*glmer*	*glmer*	✓	✓	2003 abundance +

* All models contained random intercepts for the measurement units

\+ Initial abundance in 2004 was used if there were no plants present in 2003 but a plant emerged from dormancy in 2004

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