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**THE INFLUENCE OF WHITE-TAILED DEER  
AND LANDSCAPE COMPOSITION AND STRUCTURE  
ON EXOTIC PLANT SUCCESS**

A Dissertation in

Ecology

By

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## ABSTRACT

Plant communities are shaped by a variety of interacting factors including geographic constraints, abiotic, and biotic factors. The research contained herein investigated how these factors interact to influence exotic plant invasions. In the Northeastern United States, the highly abundant native white tailed deer (*Odocoileus virginianus* Zimm.), and landscape fragmentation are known to facilitate plant invasion independently. At the same time, biologically diverse native plant communities are broadly expected to limit invasion. In this work, primary producer-consumer interactions, plot-level native diversity, and surrounding landscape configuration were investigated to assess their association with exotic plant invasion across the region.

Using floristic composition data from 24 deer exclusion research sites distributed across the Northeastern US, the effect of deer on exotic versus native plants was investigated at species and community levels. Results indicated that deer facilitate the abundance of some exotic plant species, but inhibit the presence and abundance of many natives. While deer did not alter absolute exotic plant richness or abundance, they increased the degree of plant invasion due to strong declines in native plant abundance. Deer altered species composition and lowered native plant richness and abundance, causing an overall reduction in Shannon diversity ( $H'$ ).

To understand why some exotic species increased and others decreased in response to deer across the region controlled multiple-choice deer preference trials were conducted. Using captive deer, relative preferences for eight invasive exotic plants and seven native plants that are currently widespread and occur frequently in the region were determined in spring, summer, and autumn. Even though deer consumed more native plant biomass overall, preferences varied strongly at the level of species. This suggests that deer facilitate the invasion of exotic plants that are relatively unpalatable due to preferential selection of palatable plants.

Last, the relative importance of site-level white-tailed deer density, multiple landscape fragmentation metrics, and plot-level native plant diversity were tested for their roles in explaining plant invasion patterns in forest understory communities. The same pooled, floristic community data from 24 sites in the Northeastern US was analyzed using a series of nonparametric and parametric, multivariate and univariate statistics to illustrate the effects of multiple factors and their interactions on several measures of plant invasion. Deer, landscape structure and composition, and native species richness all affected patterns of exotic plant invasion. Results showed that deer density was highly correlated to landscape structure and that, as deer density increased, the percentage of exotic plant species also increased. Generally, landscape fragmentation was positively correlated with plant invasion. However, several interactions among deer presence, native plant diversity, and landscape attributes were identified. Exotic plant richness increased with native plant richness, but some evidence was found for native plant diversity limiting the degree of invasion in non-fragmented landscapes. Overall, to more fully understand the factors that influence plant invasion, the context of deer abundance, surrounding landscape structure and composition, and native plant species diversity must be considered.

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## **Prologue**

In this dissertation, multiscale approaches were used to increase understanding of factors driving exotic plant invasion in Northeastern United States (US) forest understories. At the local scale, deer food preference was tested for its role in producing mesoscale community-level patterns of plant invasion, specifically invasive exotic plant abundance, exotic species richness, and the degree of invasion in the plant community. At the landscape scale, several fragmentation metrics were used to determine the influence of landscape structure and composition on plant invasion patterns across the Northeastern US. This hierarchical approach aimed to elucidate factors driving invasive plant success across a range of scales.

Severe pressures brought about by the expanding reach and influence of humans are challenging the integrity of ecosystems around the world (Chapin et al. 2000). Modern landscapes are largely anthropogenically-altered (Hannah et al. 1994). In particular, humans have accelerated species homogenization, drastically modified species habitats, and triggered a dramatic reduction in biodiversity (Alroy 2008). Understanding the consequences of these human-driven global changes is a prominent goal in ecology. A major change accompanying globalization is the current mass invasion of organisms. Because humans have transported numerous species far from their ecological zones of origin, exotic species now make up considerable portions of species richness and abundance (Vitousek et al. 1996) and are important components of modern ecological communities.

Why plant colonization, establishment, and invasion vary temporally and spatially across the landscape is a central question in ecology. International trade and travel, landscape fragmentation, habitat disturbances, native plant diversity, and herbivore pressure all affect exotic plant invasion. While many plant species are introduced into novel ranges, only a few become

invasive (Williamson and Fitter 1996) in part because they are unpalatable to local herbivores or resistant to local pathogens (Keane and Crawley 2002).

Invasive plants are often correlated with decreases in native plant species richness and modified community composition and structure (Vitousek et al. 1997, Levine et al. 2003). They are also associated with altered ecosystem processes, such as novel fire regimes and biogeochemical cycling (Mack et al. 2000, Ehrenfeld 2010). However, these associations do not necessarily mean that invasive plants are the drivers of ecological change. In fact, alterations in disturbance regimes and/or environmental factors might be the ultimate drivers of plant invasion (MacDougall and Turkington 2005). In particular, changes in land cover/land use, such as increasing agricultural or developed cover, concomitantly result in the loss of forest habitat. Land cover changes can also cause patterns of landscape fragmentation, where large contiguous landscape patches are broken apart (Fahrig 2003). Both the loss of habitat and fragmented landscape patterns alter environmental conditions and the flow of resources and organisms (Wu 2009).

Plant invasion autecology offers benefits for understanding and managing individually problematic species (e.g., Averill et al. 2008, Rauschert et al. 2009, Nord et al. 2010, Averill et al. 2010, Averill et al. 2011). However, exotic species often occur together and can facilitate further invasion, i.e., invasional meltdown (Simberloff and von Holle 1999). Community ecology offers a framework for understanding the integration of exotic species into native assemblages (Shea and Chesson 2002). Focusing management of biotic invasions at a community or ecosystem scale is more effective than managing individual species (Mack et al. 2000), because controlling one invasive plant at a time can result in replacement of one invader with another (e.g., Reid et al. 2009).

While dispersal and climatic conditions filter plant species at the regional and landscape scales (Harper 1977), abiotic context (e.g., microsite suitability) (Gerhardt and Collinge 2007)

and biotic interactions with enemies (e.g., herbivores and diseases) and competitors (e.g., native plants) determine whether plant invaders establish and persist in an introduced range. Together, this suite of selection filters or pressures regulate the process of community assembly (Drake 1990, Booth and Swanton 2002). Many mechanisms that explain plant invasions have been investigated and they can all be considered within a community ecology framework (Shea and Chesson 2002, Vellend 2010, Gurevitch et al. 2011). The propagule pressure mechanism (Lockwood et al. 2005, von Holle and Simberloff 2005, Simberloff 2009) is considered the null model (Colautti et al. 2006) of plant invasion and evokes the dispersal element in community assembly. The biotic resistance (Elton 1958, Levine et al. 2004), enemy release (Keane and Crawley 2002, Colautti et al. 2004, Agrawal et al. 2005, Liu and Stiling 2006), and the evolution of increased competitive ability (Blossey and Notzold 1995) hypotheses are all relevant to community-level selection via biotic interactions. Last, the fluctuating resources hypothesis (Davis et al. 2000) and the hypothesis that changes in disturbance regimes facilitate plant invasion (Moles et al. 2012) are relevant to abiotic selection in community assembly. However, theoretical models and reviews indicate that multiple factors simultaneously influence the establishment and persistence of exotic plant species (e.g., Shea and Chesson 2002, Mitchell et al. 2006, Barney and Whitlow 2008, see Gurevitch et al. 2011 for a review), yet most empirical studies to date have considered only one or two drivers simultaneously (e.g., Eschtruth and Battles 2009).

The role of native herbivores in the invasion process is directly relevant to both the biotic resistance and enemy release hypotheses, but has not been investigated in the scenario of regionally abundant herbivores. Herbivory is an important producer-consumer interaction, which results in the transfer of energy to higher trophic levels and which affects the physical structure and productivity of plant communities (Harper 1977, Côté et al. 2004). Plant invaders potentially leave behind herbivore and other enemies in the native range but also encounter new enemies in

the introduced range (Parker et al. 2006, Morrison and Hay 2011). Thus, invading plants could be successful in the introduced range if they are subjected to little or no herbivory relative to native plants [enemy release (Keane and Crawley 2002)] or unsuccessful (i.e., they fail to invade) if native herbivores selectively consume them [biotic resistance (Elton 1958, Levine et al. 2004)].

The currently dominant and abundant wild ruminant herbivore in the Eastern United States, white-tailed deer (*Odocoileus virginianus* Zimm.), rivals invasive plants as an ecological and management concern (McShea et al. 1997, Rooney 2001). However, during the late 1800s, deer numbers severely declined due to over-hunting. By the early 1900s, Aldo Leopold advised increasing edge habitat and forest openings to increase deer populations (Leopold 1933) and these landscape alterations soon followed. Habitat creation combined with declining predator populations and game laws that restricted hunting resulted in increased deer populations (McShea et al. 1997). Additionally, increasing agricultural and silvicultural land cover enhanced deer habitat by supplementing forage availability (Alverson et al. 1988, Côté et al. 2004). While archeological evidence suggests pre-European settlement deer densities were 2 to 4 deer km<sup>-2</sup> across the North American range (Alverson et al. 1988, McCabe and McCabe 1997), current estimates exceed 10 deer km<sup>-2</sup> (Diefenbach et al. 1997). In Pennsylvania, an experiment in which deer density was manipulated showed that forests with deer densities above 8 deer km<sup>-2</sup> are expected to have very limited natural regeneration (Tilghman 1989). A more recent study in NY found that tree regeneration during a 12-year period could be maintained at a density of 12 deer km<sup>-2</sup> (Levine et al. 2012). Thus deer densities at or below 12 deer km<sup>-2</sup> should be targeted to maintain native tree regeneration.

Deer density varies across landscapes in response to predation pressure (Martin and Baltzinger 2011), habitat quality (Alverson et al. 1988), and landscape structure (Augustine and Frelich 1998). Because deer densities are known to be heterogeneous, the patchy occurrence of herbivore-free space likely plays a role in plant invasion (Agrawal et al. 2005). Intermittent

patterns of deer pressure and native plant growth can result in windows of opportunity for invading plants. Furthermore, patchy patterns of selection pressure can be explained in part by forest fragmentation (Augustine and Frelich 1998). Deer prefer early successional plant communities, such as open fields, compared to mature forests (Russell et al. 2001, Crimmins et al. 2010) and browsing damage has been found to be more severe close to habitat edges and less severe adjacent to roads, where roadside disturbance is more frequent (Gill 1992). Increased activity of deer in habitat edges spills over to adjacent forest communities. The fact that deer wander widely and take cover in forests causes severe herbivore impacts on forest understory plant communities (Alverson et al. 1988). Generally, greater deer impacts on vegetation are observed in fragmented landscapes (Augustine and Frelich 1998, Côté et al. 2004), which are also more susceptible to invasion by exotic species (Minor et al. 2009, Flory and Clay 2009). However, research on the effects of deer herbivory on plant communities and plant invasion at landscape scales is lacking (Maron and Vilà 2001, Russell et al. 2001, Mosbacher and Williams 2009).

Leopold was also one of the first scientists to openly warn that increasing white-tailed deer populations could negatively impact forest regeneration (Leopold et al. 1947). High deer densities have strong negative effects on plant community composition and structure (Alverson et al. 1988, Côté et al. 2004). For example, deer herbivory of tree seedlings reduces tree growth, which can impact forest regeneration, economic value, ecological stability (e.g., erosion and flood protection), and forest species diversity (Côté et al. 2004). Selective over-browsing results in a reduction or elimination of the most palatable plant species, with a concomitant increase in less preferred or unpalatable species (Leopold et al. 1947, Horsley et al. 2003, Côté et al. 2004). Herbivores acquire behavioral preferences for plants that result in the sensation of satiety and also avoid plants that cause malaise due to excess nutrients, toxins, or nutrient deficits (Provenza 1995). Herbivores generally prefer plant material with higher concentrations of protein (Mattson

1980) and higher quantities of carbohydrates (Berteaux et al. 1998). Deer selectivity can affect the competitive relationships among plant species. Shifts in plant species dominance as a result of increased deer abundance can result in alternative stable states (Stromayer and Warren 1997, Augustine et al. 1998), with the potential to lower resistance to exotic plant invasion (Tilghman 1989, Horsley et al. 2003, Latham et al. 2005, Vavra et al. 2007). Furthermore, deer overbrowsing is likely to reduce the ability of temperate tree species to respond to global climate change and expand northward because heavy browse pressure can wipe out the increased growth of temperate broadleaf species at warmer sites and facilitate growth rates of less palatable boreal species (Fisichelli et al. 2012). Consequently, the combination of landscape fragmentation, high deer abundance, increased plant invasion, and climate change represent multiple and interacting selection pressures against native plant species.

Deer herbivory is an important top-down process regulating community assembly, composition, and structure, as well as ecosystem productivity (Leopold et al. 1947, Hobbs 1996, Rooney 2001, Wisdom et al. 2006). Deer limit and, in cases of overabundance, regulate plant species composition and abundance (McShea et al. 1997). While deer are also influenced by the availability and palatability of forage, heavily browsed vegetation is associated with reductions in body mass and reproduction, instead of with lowered population densities (Simard et al. 2008). Questions about whether top-down or bottom-up forces govern populations and communities are pervasive in the ecological literature (Hairston et al. 1960, Hunter and Price 1992, Power 1992, Martin et al. 2010). High deer densities are partially driven by landscape composition, suggesting that large-scale top-down constraints are relevant across the Northeastern US. However, bottom-level forces (e.g., resource availability) and intra-trophic forces (e.g., direct and indirect plant competition resulting from efficiency of resource acquisition and plant palatability, respectively) are also known to be important in determining plant community composition and abundance. Landscape hierarchy theory suggests that top-level forces constrain mesoscale patterns and

processes (e.g., landscape fragmentation constrains plant community assembly), while bottom-level forces explain those patterns and processes (e.g., resource availability and plant traits help explain the occurrence and abundance of plant species) (Ahl and Allen 1996). Exotic species often out-compete native species for resources (e.g., Bazzaz 1986). Additionally, if native plants are more heavily browsed by deer than exotic plants (particularly in fragmented landscapes where deer and exotic plants are more abundant), then exotic plant invasion and abundant deer are liable to alter top-level and bottom-level selection pressures, ultimately reducing native plant diversity and increasing the degree of invasion in plant communities.

Broadly, the aim of this dissertation was to quantify the role of deer in invasive plant success across a broad geographic region comprising a diversity of study sites, landscape contexts, local floras, and deer densities. My dissertation research broke out into three broad areas. In the first chapter, I conducted a pooled analysis across 24 study sites in the Northeastern US to determine the regional effect of white-tailed deer on patterns of plant invasion. This analysis takes a species-level approach to identify the invasive plants released and those suppressed by white-tailed deer. In the second chapter, I set out to determine the role of differential palatability in invasive plant success, using a set of commonly occurring invasive exotic and native plants. In the third chapter, I took a multiscalar approach to identify the relative importance of white-tailed deer, native plant diversity, and surrounding landscape structure and composition on plant invasion patterns. Chapters 1 and 3 transcend spatial scales from plot level summaries in Chapter 1 to a regional analysis in which landscape context is considered in Chapter 3. To perform these unique analyses, I collected or had access to an unprecedented large and rich collection of multi-year deer exclosure datasets. My work provides the most comprehensive analysis to date on the impacts of deer across a broad range of sites, landscape types, floristic communities, and suites of invasive plants. From my Chapter 1 analyses and Chapter 2 palatability experiments, several “plant species of concern” clearly were favored under

high deer densities. An intriguing finding of this body of work is that some plants appear to be facilitated while others are selected against under high deer pressure. Three invasive plants that benefited under high deer pressure included *Ailanthus altissima* tree-of-heaven, *Alliaria petiolata* garlic mustard, and *Microstegium vimineum* Japanese stiltgrass. Interestingly, the controlled deer preference study corroborated this finding with *A. petiolata* and *M. vimineum* being the least preferred of all species studied. The findings reported in the third chapter provide compelling evidence of the association between high deer densities and fragmented landscapes and a high degree of plant invasion. Taken together, this work shows the illuminating power of multiple datasets in elucidating consistent patterns of invasive plant success, specifically highlighting the degree to which that success is mediated by landscape context and deer density.

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## Chapter 1

### Effects of deer on invasive plants: results from a region-wide pooled analysis

#### Abstract

Herbivores can profoundly influence plant species assembly and resulting community composition. Human-aided plant invasion and extreme population escalation of the dominant native herbivore, white-tailed deer (*Odocoileus virginianus* Zimm.), raise concerns for native plant diversity. While several researchers have tested for deer effects on invasive plants at one or two sites, the overarching role of deer presence in plant invasion is unclear. Using data from 24 deer exclusion research sites distributed across the Northeastern US, the effect of deer on exotic versus native plants was investigated at species and community levels. Results indicate that deer facilitate high abundance of some plant species, while inhibiting the presence and abundance of many others. Furthermore, a suite of plant species, including several regionally invasive exotic plants, acted as good indicators of deer presence. Deer presence did not directly affect exotic plant richness or abundance; instead deer increased the relative abundance of exotics due to their strong negative effects on native plant abundance. Deer altered species composition, lowered native plant richness and abundance, and reduced Shannon diversity ( $H'$ ). Deer increased the potential ecological influence of exotic plants by increasing their relative abundance in plant communities. Based on these results, deer reductions might increase native plant richness and abundance, increase species diversity, and reduce the degree of plant community invasion.

## Introduction

Herbivores can profoundly influence plant species assembly and resulting community composition (Booth and Swanton 2002). However, the degree to which native herbivores influence exotic plant invasions is unclear. Invasive plants are an increasing ecological and management concern (Pimentel et al. 2005) and in many cases high herbivore abundance is a concomitant concern. In the Northeastern United States, white-tailed deer (*Odocoileus virginianus* Zimm.) populations escalated several-fold within the past century (McCabe and McCabe 1997) threatening the integrity of native plant communities (Côté et al. 2004). Simultaneously, plant invasions have resulted in altered ecosystem functioning (Ehrendfeld 2010) and in environmental damages and losses that exceed \$100 billion annually (Pimentel et al. 2005). In the Northeastern US, deer populations are an order of magnitude greater than pre-European settlement densities and, in the same region and time period, many invasive exotic plants' ranges have expanded, suggesting that abundant deer might foster plant invasions (Vavra et al. 2007). However, previous research on the issue appears contradictory. In site-level studies, deer were found to increase invasive plant abundance (Caraher 2009, Knight et al. 2009, Eschtruth and Battles 2009a, Kalisz et al. 2014), but have also been reported to have the opposite (Rossell et al. 2007) or no effect (Bowers 1993, Levine et al. 2012). In an attempt to reconcile and understand these inconsistent patterns, I present results from a multi-site and region-wide field plot analysis of the effects of white-tailed deer on the richness and abundance of exotic and native plants.

In North America, white-tailed deer are the dominant wild ruminant and their numbers and influence have reached historically high levels (McShea et al. 1997). Deer browsing is widely considered one of the main determinants of understory species composition and structure (Alverson et al. 1988, Côté et al. 2004). For example, deer browsing of tree seedlings reduces tree

growth and alters forest understory composition and evenness (Côté et al. 2004). Such impacts can limit forest regeneration, reduce economic value of forests, and lower ecological stability (e.g., erosion and flood protection).

Deer are generalist herbivores, yet they are selective foragers. Herbivore selectivity can alter plant species dominance and result in alternative stable states and disrupted ecosystem functioning and service provision (Côté et al. 2004), which can lead to exotic plant invasion (Stromayer and Warren 1997, Augustine et al. 1998, Vavra et al. 2007). Effects of selectivity are exacerbated under conditions of high herbivore abundance (Vavra et al. 2007). Exotic species might fail to invade due to resistance from the native community (Elton 1958, Levine et al. 2004). However, deer-mediated shifts in community composition, structure, and/or function can lower community resistance to invading species (Tilghman 1989, Horsley et al. 2003, Latham et al. 2005, Vavra et al. 2007). Generalist herbivores influence plant communities via direct and indirect effects of their selective foraging. Herbivores can directly influence plant community composition and structure by means of herbivore-mediated plant mortality. However, the primary effects of herbivory occur through alterations in the outcome of interspecific competition (Bowers 1993, Crawley 1997). Consequently, herbivores indirectly affect competitive interactions as a result of differential herbivore selectivity; unpalatable plants gain a competitive advantage relative to more palatable ones and are more strongly represented in the flora (Senft et al. 1987, Keane and Crawley 2002). The combination of abundant herbivores and selective feeding behavior can severely jeopardize native plant communities as well as provide opportunities for exotic plants to invade (Hobbs and Huenneke 1992), yet the handful of studies assessing these interactions have been equivocal.

Since the early 1900s, numerous, isolated enclosure experiments have been conducted to gauge the impact of deer on forest plant communities (McShea et al. 1997, Côté et al. 2004). The use of paired plots affords valuable insight into the effects of large herbivores on floristic

composition and response to herbivore pressure. Previous research using paired plots has shown that the effect of deer herbivory on exotic plants is inconsistent across the Northeastern US. Individual exclosure experiments revealed that deer increase, decrease, or have no effect on invasive exotic plants. Deer facilitated an increase in the abundance of several problematic invasive plants, including *Alliaria petiolata* garlic mustard and *Microstegium vimineum* Japanese stilt-grass, in New Jersey and Pennsylvania forests compared to fenced exclusion plots (Knight et al. 2009, Eschtruth and Battles 2009). In contrast, deer reduced abundance of the invasive exotic vine *Celastrus orbiculatus* Oriental bittersweet in an oak-beech forest (Rossell et al. 2007) and the invasive shrub *Rosa multiflora* multiflora rose in one of two New Jersey Piedmont fields (Cadenasso et al. 2002). In a Virginia old field, deer had no effect on exotic plant abundance (Bowers 1993). A global meta-analysis of 63 studies and over 100 exotic plant species showed that native herbivores suppress exotic more than native plants (Parker et al. 2006). However, the meta-analysis included experiments studying the exclusion of many herbivore types (e.g., insects, rodents, and cervids) as well as covering a global extent of ecosystems. While informative for plant-herbivore interactions generally, such an extensive analysis is not useful for understanding the effect of a particular herbivore. In the study presented here, the focus is on white-tailed deer whose regional populations are at historically high levels.

Site-level investigation can provide practical insights for local species and conditions, but precludes region-wide conclusions about herbivory and plant invasion. Regional assessment requires plant community data from sites that range in herbivore abundance and in plant species composition and structure. Spatially and temporally large investigations bolster generalizations and forecasts made about ecological processes (Clark et al. 1999, Clark et al. 2001), such as elucidating the factors important to community assembly and plant invasion (Gill and Beardall 2001).

The objective of this work was to determine the effect of deer on the composition, richness, and abundance of exotic versus native plant species in northeastern US forest understory communities. Data were pooled from 24 exclosure experiments across the region, spanning a broad gradient of forest types and deer densities. While experimental procedures varied, each dataset had the same basic structure, including vascular plant species abundance data from two plot types, fenced deer exclosures and unfenced controls. The pooling approach has the benefit of increasing statistical power and reducing type II error rates (i.e., false negatives) (Blettner et al. 1999). First, the hypothesis that white-tailed deer alter floristic composition was tested. Second, deer were hypothesized to increase the richness and abundance of exotic plants and decrease those of native plants at the species and community levels. Third, deer were hypothesized to reduce plant species Shannon diversity ( $H'$ ).

## **Methods**

### **Data description**

Datasets in which floristic composition and abundance were quantified in fenced deer exclusion and unfenced control plots were compiled. I collected data at two sites in Northwestern Pennsylvania, Long Run (LR) and Marienville (MV) that were initially established by A. Royo (Tab. 1-1). Additionally, other scientists in the Northeastern US, known to have floristic datasets based on paired, unfenced deer plots and adjacent fenced deer exclusion plots, were invited to contribute their data for this pooled meta-analysis and to co-author resulting peer-reviewed publications. The compilation yielded 458 experimental units, i.e., 229 plot pairs, across 24 sites (Tab. 1-1). Abundance data of herbaceous and woody species growing up to 2 m in height were reported in each dataset. All datasets included forest understory floristic composition, except for

one old-field site (IT). Some, but not all, of the contributed datasets have been previously published (Tab. 1-1).

Sites were located in deciduous forests and in one old-field in the Northeastern US (north to Ithaca, New York, east to Morristown, New Jersey, south to the Shenandoah National Park in Virginia, and west to Fermilab in Illinois) (Fig. 1-A1). Overstory species included oak (*Quercus* spp.) (17 of 23 sites; not including the one old-field site), maple (*Acer* spp.) (9 of 23), or beech (*Fagus grandifolia*) (8 of 23) (Tab. 1-2). Forests dominated by tulip poplar (*Liriodendron tulipifera*) and cherry (*Prunus* spp.) were also well-represented. In addition to being a diverse and regionally distributed network of deer exclusion experiments, the timeframe and duration of deer exclusion varied across sites (Tab. 1-1). Six sites were established in the late 1980s/early 1990s, and the remaining 18 sites in the 2000s. However, the floristic censuses reported here represent a shorter timeframe of regional patterns; data were recorded at 22 of the 24 sites between 2005 and 2012. Data were collected during the summer months of the growing season.

Adjacency of plots varied, but at most sites (22 of 24) unfenced and fenced plots were separated by 5 to 60 m. Sampling intensity varied across sites, with some sites having very high plot-pair replication and others with low replication, but large area sampled (Tab. 1-1). Fence height was consistent across sites and was always at least 2 m. Mesh size varied, indicating that deer might not have been the only mammalian herbivore excluded; fenced plots could have excluded other animals as well (e.g., see Bowers 1993).

## **Data processing**

The most recent censuses (when floristic abundance data of fenced and unfenced plots were simultaneously measured) were processed for analysis. Segments of certain datasets were omitted because enclosure experiments were sometimes conducted to investigate the role of

multiple factors, not just deer presence/absence. For example, plots were excluded from analysis if additional treatments such as burning or herbicide were also imposed. Equal numbers of fenced and unfenced plots were analyzed from each dataset. For datasets provided at the subplot level, plot-level means were determined and used for analysis on a  $m^2$ -basis. Subplots were nested within plots, which were nested within fenced/unfenced pair, which were nested within sites. Plots were paired based on initial investigator-designated pairings or according to plot numbers.

The plant abundance metrics reported in the datasets were: stem density (e.g., stems  $m^{-2}$ ), the percentage of ground covered by the species (i.e., percentage cover, with 1- or 5- percentage point increments), cover classes or categories (varying ranges of percentage point increments) (Fig. 1-1) and density classes (Tab. 1-1). Attempts were made to pool data that was collected using different abundance metrics for joint analysis. However, strong relationships between metrics could not be determined and this prevented pooling. Consequently, each abundance metric was analyzed separately. Cover class data were converted to cover class midpoint (herein midpoint) for analyses and were analyzed separately from cover data. At six sites, a density class of “>10 stems” was sometimes employed, in which case the most conservative value of “11” was substituted for analyses. Density class data were recorded at one site (SH), so the following conversions were used: “2-3 stems” = 2.5 stems; “4-5 stems” = 4.5 stems; and “>5 stems” = 6 stems. At ten sites (e.g., AN, CA, and VJ), different plant habits were recorded with separate measures, for example cover or cover class for the more numerous herbs and grasses and density for less numerous woody species; thus floristic censuses were split accordingly and analyzed only with other data of the same measure. Consequently, results reported here should be interpreted conservatively as the effects of deer presence according to species habits. At other sites (FN, MA, and MG), cover and density were recorded, thus both measures of flora at those sites were included in respective analyses. It follows that the separate plant abundance analyses were not wholly independent and should be interpreted individually to test the hypotheses. Regardless,

when sites FN, MA, and MG were entirely excluded from community-level analyses, statistical results were the same as when they were included.

Some plant species in almost every dataset were unidentified and marked as unknown at the genus, family, or growth habit level (e.g., forb, fern, woody seedling). These were necessarily excluded from analyses that relied on knowing species' native/exotic status, but were included when determining total abundance and total species richness. Observations of mosses, coarse woody debris, and bareground cover were excluded from analyses because they were not consistently recorded across datasets. Species taxonomy and native/exotic status were standardized according to the United States Department of Agriculture Plants Database (USDA, NRCS 2012). Plants with a native status code of "Native and Introduced" (i.e., some infra-taxa are native and some are introduced) were considered native.

## **Data analysis**

### ***Effects of deer on plant species composition***

Linear mixed effects analysis of variance (ANOVA) was used to test the main effect of deer on individual exotic and native plant species abundance. Plot and site pair were included as random effects to control for within- and between-site variability, respectively. Species-level abundance analyses were conducted for the most frequently occurring exotic plants, i.e., those present in at least 5% of all plots (13 exotic species). Native plant analyses were conducted for the 20 most frequent native species. Separate analyses were conducted for each abundance metric and some species were tested more than once with different metrics. Stem density analyses included 10 exotic and 20 native species; cover analyses included 3 exotics and 8 natives; and midpoint analyses included 4 exotics and 11 natives.

Indicator species analysis (ISA) was used to test for the deer effect on floristic composition (Dufrêne and Legendre 1997). The ISA results indicate which plant species associate with the presence or absence of deer. The indicator value represents the degree to which a species is an adequate indicator of treatment conditions. A Monte Carlo randomization test determines significance of the indicator value. First, an analysis was conducted based on species presence/absence and then separate analyses were conducted for each of the three abundance metrics. If none of the most frequent species occurred in a plot, that plot was necessarily excluded from analysis. PC-ORD software was used for the ISAs (McCune and Grace 2002). Species were reported as associated with a treatment at the  $\alpha = 0.1$  level.

#### ***Effects of deer on exotic and native plant species richness and abundance***

Linear mixed effects ANOVA was used to test for effects of deer on exotic, percentage exotic, native, and total plant richness and abundance and on Shannon's diversity index. Deer presence/absence (exclosure treatment) was the fixed effect and plot pair and site were the random effects. For each plot, abundance was calculated by summing across species within each abundance metric for exotic, native, and total components. Total cover could exceed 100% due to overlapping leaves of different species. The percentage of vegetation composed of exotic plants (i.e., relative abundance) was determined within each abundance metric by dividing exotic abundance by total abundance within the metric and multiplying by 100. Both absolute and relative exotic plant abundance were measured because they represent different measures of plant invasion; the former represents deer effects on actual exotic plant abundance, while the latter represents the portion of the community composed of exotic plants. A change in one metric does not necessitate a change in the other. If an abundance metric was not measured at a site, the site was excluded from analysis of that metric. If no exotic plants were recorded at a site, the site was

excluded from the exotic and percentage exotic analyses. If plants were absent from a plot, percentage exotic richness or percentage abundance was set to zero.

The Shannon diversity index ( $H'$ ) (Shannon 1948), a combined measure of species richness and relative abundance (Hill 1973, McCune and Grace 2002), was calculated for each plot and for each abundance metric that was measured in each plot as follows:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

where  $p_i$  is the proportional abundance of species  $i$  in the plot and  $S$  is the total number of species measured with each abundance metric. Plots were excluded from statistical analysis if  $S = 0$  because  $H'$  is undefined in such cases.

Linear mixed effects analysis of covariance (ANCOVA) was used to determine the effect of deer on relationships between native and exotic vegetation. Exotic vegetation was the response variable, native vegetation the covariate, deer presence/absence the fixed effect, and plot pair and site were random effects. Separate analyses were conducted for richness and for each abundance metric. The interaction between deer presence/absence and native vegetation was initially included, but due to no significance in all four models, was removed from final analyses.

Square root, natural log, or arc sine square root transformations of response variables were used to meet statistical assumptions of normality and homogeneity of residuals. For models with a significant deer treatment effect ( $\alpha < 0.05$ ), least square means were determined using  $t$  tests (based on the Satterthwaite approximation for denominator degrees of freedom). Log-likelihood ratio tests (with one degree of freedom, i.e., one effect tested at a time) were used to determine significance of random factors. In community-level analyses, 95% confidence intervals for significant fixed effects are reported. The lme4, lmerTest, and vegan packages were used for analyses in R version 3.0.1 (R Development Core Team 2006). Means are reported at the plot-level  $\pm$  one standard error.

## Results

Across the 24 sites, 699 plant taxa were recorded; 111 were exotic species, 383 were native species, and 205 taxa were unknown to the species level. Across sites, 97 species occurred only where deer were present and 125 occurred only where deer were absent; the remaining 477 species occurred in both treatments (Fig. 1-2). Mean plot-level exotic species richness was  $3.3 \pm 0.3$  (Fig. 1-A2). Native species richness was  $12.2 \pm 0.4$  regardless of whether the site was invaded (exotics present:  $12.2 \pm 0.5$ ; exotics absent:  $12 \pm 2$ ). Total species richness was  $19.0 \pm 0.7$ , and was higher at sites where exotics were present (19.5) versus where they were absent (15). At invaded sites, exotic stem density ( $7.7 \pm 0.7$  exotic stems  $m^{-2}$ ) made up  $23 \pm 1\%$  of total stem density; exotic cover ( $47 \pm 5\%$ ) made up  $31 \pm 3\%$  of total cover; and exotic midpoint ( $11 \pm 1\%$ ) made up  $25 \pm 2\%$  of total midpoint (Fig. 1-A3). Across all sites, native stem density was  $10.1 \pm 0.6$  stems  $m^{-2}$ , native cover was  $75 \pm 5\%$ , and native midpoint was  $13 \pm 1\%$ , while total stem density was  $22 \pm 1$  stems  $m^{-2}$ , total cover was  $107 \pm 7\%$ , and total midpoint was  $27 \pm 2\%$  (Figs. 1-A4, 1-A5, 1-A6).

### Effects of deer on plant species composition

Where deer were present (unfenced control), over 40% of the indicator species were exotic, while where deer were absent (fenced enclosure), only 16% were exotic. Despite this large difference in the proportion of exotic indicator species across deer and no-deer plots, about the same number of exotic species were indicators of plots with deer (6 spp.) as without deer (5 spp.) (Tab. 1-2). In contrast, many fewer native species were significantly associated with deer plots (8 spp.) compared to no-deer plots (27 spp.). Two exotic plants, *Alliaria petiolata* and *Microstegium vimineum*, were the best indicators of deer presence (according to indicator values) and they

occurred in a large proportion of plots and sites. The best indicators of deer absence included the exotic vine *Lonicera japonica* and the natives *Lindera benzoin*, *Parthenocissus quinquefolia*, *Prunus serotina*, and *Toxicodendron radicans*.

Many of the species identified as indicator species for deer plots were also statistically more abundant in deer plots and indicator species for no-deer plots were more abundant in no-deer plots (Tab. 1-3) (Figs. 1-A7, 1-A8, 1-A9). Deer presence increased the abundance of three exotic species, *Ailanthus altissima*, *A. petiolata*, and *M. vimineum* and two native species, *Liriodendron tulipifera* and *Pilea pumila*, relative to no-deer plots. Deer presence decreased the abundance of two exotic species, *Duchesnea indica* and *L. japonica*, and nine native species, including *P. quinquefolia*, *P. serotina*, and *T. radicans*.

The most frequently encountered unknown plants were from the following genera (with percentage occurrence across all plots): *Viola* (30%), *Vitis* (30%), *Carex* (25%), *Rubus* (18%), *Fraxinus* (17%), *Polygonum* (10%), *Carya* (8.5%), and *Solidago* (7.6%).

### **Effects of deer on exotic and native plant species richness and abundance**

Deer presence reduced native vegetation richness and abundance and increased the relative abundance of exotic vegetation (i.e., the proportion of exotic abundance in the plant community). Deer had no effect on exotic plant richness or on absolute exotic plant abundance (Tabs. 1-4, 1-5). Exotic plant richness was  $3.3 \pm 0.3$  species/plot regardless of deer presence (Fig. 1-A2). Deer decreased native plant species richness by 14% to  $11.2 \pm 0.6$  species/plot, compared to no-deer plots ( $13.1 \pm 0.6$  species/plot). Deer also decreased total plant species richness by 9% from  $20.0 \pm 0.9$  species/plot in no-deer plots to  $18.1 \pm 1.0$  species/plot in deer plots.

Deer increased exotic plant abundance across the region, but the effect was not significant (Tab. 1-5). Exotic density (deer:  $8 \pm 1$  stems  $m^{-2}$ ; no deer:  $6.9 \pm 0.9$  stems  $m^{-2}$  exotic),

exotic cover (deer:  $50 \pm 8\%$ ; no deer:  $45 \pm 7\%$ ), and exotic midpoint (deer:  $13 \pm 2\%$ ; no deer:  $10 \pm 2\%$ ) were statistically unaffected by deer (Figs. 1-A4, 1-A5, 1-A6). However, due to the large reduction in native plant abundance, deer increased the proportion of vegetation comprised of exotic plants. Deer increased the percentage of exotic cover by 18% (deer:  $33 \pm 4\%$ ; no-deer:  $28 \pm 3\%$ ) and exotic midpoint by 45% (deer:  $29 \pm 3\%$ ; no deer:  $20 \pm 2\%$ ), but did not have a significant effect on the percentage of exotic stems (deer:  $24 \pm 2\%$ ; no-deer:  $22 \pm 2\%$ ) (Fig. 1-A3).

Deer decreased native plant abundance regardless of the abundance metric used (Tab. 1-5). Deer reduced native stem density by 16% (deer:  $9.3 \pm 0.8$  stems  $m^{-2}$ ; no-deer:  $11.0 \pm 0.8$  stems  $m^{-2}$ ), native percentage cover by 15% (deer:  $69 \pm 7\%$ ; no-deer:  $81 \pm 7\%$ ), and native midpoint by 73% (deer:  $5.4 \pm 0.8\%$ ; no-deer:  $20 \pm 3\%$ ) (Figs. 1-A7, 1-A8, 1-A9). The negative effect of deer on native plants translated into a consistent decrease in total plant abundance. Deer reduced total stem density by 2% (deer:  $21 \pm 2$  stems  $m^{-2}$ ; no-deer:  $22 \pm 2$  stems  $m^{-2}$ ), total percentage cover by 8% (deer:  $103 \pm 10\%$ ; no-deer:  $111 \pm 10\%$ ), and total midpoint by 37% (deer:  $21 \pm 2\%$ ; no-deer:  $33 \pm 4\%$ ). Deer also reduced Shannon diversity ( $H'$ ) in terms of stem density (deer:  $1.66 \pm 0.06$ ; no deer:  $1.79 \pm 0.06$ ) and midpoint (deer:  $0.90 \pm 0.07$ ; no deer:  $1.12 \pm 0.07$ ), but not of cover (deer and no-deer:  $1.9 \pm 0.1$ ) (Tab. 1-5).

Despite divergent effects of deer on exotic (no effect) versus native (decreasing effect) plant species abundance, positive relationships were found between exotic and native vegetation in terms of species richness, stem density, and midpoint, but not of cover (Tab. 1-6) (Fig. 1-A10). This means that plots where native species richness and abundance were high also had higher exotic species richness and abundance. In almost all models, the random factors, plot pair and site, were significant (Tabs. 1-4, 1-5), however, despite such high within- and between-site variability, strong and consistent effects of deer were detected.

## Discussion

Abundant native deer are strongly linked with the abundance of several invasive exotic plants currently encroaching on Northeastern US forest understories, including *Ailanthus altissima* tree-of-heaven, *Alliaria petiolata* garlic mustard, and *Microstegium vimineum* Japanese stilt-grass. Furthermore, the pooled analysis of regional plant communities showed that deer increase the degree of plant invasion, i.e., they increased the abundance of exotic plant species relative to total abundance. Importantly, white-tailed deer indirectly increased the exotic segment of Northeastern US forest understory plant communities by decreasing native plant species richness and abundance. While deer strongly limited native plants, they had no effect on exotic plant abundance or on exotic species richness. Overall, the hypotheses that white-tailed deer would alter plant species composition and decrease native species were supported based on multiple lines of evidence represented by the various abundance metrics used across the sites. However, deer were not found to increase exotic plant abundance at the community-level, instead deer increased some exotic species while reducing others.

### Effects of deer on plant species composition

Previously reported results testing the role of deer in exotic plant success varied in the direction of effects and thus raised questions about the overarching effects of deer on susceptibility of eastern deciduous forests to plant invasion. This pooled analysis goes a long way toward clarifying those effects by revealing clear species-level impacts of deer. Deer increased the abundance of several prominent invasive plants in the Northeastern US, *A. altissima*, *A. petiolata*, and *M. vimineum*. However, deer effects on plant abundance were species-specific; deer increased some species and decreased others regardless of their native/exotic status (Tab. 1-

3). This finding is consistent with previous research that tested the effect of deer on exotic plants and which showed that deer can increase (Knight et al. 2009, Kalisz et al. 2014), decrease (Rossell et al. 2007), or have no effect (Bowers 1993, Levine et al. 2012) on exotic plants. This work emphasizes that deer affect plants on a species-basis, which is likely determined by relative palatability in the plant community (Senft et al. 1987, Keane and Crawley 2002).

The three exotic species whose abundances increased with deer are not just naturalized species, but are considered invasive in the Eastern U.S. (USDA Forest Service 1998) and, furthermore, the states of Connecticut and Massachusetts have prohibited them (USDA, NRCS 2012). Positive effects of deer on *A. petiolata* and *M. vimineum* have also been found in site-level experiments (Knight et al. 2009, Eschtruth and Battles 2009b, Eschtruth and Battles 2009a, Kalisz et al. 2014). The facilitative effect of deer on these species appears to be a result of their unpalatability relative to other plants, which can result in altered competitive hierarchies; *A. petiolata* and *M. vimineum* were the least palatable species of those included in controlled native and exotic species multiple-choice deer preference trials (Figs. 2-1, 2-2). Additionally, *A. petiolata* and *M. vimineum* were the best indicator species of plots with deer (Tab. 1-2), implying that where these plant species are observed in high abundance, high deer pressure is likely an indirect driver.

In contrast to their facilitative effect on some invasive plants, deer reduced the abundance of the invasive vine *Lonicera japonica* Japanese honeysuckle (Tabs. 1-2, 1-3), likely due to its high palatability to deer. The species is palatable enough that hunters are known to plant it to attract deer to hunting grounds (pers. comm.). Additionally, an invasive shrub in the same genus, *Lonicera morrowii*, was found to be one of the most palatable species in controlled deer preference trials (Figs. 2-1, 2-2). In heavily browsed plant communities, the most palatable species are the most susceptible to being eaten and reduced in abundance relative to where herbivores are excluded (Royo and Carson 2006). Importantly, this vine species might have been

more abundant in fenced plots not only because of protection against deer browsing, but also because it can climb over the more abundant vegetation in deer exclusion plots and on the fences themselves. In trying to control for this effect, investigators at Valley Forge sites (VJ, VM) placed a metal stake in the center of control plots (Abrams and Johnson 2012). Deer effects on exotic plants were minimal at these two sites (Figs. 1-A7, 1-A9), but the four occurrences of *L. japonica* at VJ were all in no-deer plots (data not shown), implicating deer preference and not a climbing effect as the cause of its differential abundance between deer and no-deer plots. Interestingly, while the native shrub *Lindera benzoin* is seldom severely damaged in landscape plantings (Perdomo et al. 2004) and is relatively unpreferred compared to commonly co-occurring species (Fig. 2-1), it was an indicator of deer absence (Tab. 1-2). This contradiction might exist if the species is reduced due to resource competition with a species that occurs where deer are present. Alternatively, while a species might not be extensively browsed by deer, certain quantities still might be important in the deer diet (Spalinger et al. 1997), so it might not be surprising that it grows better without any deer pressure at all. Indeed, in controlled deer preference trials, *L. benzoin* biomass was intermediately consumed relative to native and exotic species (Fig. 2-2). Deer also reduced native species known to be palatable to deer, including *Geum canadense*, *Maianthemum racemosum*, and *Quercus rubra* (Tab. 1-3) (Perdomo et al. 2004). Notably, many more native species were associated with deer absence than with deer presence (Tab. 1-3), demonstrating the strong limiting effects of deer on native plants.

Protection from deer in fenced plots offers more habitat (e.g., food, shelter, and perch points) for birds and other seed dispersing animals (McShea and Rappole 2000). In this work, all of the exotic species, including *L. japonica*, that were associated with deer absence produce fleshy-fruits (Tab. 1-2), which lends support to the importance of mutualistic interactions in plant invasion (Richardson et al. 2000, Gleditsch and Carlo 2011). Consequently, propagule pressure via bird- and small mammal-dispersal could account for the increased plant abundance and

diversity observed in fenced plots. Bird dispersal might also explain why fleshy-fruited species, in particular, were more abundant in or associated with fenced deer exclosures in this study, as well as shed light on previous experimental results in which deer were found to decrease a fleshy-fruited species in unfenced plots relevant to fenced plots (Russell et al. 2007).

Deer presence shifted species composition toward unpalatable species, a well-studied effect of abundant deer (Côté et al. 2004). The outcome for unpalatable species is a competitive advantage and potential dominance (Royo and Carson 2006) or opportunity for plant invasion (Hobbs and Huenneke 1992, Vavra et al. 2007). This research suggests that deer facilitate or accelerate some plant invasions indirectly by avoiding them and preferentially browsing native plants, which lends support to the enemy release hypothesis since a primary tenet of the hypothesis is that natural enemies have a greater impact on native versus exotic species (Keane and Crawley 2002). Furthermore, these findings imply that researchers must not evaluate relationships between deer and exotic plants in isolation, but they must also consider deer effects on native plants.

### **Effects of deer on exotic and native plant species richness and abundance**

Abundant deer in the region also altered plant community composition by increasing the exotic to native ratio of plants, a result that appears to refute the biotic resistance hypothesis of plant invasion, that native plant and animal communities resist invader establishment (Levine et al. 2004). Instead, these results represent a reversal of the broadly observed pattern in which native herbivores reduce the exotic: native ratio (Parker et al. 2006). A distinguishing phenomenon in the region studied here is the historically high native herbivore pressure, which might explain the reversal (Côté et al. 2004) and which implies that native herbivore abundance and not just presence is important. Consequently, where deer densities are high, the negative

effect of selective browsing of native plants appears to offer a window of opportunity for invading unpalatable species (Harper 1977, Johnstone 1986, Shea and Chesson 2002). While deer can actually increase floristic diversity at low deer abundance (Royo et al. 2010a), abundant deer have the opposite effect of limiting diversity and promoting homogeneity (Rooney et al. 2004). Increased homogeneity where deer were present was the pattern observed in this study, demonstrated by reductions in Shannon diversity ( $H'$ ) (Tab. 1-5).

Despite the fact that deer were associated with increased plant community invasion, exotic plant invasion patterns were positively correlated with native plant richness and abundance regardless of deer presence (Tab. 1-6). This finding supports previous research showing that exotic plant species invade “hot spots” of diversity (Stohlgren et al. 1999) and that underlying environmental gradients might drive both native and exotic species diversity. However, exotics could occur across deer and no-deer plots as a result of deer exerting an influence prior to experimentation and deer exclusion (Russell et al. 2001) and leaving behind legacy effects (Royo et al. 2010b, Nuttle et al. 2011), such as by altering seedbank composition (DiTommaso et al. 2014). Consequently, even when deer are excluded or vastly limited, community re-assembly could take a long time and result in communities that are very different from those that previously occurred (Tanentzap et al 2012). Currently, because white-tailed deer numbers are an order of magnitude greater than during pre-European settlement (McCabe and McCabe 1997), the cervids appear to be exerting strong community-level selection for a reordered flora comprised primarily of unpalatable and fast-growing early successional species.

### **Site influences**

Abiotic conditions vary across space, resulting in myriad combinations of temperature, moisture, light, and substrata and therefore different sets (i.e., communities) of species. Deer

density, overstory and understory species composition, and duration of deer exclusion were some of the factors known to vary among sites (Tab. 1-1). Furthermore, deer density can vary spatially and temporally within a site and is influenced by roads, quantity of forest-field edge habitat, and by predators (McShea et al. 1997), factors which likely varied across the sites investigated here. The influence of site differences, including deer density and surrounding landscape structure and composition was explored elsewhere (Chapter 3).

Interestingly, five sites were uninvaded by exotic plants. The native fern *Dennstaedtia punctilobula* is dominant at two of the sites (LR and MV), both forest understory sites in northeastern Pennsylvania. The fern species is widely considered a native invasive plant, increasing in response to overstory thinning in conjunction with abundant deer (de la Cretaz and Kelty 1999). At the other three sites (FN, MG, and Z1), deer densities were considerably lower (~6 deer km<sup>-2</sup>) than the average across sites (mean = 35 deer km<sup>-2</sup>; median = 26 deer km<sup>-2</sup>), suggesting that lower deer density at a site might enable biotic resistance to invaders (Tab. 1-1). Indeed, as deer density increases, so does the magnitude of deer impact on vegetation (Tilghman 1989). Deer density estimates were positively correlated with increases in the percentage of exotic cover and the percentage of exotic species (Fig. 3-8a, 3-8c). In contrast, at FN and MG, low deer densities were shown to promote herbaceous richness and abundance by reducing fast-growing early-successional species (Royo et al. 2010a). However, because deer density was not necessarily estimated at the same time as plant censuses were recorded, correlations need to be interpreted with caution.

While deer presence increased the prevalence of several invasive exotic species, other factors such as propagule pressure, resource availability, and presence of mutualists are known to strongly influence plant invasions. Plant invasions cannot occur without nearby propagule sources. Additionally, soil moisture, nitrogen, and pH are known to affect *M. vimineum* populations in deciduous forests in Pennsylvania (Nord et al. 2010). Also, canopy disturbance

(i.e., increased light in the understory) and propagule pressure were more important than deer herbivory for *M. vimineum* invasion in eastern hemlock forests (Eschtruth and Battles 2009a). Similarly, previous work at the uninvaded and contiguously forested West Virginia sites (FN, MG) showed that fire and canopy gaps were more important than deer in altering plant communities (Royo et al. 2010a).

After accounting for significant plot- and site-level variation by using plot and site as random variables, deer presence still had major effects on plant diversity, abundance, and composition. The fact that deer have negative impacts on native plants and indirect facilitative effects on exotic plants across sites that vary so much in context, particularly in deer density, indicates that the damaging effects of deer on vegetation are widespread and frequent in the region (Russell et al. 2001).

## **Limitations**

In floristic censuses, plant abundance is sometimes sampled using different metrics for different plant habits (Tab. 1-1), which presents issues for meta-analysis, such as requiring interpretation of multiple abundance-metric based analyses. Additionally, internal, site-level dynamics might be masked. For example, pooled analysis obscures counter-balancing deer effects, such as where some invasive plants are facilitated and others are reduced by deer within the same site. For example, at Antietam National Battlefield, deer increased the midpoint of *A. petiolata* and *M. vimineum*, but decreased the density of *L. japonica* (data not shown). The result is a conflicting observation of deer impact at the community-level in which deer increase exotic cover midpoint, but decrease exotic stem density. Separate analyses at the species level can protect against concealed patterns, yet this approach also has issues. For example, determining total stem density or total cover, and therefore total vegetation abundance, depends on having

every species sampled in the same way. Total plant abundance is a particularly useful metric when relating primary productivity to ecosystem functioning (Chapin et al. 2002), but could not be calculated here due to multiple abundance metrics being used. Additional meta-analytical limitations can be found in Koricheva et al. (2013).

Analyzing plant community data suffers with the high number of unknown taxa. This emphasizes the importance of botanical knowledge and taxonomic education in plant community ecology. Many of the unknown species occurred within genera that are notoriously difficult to identify (e.g., *Viola* and *Carex*) and that are almost completely native to the United States (USDA, NRCS 2012). While analytical methods detected strong negative effects of deer on native vegetation, statistical ability to detect deer effects likely would have been greater had unknown plants been identified to species level. Last, the paired plot approach itself also has downsides, including fence line effects, fences providing artificial support for vines, and an unrealistic absence of deer in fenced plots (Russell et al. 2001, White 2012). Additionally, paired plots are assumed to have the same abiotic and biotic characteristics at establishment, but microsite heterogeneity is still liable to exist.

## **Conclusions**

In this work, deer altered plant community composition and increased plant community invasion. The negative effect of deer on native plants provides a window of opportunity for invaders (Johnstone 1986, Shea and Chesson 2002), which was observed, but only for unpalatable exotic plants. This regional meta-analysis broadens and deepens understanding of some key factors in the invasion process. Some invasives appear to be particularly capable of benefiting in the face of deer herbivory, an advantage that at least in part is driven by differences in palatability. The fact that patterns occurred unevenly across sites is likely a result of differences

in propagule pressure, as well as important abiotic and biotic differences across the region that shape local flora.

The displacement of palatable native plants with unpalatable exotic plants has implications for bottom-up alteration of food webs (Richardson et al. 2000, Gleditsch and Carlo 2011). Furthermore, while exotic plant invasion has been causally implicated in native plant decline (Wiegmann and Waller 2006), ruminant herbivory appears to be a key factor affecting both processes. Dominant native herbivores such as deer appear to be important agents of ecosystem change as their presence reduces biodiversity and increases the degree of exotic plant invasion, two of the major drivers that have altered modern ecosystems (Hooper et al. 2012).

To optimize vegetation management, understanding the mechanistic interplay among the dominant and damaging organisms is an important first step. This research shows that abundant native herbivores increase the abundance of certain invasive exotic plants and are likely to have indirectly facilitated their invasion. Thus, in addition to facilitating the conservation of native species diversity in forest understories, deer reductions might also alleviate the burden of plant invasions across the region.

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**Table 1-1:** Descriptions of sites and data used in pooled analyses testing the role of white-tailed deer in exotic plant invasion across the Northeastern United States. Floristic composition data were collected from unfenced (deer) and fenced (no-deer) plots at each site.

Site (code)	US State	Latitude — decimal degrees	Longitude — decimal degrees	Dominant overstory species	Vegetation abundance measurement	Reference used for plant classification
Antietam National Battlefield (AN)	MD	39.4763	-77.7490	maple, white ash, cherry	counts, cover classes <sup>1</sup> , or density classes in subplots; sapling counts in main plot	Strausbaugh and Core 1978
Catoctin Mountain Park (CA)	MD	39.6561	-77.4786	maple, tulip poplar	counts or cover classes	Newcomb 1977; USDA NRCS 2012
Chesapeake & Ohio Canal National Historical Park (CH)	MD	39.0882	-77.4619	maple, white ash, cherry	counts, cover classes <sup>1</sup> , or density classes in subplots; sapling counts in main plot	Strausbaugh and Core 1978
Smithsonian Conservation Biology Institute (CRC)	VA	38.8951	-72.1463	oak, beech	counts, cover classes <sup>1</sup> , or density classes	Strausbaugh and Core 1978
Edgewater (ED)	MD	38.8908	-76.5646	tulip poplar, sweet gum, beech	percentage cover	Gleason and Cronquist 1991; botanists (see note)
Fermilab (FE)	IL	41.8423	-88.2631	oak	percentage cover	Swink and Wilhelm 1994
Fernow (FN)	WV	39.0167	-79.7000	oak, maple, beech	counts and percentage cover	Gleason and Cronquist 1991; USDA NRCS 2012
Gold Mine Tract of C&O Canal (GM)	MD	38.9931	-77.2392	oak, beech	counts, cover classes <sup>1</sup> , or density classes	Strausbaugh and Core 1978
Great Falls Park (GF)	VA	38.9840	-77.2531	oak, beech	counts, cover classes <sup>1</sup> , or density classes	Strausbaugh and Core 1978
Ithaca (IT)	NY	42.4665	-76.4416	NA (old field)	percentage cover	Gleason and Cronquist 1991
Long Run (LR)	PA	41.6288	-78.7211	black cherry, red maple	percentage cover	Rhoads and Block 2007; USDA NRCS 2012; botanists (see note)
Manassas National Battlefield Park (MA)	VA	38.8266	-77.5279	oak, hickory, VA pine, northern red cedar	counts and percentage cover	Strausbaugh and Core 1978
Marienville (MV)	PA	41.5347	-79.1643	black cherry, red maple	percentage cover	Rhoads and Block 2007; USDA NRCS 2012; botanists (see note)
Monocacy National Battlefield (MO)	MD	39.3697	-77.3924	dry oak, tulip poplar	counts or cover classes <sup>1</sup> in subplots; sapling counts in main plot	Strausbaugh and Core 1978
Monongahela (MG)	WV	39.1000	-79.7167	oak, maple, beech	counts and percentage cover	Gleason and Cronquist 1991; USDA NRCS 2012
Morristown National Historic Park (MP)	NJ	40.7760	-74.5301	tulip poplar, white ash, oak, black locust	cover classes	Newcomb 1977; Gleason and Cronquist 1991
Raccoon Ecological Management Area (R1)	OH	39.1997	-82.4093	oak, hickory	cover classes	Gleason and Cronquist 1991
Riverbend Park (RB)	VA	39.0093	-77.2580	oak, beech	counts, cover classes <sup>1</sup> , or density classes	Strausbaugh and Core 1978
Shenandoah National Park (SH)	VA	38.7438	-78.2992	oak, hickory, pine	counts or density classes	Gleason and Cronquist 1991
Trillium Trail (TR)	PA	40.5201	-79.9011	oak, beech, maple, tulip poplar	percentage cover	Gleason and Cronquist 1991
Valley Forge National Historical Park—Mt Joy (VJ)	PA	40.0940	-75.4543	tulip poplar, dry oak	cover classes or counts	Gleason and Cronquist 1991
Valley Forge National Historical Park—Mt Misery (VM)	PA	40.0932	-75.4611	dry oak	cover classes or counts	Gleason and Cronquist 1991
West Point (WP)	NY	41.3636	-74.0239	oak, sugar maple	cover classes	Rhoads and Block 2007; USDA NRCS 2012
Zaleski (Z1)	OH	39.3032	-82.3461	oak, hickory	cover classes	Gleason and Cronquist 1991

<sup>1</sup> McShea/Bourg cover classes were used.

**Table 1-1: (Extended)**

Site (code)	Estimated deer density <sup>2</sup> deer km <sup>-2</sup>	Duration of deer exclusion yrs	Years of study	# Plot pairs	Plot area <sup>3</sup> m <sup>2</sup>	Subplot area m <sup>2</sup>	Total area sampled/ plot	Distance between paired plots m	Fence height	Fence mesh size cm	References/notes
Antietam National Battlefield (AN)	53	6	2003–2009	12	25	1	4	<5	2.4	10 x 10	McShea and Bourg 2009
Catoctin Mountain Park (CA)	44	3	2005–2008	7	25	NA	25	5	3	10 x 20	Caraher 2009; plots established in hurricane Ivan blow-down gaps
Chesapeake & Ohio Canal National Historical Park (CH)	54	6	2003–2009	28	25	1	4	<5	2.4	10 x 10	McShea and Bourg 2009
Smithsonian Conservation Biology Institute (CRC)	107	4	2005–2009	14	16	1	4	50	2.4	5 x 5	unpublished data, W. McShea and N. Bourg, SI Conservation Biology Institute
Edgewater (ED)	4	2	2009–2011	16	100	1	5	3–10	2.3	50 x 50	unpublished data, J. Parker, SI; species ID: pers. comm. with botanists at SI Museum of Natural History
Fermilab (FE)	6	14	1992–2006	3	594	1	25	5	3	15 x 15	unpublished data, V. Nuzzo, Natural Area Consultants; 90% deer herd cull in 1998
Fernow (FN)	6	6	2000–2006	4	400	1	5	>20	2	15 x 15 or 30	Royo et al. 2010
Gold Mine Tract of C&O Canal (GM)	45	4	2005–2009	10	16	1	4	50	2.4	5 x 5	McShea and Bourg 2008
Great Falls Park (GF)	26	4	2005–2009	22	16	1	4	50	2.4	5 x 5	McShea and Bourg 2008
Ithaca (IT)	39	3	2005–2008	6	256	49	196	64–400	2.4	5 x 5	DiTommaso et al. 2014
Long Run (LR)	5	11	2000–2011	5	280	1	4	10–30	2	5 x 5	unpublished data, K. Averill and D. Mortensen and A. Royo, USDA Forest Service; species ID: pers. comm. with botanists at Penn State
Manassas National Battlefield Park (MA)	63	9	2000–2009	23	12	1	4	1	2	5 x 10	McShea et al. 2010
Marienville (MV)	5	11	2000–2011	5	280	1	4	10–30	2	5 x 5	unpublished data, K. Averill and D. Mortensen and A. Royo, USDA Forest Service
Monocacy National Battlefield (MO)	77	6	2003–2009	6	25	1	4	<5	2.4	10 x 10	McShea and Bourg 2009
Monongahela (MG)	6	6	2000–2006	4	400	1	5	>20	2	15 x 15 or 30	Royo et al. 2010
Morristown National Historic Park (MP)	19	14–17	1987–2005	5	36	1	9	~9	3.7	11 x 15	unpublished data, R. Masson, National Park Service
Raccoon Ecological Management Area (R1)	11	5	2001–2006	3	400	1	12	10–15	2.4	4.4 x 5	unpublished data, T. Hutchinson and D. Apsley, USDA Forest Service
Riverbend Park (RB)	26	3	2006–2009	2	16	1	4	50	2.4	5 x 5	McShea and Bourg 2008
Shenandoah National Park (SH)	10	4–6	1990–1996	6	4 ha	1	18	see note	2.4	15 x 15	unpublished data, W. McShea, SI Conservation Biology Institute; plots paired regionally, with one 4 ha plot per site, each with 3 24 x 24 m plots
Trillium Trail (TR)	32	8	1994–2002	3	100	NA	100	~60	2.5	6 x 6	Knight et al. 2009
Valley Forge National Historical Park–Mt Joy (VJ)	84	17	1993–2010	15	9	4	4	20–36	2	5 x 10	Abrams and Johnson 2012; 2 m metal stake in centers of control plots
Valley Forge National Historical Park–Mt Misery (VM)	84	17	1993–2010	15	9	4	4	20–36	2	5 x 10	Abrams and Johnson 2012; 2 m metal stake in centers of control plots
West Point (WP)	no estimate available	4	2008–2012	12	900	1	10	5–50	2.4	5 x 5	unpublished data, B. Blossey, Cornell University and V. Nuzzo, Natural Area Consultants
Zaleski (Z1)	11	5	2001–2006	3	400	1	12	10–15	2.4	4.4 x 5	unpublished data, T. Hutchinson and D. Apsley, USDA Forest Service

<sup>2</sup> See appendix for methods and references.

NA = not applicable

**Table 1-2:** Indicator species analysis results showing which exotic and native plant species were associated with white-tailed deer or with no deer across the Northeastern United States. Indicator values range from 0 (no indication of association with treatment) to 100 (perfect indication) and were determined according to the metric used to record species' abundance, presence/absence (p/a), density, cover, or cover class midpoint (midpoint). Results are based on floristic composition data collected from unfenced (deer) and fenced (no-deer) plots at 24 sites across the region.

	Native/ Exotic status	Species	Habit	Abundance measurement	Indicator Value	p value	# plots (n)	# sites		
Deer	Exotic	<i>Ailanthus altissima</i>	Tree	density	9.5	0.08	36	7		
		<i>Alliaria petiolata</i>	Forb/herb	density	29.3	0.03	133	9		
		<i>Microstegium vimineum</i>	Graminoid	p/a	21.8	0.02	148	14		
	Native	<i>Perilla frutescens</i>	Forb/herb	p/a	41.3	0.0002	131	12		
		<i>Polygonum cespitosum</i>	Forb/herb	p/a	5.4	0.06	26	7		
		<i>Rubus phoenicolasius</i>	Subshrub	density	6.6	0.08	35	9		
		<i>Acalypha rhomboidea</i>	Forb/herb	density	4.2	0.09	12	6		
				p/a	4.1	0.09	18	3		
				density	4.9	0.009	9	2		
		<i>Cinna arundinacea</i>	Graminoid	midpoint	3.4	0.03	5	1		
		<i>Oxalis stricta</i>	Forb/herb	density	7.7	0.02	21	4		
		<i>Oxalis violacea</i>	Forb/herb	density	2.5	0.06	4	2		
		<i>Pilea pumila</i>	Forb/herb	p/a	7.4	0.07	40	10		
				density	11.1	0.01	33	5		
				p/a	3.1	0.04	9	3		
				density	4.8	0.01	9	3		
		<i>Symphoricarpos orbiculatus</i>	Shrub	density	5.8	0.07	17	2		
		<i>Urtica dioica</i>	Forb/herb	density	4.2	0.1	11	2		
No deer	Exotic	<i>Lonicera japonica</i>	Vine	p/a	21.7	0.06	156	15		
				midpoint	16.3	0.002	39	5		
				density	25.4	0.04	118	9		
		<i>Lonicera maackii</i>	Shrub	p/a	3.1	0.01	7	3		
		<i>Morus alba</i>	Tree, Shrub	p/a	2.7	0.07	8	3		
				density	3.3	0.07	7	2		
	Native	<i>Rosa multiflora</i>	Vine, Subshrub	p/a	13.7	0.04	86	12		
				midpoint	6	0.03	12	5		
				density	13.8	0.07	56	6		
				<i>Rubus phoenicolasius</i>	Subshrub	midpoint	5.8	0.10	16	4
				<i>Actaea racemosa</i>	Forb/herb	midpoint	5.1	0.06	11	4
				<i>Carya alba</i>	Tree	p/a	6.2	0.07	31	11
		<i>Carya cordiformis</i>	Tree	midpoint	5.6	0.007	10	3		
				density	6.3	0.02	17	7		
				p/a	9.5	0.01	47	13		
				density	10.9	0.004	31	8		
				<i>Carya glabra</i>	Tree	density	6.8	0.05	22	8
				<i>Cercis canadensis</i>	Tree, Shrub	density	9	0.07	31	6
<i>Circaea alpina</i>	Forb/herb	p/a	2.6	0.03	6	1				
		midpoint	4.1	0.03	6	1				

Table 1-2: (Continued)

	Native/ Exotic status	Species	Habit	Abundance measurement	Indicator Value	p value	# plots (n)	# sites	
No deer		<i>Fraxinus americana</i>	Tree	p/a	14.7	0.09	100	17	
		<i>Geum canadense</i>	Forb/herb	midpoint	5.4	0.008	8	3	
				density	10.1	0.08	38	6	
			<i>Juglans nigra</i>	Tree	density	3	0.06	5	1
			<i>Lindera benzoin</i>	Tree, Shrub	p/a	21.8	0.07	159	15
					midpoint	9.3	0.03	22	5
			<i>Maianthemum racemosum</i>	Forb/herb	p/a	12	0.008	61	16
					midpoint	11	0.007	25	8
					density	8	0.02	23	5
					cover	19.5	0.08	17	4
			<i>Parthenocissus quinquefolia</i>	Vine	midpoint	24.7	0.009	78	8
			<i>Podophyllum peltatum</i>	Forb/herb	midpoint	4.1	0.04	7	2
			<i>Polygonatum biflorum</i>	Forb/herb	p/a	8	0.02	37	13
					midpoint	8.1	0.007	14	6
					density	4.3	0.09	12	5
			<i>Prunus serotina</i>	Tree, Shrub	p/a	23.9	0.02	165	21
					density	23.6	0.08	110	12
			<i>Quercus prinus</i>	Tree	density	12.4	0.06	45	7
					p/a	9.4	0.09	57	12
					midpoint	10.7	0.05	28	4
					density	10.8	0.009	33	7
			<i>Rhododendron periclymenoides</i>	Shrub	p/a	3.5	0.02	10	4
					midpoint	4.1	0.03	6	2
			<i>Rhus typhina</i>	Shrub, Tree	cover	13	0.06	8	1
			<i>Rubus flagellaris</i>	Subshrub	midpoint	4	0.06	7	2
			<i>Rubus pensilvanicus</i>	Subshrub	p/a	2.6	0.03	6	3
					midpoint	3.4	0.07	5	2
			<i>Sassafras albidum</i>	Tree, Shrub	density	14.1	0.08	60	10
			<i>Toxicodendron radicans</i>	Shrub, Forb/herb, Subshrub, Vine	p/a	22.1	0.07	160	19
					midpoint	16.6	0.06	58	8
					density	19.8	0.04	86	9
			<i>Ulmus americana</i>	Tree	p/a	3.4	0.09	13	2
				density	4.7	0.05	13	2	
		<i>Ulmus rubra</i>	Tree	p/a	11.3	0.007	56	9	
				density	13.5	0.006	45	8	
		<i>Uvularia perfoliata</i>	Forb/herb	p/a	6.4	0.07	33	11	
				midpoint	7	0.03	18	7	
		<i>Vaccinium angustifolium</i>	Subshrub, Shrub	midpoint	6.9	0.07	19	3	
		<i>Viburnum acerifolium</i>	Shrub, Subshrub	p/a	9.3	0.002	37	10	
				midpoint	12.6	0.001	25	7	

**Table 1-3:** Significant effects of white-tailed deer on the abundance of the most frequent exotic and native plant species in the Northeastern US based on mixed models. Metrics used to record species' abundance included density, cover, and cover class midpoint (midpoint). Variation due to plot pair and site was accounted for using random effects. Results are based on floristic composition data collected from unfenced (deer) and fenced (no-deer) plots at 24 sites across the region.

	Native/ Exotic status	Species	Habit	Abundance measurement	p value	Number of plots in analysis (n)	Number of pairs in analysis	Number of sites in analysis	
Deer	Exotic	<i>Ailanthus altissima</i>	Tree	Density	0.04	190	95	7	
		<i>Alliaria petiolata</i>	Forb/herb	Density	0.0002	246	123	9	
		<i>Microstegium vimineum</i>	Graminoid	Cover class midpoint	<0.0001	312	156	12	
	Native	<i>Pilea pumila</i>	Forb/herb	Density	0.005	166	83	5	
No deer	Exotic	<i>Duchesnea indica</i>	Forb/herb	Density	0.03	170	85	4	
		<i>Lonicera japonica</i>	Vine	Cover class midpoint	<0.0001	116	58	5	
				Density	0.0005	246	123	9	
		<i>Rosa multiflora</i>	Vine, Subshrub	Density	0.02	210	105	6	
	Native	<i>Carya cordiformis</i>	Tree	Density	0.001	236	118	8	
		<i>Fraxinus americana</i>	Tree	Cover class midpoint	0.02	62	31	3	
		<i>Geum canadense</i>	Forb/herb	Density	0.03	190	95	6	
		<i>Maianthemum racemosum</i>	Forb/herb	Cover class midpoint	0.001	166	83	8	
				Density	0.01	186	93	5	
		<i>Parthenocissus quinquefolia</i>	Vine	Cover class midpoint	0.0003	166	83	8	
				Density	0.02	254	127	10	
		<i>Prunus serotina</i>	Tree, Shrub	Cover class midpoint	0.02	76	38	3	
		<i>Quercus rubra</i>	Tree	Cover class midpoint	0.05	82	41	4	
				Density	0.002	238	119	7	
		<i>Sassafras albidum</i>	Tree, Shrub	Density	0.01	292	146	10	
			Shrub, Forb/herb,						
		<i>Toxicodendron radicans</i>	Subshrub, Vine	Cover class midpoint	0.01	166	83	8	
			Density	0.007	246	123	9		
	<i>Ulmus rubra</i>	Tree	Density	0.0009	252	126	8		
	<i>Viburnum acerifolium</i>	Shrub, Subshrub	Cover class midpoint	0.0009	152	76	7		

**Table 1-4:** Mixed model effects of white-tailed deer presence on exotic, native, and total plant community species richness based on a Northeastern United States network of 24 deer research sites where paired unfenced deer or fenced deer exclusion plots were established.<sup>1</sup>

	Exotic species richness	Percentage exotic	Native species	Total species richness
<i>Fixed effects</i>				
Intercept (SE)	1.2 (0.3)	2.7 (0.4)	3.3 (0.3)	4.2 (0.3)
Deer presence coefficient (SE)	0.05 (0.04)	-0.1 (0.1)	0.38 (0.05)	0.31 (0.06)
p value	0.2	0.3	<b>&lt; 0.0001</b>	<b>&lt; 0.0001</b>
LSmeans treatment test	-	-	<b>ND &gt; D</b>	<b>ND &gt; D</b>
D estimate (LCI-UCI)	-	-	3.3 (2.8-3.9)	4.2 (3.5-4.8)
ND estimate (LCI-UCI)	-	-	3.7 (3.2-4.3)	4.5 (3.8-5.1)
<i>Random effects</i>				
Plot pair variance (SD)	0.2 (0.4)	1 (1)	0.1 (0.4)	0.2 (0.5)
p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Site variance (SD)	2 (1)	4 (2)	2 (1)	2 (1)
p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Residual	0.2 (0.4)	1 (1)	0.3 (0.6)	0.4 (0.7)
<i>n</i>	458	458	458	458
# Fenced/unfenced plot pairs	229	229	229	229
# Sites	24	24	24	24

<sup>1</sup> Square-root transformations of species richness were necessary to meet the assumption of homogeneity of residuals. SE = standard error; D = deer; ND = no deer; LCI = lower confidence interval; UCI = upper confidence interval; SD = standard deviation; n = number of observations.

**Table 1-5:** Mixed model effects of white-tailed deer presence on exotic, native, and total plant community density, cover, and cover class midpoint based on a Northeastern United States network of 24 deer research sites where paired unfenced deer or fenced deer exclusion plots were established. Deer effects on Shannon diversity ( $H'$ ) are also reported.<sup>1</sup>

	Exotic stem density	Percentage exotic density	Native stem density	Total stem density	Shannon diversity (density)	Exotic cover	Percentage exotic cover	Native cover	Total cover	Shannon diversity (cover)
<i>Fixed effects</i>										
Intercept (SE)	1.4 (0.3)	0.43 (0.07)	1.8 (0.2)	2.3 (0.3)	1.6 (0.2)	5 (2)	0.5 (0.1)	7 (1)	8 (1)	1.8 (0.2)
Deer presence coefficient (SE)	-0.04 (0.08)	-0.01 (0.02)	0.3 (0.07)	0.27 (0.06)	0.19 (0.04)	-0.3 (0.3)	-0.07 (0.03)	0.8 (0.2)	0.5 (0.2)	0.01 (0.07)
p value	0.6	0.6	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.3	<b>0.02</b>	<b>0.003</b>	<b>0.03</b>	0.9
LSmeans treatment test	-	-	<b>ND &gt; D</b>	<b>ND &gt; D</b>	<b>ND &gt; D</b>	-	<b>D &gt; ND</b>	<b>ND &gt; D</b>	<b>ND &gt; D</b>	-
D estimate (LCI-UCI)	-	-	1.8 (1.3-2.2)	2.3 (1.7-2.9)	1.6 (1.2-2.0)	-	0.53 (0.18-0.87)	7.1 (4.1-10)	8.3 (4.7-12)	-
ND estimate (LCI-UCI)	-	-	2.1 (1.6-2.5)	2.6 (1.9-3.2)	1.8 (1.4-2.2)	-	0.46 (0.11-0.80)	7.9 (4.8-11)	8.8 (5.2-12)	-
<i>Random effects</i>										
Plot pair variance (SD)	0.2 (0.5)	0.02 (0.2)	*	0.01 (0.1)	0.1 (0.3)	6 (2)	0.04 (0.2)	1 (1)	3 (2)	0.1 (0.2)
p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	*	0.6	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0004</b>	<b>&lt;0.0001</b>	<b>0.01</b>
Site variance (SD)	1 (1)	0.05 (0.2)	0.7 (0.8)	1 (1)	0.4 (0.7)	9 (3)	0.03 (0.2)	12 (3)	17 (4)	0.4 (0.6)
p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.02</b>	0.2	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Residual	0.4 (0.6)	0.04 (0.2)	0.4 (0.7)	0.3 (0.6)	0.2 (0.4)	1 (1)	0.01 (0.1)	1 (1)	1 (1)	0.1 (0.3)
<i>n</i>	290	290	336	336	325	56	56	92	92	92
# Fenced/unfenced plot pairs	145	145	168	168	167	28	28	46	46	46
# Sites	11	11	14	14	14	4	4	8	8	8

<sup>1</sup> Natural log +1 transformations of stem density, square-root transformations of cover, and arc sin square-root transformations of percentage exotic abundance data were necessary to meet the assumption of homogeneity of residuals. SE = standard error; D = deer; ND = no deer; LCI = lower confidence interval; UCI = upper confidence interval; SD = standard deviation; n = number of observations.

\* Excluded pair from model because the model term did not account for variation and prevented convergence.

**Table 1-5: (Extended)**

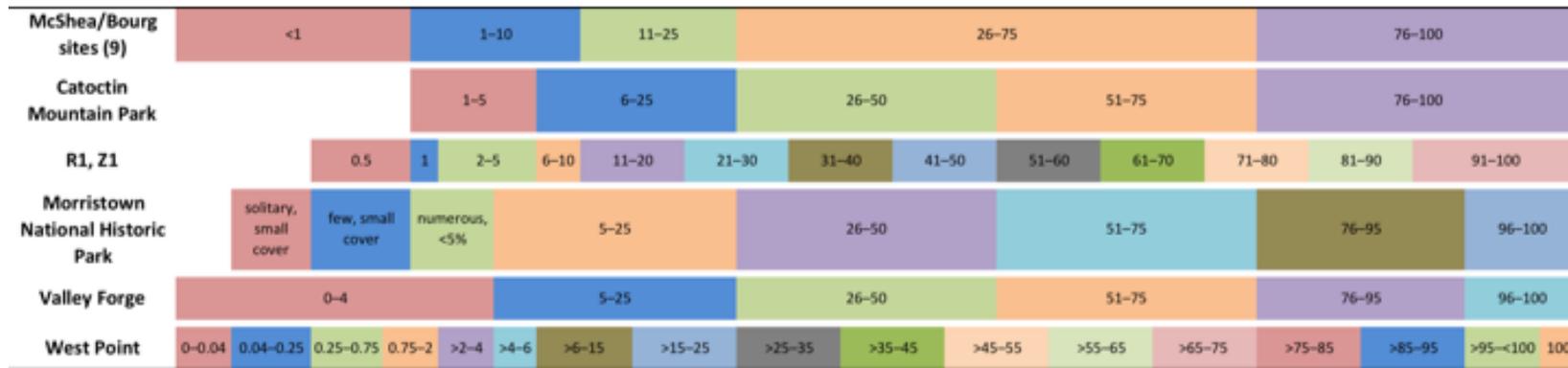
	Exotic cover class midpoint	Percentage exotic cover class midpoint	Native cover class midpoint	Total cover class midpoint	Shannon diversity (cover class midpoint)
<i>Fixed effects</i>					
Intercept (SE)	1.3 (0.3)	0.50 (0.08)	1.2 (0.3)	2.2 (0.3)	1.0 (0.2)
Deer presence coefficient (SE)	-0.1 (0.1)	-0.12 (0.04)	0.7 (0.1)	0.3 (0.1)	0.22 (0.06)
p value	0.4	<b>0.006</b>	<b>&lt;0.0001</b>	<b>0.006</b>	<b>0.0007</b>
LMeans treatment test	-	<b>D &gt; ND</b>	<b>ND &gt; D</b>	<b>ND &gt; D</b>	<b>ND &gt; D</b>
D estimate (LCI-UCI)	-	0.50 (0.33-0.66)	1.2 (0.49-1.9)	2.2 (1.6-2.8)	0.97 (0.50-1.4)
ND estimate (LCI-UCI)	-	0.38 (0.22-0.54)	1.9 (1.2-2.6)	2.6 (1.9-3.2)	1.2 (0.71-1.7)
<i>Random effects</i>					
Plot pair variance (Std.Dev.)	0.6 (0.8)	0.05 (0.2)	*	0.3 (0.6)	*
p value	<b>&lt;0.0001</b>	<b>0.0007</b>	*	<b>0.009</b>	*
Site variance (Std.Dev.)	0.8 (0.9)	0.06 (0.2)	1 (1)	1 (1)	0.7 (0.8)
p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Residual	1 (1)	0.2 (0.4)	1 (1)	1 (1)	0.3 (0.5)
<i>n</i>	348	348	354	354	293
# Fenced/unfenced plot pairs	174	174	177	177	169
# Sites	14	14	15	15	15

<sup>1</sup> Square-root transformations of midpoint and arc sin square root transformations of percentage midpoint data were necessary to meet the assumption of homogeneity of residuals. SE = standard error; D = deer; ND = no deer; LCI = lower confidence interval; UCI = upper confidence interval; SD = standard deviation; n = number of observations.

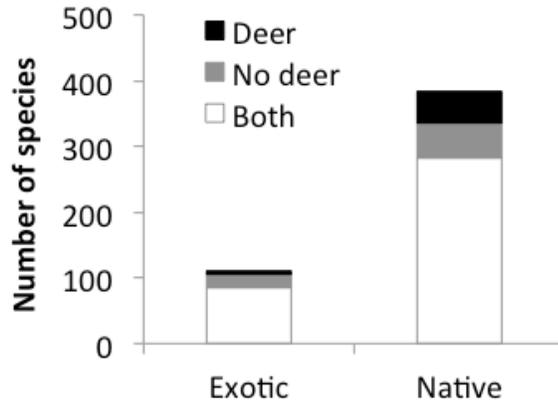
\* Excluded pair from model because the model term did not account for variation and prevented convergence.

**Table 1-6:** Mixed model effects of white-tailed deer on the relationship between exotic and native abundance across Northeastern US forest understories. Results are based on floristic composition data collected from unfenced (deer) and fenced (no-deer) plots at 24 sites across the region.

	Exotic species richness	Exotic stems	Exotic cover	Exotic cover class midpoint
<i>Fixed effects</i>				
Intercept (SE)	0.3 (0.3)	0.8 (0.3)	6 (2)	1.0 (0.3)
Deer presence coefficient (SE)	-0.05 (0.04)	-0.13 (0.07)	-0.2 (0.4)	-0.2 (0.1)
p value	0.2	0.071	0.5	<b>0.04</b>
Post-hoc treatment test	-	-	-	<b>D &gt; ND</b>
D estimate (LCI-UCI)	-	-	-	1.3 (0.79-1.9)
ND estimate (LCI-UCI)	-	-	-	1.1 (0.54-1.7)
Native vegetation covariate coefficient (SE)	0.27 (0.03)	0.33 (0.07)	-0.1 (0.1)	0.22 (0.06)
p value	<b>&lt; 0.0001</b>	<b>&lt; 0.0001</b>	0.6	<b>0.0006</b>
<i>Random effects</i>				
Plot pair variance (Std.Dev.)	0.1 (0.4)	0.3 (0.5)	6 (2)	0.6 (0.8)
p value	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
Site variance (Std.Dev.)	1 (1)	0.7 (0.8)	10 (3)	0.8 (0.9)
p value	<b>0.0001</b>	<b>0.0001</b>	<b>0.02</b>	<b>0.0001</b>
Residual	0.2 (0.4)	0.4 (0.6)	1 (1)	1 (1)
<i>n</i>	458	290	56	348
# Fenced/unfenced plot pairs	229	145	28	174
# Sites	24	11	4	14



**Figure 1-1:** Cover class categories used within 15 floristic composition datasets that measured plant abundance with cover classes in unfenced (deer) and fenced (no-deer) plots across the Northeastern United States region.

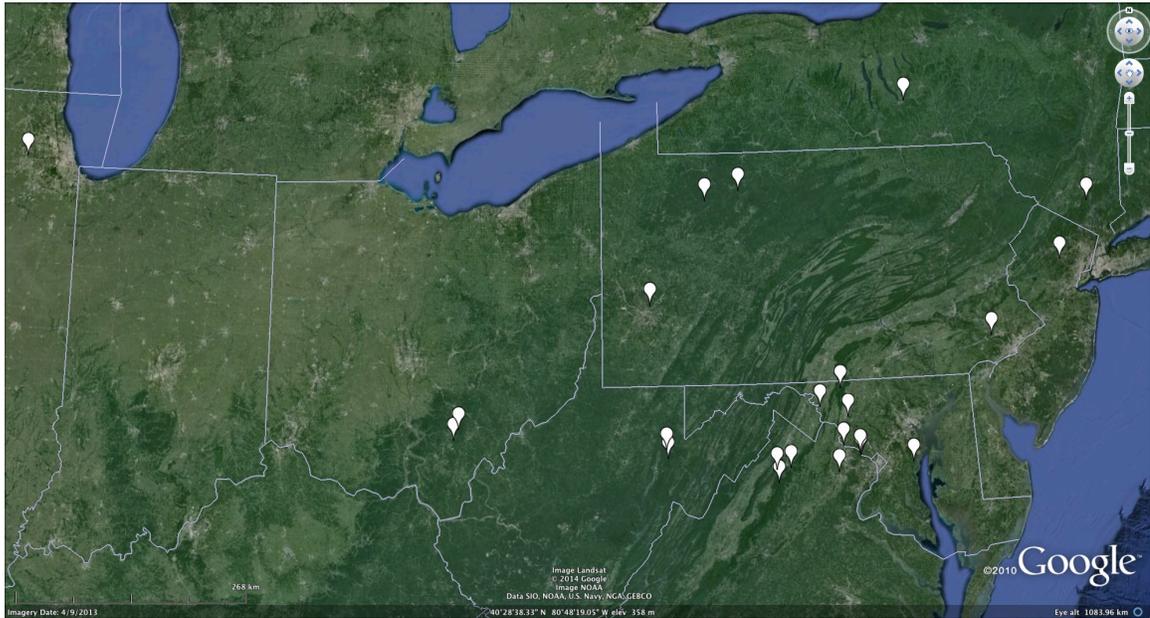


**Figure 1-2:** Total number of exotic and native plant species occurring in deer plots, no-deer plots, or in both across the Northeastern United States. Results are based on floristic composition data collected from unfenced (deer) and fenced (no-deer) plots at 24 sites across the region.

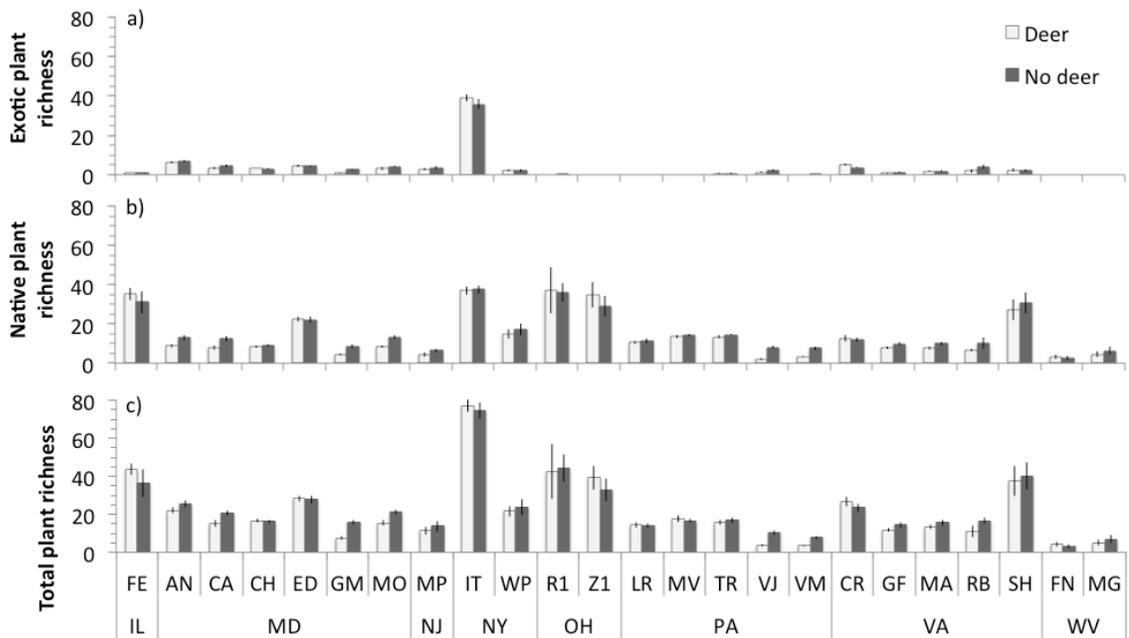
## Appendices

**Table 1-A1:** Deer density estimates at sites used in pooled analyses testing the effects of deer presence on exotic plant invasion based on unfenced (deer) and fenced (no-deer) plots at 24 sites across the Northeastern United States region.

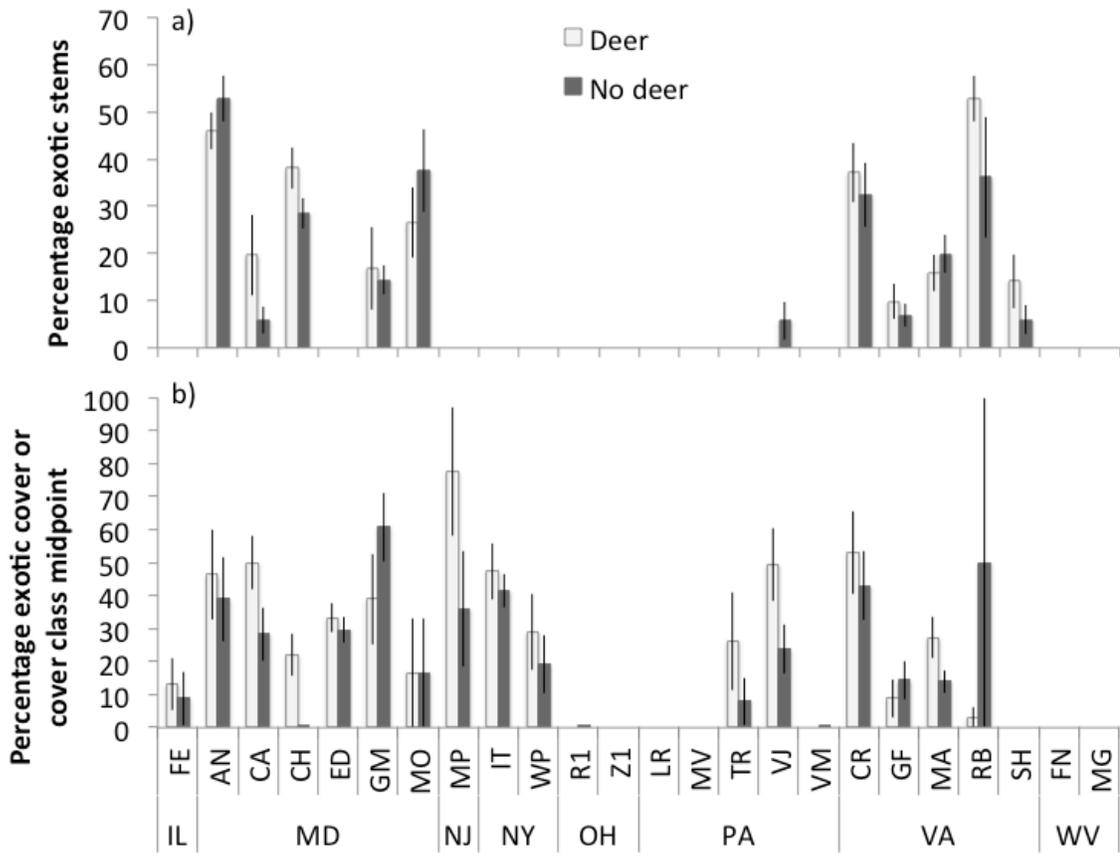
Site	Estimated deer density deer km <sup>-2</sup>	Year/s of estimate	Extent of estimate	Methods	Source
Antietam National Battlefield (AN)	53	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 41–68 deer km <sup>-2</sup>	Bates 2009
Catoctin Mountain Park (CA)	44	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 37–52 deer km <sup>-2</sup>	Bates 2009
Chesapeake & Ohio Canal National Historical Park (CH)	54	2003	site	combination of spotlight, helicopter, and forward-looking infrared surveys during autumn and winter	Gibbs et al. 2004
Smithsonian Conservation Biology Institute (CRC)	107	1999	site	95% CI: 95-151 deer km <sup>-2</sup>	Kocka and Steffen 2000
Edgewater (ED)	4	2013	site	aerial survey	Pers. comm. with J. Parker (Smithsonian Institution)
Fermilab (FE)	6	2005, 2007	site	winter aerial surveys; mean of 2005 (7) and 2007 (5) estimates	Pers. comm. with R. Walton (Fermi National Accelerator Laboratory)
Fernow (FN)	6	~2000-2010	county		Royo et al. 2010
Gold Mine Tract of C&O Canal (GM)	45	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 25–80 deer km <sup>-2</sup>	Bates 2009
Great Falls Park (GF)	26	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 16–41 deer km <sup>-2</sup>	Bates 2009
Ithaca (IT)	39	2013	site	motion-sensing camera survey	DiTommaso et al. 2014
Long Run (LR)	5	2011	site		Pers. comm. with A. Royo (USDA Forest Service)
Manassas National Battlefield Park (MA)	63	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 28–140 deer km <sup>-2</sup>	Bates 2009
Marienville (MV)	5	2011	site		Pers. comm. with A. Royo (USDA Forest Service)
Monocacy National Battlefield (MO)	77	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 38–158 deer km <sup>-2</sup>	Bates 2009
Monongahela (MG)	6	~2000-2010	county		Royo et al. 2010
Morristown National Historic Park (MP)	19	2009-2010	site	spotlight surveys and distance sampling; average of autumn '09 (17 deer km <sup>-2</sup> ) and spring '10 (20 deer km <sup>-2</sup> ) estimates	Pers. comm. with R. Masson (National Park Service)
Raccoon Ecological Management Area (R1)	11	2006	county	harvest-based estimates	Pers. comm. With M. Tonkovich (Ohio Department Natural Resources)
Riverbend Park (RB)	26	2008	site	autumn spotlight surveys and distance sampling; 95% CI = 16–41 deer km <sup>-2</sup>	Bates 2009
Shenandoah National Park (SH)	10	2013	park	autumn spotlight survey; 95% CI = 7–15 deer km <sup>-2</sup>	Pers. comm. with W. McShea (Smithsonian Institution)
Trillium Trail (TR)	32	1992-2002	city borough	annual aerial surveys; estimate range = 25–40 deer km <sup>-2</sup>	Knight et al. 2009
Valley Forge National Historical Park–Mt Joy (VJ)	84	1997-2010	site	mark-resight surveys; average across 14 yrs; estimate range = 56–120 deer km <sup>-2</sup>	Pers. Comm. with K. Heister (National Park Service)
Valley Forge National Historical Park–Mt Misery (VM)	84	1997-2010	site	mark-resight surveys; average across 14 yrs; estimate range = 56–120 deer km <sup>-2</sup>	Pers. Comm. with K. Heister (National Park Service)
West Point (WP)	no estimate available				
Zaleski (Z1)	11	2006	county	harvest-based estimates	Pers. comm. With M. Tonkovich (Ohio Department Natural Resources)



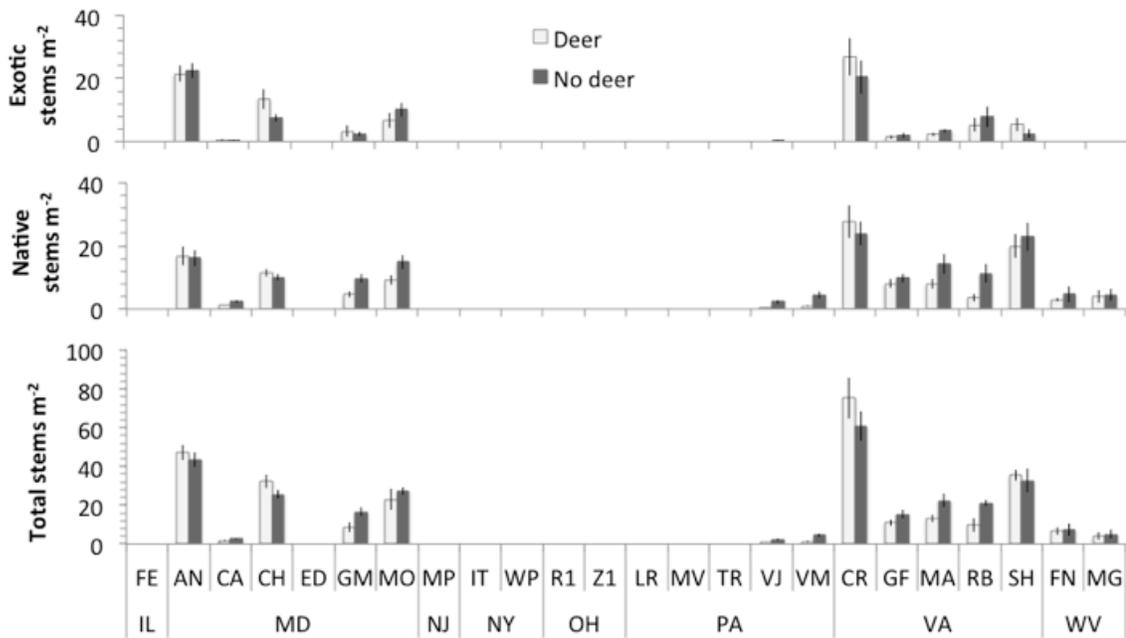
**Figure 1-A1:** Mapped locations of deer research sites. Note that some sites were so close in proximity that location markers overlap.



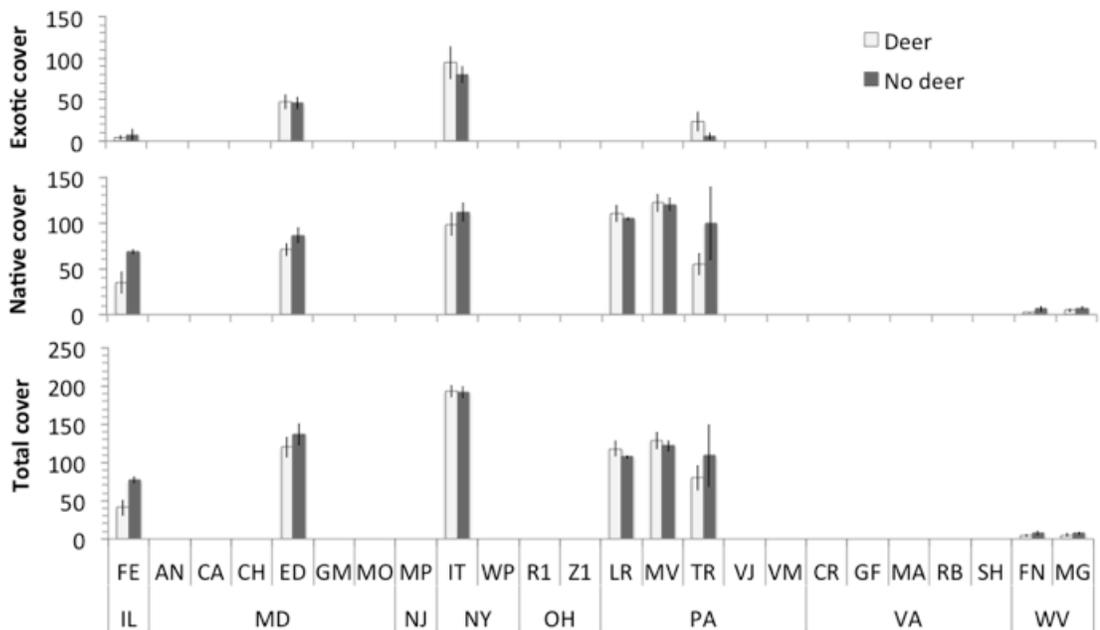
**Figure 1-A2:** The mean number of a) exotic, b) native, and c) total species occurring with or without white-tailed deer at 24 sites across eight states in the Northeastern US. No exotic plant species were recorded at FN, LR, MG, MV, or Z1. See Tab. 1-1 for site codes.



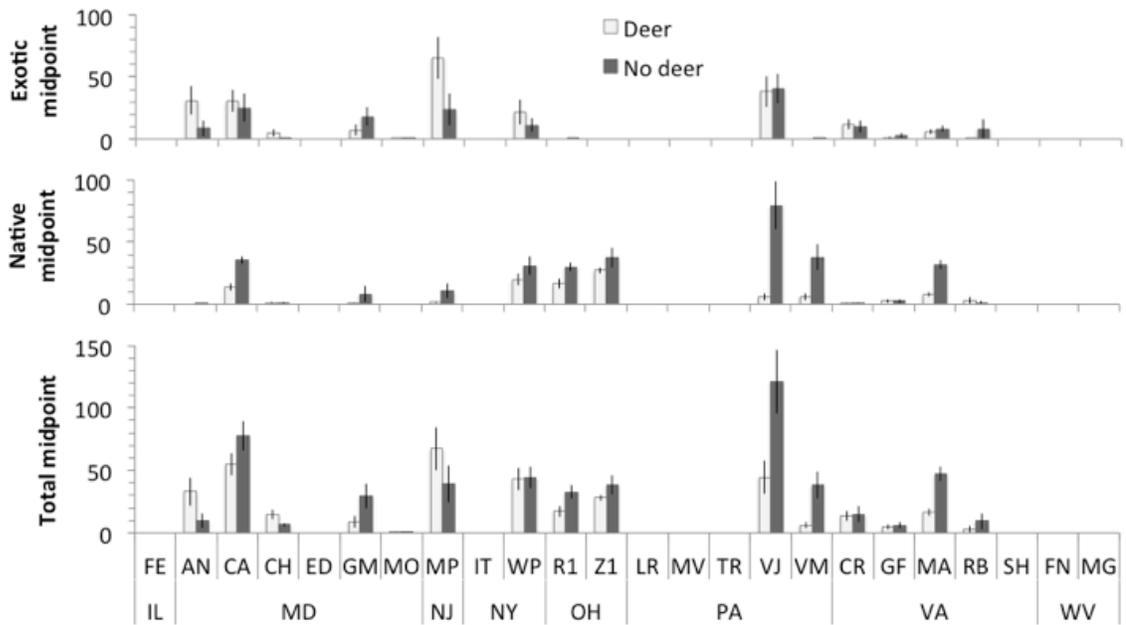
**Figure 1-A3:** Percentage of total a) stem or b) cover abundance comprised of exotic vegetation across white-tailed deer and no-deer plots at 24 sites across eight states in the Northeastern US. In b, percentage cover was reported for four sites (ED, FE, IT, and TR) and percentage cover class midpoint for the others. See Tab. 1-1 for site codes.



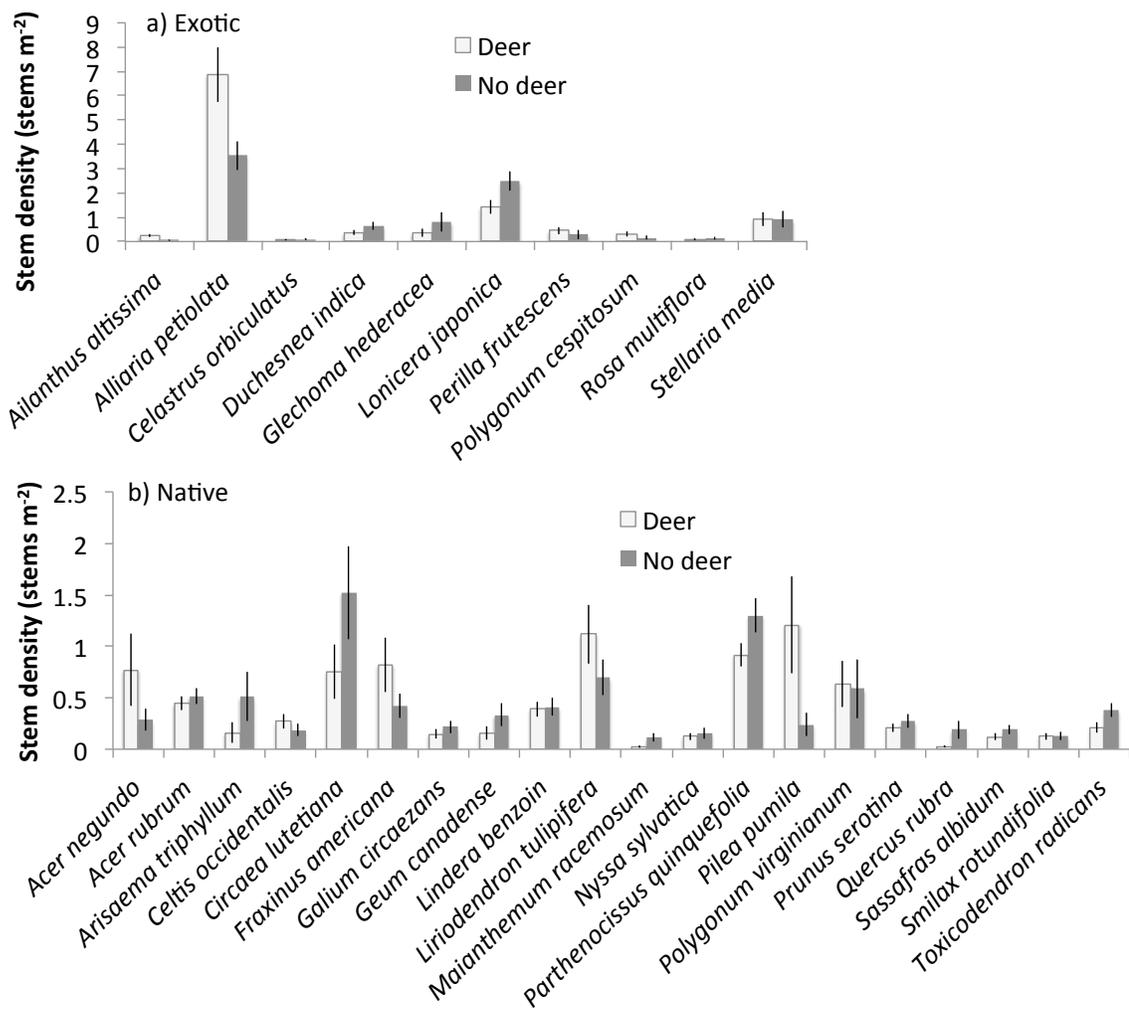
**Figure 1-A4.** Stem density of exotic, native, and all vegetation across the Northeastern US depending on deer presence or absence.



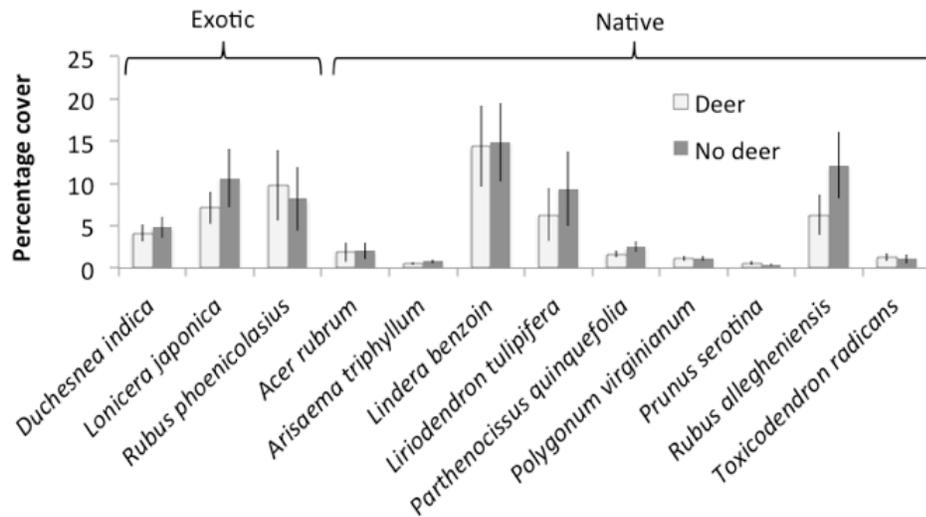
**Figure 1-A5.** Percentage cover of exotic, native, and all vegetation across the Northeastern US depending on deer presence or absence.



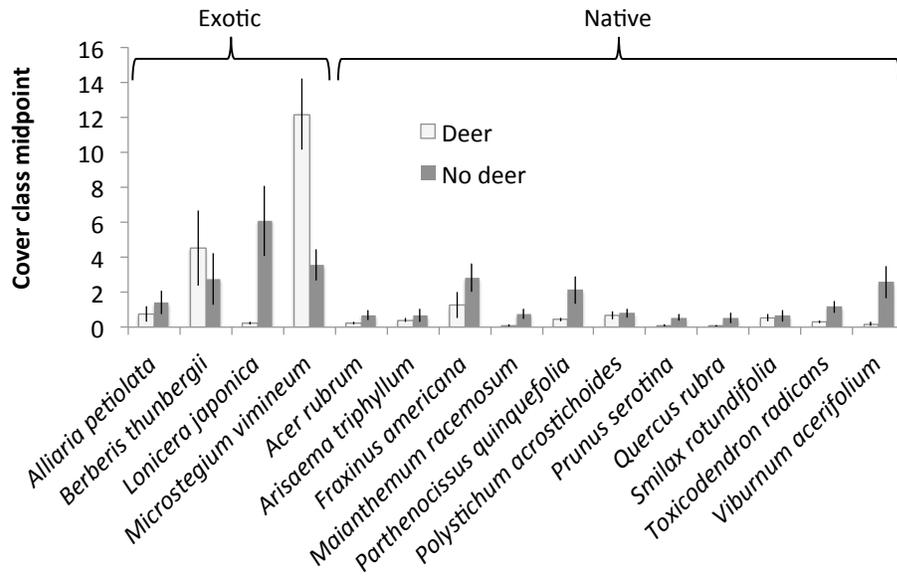
**Figure 1-A6.** Midpoint of cover class of exotic, native, and all vegetation across the Northeastern US depending on deer presence or absence.



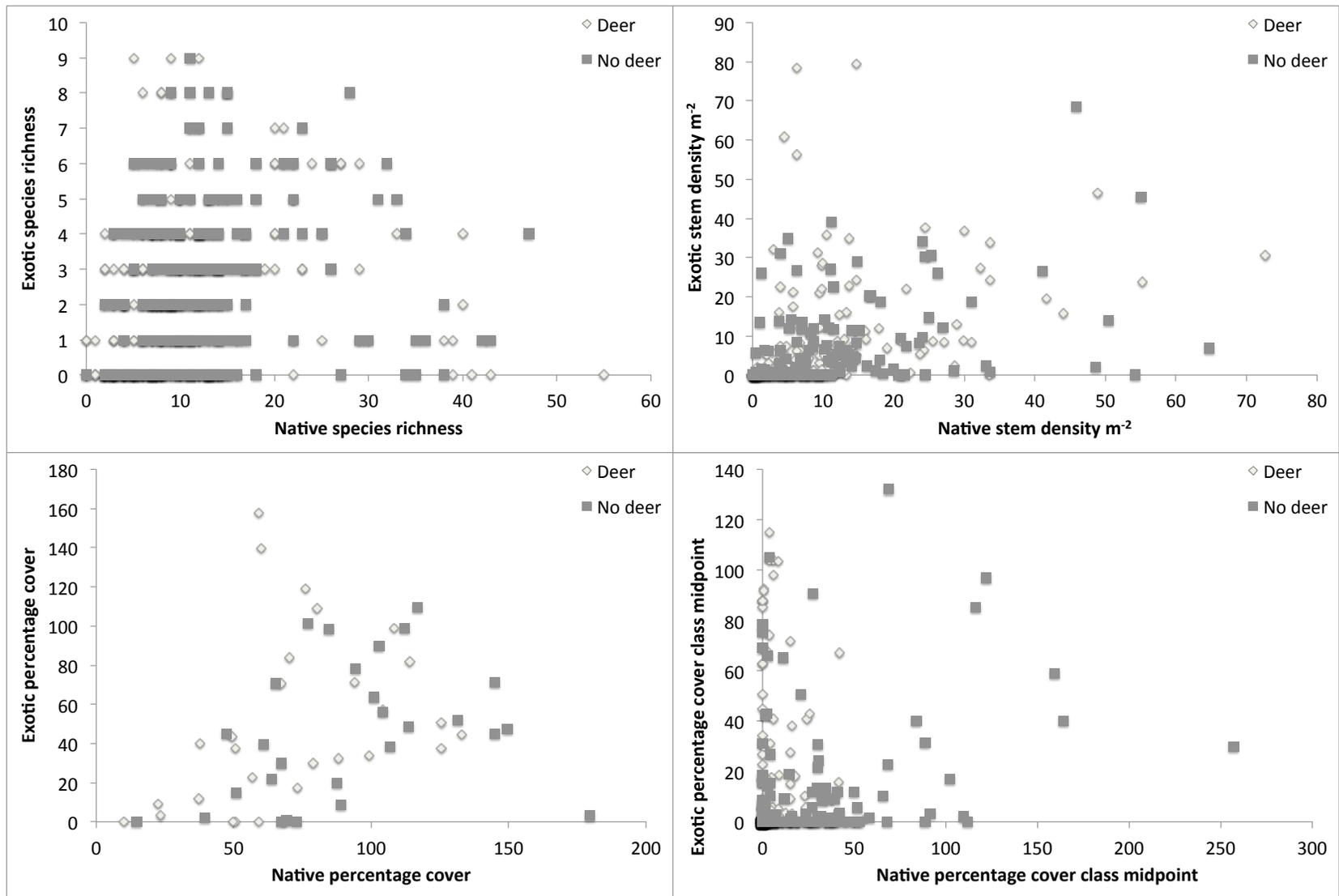
**Figure 1-A7.** Stem density of frequently occurring a) exotic and b) native plant species in the Northeastern US according to deer presence or absence.



**Figure 1-A8.** Percentage ground cover of frequently occurring exotic and native plant species in the Northeastern US according to deer presence or absence.



**Figure 1-A9.** Midpoint of percentage ground cover class of frequently occurring exotic and native plant species in the Northeastern US according to deer presence or absence.



**Figure 1-A10:** Relationships between exotic and native plant species richness and abundance in the Northeastern US with or without white-tailed deer.

## Chapter 2

### Deer strongly avoid consumption of some but not all invasive exotic plants

#### Abstract

Herbivore food preferences have major influences on plant community composition, yet little is known about herbivore selectivity for invasive exotic vs. native plants. I explored whether herbivore food selection occurs at the functional group level (native vs. exotic) or at the species level. White-tailed deer (*Odocoileus virginianus* Zimm.) preferences were simultaneously tested for eight invasive exotic plants and seven widespread and frequently occurring native plants in the Northeastern United States. Multiple-choice deer preference trials were conducted using captive does in spring, summer, and autumn (eight trials per season). Avoidance and preference were determined based on percentage biomass consumed, Vanderploeg and Scavia's electivity index, and video-recorded feeding behavior. Overall, more native than exotic biomass was consumed, but deer preferences varied strongly at the level of species as opposed to varying at the level of functional group. Results show consistent deer avoidance of several invasive exotic plants (*Alliaria petiolata* garlic mustard, *Berberis thunbergii* Japanese barberry, and *Microstegium vimineum* Japanese stiltgrass). Other invasive plants were highly preferred (e.g., *Celastrus orbiculatus* Oriental bittersweet, *Ligustrum vulgare* European privet, and *Lonicera morrowii* Morrow's bush honeysuckle). Deer preferences for these avoided and preferred species were consistent across season, but varied by season for other species (e.g., invasive plants *Elaeagnus umbellata* autumn olive and *Rosa multiflora* multiflora rose were less preferred in summer). Highest biomass consumption occurred in spring, particularly for native species. While avoidance-preference gradients were observed in both native and exotic plant groups, extremes

were greater among exotic species. Behavior data correlated with deer avoidance and consumption patterns, especially for invasive exotic plants. The number of deer bites per sniff provided the best indicator of biomass consumption and electivity index. This work has implications for understanding effects of deer selectivity on community-level dynamics, such as plant invasion. Deer are expected to facilitate the invasion of exotic plants that are relatively unpalatable due to preferential selection of palatable plants.

## Introduction

Biotic constraints such as herbivore food preferences influence the internal dynamics of plant community assembly and invasion (Drake 1990, Booth and Swanton 2002). However, whether historical coevolution between plants and herbivores affects ruminant food preferences has not been explored. In the deciduous forests of eastern North America, invasive exotic plants are increasing in number and spatial extent (Vitousek et al. 1997, Pimentel et al. 2005, Rauschert et al. 2009). Concurrently, white-tailed deer (*Odocoileus virginianus* Zimm.) populations have increased up to 15-fold since the early 1900s (McCabe and McCabe 1997, Rooney 2001), e.g., up to 84 deer km<sup>-2</sup> in Valley Forge National Historical Park (Tab. 1-A1), leading ecologists to question their role in facilitating plant invasion (Vavra et al. 2007). Literature on the subject is equivocal, with some studies showing increases of invasive exotic plants where deer are present (Eschtruth and Battles 2009, Kalisz et al 2014) and others showing the opposite (Rossell et al. 2007) or no effect (Bowers 1993, Levine et al. 2012). Deer are known to selectively browse at the individual and species levels (Augustine and McNaughton 1998), but selectivity across broader groups of native versus invasive exotic plants has not previously been tested.

Invasive plants and deer are often cited as pressing ecological and management concerns. Plant invasions can reduce floristic biodiversity (Chapin et al. 2000, Hejda et al. 2009), interfere

with ecosystem function (Ehrenfeld 2010), and are very costly to manage (Pimentel et al. 2005). The increasing deer densities reported in northeastern US forests are known to limit tree regeneration (Levine et al. 2012) and are a highly influential driver of vegetation change (Rooney et al. 2004, Nuttle et al. 2013), profoundly affecting plant community composition, structure, and function (Alverson et al. 1988, Augustine and McNaughton 1998, Côté et al. 2004).

Despite being considered generalist herbivores, deer selectively choose food plants and thereby strongly influence plant community composition. Selectivity reduces the abundance of the most palatable plant species and indirectly increases the abundance of less preferred or unpalatable species (Leopold et al. 1947, Horsley et al. 2003, Côté et al. 2004), which are thereby released from competition with their neighbors (Augustine and McNaughton 1998). Ultimately, herbivore selectivity affects plant community richness and evenness (Gill 1992a, Côté et al. 2004), causing a trophic cascade of effects within the food web (Nuttle et al. 2011) and altering ecosystem function (Hobbs 1996). For example, heavy deer browsing decreases the number of forest vegetation layers, which results in a corresponding decline in bird species diversity and abundance (MacArthur and MacArthur 1961, Nuttle et al. 2011, Chollet and Martin 2013). Selective browsing can also alter nutrient cycling, net primary productivity, and fire regimes (Hobbs 1996). Additionally, selective over-browsing has been shown to increase forest susceptibility to plant invasion (Vavra et al. 2007).

Deer choose among foods based on antifeedant properties and nutritional quality (Augustine and McNaughton 1998, Alm et al. 2002, Côté et al. 2004). Feeding behavior is learned through complex interactions among pre- and post-ingestion feedback cues via the senses, i.e., taste, smell, sight, and the viscera (Provenza 1995). Plant physical protection in the form of spines and thorns decreases herbivory (Campbell and Reece 2002). Additionally, structural compounds (e.g., lignin) and secondary compounds (e.g., tannins) are known to reduce palatability (Augustine and McNaughton 1998, Alm et al. 2002). Seasonal timing of herbivory is

known to affect deer preference due to differences in plant availability and quality and varying deer nutritional requirements throughout the year (Crawford 1982, Dumont et al. 2005, Estevez et al. 2010).

Native and exotic plants often differ in that exotics are more likely to have higher specific leaf area, lower canopy height, and smaller seeds (Ordonez et al. 2010), traits that are associated with fast-growing, earlier successional species that invest less in structure and defense and more in palatable foliage (Lambers and Poorter 1992, Ordonez et al. 2010). Indeed, preference tests suggest earlier successional species are more palatable to herbivores than later successional species (Cates and Orians 1975). All else being equal, these observations indicate that exotic plants should be more palatable to native herbivores. A meta-analysis of 63 herbivore exclusion experiments including over 100 exotic plant species and both vertebrate and invertebrate herbivores found that native herbivores preferentially browsed exotic compared to native plant species (Parker et al. 2006).

The work by Parker and colleagues (2006) supports the prominent biotic resistance hypothesis, which posits that interactions with native species, including natural enemies, limit the establishment or spread of exotic species (Elton 1958, Mitchell and Power 2003). However, examples of exotic species increasing despite the presence of abundant native generalists (Knight et al 2009, Eschtruth and Battles 2009) support the other prominent hypothesis in plant invasion, the enemy release hypothesis, positing that exotic plants succeed if they are introduced without coevolved enemies from their endemic range (Darwin 1859, Mitchell and Power 2003). This hypothesis also predicts that generalist enemies in the novel range will have a lesser impact on exotics compared to natives, either because exotics are more tolerant of generalist enemy attack or generalists prefer natives as food plants (Keane and Crawley 2002). Exotic plants might exhibit herbivore resistance or tolerance, which could provide a “natural enemy escape opportunity” (Johnstone 1986, Shea and Chesson 2002), thus enabling them to become invasive.

Indeed, in northeastern North America, exotic plants suffered less insect herbivory than native plants (Cappuccino and Carpenter 2005, Agrawal et al. 2005) and plants ranked as highly invasive sustained less herbivory than less invasive plants in the same region (Carpenter and Cappuccino 2005). Exotic plants were more likely to have novel secondary chemistry compared to native plants (Cappuccino and Arnason 2006, but see Lind and Parker 2010). While the invasion of some exotic plants might be effectively prevented as a result of native herbivore attack, others might become invasive due to native herbivore avoidance (Davis and Thompson 2000, Smith and Knapp 2001). Overall, herbivore food preferences appear important in determining exotic plant success.

Field research focused on the effects of white-tailed deer on exotic plants has varied by experiment and study site. Several field experiments have shown that the presence of white-tailed deer facilitates an increase in the abundance of invasive plants, e.g., *Microstegium vimineum* and *Alliaria petiolata* (Knight et al. 2009, Eschtruth and Battles 2009, Kalisz et al. 2014). Conversely, deer decreased the frequency of the invasive vine *Celastrus orbiculatus* in an interior forest (Rossell et al. 2007) and the abundance of the invasive shrub, *Rosa multiflora*, in one of two old-fields (Cadenasso et al. 2002). Last, other evidence from the field shows no general effect of deer on exotic plants (Bowers 1993, Levine et al. 2012). Deer feeding preferences might help explain this variability.

The goal of this research is to deepen understanding of deer preference patterns and to determine whether deer preferences vary for native and invasive exotic plants at the level of functional group (native vs. exotic) or at the level of species. Species level differences may resolve contradictory findings in selective herbivory. Even though invasive plants share characteristics such as rapid rates of growth and expansion, palatability is likely to vary strongly within functional groups, such as native/exotic status (Smith and Knapp 2001). To explore palatability, I used multiple choice feeding preference experiments. Controlled herbivore feeding

preference tests offer a direct way of determining base-level relationships between herbivores and plants and have been used widely as an ecological tool to explore producer-consumer interactions. They have been used to demonstrate increased palatability in earlier successional plants (Cates and Orians 1975) and to show that palatability can explain relative plant species abundance at the community level (Landa and Rabinowitz 1983). However, these methods have not been used to explore whether deer preferences vary for native and invasive exotic plants. Here, it was hypothesized that deer preferences would vary at the species level instead of by native/exotic status.

## **Methods**

Deer preference experiments were conducted at The Pennsylvania State University Deer Research Center in State College, Pennsylvania. The Center has a captive deer population of 75–100 white-tailed deer and provided an ideal venue for testing deer diet preference in a controlled setting, a 0.4 ha pen seeded with a mix of clovers and grasses (see Appendix for species list). Preference was assessed with feeding trials in late summer (August 2011), early autumn (September and October 2011), and in spring (May 2012) to account for variation in appetite and palatability of the vegetation. Feeding trials consisted of a cafeteria-style (multiple choice) preference test in which deer were offered a suite of 15 plant species (Tab. 2-1) simultaneously and were replicated 8 times in spring and summer and 7 times in autumn. A trial lasted 20 h, during which plant material was offered to the deer at 3 PM and uneaten plant material was collected at 11AM the following day.

The following criteria guided the selection of plant species included in the study. Commonly occurring, representative native and exotic plant species, spanning a range of expected preferences and growth habits, were selected (Tab. 2-1). Species were included based on

reports in the literature (Tab. 2-1), expert opinion, and access to plant material. All exotic species are considered moderately or highly invasive in the Eastern U.S. (USDA Forest Service 1998).

Eight mature (> two yrs), calm-tempered does without fawns were selected for the experiments. Because preliminary testing revealed deer feeding behavior was altered when individual animals were isolated in a pen, deer were randomly paired for each trial. Each deer was used in two trials per season, pairs were not repeated within each season, and sibling and mother-daughter pairings were avoided. Deer were offered their regular diet of commercial deer pellets (Record Rack Breeder, Cargill, Minneapolis, Minnesota 55440) and dry hay prior to and during preference trials. All plant species were presented to deer during a priming phase at least once within the three days before experimental trial to allow animals to become familiar with the plants and feeding stations. Deer were moved into the feeding trial pen after feeding stations were in place.

Within 6 hrs prior to each trial, representative samples of each species were collected from forest edge and understory habitats at the Russell E. Larson Agricultural Research Center at Rock Springs, Centre County, Pennsylvania. Plant stems were immediately placed in water, where they were kept throughout the feeding trial. Sampling was restricted to the range of deer reach (0–2 m above ground) and ~50 cm length stems were taken from the outer edge of individuals with canopies. The volume of plant material was kept as consistent as possible among species and across trials and seasons. However, due to different plant habits represented in the trials, e.g., grasses and woody species, variation across species occurred in the weights of leafy fresh matter offered [mean  $\pm$  standard error (SE) =  $87 \pm 3$ g; median = 78 g; range = 14–368 g]. Flowers, seeds, or fruits were included if present and samples were collected from at least four individual plants. Plant material for each of the 15 plant species were bundled and placed in a 13 L, 30 cm diameter bucket filled with water. Each bucket was covered with a lid with a 3 cm hole in the center and two layers of mesh wire on the underside used to secure stems in an upright

position. The 15 buckets were arranged ~50 cm apart from one another over an area spanning ~4 m by 4 m.

Fresh, wet weights were determined for the plant samples immediately before and following each feeding trial. After trials, woody plant material was separated, weighed, and then excluded from analysis. Species-specific water loss was determined using a set of control plant samples collected, weighed, and treated the same as preference test plant material only in the absence of deer (Manly 1993). Biomass intake by deer (i.e., consumption) was assessed by calculating the percentage of non-woody biomass consumed during trials after accounting for species-specific water loss.

Vanderploeg and Scavia's electivity index ( $E^*$ ) (Vanderploeg and Scavia 1979) was also used to determine deer preference. The index provides a measure of deer perception of a species' value as a function of its abundance as well as the abundance of the other species offered (Manly et al. 1993) and was calculated as follows:

$$E^*_i = \frac{W_i - \frac{1}{n}}{W_i + \frac{1}{n}}$$
$$W_i = \frac{r_i / p_i}{\sum_i^n \frac{r_i}{p_i}}$$

where  $W_i$  is the selectivity coefficient,  $n$  is the number of species in the trial,  $r_i$  is the proportion of species  $i$  consumed of all biomass consumed, and  $p_i$  is the proportion of species  $i$  in the total biomass offered. The  $E^*$  varies between “-1” (never used) to “+1” (exclusively used), so a positive value indicates preference and a negative value indicates avoidance. A value of zero indicates random feeding, i.e., intake of that species was in similar proportion to the proportion offered. I used the non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952) to determine the rank order of preference for species within each season (Lechowicz 1982).

Each trial was recorded using a motion-sensor trail camera (Trophy Cam, Bushnell Corporation, Overland Park, Kansas 66214), which records color video during the day and infrared video during the night. Sniffing and biting events were quantified using JWatcher (Blumstein and Daniel 2007). Sniffing occurred when a deer smelled a plant, while biting entailed consumption of the plant. An event was considered one initiation of a browsing behavior, thus event duration varied. When a deer pulled its head away from the plant, the event ended; if the deer began sniffing or biting the same plant again, it was recorded as a new event. The biting to sniffing ratio, i.e., bites per sniff, was calculated by dividing the number of bite events by the number of sniffing events for each species within a trial.

Linear mixed effect analysis of variance (ANOVA) was used to analyze percentage biomass intake and behavior events. The fixed effects were native/exotic status, species nested within native/exotic status (species[native/exotic]), season, and their interactions and the random effect was deer pair (i.e., trial). An arc-sine square-root transformation of percentage biomass consumed and square-root transformations of behavior events were necessary to satisfy statistical assumptions of normality and homogeneity of residuals. Because *M. vimineum* was too small to include in the spring trials, I performed two sets of analyses, either including data from all seasons but excluding *M. vimineum* or including data from summer and autumn but excluding spring data. Linear regression was used to test for correlations between sniffing and biting events and between those behavior events, as well as bites per sniff, and biomass consumption and electivity index. JMP 10.0 (SAS 2012) was used for statistical analyses. Means are presented  $\pm$  standard error (SE).

## Results

### Biomass consumption

Across all plant species and seasons, deer consumed more native ( $67 \pm 4$  g;  $66 \pm 2\%$ ) than invasive exotic plant biomass ( $53 \pm 4$  g;  $56 \pm 3\%$ ) (Fig. 2-1; Tab. 2-2). However, an interaction between plant species and season was detected ( $P < 0.0001$ ). Overall, deer preference patterns varied strongly according to plant species identity instead of by plant native/exotic status, supporting the hypothesis tested in this work. Deer consistently avoided consumption of the invasive exotic plants *Alliaria petiolata*, *Berberis thunbergii*, and *Microstegium vimineum* across all seasons. In contrast, deer consumption and therefore preference of several invasive exotic species was consistently high across seasons (e.g. *Celastrus orbiculatus* and shrubs *Ligustrum vulgare* and *Lonicera morrowii*). Consumption of some species varied by season, e.g., invasive exotic plants *Elaeagnus umbellata* and *Rosa multiflora* were less preferred in summer, consumption of native plants *Dennstaedtia punctilobula* and *Rubus allegheniensis* was higher in spring, and consumption of native plants *Lindera benzoin* and *Rhus typhina* was lower in summer (Fig. 2-1). Overall, deer consumed the most biomass in the spring ( $90 \pm 6$  g;  $73 \pm 3\%$ ), less in autumn ( $54 \pm 4$  g;  $60 \pm 3\%$ ), and least in the summer ( $36 \pm 3$  g;  $50 \pm 3\%$ ) (Fig. 2-1). Because it was only beginning to germinate, *M. vimineum* was not included in the spring trials. This species had the lowest mean biomass consumption compared to other species across summer and autumn trials. Analyses using summer and autumn data showed very low deer preference for *M. vimineum* (Tab. 2-2).

## Electivity index and preference

Overall, deer showed stronger avoidance of invasive exotic species ( $-0.17 \pm 0.03$  electivity index,  $E^*$ ) than of native species ( $-0.04 \pm 0.03 E^*$ ). Deer especially preferred native species in the spring (Fig. 2-2). However, more pronounced preference differences were seen at the species level. Deer avoided invasive plants with known defenses, including *A. petiolata* and *B. thunbergii* (Tab. 2-1), and also avoided *M. vimineum*. Deer preferred the invasive vine *C. orbiculatus* and shrubs *L. vulgare* and *L. morrowii*. Deer showed high preference for the native tree *Acer rubrum* and for the native vine *Parthenocissus quinquefolia*. Among natives, lowest preference was shown for the chemically-defended fern *D. punctilobula* and the physically-defended subshrub *R. allegheniensis* (Fig. 2-2; Tab. 2-1). In the spring, deer preferred the native tree *Quercus rubra*, shrub *R. typhina*, and subshrub *R. allegheniensis* significantly more than in summer or autumn. The shrub *L. benzoin* was least preferred in the summer (Figs. 2-1 and 2-2).

## Deer behavior and biomass consumption

The number of biting events varied by the interaction between species and season. However, sniffing events only varied among species (Tab. 2-2). Biting events were positively correlated with sniffing events among invasive exotic plants (bites =  $2.10 + 0.950 \cdot \text{sniffs}$ ;  $R^2 = 0.40$ ) and native plants (bites =  $2.0 + 0.79 \cdot \text{sniffs}$ ;  $R^2 = 0.44$ ). Most importantly, the selective patterns of deer biomass consumption and electivity were positively correlated with deer feeding behaviors. These relationships were only evident among exotic species and were observed in all seasons except for sniffing events in the summer (Fig. 2-3). While the native species relationships were mainly positive, they were not significant. The number of biting events was a better predictor of biomass consumed and electivity than the number of sniffing events for exotic

species (Fig. 2-3). However, the number of bites per sniff was the best overall behavioral predictor of biomass consumption and electivity (Fig. 2-4). Exotic and native species with higher percentage biomass consumed and higher electivity had relatively more bites per sniff than the less-consumed species. Simply put, if the exotic plant material was palatable to the deer, more biomass was consumed per investigative sniff. Plant species for which the number of bites per sniff was above one were most preferred (Fig. 2-5), while a bite to sniff ratio below one indicated avoidance. Observations of deer sniffing and biting behavior could provide a good indication of preference when quantifying biomass consumption is prohibitive.

### **Discussion**

White-tailed deer consumed more native plant biomass than invasive exotic biomass, supporting the enemy release hypothesis of plant invasion (Keane and Crawley 2002, Carpenter and Cappuccino 2005). However, large species-level differences across native/exotic status were observed and it appears that a small subset of unpalatable invasive exotic plants drove this avoidance. Deer preferences varied for native and invasive exotic plants at the species level, supporting the hypothesis tested in this work. Instead, regardless of native/exotic status, deer limited their intake of plants with known defenses in favor of those that were less well defended (Tab. 2-1).

Generalist herbivores are expected to respond to plants at the trait level (Augustine and McNaughton 1998), suggesting that the dividing line between native and exotic species might be irrelevant from the generalist consumer perspective. Indeed, chemical extracts from 19 invasive plants were found to be no different overall in deterring a generalist insect herbivore than biochemistry from 21 native plants; deterrence varied widely at the species level (Lind and Parker

2010). Likewise, results from the preference trials described here point to the importance of plant species rather than broad groupings of native versus exotic plants in plant-herbivore interactions.

Strong deer avoidance of *Alliaria petiolata*, *Berberis thunbergii*, and *Microstegium vimineum* observed in this study is correlated with the success of these plants in eastern forests of North America. Success of invasive plants has been linked to reduced herbivory (Cappuccino and Carpenter 2005, Carpenter and Cappuccino 2005) and abundant deer may be facilitating their success by reducing competition from more palatable plant neighbors, including many native plants. Anti-herbivore traits, such as novel chemistry or morphological adaptations, are known to occur in many of the least preferred plants in experiments presented here (Tab. 2-1). Secondary defense compounds found in *A. petiolata* (e.g., glucosinolates, trypsin inhibitor, and peroxidase) are known to deter herbivores (Stowe 1998, Cipollini 2002). Additionally, this plant achieves greater abundance in the presence of deer (Knight et al. 2009, Kalisz et al. 2014) and rarely experiences growth- or fitness-reducing effects related to herbivory (Rosenthal and Kotanen 1994, Strauss and Agrawal 1999). The sharp spines of *B. thunbergii* could explain the limited consumption of this species (Campbell and Reece 2002), as could deterrent chemistry, which also has been found to reduce feeding of this species by a generalist caterpillar (Lind and Parker 2010). Although *M. vimineum* has been observed to lack natural enemies in the invaded range (Rauschert et al. 2009), specific anti-herbivore traits are unknown for this species.

Just as the deer avoided certain invasive exotic species, deer also avoided the native fern *Dennstaedtia punctilobula*, a species predicted to be unpalatable (Tab. 2-1). In many forest understories across the Northeastern U.S., *D. punctilobula* is considered an invasive native plant (de la Cretaz and Kelty 1999) and deer are already known to play a key role in its success. The fern increases in abundance as deer pressure increases (Tilghman 1989), because deer consume co-occurring species and avoid the fern. Ferns often contain abundant secondary phenolic compounds and *D. punctilobula* contains the herbivore-deterrent compound coumarin (Link

1959, Bohm and Tryon 1967). Ferns are an ancient and globally widespread plant group (Campbell and Reece 2002) and many species are rarely damaged by deer (Perdomo et al. 2004). Overall, whether exotic or native, plant unpalatability might facilitate exotic plant invasion or native plant dominance.

Herbivory is a strong selective force acting on the internal dynamics of plant community interactions and favors species that effectively avoid, resist, or tolerate it. Plants avoid deer browsing by growing in places inaccessible to deer (Comisky et al. 2005) or by growing when deer pressure is low. In this research, *M. vimineum* had not yet emerged in the spring, which was the season when deer consumed the most biomass, suggesting a partial temporal avoidance of this species. Younger plant tissue is typically more palatable (Gill 1992b) due to higher digestible energy and nitrogen (Oh et al. 1970, Bryant et al. 1983) and due to immature defenses (Oh et al. 1970), which might explain the elevated biomass consumption observed in the spring. Next, resistance to herbivory is attained via plant chemical and physical defenses (Campbell and Reece 2002), as in *A. petiolata* and *B. thunbergii*, respectively. Last, herbivore tolerance is achieved by rapid re-growth or compensation for lost biomass following herbivory (Hawkes and Sullivan 2001), traits that might facilitate the success of the palatable invasive exotic plants tested.

Although anti-herbivore characteristics likely contribute to plant invasiveness, other plant characteristics and habitat conditions are known to promote plant invasion as well, and plants often become invasive for multiple reasons (Cappuccino and Arnason 2006). For instance, *A. petiolata* not only has secondary compounds that influence aboveground interactions, but also releases root exudates that reduce the germination of other species (Prati and Bossdorf 2004). Additionally, *B. thunbergii* is known to alter soil functions such as increasing nitrification rates (Ehrenfeld et al. 2001). Also, when intense deer browsing is combined with overstory thinning, the native fern *D. punctilobula* limits tree seedling establishment (de la Cretaz and Kelty 1999, Pinchot 2011). Last, plant species that have a mutualistic relationship with herbivores, such as

those possessing fleshy fruits, are more likely to become invasive (Rejmánek 1996). In this research, several of the invasive exotic plants were as much or more preferred than many of the natives, including *C. orbiculatus*, *L. morrowii*, and *L. vulgare*, and they all reproduce and disperse via a fleshy fruit. High biomass consumption typically decreases fitness, yet, if combined with animal-dispersed fruit and rapid regrowth, such species could be invasive in a landscape with abundant deer (Richardson et al. 2000, Buckley et al. 2006).

### **Deer feeding behavior**

Deer feeding behaviors were strongly correlated, suggesting that, in general, sniffing investigation led to biting (i.e., eating) and therefore consumption. The stronger relationship between biomass consumption or electivity and biting vs. sniffing implies that deer might sniff and then elect not to eat. Furthermore, a low number of sniffs for the unpalatable species demonstrates that deer learn to avoid such plants even before sniffing, i.e., by visual cues.

Animal- or plant-based changes could explain observed electivity differences across seasons. Physiological needs of deer vary across seasons (Crawford 1982, Dumont et al. 2005, Estevez et al. 2010) and plants also change throughout the year according to species' life cycles. For example, woody species such as the native tree *Quercus rubra* and shrub *R. allegheniensis* became less palatable during the growing season and this could be a result of increasing lignin and/or starch content. These compounds are known to be less palatable because they have lower nutritional value (Augustine and McNaughton 1998, Alm et al. 2002).

Food selection is considered an innate behavior in white-tailed deer and is expected to be quite similar among wild and captive individuals (Spalinger et al. 1997). However, differences might occur because the regular diet of captive deer is limited (e.g., the deer in this study are typically fed food pellets, dried hay, and species growing in the penned environment). While wild

deer use different plants to meet nutritional requirements, this is more difficult for captive deer (Spalinger et al. 1997). Thus when captive deer are offered fresh plant biomass, some food consumption might be attributed to satisfying requirements particular to the conditions of their captivity. For example, even though I expected *L. vulgare* and *Acer rubrum* to be unpalatable, perhaps they contained a nutritional requirement that the captive deer were lacking, causing the deer to consume more of these species in captivity than in the wild (Abrams 1998 and references therein).

## **Conclusions**

Together, biomass consumption and behavior data indicate that deer preference depends more on species and season than on native or invasive exotic status. These results imply that a history of coevolution between plants and herbivores does not affect generalist herbivore preferences. However, differences in deer preference within the exotic plant group were greater than those observed within the native plant group. Of the eight invasive exotic species studied, three were consistently avoided while three were consistently preferred across seasons. The high level of preference for fleshy-fruited species could have important implications for invasive plant spread. In contrast, of the seven native species, only one was avoided and only one was consistently preferred across seasons (Fig. 2-2). Similarly, deer sniffing and biting behavior was strongly positively correlated with biomass consumption and electivity of exotic species, but this pattern of association was not observed for native species (Fig. 2-3). The number of bites a deer takes provides a good estimate of how much deer consume of exotic species, but not for native species. However, the number of bites per sniff appears to be an appropriate predictor of biomass consumption and electivity for both exotic and native species.

This work has implications for understanding the effect of deer selectivity on community-level dynamics (i.e., the changing proportion of exotic plants under high deer numbers) in field settings. The results also have implications for understanding the relative patterns of native and exotic plants through evolutionary time. Within the Northeastern US, deer are several times more abundant now than during the evolutionary histories of the native plants (McCabe and McCabe 1997), thus low deer densities provided the backdrop for native plant evolution. The increase in deer densities might help explain native plant declines as well as why certain (i.e., unpalatable) exotic plants have become invasive in the region.

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**Table 2-1:** Plant species used in multiple-choice feeding preference trials for white-tailed deer conducted at the Penn State Deer Research Center. In addition to species characteristics, ranked palatability results from deer preference trials are reported for each season (1=most preferred; 15=least preferred).

Species <sup>a</sup> (Family)	Habit <sup>a</sup>	Known plant defense/s <sup>a</sup>	Palatable to browse animals <sup>a</sup>	Woody plant resprout ability <sup>a</sup>	Predicted relative palatability <sup>b</sup>	Reference/s for predicted palatability	Ranked preference trial palatability (sp, su, au) <sup>c</sup>
<b>Exotic species</b>							
<i>Alliaria petiolata</i> (M. Bieb) Cavara & Grande (Brassicaceae)	Forb	glucosinolates*	low*	NA <sup>d</sup>	u	Knight et al. 2009, Eschtruth and Battles 2009	14, 13, 14
<i>Berberis thunbergii</i> DC (Berberidaceae)	Shrub	spines; toxicity*	low	yes	u	Eschtruth and Battles 2009, Lind and Parker 2010	13, 15, 13
<i>Celastrus orbiculatus</i> Thunb. (Celastraceae)	Vine	none	low	no	p	Rossell et al. 2007	6, 2, 2
<i>Elaeagnus umbellata</i> Thunb. (Elaeagnaceae)	Shrub	none	medium	yes	p	Williams and Ward 2006, Knapp et al. 2008	4, 10, 5
<i>Ligustrum vulgare</i> L. (Oleaceae)	Shrub	none	low	yes	u	Perdomo et al. 2004	5, 3, 3
<i>Lonicera morrowii</i> A. Gray (Caprifoliaceae)	Shrub	none ( <i>L. maackii</i> )	low ( <i>L. maackii</i> )	yes ( <i>L. maackii</i> )	p	Averill dissertation chapter 1	7, 4, 4
<i>Microstegium vimineum</i> (Trin.) A. Camus (Poaceae)	Grass	none*	low*	NA	u	Averill dissertation chapter 1, Rauschert et al. 2009	NA, 14, 15
<i>Rosa multiflora</i> Thunb. (Rosaceae)	Shrub	prickles*	medium*	yes*	p	Averill dissertation chapter 1, Cadenasso et al. 2002	11, 8, 6

<sup>a</sup> Taxonomy and plant characteristics according to the USDA Plants Database (<http://plants.usda.gov/>; (USDA, NRCS 2012). Asterisks indicate data are from references listed. For *L. morrowii* and *R. typhina*, data were only available for the closely related congener listed. NA indicates information was not available.

<sup>b</sup> Predicted palatability based on previous research, p = palatable; u = unpalatable.

<sup>c</sup> Results from feeding preference trials based on the electivity index, E\*, for spring (sp), summer (su), and autumn (au).

<sup>d</sup> NA = not applicable for herbaceous plants

**Table 2-1:** (Continued)

Species <sup>a</sup> (Family)	Habit <sup>a</sup>	Known plant defense/s <sup>a</sup>	Palatable to browse animals <sup>a</sup>	Woody plant resprout ability <sup>a</sup>	Predicted relative palatability <sup>b</sup>	Reference/s for predicted palatability	Ranked preference trial palatability (sp, su, au) <sup>c</sup>
<b>Native species</b>							
<i>Acer rubrum</i> L. (Aceraceae)	Tree	slight toxicity	medium	yes	u	Averill dissertation chapter 1, Horsley et al. 2003	8, 1, 1
<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore (Dennstaedtiaceae)	Fern	coumarin*	low*	NA	u	Bohm et al. 1967, de la Cretaz and Kelty 1999	12, 12, 12
<i>Lindera benzoin</i> (L.) Blume (Lauraceae)	Shrub	none	medium	yes	p	Averill dissertation chapter 1	10, 9, 7
<i>Parthenocissus quinquefolia</i> (L.) Planch. (Vitaceae)	Vine	none	medium	yes	p	Averill dissertation chapter 1, Perdomo et al. 2004	3, 5, 8
∞ <i>Quercus rubra</i> L. (Fagaceae)	Tree	tannins*	medium	yes	p	Averill dissertation chapter 1, Campbell et al. 2006	1, 6, 9
<i>Rhus typhina</i> L. (Anacardiaceae)	Shrub	none ( <i>R. glabra</i> )	low ( <i>R. glabra</i> )	yes ( <i>R. glabra</i> )	p	Perdomo et al. 2004	2, 7, 10
<i>Rubus allegheniensis</i> Porter (Rosaceae)	Subshrub	prickles*	high	yes	p	Horsley and Marquis 1983, Crimmins et al. 2010	9, 11, 11

<sup>a</sup> Taxonomy and plant characteristics according to the USDA Plants Database (<http://plants.usda.gov/>; (USDA, NRCS 2012). Asterisks indicate data are from references listed. For *L. morrowii* and *R. typhina*, data were only available for the closely related congener listed. NA indicates information was not available.

<sup>b</sup> Predicted palatability based on previous research, p = palatable; u = unpalatable.

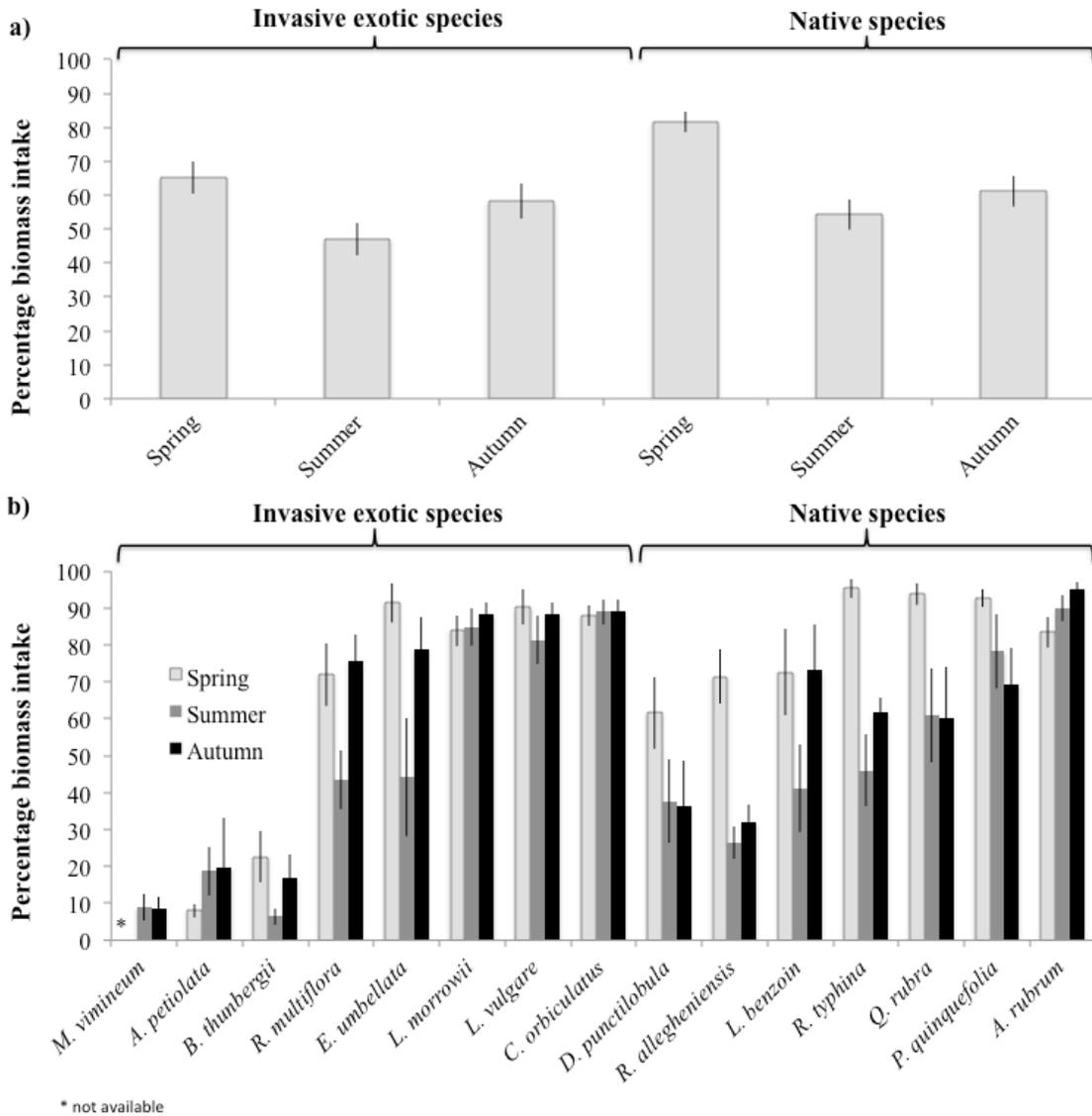
<sup>c</sup> Results from feeding preference trials based on the electivity index, E\*, for spring (sp), summer (su), and autumn (au).

<sup>d</sup> NA = not applicable for herbaceous plants

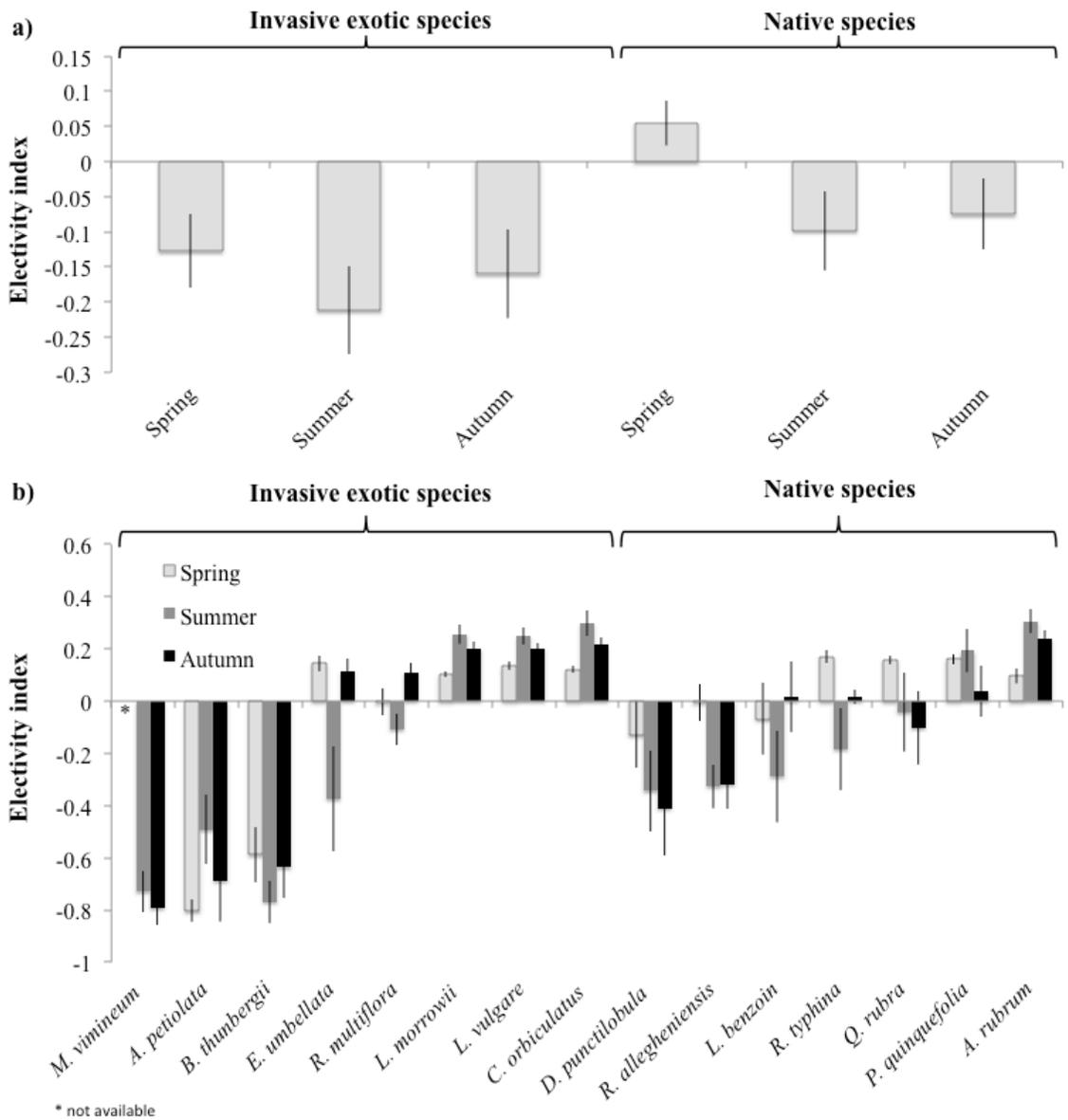
**Table 2-2:** Mixed model ANOVA results for effects of plant species, their native/exotic status (N/E status), and season on several measures of deer preference with (w/) and without (w/o) *Microstegium vimineum* (*M.v.*), which was not available in the spring. Results are from 24 one-day/one-night multiple choice preference trials for white-tailed deer using a suite of eight invasive exotic and seven native species frequently occurring across the Northeastern United States. Model F and P values are shown<sup>a</sup>. Trial ID (i.e., deer pair) was the random effect.

	% biomass consumption (w/o <i>M.v.</i> )		% biomass consumption (w/ <i>M.v.</i> )		Sniffing events (w/o <i>M.v.</i> )		Sniffing events (w/ <i>M.v.</i> )		Biting events (w/o <i>M.v.</i> )		Biting events (w/ <i>M.v.</i> )	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
N/E status	5.3 <sub>1,258</sub>	<b>0.02</b>	4.9 <sub>1,180</sub>	<b>0.03</b>	1.1 <sub>1,257</sub>	0.3	2.9 <sub>1,179</sub>	0.09	0.99 <sub>1,257</sub>	0.3	0.19 <sub>1,179</sub>	0.7
Species[N/E status]	40 <sub>12,258</sub>	<b>&lt;0.0001</b>	30 <sub>13,180</sub>	<b>&lt;0.0001</b>	7.0 <sub>12,257</sub>	<b>&lt;0.0001</b>	5.7 <sub>13,179</sub>	<b>&lt;0.0001</b>	39 <sub>12,257</sub>	<b>&lt;0.0001</b>	27 <sub>13,179</sub>	<b>&lt;0.0001</b>
Season	4.4 <sub>2,20</sub>	<b>0.03</b>	1.5 <sub>1,13</sub>	0.2	2.8 <sub>2,20</sub>	0.08	2.3 <sub>1,13</sub>	0.1	4.4 <sub>2,20</sub>	<b>0.02</b>	3.9 <sub>1,13</sub>	0.07
Species[N/E status] * Season	3.5 <sub>24,258</sub>	<b>&lt;0.0001</b>	2.1 <sub>13,180</sub>	<b>0.01</b>	1.3 <sub>24,257</sub>	0.2	1.5 <sub>13,179</sub>	0.1	1.9 <sub>24,257</sub>	<b>0.007</b>	1.1 <sub>13,179</sub>	0.3
N/E status * Season	6.3 <sub>2,258</sub>	<b>0.02</b>	0.49 <sub>1,180</sub>	0.5	0.60 <sub>2,257</sub>	0.5	1.8 <sub>1,179</sub>	0.2	3.7 <sub>2,257</sub>	<b>0.03</b>	0.15 <sub>1,179</sub>	0.7

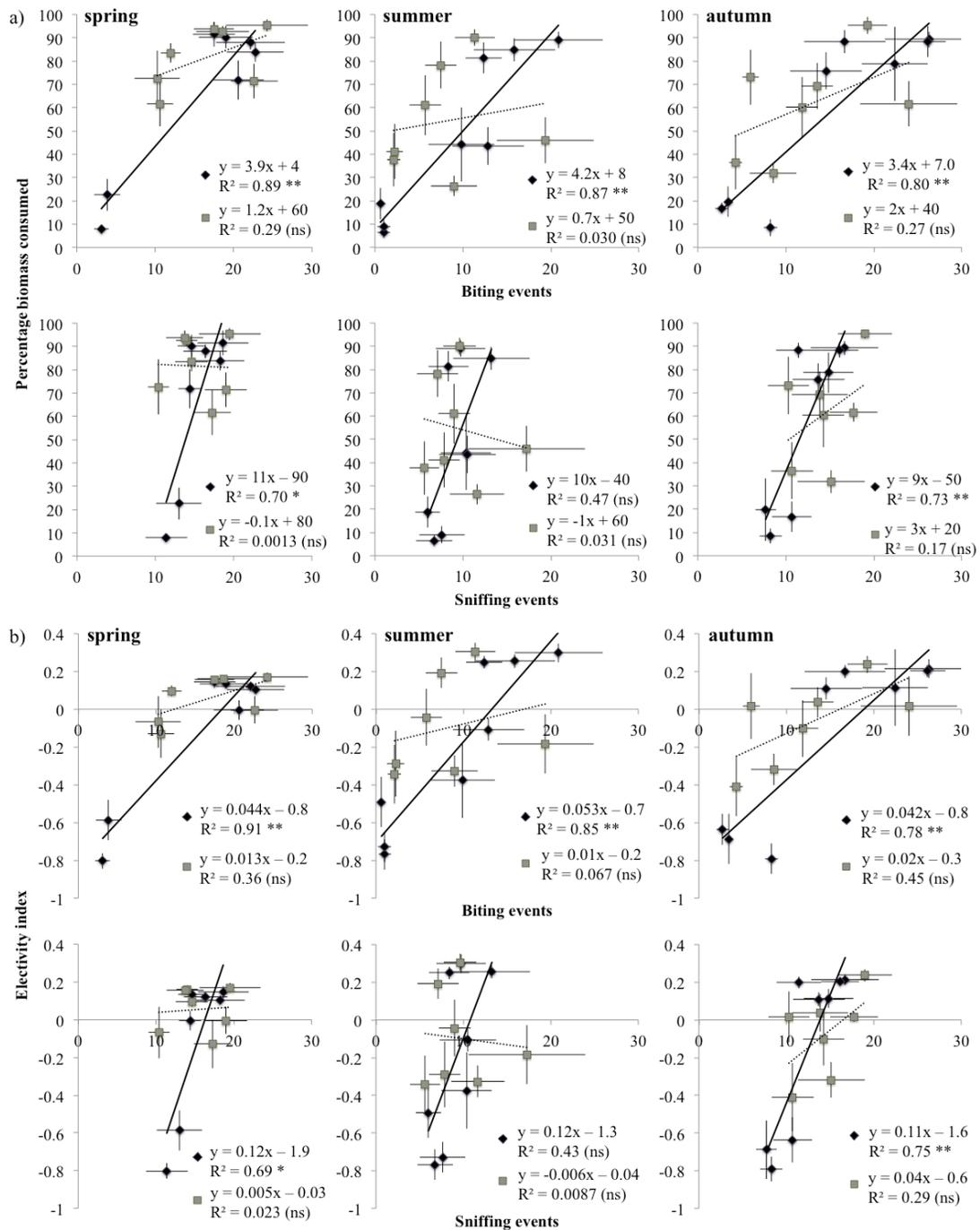
<sup>a</sup> F values are reported with subscript numerator and denominator degrees of freedom. P values are bolded if significant at  $\alpha = 0.05$ .



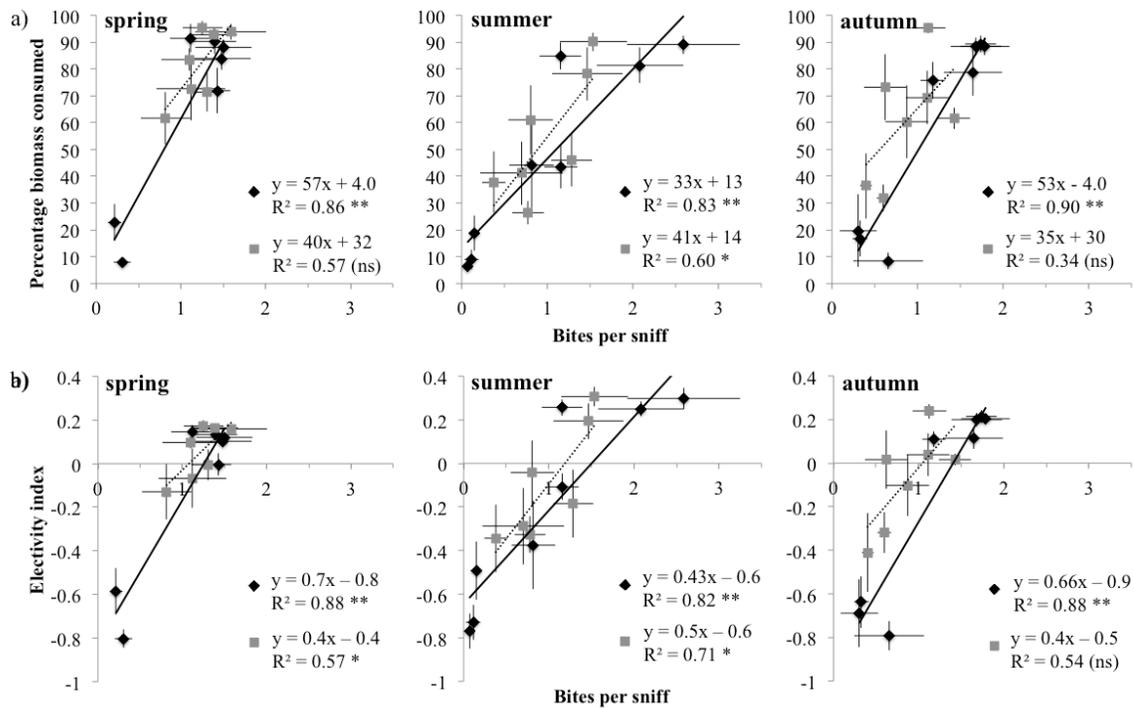
**Figure 2-1:** Leaf biomass consumed ( $\pm 1$  SE) by adult white-tailed deer in three seasons during 24 one-day/one-night multiple-choice preference trials conducted at the Penn State Deer Research Center a) pooled across species and b) by species. Plant species occur widely across the Northeastern United States.



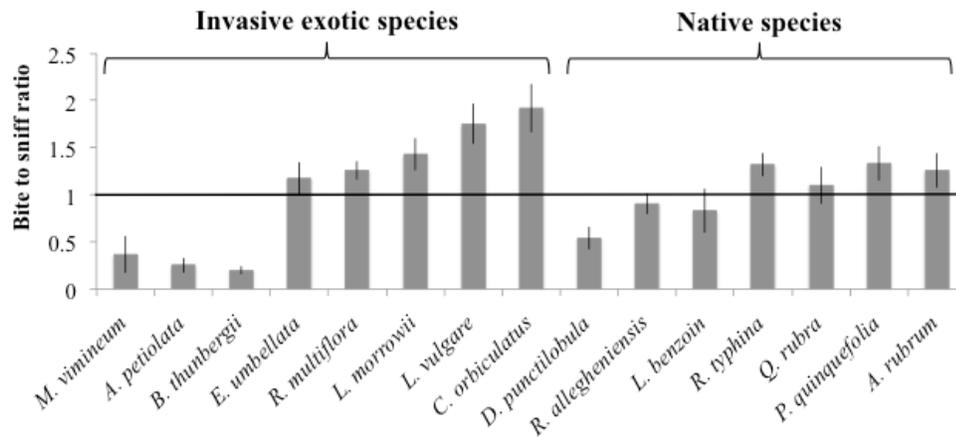
**Figure 2-2:** Relative preferences of adult white-tailed deer for native and exotic plant species across three seasons a) pooled across species and b) by species based on 24 one-day/one-night multiple-choice preference trials conducted at the Penn State Deer Research Center. The electivity index ranges from “-1” (strong avoidance) to “+1” (high preference) and a value of zero indicates random feeding.



**Figure 2-3:** Relationships between browsing behaviors and a) non-woody biomass consumed and b) electivity index exhibited by white-tailed deer in three seasons based on 24 multiple-choice deer preference trials conducted at the Penn State Deer Research Center. Observations represent eight exotic (black diamonds) and seven native (gray squares) species abundant across the Northeastern United States. Linear regression relationships are shown by species groups and are labeled as significant at levels,  $\alpha = 0.0001$  (\*\*\*) ,  $\alpha = 0.01$  (\*\*),  $\alpha = 0.05$  (\*) or as not significant (ns).



**Figure 2-4:** The ratio of biting to sniffing events (i.e., bites per sniff) correlates strongly to a) biomass consumed by deer and to b) electivity index based on 24 one-day/one-night multiple-choice deer preference trials conducted at the Penn State Deer Research Center. Observations represent eight exotic species (black diamonds) and seven native species (gray squares). Linear regression relationships are shown for native and exotic species groups and are labeled as significant at levels,  $\alpha = 0.0001$  (\*\*\*),  $\alpha = 0.01$  (\*\*),  $\alpha = 0.05$  (\*) or as not significant (ns).



**Figure 2-5:** Ratio of white-tailed deer biting events to sniffing events during 24 one-day/one-night multiple-choice preference trials using a suite of eight exotic and seven native plant species that frequently occur across the Northeastern United States. The 1:1 line provides a reference point for equal numbers of biting and sniffing events.

## Appendix

**Table 2-A1:** Species sown in May 2011 at the Penn State Deer Research Center paddock later used for white-tailed deer preference experiments.

Common name	Scientific name	Percentage
alsike clover	<i>Trifolium hybridum</i> L.	20.67
"Climax" timothy	<i>Phleum pratense</i> L.	17.94
perennial ryegrass	<i>Lolium perenne</i> L.	17.93
orchardgrass	<i>Dactylis glomerata</i> L.	16.49
annual ryegrass	<i>Lolium multiflorum</i> Lam.	12.74
white clover	<i>Trifolium repens</i> L.	4.94
birdsfoot trefoil	<i>Lotus corniculatus</i> L.	4.1
other crop seed		3.0
inert matter		1.94
weed seed		0.25

### Chapter 3

## **Effects of native deer, landscape structure and composition, and native plant diversity on plant invasion across the Northeastern United States**

### **Abstract**

Plant communities are shaped by a variety of factors including geographic constraints, abiotic, and biotic factors. In plant invasion research, however, few studies have compared the importance of multiple factors simultaneously. In the Northeastern United States, the highly abundant native white tailed deer (*Odocoileus virginianus* Zimm.), and landscape fragmentation are known to facilitate plant invasion. In contrast, biologically diverse native communities are broadly expected to limit invasion (sensu biotic resistance). In this multiscale work, site-level density of white-tailed deer, several landscape fragmentation metrics, which measured both habitat loss and the breaking apart of forested habitat, and plot-level native plant diversity were tested for their roles in forest understory community invasion. In pooled analyses of floristic community data from 24 widely distributed sites with paired unfenced (deer) and fenced (no deer) plots in the Northeastern US, a series of nonparametric and parametric, multivariate and univariate statistics were used to elucidate the effects of multiple factors and their interactions on several measures of plant invasion. Deer, landscape structure and composition, and native species richness all affected exotic plant invasion. The perimeter to area ratio of landscape patches was a highly important factor in predicting plant invasion patterns. Overall, landscape fragmentation and developed cover were associated with increased plant invasion, although several interactions were detected among deer presence, native plant diversity, and landscape predictor variables. Exotic plant richness was positively correlated with native species diversity, but some evidence

was found for native diversity limiting plant invasion in non-fragmented landscapes. When data were subsetted according to fencing treatment, the percentage of exotic plant species was greater where deer density was higher (unfenced plots) and tended to be lower where deer were excluded for a longer duration of time (fenced plots). Overall, this work suggests that to fully understand the factors that influence plant invasion, the context of deer abundance, surrounding landscape structure and composition, and native plant species diversity must be considered.

### **Introduction**

Accounting for the range of factors that influence plant invasion is valuable for understanding plant community assembly and for managing plant communities knowledgeably. Numerous theoretical models and reviews suggest that multiple factors influence the degree of plant invasion (see Gurevitch et al. 2011 for a review). However, few empirical studies have compared the importance of multiple factors simultaneously (Rouget and Richardson 2003, Pauchard and Alaback 2004, Eschtruth and Battles 2009). In the Northeastern United States, the highly abundant native white-tailed deer (*Odocoileus virginianus* Zimm.) (Eschtruth and Battles 2009, Kalisz et al. 2014) and landscape fragmentation (Buckley et al. 2006, Vilà and Ibáñez 2011) are known to facilitate plant invasion. Fragmented landscapes are typically characterized by increased edge habitat, which increase deer populations (Leopold 1933, Alverson et al. 1988). This suggests that landscape scale forest fragmentation might indirectly influence plant community invasion through its effects on deer populations. Furthermore, at the local scale, biologically diverse native communities are expected to limit invasion (Elton 1958), i.e., via biotic resistance, and thus native plant diversity is expected to be important in understanding gradients of plant invasion (Naeem et al. 2000, Levine et al. 2004). In the multiscale work

presented here, native deer density, landscape structure and composition, and native plant diversity were investigated for their relative roles in forest understory community invasion.

Deer (Cervidae) are a widely distributed ruminant herbivore, occurring on all continents except Antarctica and Australia. In northeastern US forests, white-tailed deer (herein deer) are the dominant large herbivores and have been shown to facilitate the invasion of unpalatable species (Chapter 1, Knight et al. 2009, Eschtruth and Battles 2009, Kalisz et al. 2014). Success of unpalatable species is partly due to an indirect competitive advantage resulting from the preferential consumption of more palatable species (Keane and Crawley 2002). The current lack of a definitive link between deer abundance and plant invasion might be because studies on the effects of deer herbivory on plant communities at larger spatial scales are lacking (Maron and Vilà 2001, Russell et al. 2001, Mosbacher and Williams 2009). Furthermore, more intense deer impacts on vegetation are observed in fragmented compared to non-fragmented landscapes (Côté et al. 2004), emphasizing the importance of drawing conclusions about factors relevant to plant invasion at the landscape scale (Kupfer et al. 2006).

Despite being at record low numbers near 1900, deer populations have increased to historically high levels (McCabe and McCabe 1997) due to hunting regulations, declining natural predator populations, and increasing foraging habitat, such as fields and forest edges (for a review, see Côté et al. 2004). Aldo Leopold advised increasing edge habitat and forest openings to facilitate recovery of deer populations (Leopold 1933) because they are more abundant in these habitats (Leopold 1933, Augustine and Frelich 1998). While forested land cover declined in many landscapes, land cover of young forest, agriculture, and silviculture increased throughout the 20th century (Augustine and Frelich 1998). This heterogeneous mosaic of land cover types is ideal habitat for supporting large deer populations (Alverson et al. 1988) and such landscape changes over the past century have facilitated the recovery and subsequent escalation of deer populations (McCabe and McCabe 1997).

Landscape fragmentation affects ecosystems by changing the composition and pattern of land use/land cover patches, entailing habitat loss and the breaking apart of habitat, respectively (Fahrig 2003). As agricultural and developed land cover increase, overall forested land cover declines and the remaining forests often become fragmented, for example by increasing quantities of edge habitat. These landscape alterations cause changes in environmental conditions (e.g., light and soil moisture) and the flow of organisms and resources (Wu 2009). Importantly, fragmented landscapes are more susceptible to exotic plant invaders than unfragmented forests (Vilà and Ibáñez 2011), an outcome that could ultimately result from historical agricultural soil disturbance in young forests (Parker et al. 2010) and proximately by altered nutrient availability (Fraterrigo et al. 2006). Fragmented landscape patterns are often correlated with proximity to human populations. Furthermore, human population density is one of the best predictors of exotic species richness at regional spatial scales and reflects the integration of proximate factors that directly determine invasion outcomes, including propagule pressure, dispersal avenues, and the intensity of human activities (Pyšek et al. 2010). Urban and suburban landscapes are known to be the primary sources for the introduction and spread of exotic plant species (Duguay et al. 2007, Vilà and Ibáñez 2011). Landscape fragmentation metrics, such as patch richness, perimeter to area ratio, and contagion (Tab. 3-1), measure landscape structure and provide a way to link ecological patterns and processes to landscape patterns (Turner 1989). For example, abrupt discontinuities in landscape patterns introduce constraints on the processes of plant community assembly and plant invasion (e.g., Duguay et al. 2007), including altered environmental factors, resulting in abrupt discontinuities in plant species assemblages (Turner 2005). Landscape composition represents land cover, including the percentage of forested, agricultural, and developed land.

Exotic plant invasion is influenced by multiple factors, including global species transportation, habitat disturbances, and herbivores (Mack et al. 2000). Furthermore, increasing evidence shows that plant invasions are outcomes of multiple interacting factors, which are not

mutually exclusive (Mitchell et al. 2006). For example, the interaction between propagule pressure and canopy disturbance (i.e., increased light availability) and deer herbivory were important determinants of plant invasions in eastern hemlock forests (Eschtruth and Battles 2009). Another study showed that propagule supply and soil nitrogen interacted to affect the abundance of a highly invasive plant, but only when herbivore abundance was reduced (Sanders et al. 2007). Last, propagule pressure was a better predictor of invasive plant abundance than environmental factors in South Africa's Agulhas Plain (Rouget and Richardson 2003). These studies show the importance of studying multiple, interacting factors, yet it is still unclear how plant community assembly factors interact across landscapes.

Basic linear models continue to represent the dominant method of ecological data analysis, including ANOVA and regression (Ellison and Dennis 2010). However, there is an increasing need to understand complex ecological problems, such as plant invasions, by analyses that take advantage of non-linearity and complex interactions (Clark et al. 2001). Advances in computing and statistical theory during recent decades allow us to analyze data with nonlinear and nonparametric patterns to maximize the usefulness of large and variable ecological datasets (e.g., Fraterrigo and Rusak 2008). Spatially and temporally large experiments bolster conclusions and forecasts researchers can make about landscape-level ecological processes (Clark et al. 1999, 2001), including community assembly and plant invasion (Gill and Beardall 2001). In this work, non-parametric and parametric statistics were used together to elucidate the factors important in exotic plant invasion at a regional scale.

The objective was to understand how abundant native deer, landscape configuration and composition, and native plant diversity affect plant invasion in the Northeastern US. This approach has not been used previously and aims to offer general insights regarding the plant invasion process. Understanding the importance of the contributing factors across ecological scales will enable better anticipation and forecasting of the effects of herbivore overabundance,

forest fragmentation, and native plant diversity on the degree of plant community invasion. Floristic composition datasets were compiled from a widely distributed network of 24 deer research sites (Tab. 1-1) for a total of 458 plots (229 with deer, 229 with no deer). Patterns of plant community invasion were based on absolute exotic plant abundance and richness and on two measures of the degree of plant invasion: (1) the percentage of plant abundance composed of exotic plants and (2) the percentage of species that were exotic. Surrounding landscape structure and composition (within 6.5 km) was determined for each site using the 2001 National Land Cover Data dataset. Deer density estimated at the site-level (Tab. 1-A1), landscape structure and composition surrounding the sites (Fig. 3-1), and native plant diversity represented currently existing biotic and landscape fragmentation gradients in the Northeastern US. Additionally, the originating experiments spanned a chronosequence of duration of deer exclusion, enabling analysis of the effect of severe deer population reductions on reversal of plant invasion. The following hypotheses were tested: 1) landscape attributes are important in explaining exotic plant invasion; specifically, sites surrounded by landscapes with greater fragmentation are more invaded; 2) high native plant diversity limits exotic plant invasion; 3) high deer density, not just deer presence, increases plant invasion; and 4) plant invasion is reversible following deer exclusion.

## **Methods**

### **Data description**

Floristic composition datasets were compiled from 24 northeastern US field experiments, which included data from paired plots: fenced deer enclosure plots and unfenced control plots. All sites were forested, except for one old-field site (IT). Scientists known to have floristic

datasets including paired, unfenced deer plots and adjacent fenced deer exclusion plots, were invited to share their data for these analyses and to co-author resulting peer-reviewed publications. The pooled datasets resulted in vascular plant community data from 458 plots (229 plot pairs). Experiments varied in duration, replication, and deer enclosure specifications (e.g., fence height and mesh size). Experiments ranged from 2 to 17 years in duration and had 2 to 28 replications (i.e., plot pairs) per site. The most recent complete floristic census for each site was used for analysis and the years of final censuses ranged between 1996 and 2011. Additional experimental information, including data acquisition and processing, was described previously (Chapter 1, Tab. 1-1).

The plant abundance metrics reported in the datasets were: stem density (e.g., stems m<sup>-2</sup>), the percentage of ground covered by the species (i.e., percentage cover, herein cover; 1- or 5- percentage point increments), cover classes or categories (varying ranges of percentage point increments) (Fig. 1-1) and density classes (Tab. 1-1). Cover class data were converted to cover class midpoint (herein midpoint) for analysis. At six sites, a density class of “>10 stems” was sometimes employed, in which case the most conservative value of “11” was substituted for analyses. Density class data were recorded at one site (SH), so the following conversions were used: “2-3 stems” = 2.5 stems; “4-5 stems” = 4.5 stems; and “>5 stems” = 6 stems. At ten sites (e.g., AN, CA, and VJ), different plant habits were recorded with separate measures, for example cover or cover class for the more numerous herbs and grasses and density for less numerous woody species and thus floristic censuses were split and analyzed accordingly. Thus, results reported here need to be interpreted conservatively as the effects of deer presence according to species habits. At other sites (FN, MA, and MG), both cover and density were recorded and were analyzed with other data of the same measure. Consequently, the separate plant abundance analyses were not wholly independent and should be interpreted conservatively as related lines of evidence used to test the hypotheses. The measures of plant invasion patterns were determined at

the plot-level and included: (1) exotic plant abundance; (2) exotic plant species richness; and two measures of the degree of plant invasion, (3) the portion of the vegetation that was exotic (i.e., the percentage of exotic vegetation = exotic/ total vegetation) and (4) the portion of species that were exotic (i.e., the percentage of exotic species richness = # exotic species/ # total species). Absolute and relative exotic plant abundance both were measured because they represent different measures of plant invasion; the absolute measure represents deer effects on actual exotic plant abundance, while relative abundance represents the portion of the entire community composed of exotic plants. Exotic plant abundance was based on the abundance metric(s) used at the site and analyses were conducted separately for each metric.

Landscape attributes surrounding each site were determined based on the 2001 National Land Cover Data (NLCD) dataset, consisting of a 16-class land cover classification scheme at 30 m spatial resolution based on Landsat satellite imagery (Homer et al. 2007). Data were accessed via the METALAND database, an online repository for 6.48 x 6.48 km land cover tiles of the conterminous US (Cardille et al. 2005) (Fig. 3-1). Sites were not necessarily located in the middle of tiles, but tiles were representative of the landscape surrounding each site. Landscape metrics (Tab. 1) were calculated using FRAGSTATS 2.0 (McGarigal et al. 2002, Cardille et al. 2005). Collinearity among the dozens of available landscape metrics was reduced by only selecting variables that measured orthogonal (i.e., not correlated) landscape attributes based on previous multivariate factor analysis (Riitters et al. 1995). However, some negative correlation occurred between contagion and agricultural cover and between contagion and developed cover (Appendix Tab. A1). Certain metrics of interest were excluded to minimize correlation among variables. For example, forest cover was excluded because it was highly correlated to contagion and agricultural cover; total patch edge length was excluded because it was highly negatively correlated to contagion (Tab. 3-1; see Appendix Tab. 3-A1 for a complete account of correlations among landscape metrics).

## **Statistical analysis**

Several complementary analyses were used to determine the importance of different factors thought to influence plant invasion. First, nonmetric multidimensional scaling (NMS) ordination was used to summarize and visualize relationships between plant communities, deer density (Tab. 1-A1), and surrounding landscape metrics (Tab. 3-1). Random Forests (RF) was then used to determine the relative importance of factors in predicting plant invasion. The three most important factors from RF analyses were then investigated using mixed effect models. Only the three most important variables were used to avoid overfitting, achieve model convergence, and simplify interpretation. Separate RF and mixed model analyses were conducted for absolute and relativized abundance using each metric (stem density, cover, and midpoint), exotic species richness, and percentage exotic species richness.

### ***Data visualization with non-parametric, multivariate statistics.***

NMS ordination was used in PC-ORD to summarize and visualize similarities among plots based on species presence and abundance (McCune and Grace 2002). The ordination was used to graph experimental plots in species space, which shows similarities and differences among species assemblages. To reduce noise from rare species, species present in fewer than 5-10% of plots were removed prior to analysis. Species were removed using a 5% removal basis for midpoint data, but for cover and density datasets, a 10% removal basis was employed to reduce ordination stress below 25. After rare species removal, some plots had no species and were necessarily excluded from analysis. To reduce the influence of highly abundant species, datasets were relativized by species abundance totals across plots prior to analysis. The Sorensen distance measure, random number seeds, 50 runs each with real and randomized data, and up to 200

iterations per run were used in each analysis. After verifying consistency of interpretation among several NMS solutions, each dataset was best characterized with three-dimensional ordinations; however, two dimensions were chosen for graphical display to simplify interpretation. The stability criterion (0.00001) was achieved and final stress for the three-dimensional solutions was  $< 23$  in each analysis. For display and summary purposes, community-level variables (e.g., species richness and the degree of invasion), landscape descriptors (Tab. 3-1), deer density, and latitude and longitude were overlaid as vectors on ordination plots if they independently explained at least 20% of variation. Ordinations were then rotated to visualize the vectors. Because one site was located in an old-field (IT) instead of in a forest, ordinations were conducted twice, one with old-field plots and one without them to show the influence of the site. Plots closer together in ordination space are more similar in species composition.

***Relative importance of plant invasion factors using non-parametric, univariate statistics.***

RF was used to rank predictor variables according to how well they predict plant invasion patterns (Breiman 2001). The RF approach was used because it is accurate, efficient in handling many predictor variables, cross-validation is internalized using out-of-bag predictions, and it does not overfit the data (Cutler et al. 2007). RF combines basic theory from classification and regression tree (CART) analysis with an iterative randomization procedure to produce not just one tree but a user-defined number of trees (Breiman 2001). Specifically, RF uses a bootstrapping approach to produce each tree with replacement; at each node in each tree, a random subset of predictor variables is used to make the next split to minimize over-fitting. In contrast to CART, RF does not prune trees and instead grows each tree to maximum depth to minimize pruning bias.

Sensitivity analysis, based on minimizing error, maximizing  $R^2$ , and maximizing node purity was used to determine the optimal number of trees in each model. Either 1000 or 2000

trees were produced in each analysis. The default of two variables was tried at each split (determined by dividing the total number of variables by 3 and rounding down). The importance measure is the mean decrease in accuracy, which shows the normalized decrease in accuracy between observed variable values and randomly permuted values. Important variables have greater decreases in accuracy. Percentage variation explained using pseudo  $R^2$  values and mean of squared residuals (MSR) are reported. The randomForest package in R was used for RF analyses.

***Effects of multiple factors on plant invasion using parametric, univariate statistics.***

Linear mixed effect model analysis of covariance (ANCOVA) was conducted using the top three most important, RF-determined factors and herbivore presence/absence as fixed effects and site and plot pair as random effects. While RF has many benefits over other methods, some evidence shows that the algorithm is biased where predictor variables vary in their scale of measurement or number of categories (Strobl et al. 2007). This occurred among the variables tested here, specifically with the herbivore treatment, which has just two levels. To ward against bias, the significance of herbivore presence and the three most important RF-determined variables were tested. Two-way and not higher order interactions among fixed effects were considered during mixed model development to avoid overfitting, ensure model convergence, and simplify interpretation (Zuur et al. 2009). Response variables were transformed to satisfy assumptions of normality and heterogeneity. Final model selection was based on automatic backward elimination of non-significant fixed and random effects in linear mixed effect models using the step function in R. Using an alpha level of 0.05, non-significant random effects were eliminated one at a time, followed by fixed effect elimination, beginning with highest order interactions; if interactions were significant, main effects were retained. P values for fixed effects were calculated from F tests based on Satterthwaite's approximation; p values for the random effects were based on log-

likelihood ratio tests. P values are reported for the intercept, fixed, and random effects and effect estimates and standard error are reported for the intercept and fixed effects.

Mixed model analysis was also used to test for relationships between deer density and duration of deer exclusion (hypotheses three and four). Data were subsetted by treatment into deer and no-deer scenarios for separate analysis. This was done because the deer-related variables of interest are particular to one type of plot or the other; deer density is only relevant in deer plots, while duration of deer exclusion is only relevant in no-deer plots. In deer analyses, deer density was the fixed effect and site was the random effect. In no-deer analyses, duration of deer exclusion was the fixed effect and site was the random effect. For visualization of significant ( $p < 0.05$ ) and marginally significant ( $p < 0.1$ ) models, simple linear regression equations and  $R^2$  values based on untransformed data and no random effects are reported. The lmer object and lme4 and lmerTest packages in R were used for all mixed model analyses. R statistical software version 3.0.1 (R Development Core Team 2006) was used for all univariate statistical analysis.

## Results

Deer, landscape structure and composition, and native species richness explained much of the wide variation in plant invasion patterns across the 24 northeastern US sites. Landscape structure and composition were significant in every plant invasion model developed, supporting hypothesis one tested in this work (Figs. 3-2 through 3-7, Tabs. 3-2, 3-3). In particular, patch richness and the mean perimeter to area ratio of landscape patches were significant explanatory variables across several of the models. Native species richness also explained a portion of the plant invasion patterns (Figs. 3-2 through 3-7, Tabs. 3-2, 3-3). A negative correlation between native species richness and the percentage of exotic stems was observed, except in landscapes with high perimeter to area ratio, providing some evidence to support hypothesis two that native

plant diversity can limit plant invasion. Deer density was positively correlated to exotic cover and the percentage of exotic species (Fig. 3-8a, 3-8c), which supported hypothesis three that increasing deer abundance increases plant invasion. The percentage of exotic cover and the percentage of exotic species trended downward as the duration of deer exclusion increased, but a statistically significant relationship was not detected (Fig. 3-8b, 3-8d), providing little support for hypothesis four, that invasion is reversible following deer removal or severe reductions.

### **Data visualization**

Strong site-level differences in plant species composition were evident in the consistent grouping of plots by sites in ordination plots (Figs. 3-2, 3-3, 3-4, 3-5). This illustrates that species assemblages were more similar within sites than between sites. When plots were coded by herbivore treatment instead of by site, no grouping of plots across sites was observed (not shown). Strong gradients of the degree of plant invasion (percentage exotic abundance and percentage exotic species richness) were evident among sites. The percentage of developed land cover also varied strongly across sites. Uninvaded sites (FN, LR, MG, and MV) were associated with high contagion (Figs. 3-3, 3-4) and therefore high forest cover (Tab. 3-1). Among sites that measured plant cover, deer density was associated with exotic species richness and, to a lesser degree, with percentage exotic species richness (Fig. 3-3). However, this association diminished when the old-field site was removed. The removal of the old-field site (IT) from this analysis also accentuated the latitudinal gradient, which was most strongly associated with perimeter to area ratio (Fig. 3-4 vs. Fig. 3-3), suggesting that the northern-most sites were surrounded by landscapes with lower average perimeter to area ratios (i.e., lower fragmentation).

Clustering of the most frequently occurring exotic species was observed in the ordinations. *Rosa multiflora* (ROMU), *Lonicera japonica* (LOJA), *Alliaria petiolata* (ALPE4),

and *Ailanthus altissima* (AIAL) generally clustered together in the density ordination (Fig. 3-2). In the cover ordinations, *R. multiflora*, *L. japonica*, *Berberis thunbergii* (BETH), and *Microstegium vimineum* (MIVI) clustered together (Figs. 3-3, 3-4). *Alliaria petiolata*, *B. thunbergii*, *M. vimineum*, and *Celastrus orbiculatus* (CEOR7) generally clustered together in the northwest quadrant of the midpoint ordination, (Fig. 3-5). Additionally, native tree species clustered together and away from exotic species. For example, in density and midpoint ordinations, *Acer rubrum* (ACRU), *Liriodendron tulipifera* (LITU), and *Quercus* spp. (QURU, QUAL, QUPR2), generally grouped together (Figs. 3-2, 3-5). Native vine species *Parthenocissus quinquefolia* (PAQU2) and *Toxicodendron radicans* (TORA2) grouped together with the exotic vine *L. japonica* in the northwest quadrants of density and midpoint ordinations (Figs. 3-2, 3-5); the exotic vine *C. orbiculatus* also clustered with the other vines in the midpoint ordination (Fig. 3-5). The fact that species within invasive exotic, tree, or vine functional groups cluster together shows that they co-occur within plots. The vectors illustrate the abiotic, biotic, or landscape configuration gradients that might drive co-occurrence.

### **Relative importance of plant invasion factors**

Landscape structure (patch richness, contagion, and perimeter to area ratio of landscapes patches) and composition (agricultural and developed cover) and native species richness explained much of the variation in invasive plant patterns. Multiple lines of evidence, based on the three plant abundance metrics utilized across the sites and both absolute and relativized plant abundance provide strong evidence that landscape structure and composition are highly important in understanding plant invasion in the region. However, models of exotic species density and cover and exotic species richness explained much more variation than models of exotic species midpoint (Figs. 3-6, 3-7). Models for the relative measures of exotic plant abundance and

richness (i.e., those measuring the degree of plant invasion) consistently had higher residual values (MSR), sometimes with several fold increases, compared to models for the absolute measures of exotic plant invasion. This suggests that relativizing exotic plant abundance and richness (i.e., dividing by total vegetation abundance or total species richness, respectively) introduced noise into the plant invasion models.

Perimeter to area ratio, agricultural land cover, and developed land cover were the most important variables predicting absolute exotic stem density; this model explained approximately 40% of variation (MSR = 81) (Fig. 3-6). Native species richness instead of developed cover was important for percentage exotic stem density and this model explained 41% of variation (MSR = 326). Patch richness, agricultural land cover, and native species richness were the most important variables for exotic cover; the absolute cover model explained ~59% of variation (MSR = 183), while the percentage exotic cover model explained ~58% of variation (MSR = 614). Native species richness, perimeter to area ratio, and contagion were the most important variables for exotic midpoint; the absolute exotic midpoint model explained ~14% of variation (MSR = 517), while the percentage exotic midpoint model explained ~9% of variation (MSR = 1122) (Fig. 3-6).

Perimeter to area ratio, patch richness, and native species richness explained a large amount of variation in absolute exotic species richness across sites (Fig. 3-7) and all variables in the model explained almost all variation (~91%; MSR = 3). In contrast, the percentage exotic species richness model explained only ~37% of variation (MSR = 125).

### **Effects of multiple factors and their interactions on plant invasion**

Landscape structure and composition were highly significant in plant invasion models and several statistical interactions among them and with deer presence and native species diversity were observed (Tabs. 3-2, 3-3). Increasing patch richness was associated with increases

in exotic and percentage exotic cover, as well as exotic and percentage exotic species richness. An interaction between patch richness and perimeter to area ratio was detected in exotic and percentage exotic species richness models. Perimeter to area ratio was significant in exotic stem density and in exotic and percentage exotic species richness models and an interaction between perimeter to area ratio and developed cover was found in the exotic stem density model. Repeatedly, significant interactions between perimeter to area ratio and native species richness were identified (in percentage exotic stem density, exotic and percentage exotic midpoint, and exotic species richness models). As native species increased, the percentage of exotic stems declined in landscapes with lower mean perimeter to area ratio, lending some support to hypothesis two. Native species richness was also significant in exotic and percentage exotic midpoint and exotic species richness models. As native species richness increased, so did exotic species richness. Last, agricultural cover and developed cover were significant in the exotic stem density model. Importantly, plot pair and site were consistently significant random effects across almost all models, indicating high variability within and between sites. Only in exotic cover and percentage exotic cover models was site not significant. In all models, large reductions in AIC values were observed in final models compared to the full models that contained all two-way interactions (Tabs. 3-2, 3-3).

Despite herbivore presence appearing unimportant in RF models, in mixed models this factor was a significant predictor of exotic and percentage exotic stem density, percentage exotic cover, and percentage exotic midpoint (Tab. 3-3). Additionally, a statistical interaction between herbivore presence and developed cover was significant in the exotic stem density model and a statistical interaction between herbivore presence and agricultural cover was found in the percentage exotic stem density model.

### **Effects of deer density and duration of deer exclusion on exotic plant patterns**

Positive correlations between deer density and the percentage of exotic cover (Fig. 3-8a;  $p = 0.049$ ;  $n = 46$  across 8 sites) and between deer density and the percentage of exotic species richness (Fig. 3-8c;  $p = 0.026$ ;  $n = 217$  across 23 sites) were observed. Exotic cover and percentage exotic species richness tended to be negatively correlated with duration of deer exclusion, but statistical tests showed marginally significant relationships (Fig. 3-8b, 3-8d), thus the results show little support for the fourth hypothesis. No relationships were detected between remaining metrics of exotic plant invasion and deer density or deer exclusion (Fig. 3-A1, Fig. 3-A2).

### **Discussion**

Immense changes in landscape pattern across the Northeastern US, namely increasing forest fragmentation, are responsible for increasing deer populations during the previous century (Leopold 1933, Alverson et al. 1988, McCabe and McCabe 1997). The work presented here shows that altered landscape structure and composition also play important roles in explaining the wide range of exotic plant abundance and the degree of plant community invasion patterns at a regional extent. Deer presence added a significant amount of explanatory power to some but not all models of the invasive plant patterns investigated at this broad scale. The degree of plant community invasion varied widely across the sites investigated and this pattern was evident in all ordinations of floristic community data (Figs. 3-2, 3-3, 3-4, 3-5). The fact that sites situated in landscape matrices with high developed cover had a greater association with plant invasion patterns is not surprising, as others have also found that increasing fragmentation and urbanization lead to biological invasions (Minor et al. 2009, Vilà and Ibáñez 2011). Importantly,

interactions among landscape structure and composition, deer presence, and native species diversity were prominent explanatory factors in regional plant invasion.

**Hypothesis 1: Landscape fragmentation is linked to exotic plant invasion.**

Landscape attributes and their interactions with herbivore presence and native species richness were important explanatory factors for exotic plant invasion and the degree of plant community invasion, supporting the first hypothesis tested in this research. These results agree with previous literature showing that invasive species richness and abundance is generally greater in more fragmented landscapes (Vilà and Ibáñez 2011). Overall, as fragmentation increased, so did exotic plant invasion patterns, demonstrating that consideration of surrounding landscape context in addition to the internal ecological dynamics of forest understory communities is highly important in understanding plant invasion.

A higher number of patch types and greater mean perimeter to area ratio of landscape patches were associated with increased exotic plant invasion and this might be a result of increased avenues of dispersal for invading species (Tab. 3-1). Exotic invaders were present at the sites with the highest patch richness (15 patch types at MP, IT, and WP) and the highest values of perimeter to area ratio. In contrast, uninvaded sites were located in landscape matrices containing fewer patch types (8-10 patch types at FN, LR, MG, MV, Z1) and lower mean perimeter to area ratio of patches. Uninvaded sites also tended to be more forested (Fig. 3-1) than invaded sites. That patch richness was positively correlated with exotic cover and exotic species richness is not surprising given that a more heterogeneous landscape composed of more patch and habitat types also supports more species and likely has more opportunities for invaders. For example, a higher diversity of geological substrates (Anderson and Ferree 2010) and topographies (Crisfield 2012) are known to inhabit greater biodiversity. Exotic invaders were present at some sites that were

largely forested (e.g., CA, SH, and WP) and this might be due to human activities (e.g., hiking in the parks) in or nearby the forests. As an example, the presence of rural housing has been associated with plant invasions in southern Wisconsin (Gavier-Pizarro et al. 2010) and forests roads are important avenues of dispersal for exotic plant invaders (Mortensen et al. 2009, Taylor et al. 2012, Pollnac et al. 2012). The observation that exotic species clustered together in ordinations suggests that they co-occur and that invaded sites often have more than one invader, lending support to the idea that exotic species might facilitate one another, sensu “invasional meltdown” (Simberloff and von Holle 1999).

**Hypothesis 2: Native plant diversity limits exotic plant invasion.**

Exotic plant invasion was positively correlated with native species diversity (Tabs. 3-2, 3-3) across the broad gradient of landscape fragmentation observed in the region and this finding supports previous research showing that the “rich get richer” (Stohlgren et al. 1999). The result suggests that areas with high native species richness might be more susceptible to exotic invaders (Stohlgren et al. 1999). However, the finding that native species richness limited the portion of exotic stems occurring in plant assemblages provides some support for hypothesis two and for the biotic resistance hypothesis, which suggests that diverse native species assemblages might limit plant invasion (Levine et al. 2004). Thus, after accounting for landscape-scale extrinsic factors that might have concealed the native plant diversity biotic resistance effect (Naeem et al. 2000), it appears that communities occurring in less fragmented, more contiguous landscapes might resist plant invasion better than those in highly fragmented landscapes. To grasp the full picture of plant invasion, considering interactions with native plant diversity appears important.

The remoteness of certain sites (e.g., LR and MV), has likely limited exotic plant dispersal, suggesting the lack of exotic plant propagule pressure has enabled the sites to remain

free of exotic invaders (Lockwood et al. 2005, Colautti et al. 2006, Eschtruth and Battles 2009). However, natural gas extraction in Northern Pennsylvania could provide dispersal avenues for invaders in the area of these sites (Mortensen et al. 2009, unpublished data). It should be noted that the native fern *Dennstaedtia punctilobula* has become a highly dominant native plant in the forest understories at LR and MV. This species is considered a native invader as a result of increased canopy gaps and deer pressure (de la Cretaz and Kelty 1999). Thus while the sites have resisted exotic invaders, the formation of a recalcitrant understory layer composed of this native fern nonetheless interferes with forest dynamics (Royo and Carson 2006).

### **Hypothesis 3: Deer abundance influences plant invasion.**

Deer density explained approximately one third (34%) of raw exotic cover variation (Fig. 3-8a) and one fifth (21%) of raw variation in the percentage of exotic species richness (Fig. 3-8c). These results support hypothesis three tested in this work as well as previous expectations that high deer density in the region, and not just deer presence increases patterns of exotic plant invasion (Knight et al. 2009, Kalisz et al. 2014). In spite of this, other metrics of exotic plant abundance besides cover were not related to deer density, showing that increasing deer density is not always associated with increased exotic abundance. Landscape structure and composition were very important for plant invasion (Tabs. 3-2, 3-3) [and for deer density (Tab. 3-4)] at this regional scale. This suggests that landscape attributes regulate these organisms in a top-down fashion, since both deer and invasive plants appear to increase in abundance in response to anthropogenically disturbed landscapes.

Conspicuously, deer presence was not identified as an important factor based on RF analyses, yet it was highly important in subsequent analyses. This could be a result of bias in the RF algorithm against predictors that have few levels. Strobl et al. (2007) detected bias in the RF

algorithm and showed that suboptimal predictor variables might be artificially preferred during variable selection, such as those that have many levels. Alternatively, the results could indicate that relative to landscape structure and composition, herbivory is less important in explaining plant invasion patterns at a landscape-scale. Landscape attributes appear to be the overarching drivers of both exotic plants and deer. Indeed, deer density (deer km<sup>-2</sup>) increased with patch richness, perimeter to area ratio, agricultural land cover, and developed land cover (Tab. 3-4). That deer density was negatively related to contagion, a proxy for forested land cover (Tab. 3-1), is not surprising given that deer prefer open habitats vs. closed canopy forest habitats (Alverson et al. 1988, Côté et al. 2004).

Intriguingly, the fact that herbivore presence was only important for percentage exotic cover and midpoint but not for the absolute measures in multi-factor mixed models suggests that deer are more important when considering the degree of plant community invasion compared to absolute exotic abundance. Deer effects on the relativized measures, but not on the absolute measures were also found when landscape factors and native plant diversity were unaccounted for in modeling these datasets (Tab. 2-4). These results could be due to the strong negative effect of deer on absolute native but not on absolute exotic plant abundance (Tab. 2-4).

#### **Hypothesis 4: Plant invasion is reversible following deer exclusion.**

As the duration of deer exclusion increased, exotic plant abundance trended downward based on all invasion metrics investigated; however, statistical relationships were marginally non-significant or non-significant (Fig. 3-8b, Appendix Figs. 3-A1, 3-A2). Previous work shows that ecosystem responses to reductions in deer are slow because modern plant communities and seed banks are often the cumulative result of decades of high deer abundance (Russell et al. 2001, Royo et al. 2010, Tanentzap et al. 2012). While deer reductions can quickly increase the

abundance of palatable species, community diversity could take decades to recover without additional restoration activities (Royo et al. 2010).

## **Limitations**

Methodological uncertainty or mismatches in time or space could account for the limited relationships observed between deer density and plant invasion. Accurately estimating deer density can be challenging and each method used to survey deer has its own assumptions and drawbacks (Stainbrook and Diefenbach 2012). Difficulties in achieving accurate measurements are evident in the broad uncertainty surrounding deer density estimates (Fig. 3-8a, 3-8c; Chapter 1, Appendix). Additionally, plant community data were collected at a finer spatial scale than deer density (Tabs. 1-1, 1-A1). For example, the deer density estimate for the Shenandoah National Park site (SH) was made at the park scale, which is several times larger than the scale at which plant data were measured. The fact that different groups of variables were important across exotic plant abundance metrics is likely because each abundance metric was based on different groups of sites. However, FN, MA, and MG were included in both density and cover analyses, thus the patterns at these sites contributed to both sets of analyses. As a consequence of this lack of independence, each analysis should be interpreted as a separate line of evidence testing the hypotheses. Despite differences in the most important factors contributing to plant invasion across plant abundance metrics, I conclude that both landscape scale factors and local scale forest understory community dynamics are important in understanding plant invasion. Even though a large number of floristic datasets were analyzed in this work, the necessity of subsetting the datasets by abundance metric might have limited broader conclusions.

Each site's history of community assembly and anthropogenic impacts, in addition to their geology, soil type, slope, aspect, and moisture regime, jointly affect current plant

communities, yet much of the variation in response variables was accounted for with the variables included here. Some variation in all invasive plant measures was attributed to within and/or between site variability, suggesting that factors other than those included here are also important in explaining plant invasion (Tabs. 3-2, 3-3). For instance, growth of the invasive grass, *Microstegium vimineum*, has been shown to depend not only on native species richness but also on plot-level environmental factors, including soil moisture, nitrogen, and pH (Nord et al. 2010). Additionally, past land-use was not considered in this work, yet is known to be important in determining plant invasion (Schramm 2008, Parker et al. 2010, Vilà and Ibáñez 2011). Historical changes in land-use are associated with increased plant invasion, suggesting that shifts in current land-use could help predict future invasions (Vilà and Ibáñez 2011).

## **Conclusions**

This work shows strong evidence that landscape structure and composition variables are key indicators of invasive plant patterns and deer density, two threats to forest regeneration. Deer are directly evoked in interactions with landscape attributes for some measures of exotic plant invasion, but overall deer and invasive plants appear to respond similarly by increasing in fragmented landscapes. Generally, this work suggests that to fully comprehend the factors that influence plant invasion, (1) surrounding landscape attributes, (2) native species richness, (3) herbivore abundance, and (4) their interactions must be considered.

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**Table 3-1:** Descriptions of metrics used to quantify landscape structure (patch richness, contagion, and perimeter to area ratio) and composition (agricultural and developed cover) surrounding study sites and their potential relevance to community assembly and plant invasion. The averages, coefficients of variation (CV), and ranges of metrics used in analyses are also shown.

Landscape metrics	Unit	Description	Relevance to community assembly	Mean (SE)	CV	Median	Range
Patch richness	number	number of patch (i.e., land cover) types	high patch richness suggests high landscape heterogeneity and increased dispersal avenues for invaders; increased landscape heterogeneity suggests more habitat heterogeneity and potentially more types of habitats for invaders	11.6 (0.4)	0.17	12	8–15
Contagion	percentage	degree of patch clumpiness or fragmentation; higher values indicate a landscape with few large, contiguous patches (less fragmentation), whereas lower values indicate many small and dispersed patches (high fragmentation); contagion was positively correlated to total forest cover (0.90) and negatively correlated to total patch edge (-0.97)	high contagion suggests landscape homogeneity and thus fewer dispersal avenues and fewer types of habitats for invaders	59 (3)	0.28	58	35–85
Perimeter to area ratio mean	none	mean ratio of patch perimeter (m) to area (m <sup>2</sup> ) across all patches in the landscape; a simple metric of shape complexity	large patch perimeter relative to patch area suggests increased edge habitat and more dispersal opportunities for invaders	848 (25)	0.14	895	644–996
Agricultural land cover	percentage of land cover	sum of cultivated crop and pasture/hay land cover; ag cover was negatively correlated to total forest cover (-0.82)	potential propagule source of early successional species; also represents forest habitat loss	19 (4)	0.98	14	0.019–72
Developed land cover	percentage of land cover	sum of developed open space and low, medium, and high intensity developed cover	altered abiotic environment (e.g., heat island effect); potential propagule source of early successional species; also represents forest habitat loss	15 (3)	0.92	10	0.65–49

**Table 3-2:** Mixed effect model results showing significant factors in models of absolute and percentage exotic plant species richness. The number of observations (n), number of pairs, and number of sites included in each analysis are shown in addition to the change ( $\Delta$ ) in AIC value between the full model with all two-way interactions and the final model.

Response variable <sup>a</sup>	Final model effects	Effect estimate (SE) <sup>b</sup>	P value	n	# pairs	# sites	$\Delta$ AIC	
Exotic species richness	intercept	-14 (5)	<b>0.02</b>	458	229	24	-47.6	
	<i>fixed effects</i>							
	patch richness	1.4 (0.5)	<b>0.005</b>					
	perimeter to area ratio	0.013 (0.006)	<b>0.03</b>					
	native species richness	-0.09 (0.04)	<b>0.02</b>					
	patch richness * perimeter to area ratio	-0.0013 (0.0005)	<b>0.02</b>					
	perimeter to area ratio * native species richness	0.00015 (0.00004)	<b>0.0006</b>					
<i>random effects</i>	plot pair		<b>&lt;0.0001</b>					
	site		<b>&lt;0.0001</b>					
Percentage exotic species richness	intercept	-33 (10)	<b>0.002</b>	458	229	24	-63	
	<i>fixed effects</i>							
	patch richness	2.8 (0.9)	<b>0.002</b>					
	perimeter to area ratio	0.04 (0.01)	<b>0.003</b>					
	patch richness * perimeter to area ratio	-0.0027 (0.001)	<b>0.008</b>					
	<i>random effects</i>	plot pair						<b>&lt;0.0001</b>
	site		<b>&lt;0.0001</b>					

<sup>a</sup> Square-root transformations were necessary to satisfy the assumption of homogeneity of residuals. <sup>b</sup> SE = standard error.

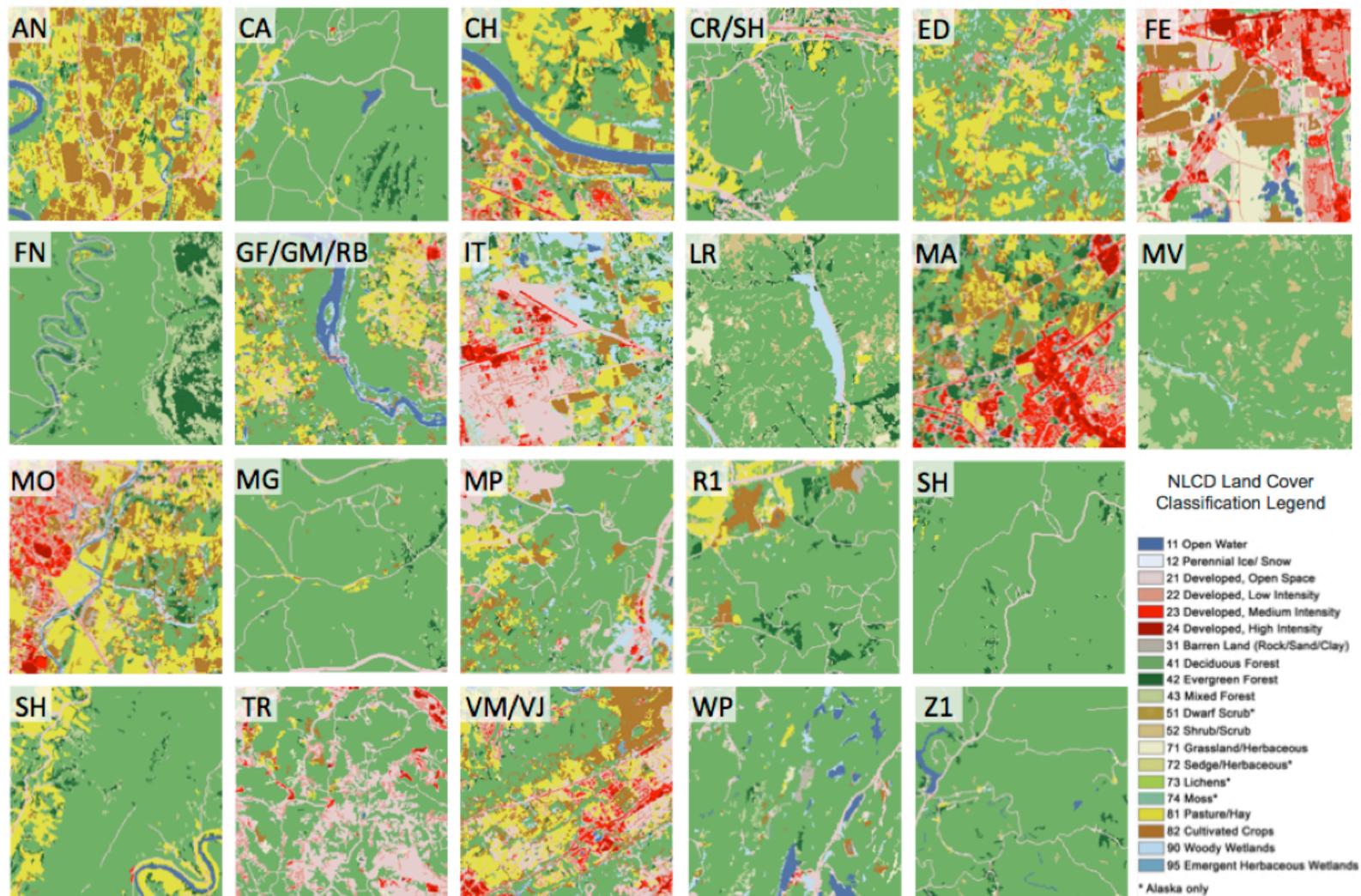
**Table 3-3:** Mixed effect model results showing significant factors in models of absolute and percentage exotic plant species abundance. The number of observations (n), number of pairs, and number of sites included in each analysis are shown in addition to the change ( $\Delta$ ) in AIC value between the full model with all two-way interactions and the final model.

Response variable <sup>a</sup>	Final model effects	Effect estimate (SE) <sup>b</sup>	P value	n	# pairs	# sites	$\Delta$ AIC
Exotic stem density <i>fixed effects</i>	intercept	-13 (4)	<b>0.005</b>	336	168	14	-52.6
	herbivore presence	0.3 (0.1)	<b>0.01</b>				
	perimeter to area ratio	0.014 (0.004)	<b>0.003</b>				
	ag cover	0.021 (0.009)	<b>0.04</b>				
	developed cover	2.1 (0.4)	<b>0.0002</b>				
	herbivore presence * developed cover	-0.016 (0.006)	<b>0.007</b>				
	perimeter to area ratio * developed cover	-0.0022 (0.0004)	<b>0.0002</b>				
	plot pair		<b>&lt;0.0001</b>				
	site		<b>&lt;0.0001</b>				
Percentage exotic stem density <i>fixed effects</i>	intercept	3 (1)	<b>0.02</b>	336	168	14	-62.8
	herbivore presence	0.1 (0.04)	<b>0.02</b>				
	perimeter to area ratio	-0.003 (0.001)	0.2				
	ag cover	0.004 (0.003)	0.2				
	native species richness	-0.12 (0.04)	<b>0.005</b>				
	herbivore presence * agricultural cover	-0.003 (0.001)	<b>0.03</b>				
	perimeter to area ratio * native species richness	0.00013 (0.00004)	<b>0.005</b>				
	plot pair		<b>&lt;0.0001</b>				
	site		<b>&lt;0.0001</b>				
Exotic cover <i>fixed effect</i> <i>random effect</i>	intercept	-13 (2)	<b>&lt;0.0001</b>	92	46	8	-51.5
	patch richness	1.4 (0.1)	<b>&lt;0.0001</b>				
	plot pair		<b>&lt;0.0001</b>				
Percentage exotic cover <i>fixed effects</i> <i>random effect</i>	intercept	-1.0 (0.1)	<b>&lt;0.0001</b>	92	46	8	-94.4
	herbivore presence	0.04 (0.02)	<b>0.03</b>				
	patch richness	0.12 (0.01)	<b>&lt;0.0001</b>				
	plot pair		<b>&lt;0.0001</b>				
Exotic midpoint <i>fixed effects</i> <i>random effects</i>	intercept	5 (3)	<b>0.06</b>	354	177	15	-61
	perimeter to area ratio		0.2				
	native species richness	-0.27 (0.09)	<b>0.002</b>				
	perimeter to area ratio * native species richness	-0.005 (0.003)	<b>0.002</b>				
	plot pair		<b>&lt;0.0001</b>				
	site		<b>&lt;0.0001</b>				
Percentage exotic midpoint <i>fixed effects</i> <i>random effects</i>	intercept	1.8 (0.8)	<b>0.04</b>	354	177	15	-74.7
	herbivore presence	0.13 (0.05)	<b>0.005</b>				
	perimeter to area ratio	-0.0014 (0.0009)	0.1				
	native species richness	-0.08 (0.03)	<b>0.01</b>				
	perimeter to area ratio * native species richness	0.00009 (0.00004)	<b>0.02</b>				
	plot pair		<b>&lt;0.0001</b>				
	site		<b>&lt;0.0001</b>				

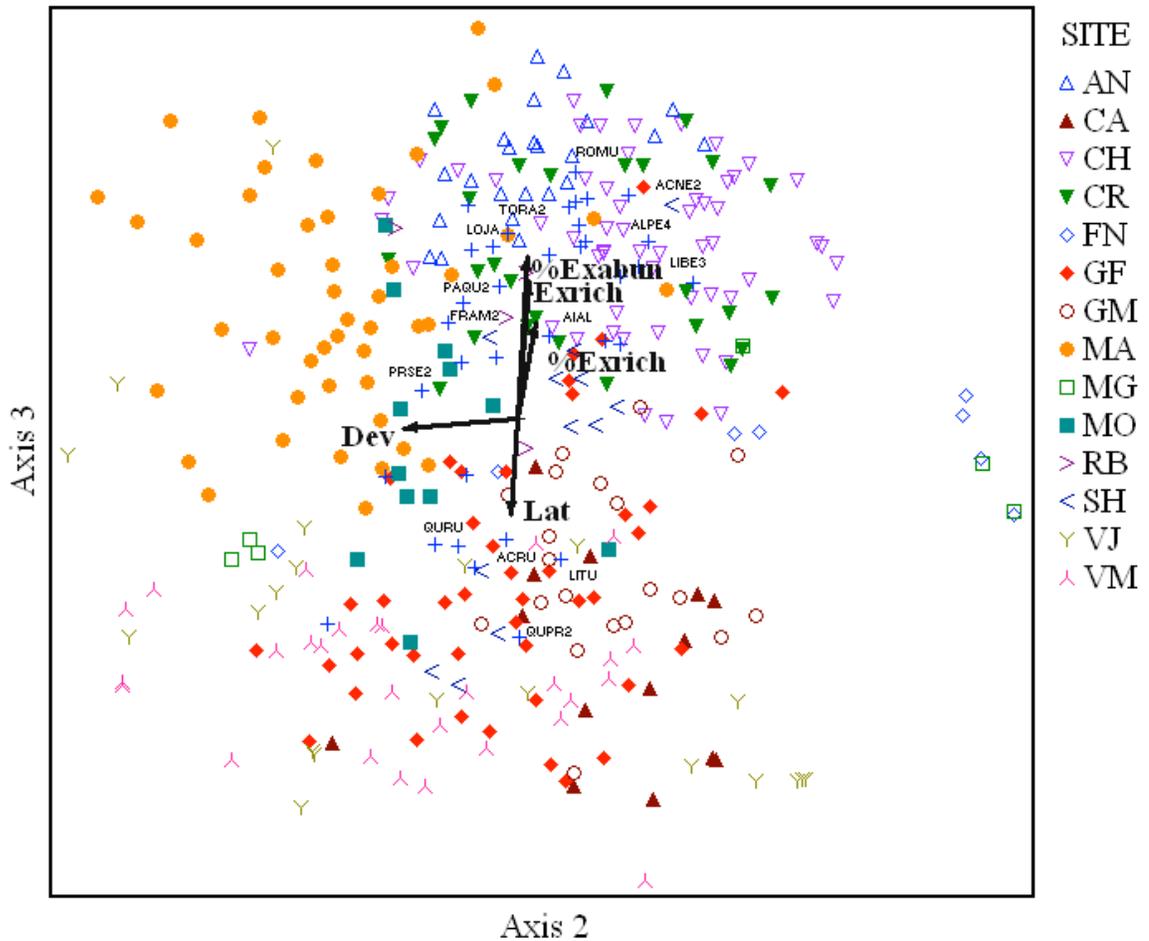
<sup>a</sup> Square-root transformations of exotic cover, natural log +1 transformations of exotic stem density and exotic midpoint, and arc sin square-root transformations of percentage exotic abundance data were necessary to satisfy the assumption of homogeneity of residuals. <sup>b</sup> SE = standard error.

**Table 3-4:** Deer density relationships with landscape structure and composition metrics based on simple linear regression for 24 sites across the Northeastern United States. *F* statistics with numerator degrees of freedom (DF) and denominator DF in subscript (DFn, DFd).

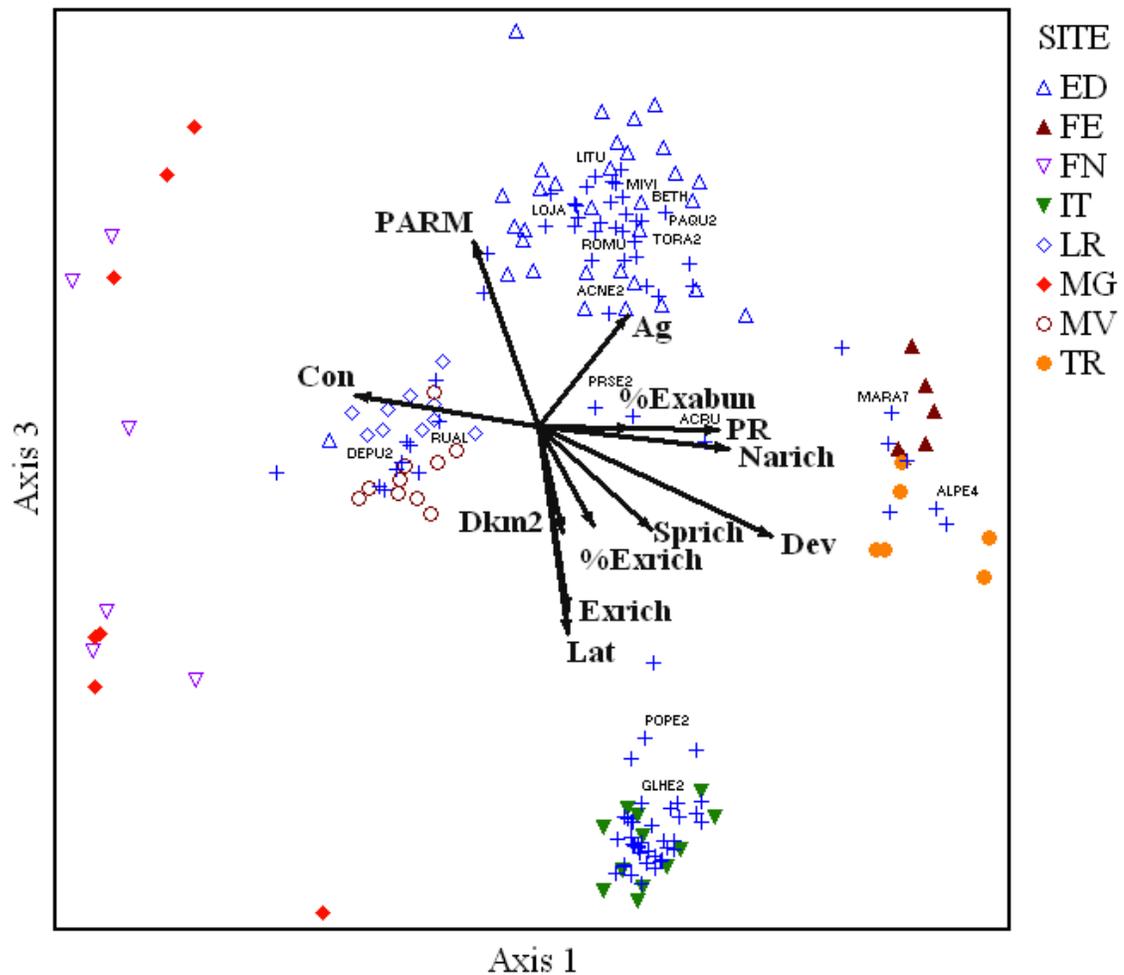
<b>Landscape metric</b>	<b>Intercept</b>	<b>Slope</b>	<b><i>F</i> (DFn, DFd)</b>	<b>p value</b>	<b>R<sup>2</sup></b>
Patch richness	5 (17)	3 (1)	5.7 <sub>1, 215</sub>	0.02	0.03
Contagion	90 (7)	-0.8 (0.1)	37 <sub>1, 215</sub>	<0.0001	0.15
Perimeter to area ratio mean	-67 (18)	0.13 (0.02)	39 <sub>1, 215</sub>	<0.0001	0.15
Percentage agricultural land cover	33 (4)	0.5 (0.1)	20 <sub>1, 215</sub>	<0.0001	0.09
Percentage developed land cover	29 (3)	1.1 (0.16)	54 <sub>1, 215</sub>	<0.0001	0.20



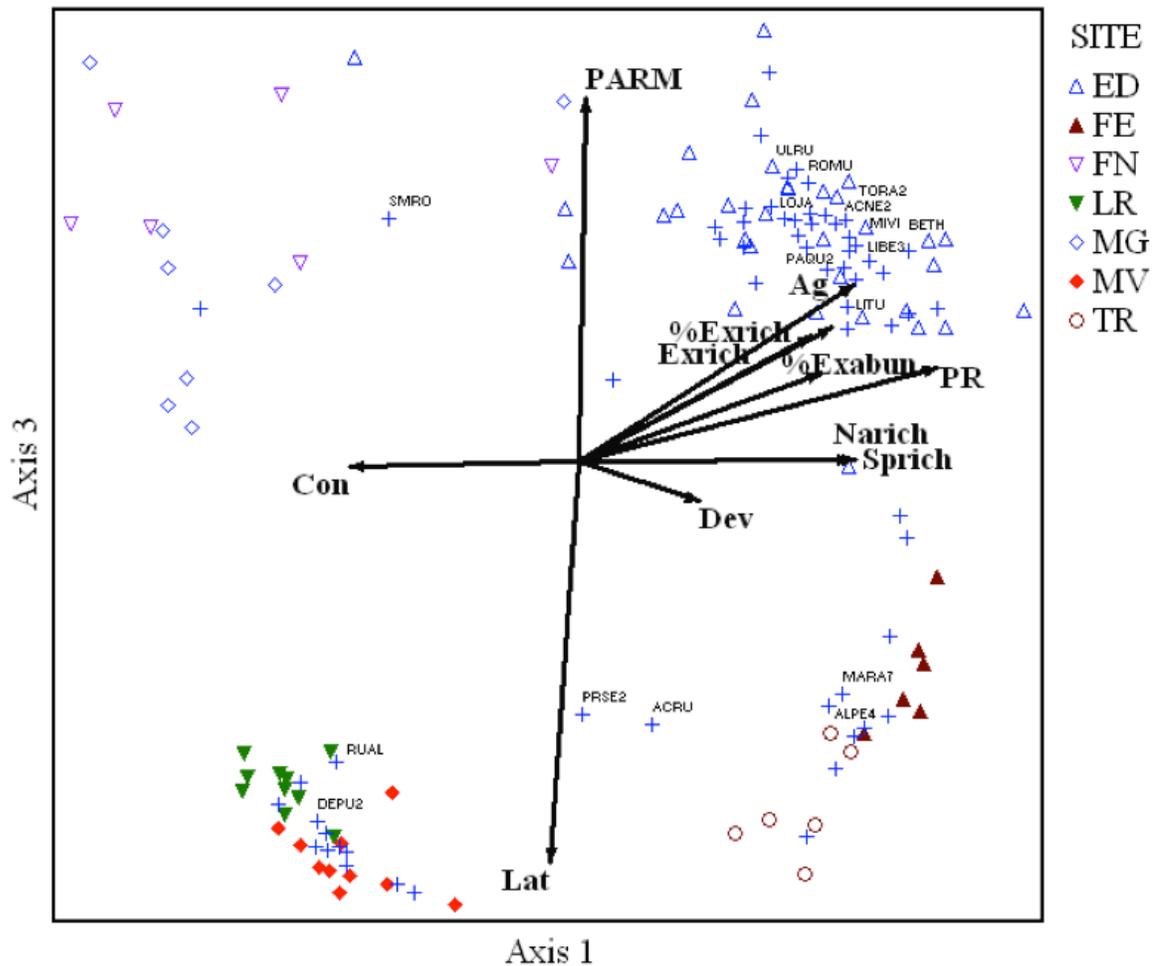
**Figure 3-1:** National Land Cover Data (NLCD) used for analysis of landscape attributes surrounding the 24 sites investigated here. Some sites were located within the same 6.48 x 6.48 km METALAND tiles shown, while Shenandoah National Park (SH) plots were located across several tiles.



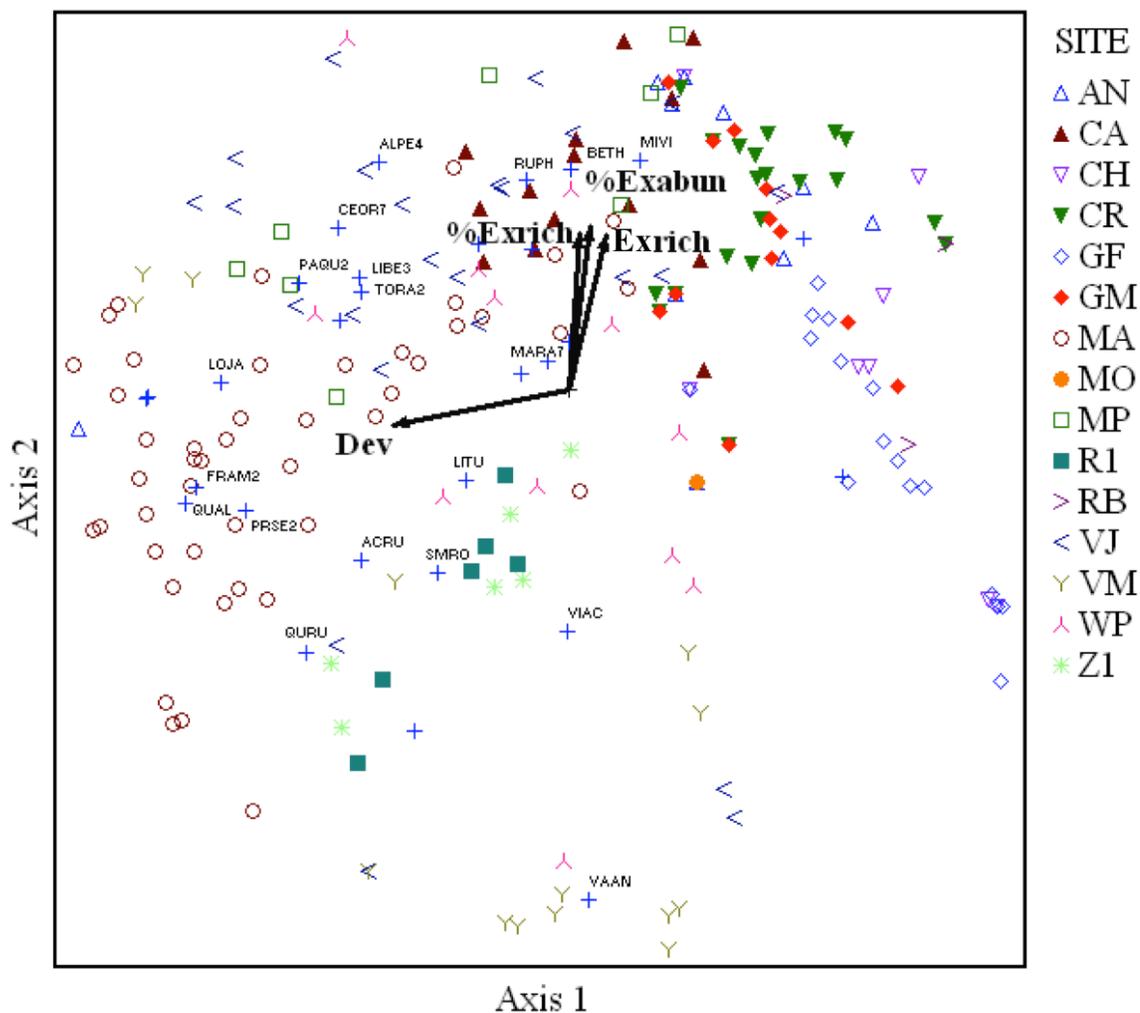
**Figure 3-2:** Non-metric multidimensional scaling ordination for stem density data showing plot similarities based on plant species assemblages at 14 northeastern US sites. The 35 species in the analysis are represented by blue cross symbols (+) and a sampling of the most frequent exotic and native species are labeled using USDA Plants Database symbols (USDA, NRCS 2012). Community-level variables (%Exrich = percentage exotic richness; %Exabun = percentage exotic stem density; Exrich = exotic species richness), percentage developed land cover (Dev) surrounding the site, and site latitude (Lat) were overlaid on the ordination (each variable independently explained >20% of variation). Overall, a three-dimensional ordination explained 44% of variation (axis 2  $R^2 = 0.20$ ; axis 3  $R^2 = 0.13$ ).



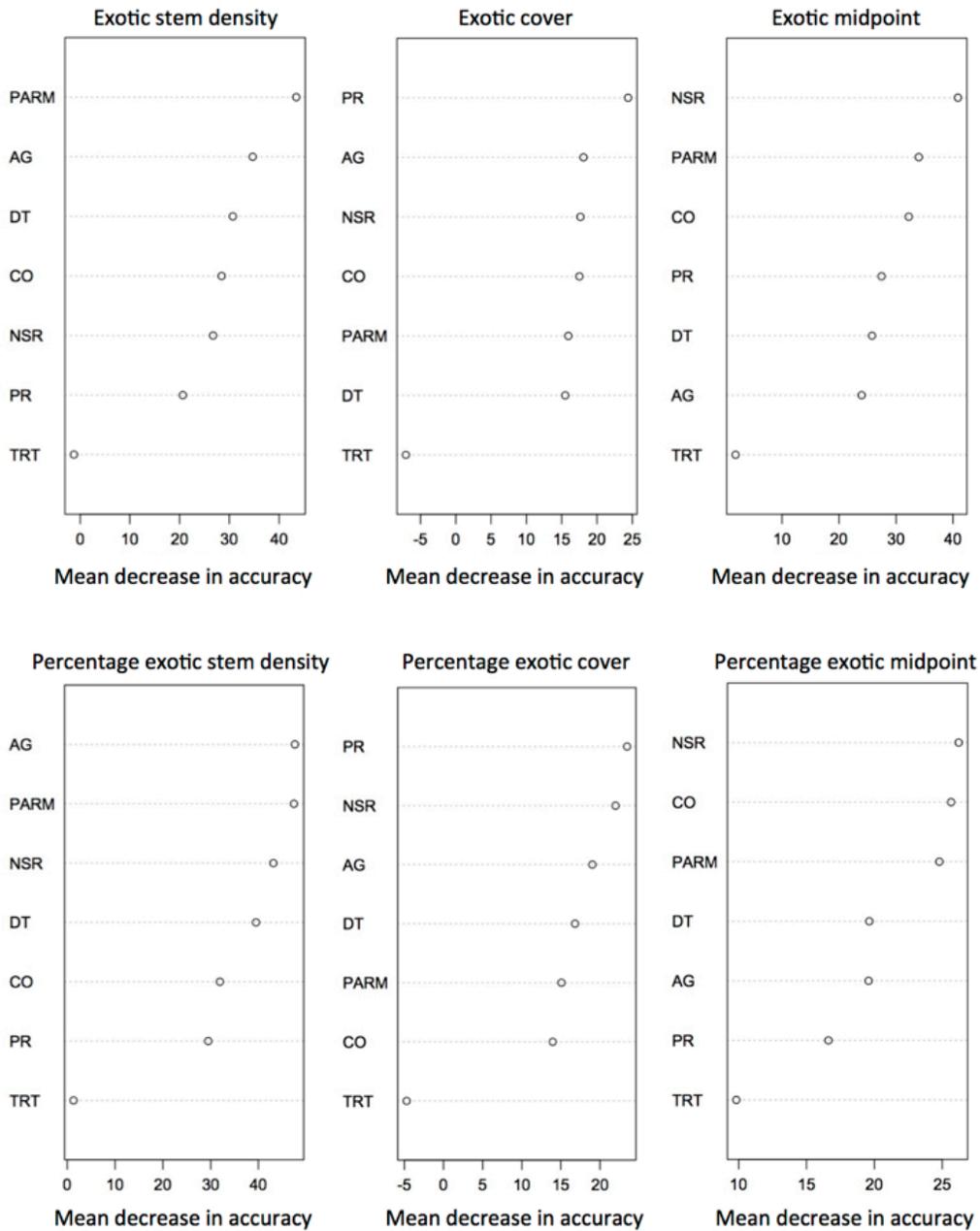
**Figure 3-3:** Non-metric multidimensional scaling ordination for cover data showing plot similarities based on plant species assemblages at 8 northeastern US sites (all sites were forested except for IT, an old field site). The 92 species in the analysis are represented by blue cross symbols (+) and a sampling of the most frequent exotic and native species are labeled using USDA Plants Database symbols (USDA, NRCS 2012). Deer density (Dkm2 = deer km<sup>-2</sup>), community-level variables (Exrich = exotic species richness; %Exrich = percentage exotic richness; %Exabun = percentage exotic cover abundance; Narich = native species richness; Sprich = total species richness), surrounding landscape descriptors (PARM = perimeter-area ratio mean; Con = contagion; Ag = percentage agricultural land cover; Dev = percentage developed land cover; PR = patch richness), and latitude (Lat) were overlaid on the ordination (each variable independently explained >20% of variation). Overall, a three-dimensional ordination explained 67% of variation (axis 1 R<sup>2</sup> = 0.21; axis 3 R<sup>2</sup> = 0.25).



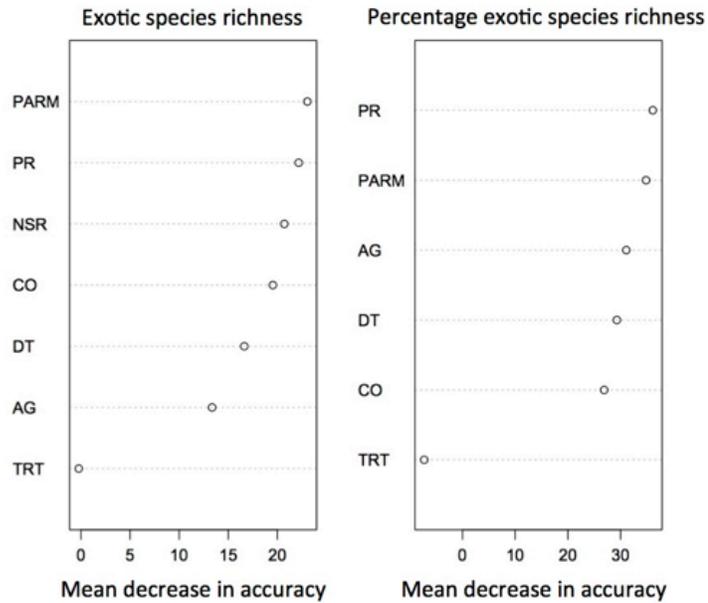
**Figure 3-4:** Non-metric multidimensional scaling ordination for cover data showing plot similarities based on plant species assemblages at 7 northeastern US sites (all sites were forested; the old field IT site was excluded). The 62 species in the analysis are represented by blue cross symbols (+) and a sampling of the most frequent exotic and native species are labeled using USDA Plants Database symbols (USDA, NRCS 2012). Community-level variables (Exrich = exotic species richness; %Exrich = percentage exotic richness; %Exabun = percentage exotic cover abundance; Narich = native species richness; Sprich = total species richness), surrounding landscape descriptors (PARM = perimeter-area ratio mean; Con = contagion; Ag = percentage agricultural land cover; Dev = percentage developed land cover; PR = patch richness), and latitude (Lat) were overlaid on the ordination (each variable independently explained >20% of variation). Overall, a three-dimensional ordination explained 67% of variation (axis 1  $R^2 = 0.25$ ; axis 3  $R^2 = 0.19$ ).



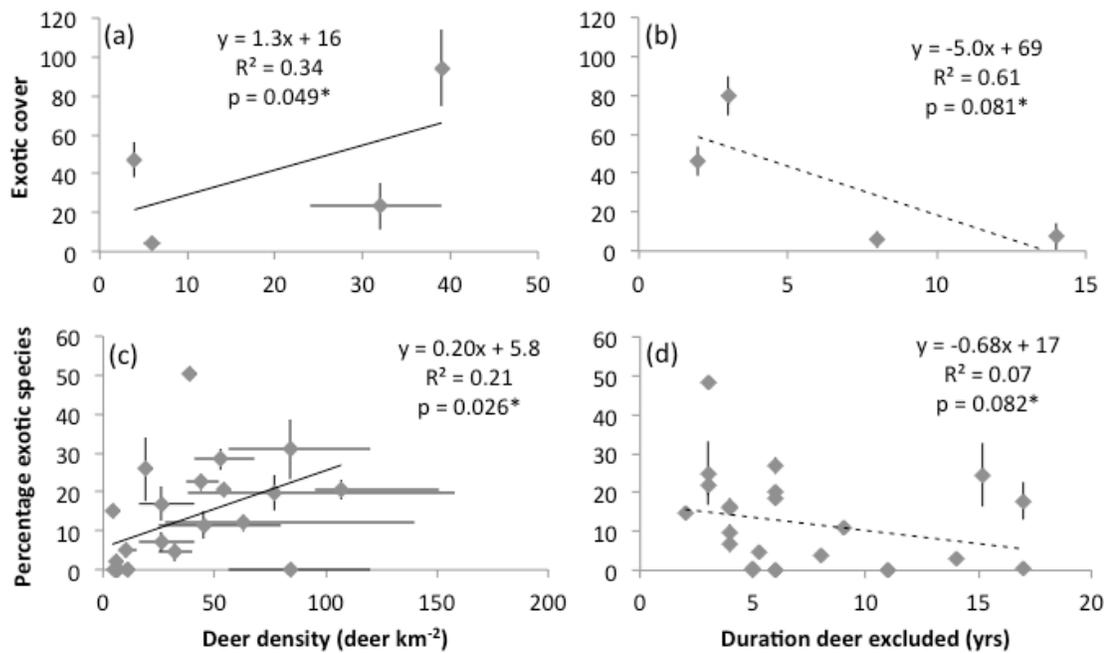
**Figure 3-5:** Non-metric multidimensional scaling ordination for midpoint data showing plot similarities based on plant species assemblages at 15 northeastern US sites. The 29 species in the analysis are represented by blue cross symbols (+) and a sampling of the most frequent exotic and native species are labeled using USDA Plants Database symbols (USDA, NRCS 2012). Community-level variables (%Exrich = percentage exotic richness; %Exabun = percentage exotic midpoint abundance; Narich = native species richness) and surrounding landscape descriptors (Dev = percentage developed land cover) were overlaid on the ordination (each variable independently explained >20% of variation). Overall, a three-dimensional ordination explained 41% of variation (axis 1  $R^2 = 0.13$ ; axis 2  $R^2 = 0.13$ ).



**Figure 3-6:** Random forests (RF) variable importance plots showing ranked importance of surrounding landscape attributes (PR = patch type richness; PARM = perimeter to area ratio mean; CO = contagion; AG = agricultural cover; DT = developed cover), native species richness (NSR), and herbivore presence (TRT), in predicting absolute and percentage exotic plant abundance. Variables are ranked according to the normalized mean decrease in accuracy resulting when variables are randomly permuted compared to when observed data is included. The most important variables cause the greatest reductions in accuracy when they are randomly permuted. Separate analyses were conducted for stem density, cover, and cover class midpoint abundance metrics.

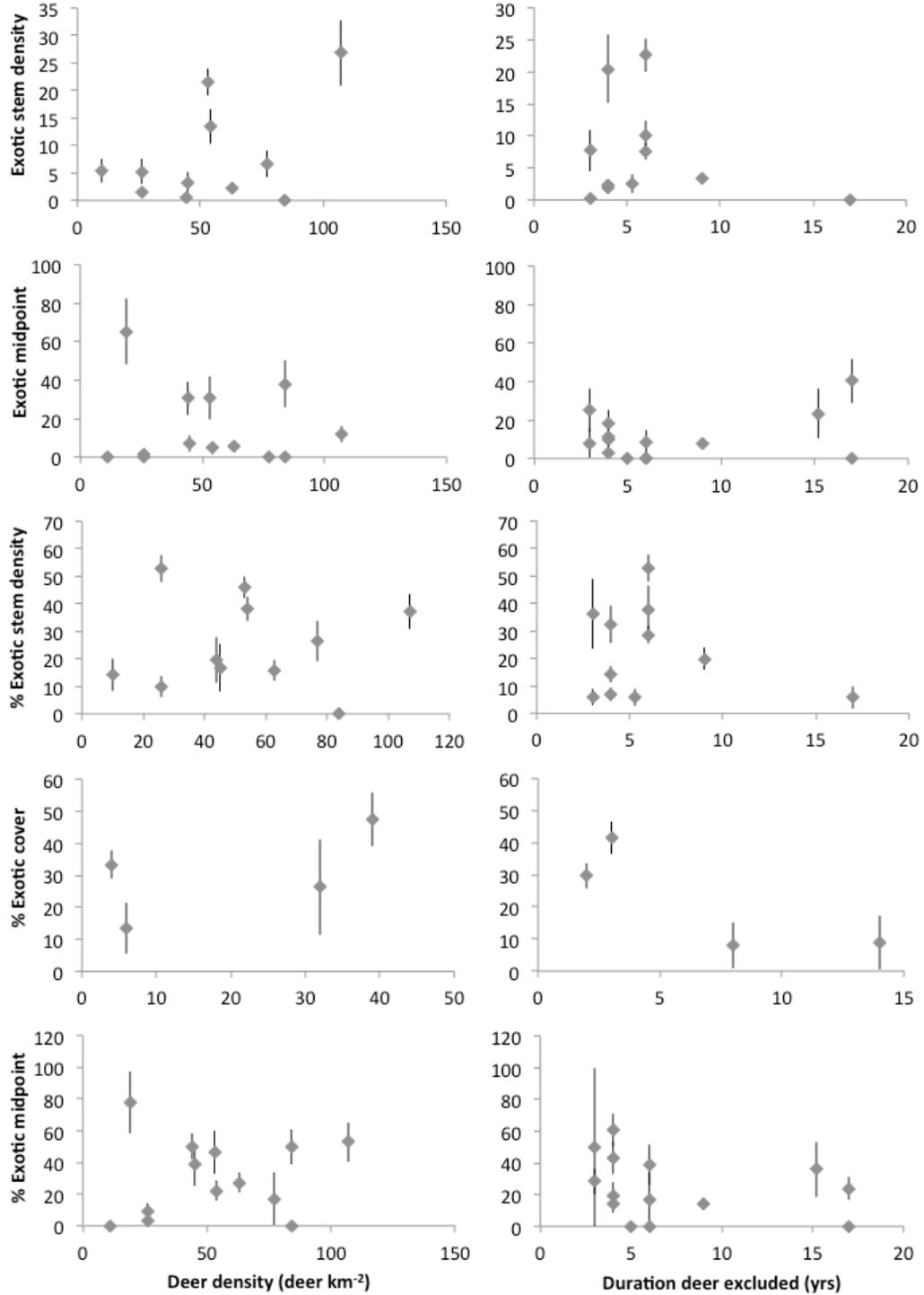


**Figure 3-7:** Random forests (RF) variable importance plots showing ranked importance of surrounding landscape attributes (PR = patch type richness; PARM = perimeter to area ratio mean; CO = contagion; AG = agricultural cover; DT = developed cover), native species richness (NSR), and herbivore presence (TRT), in predicting absolute and percentage exotic species richness. Variables are ranked according to the normalized mean decrease in accuracy resulting when variables are randomly permuted compared to when observed data is included. The most important variables cause the greatest reductions in accuracy when they are randomly permuted. NSR was not included in percentage exotic species richness model.

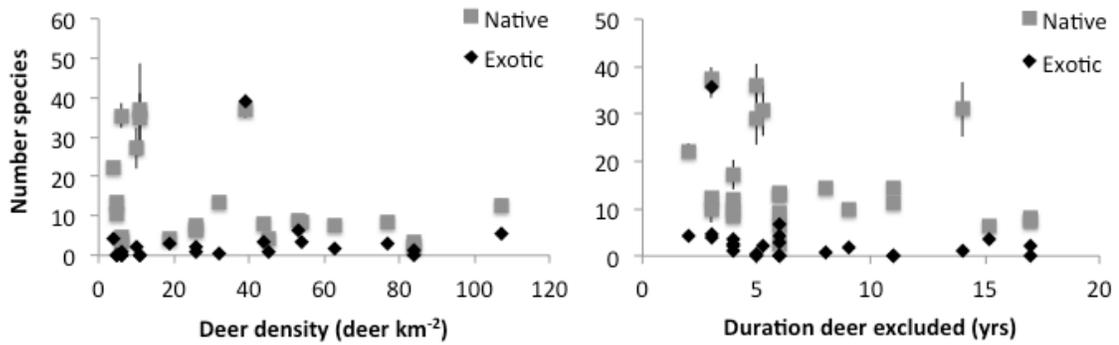


**Figure 3-8:** Exotic plant species cover in relation to (a) site-level deer density estimates or to (b) duration of time deer were excluded and percentage exotic species richness in relation to (c) deer density or to (d) duration of time deer were excluded. Data points represent site means ( $\pm$  SE). Dotted lines indicate trends that were not statistically significant at  $\alpha = 0.05$ . \*P values were based on mixed effect model analysis, while equations and  $R^2$  values were based on simple linear regression for visualization. Deer density estimate confidence intervals (Tab. 1-A1) are included for visualization if available (they were not incorporated into statistical analysis).

## Appendices



**Figure 3-A1:** Scatterplots showing absolute exotic or percentage exotic plant abundance in relation to site-level deer density estimates or duration of time deer were excluded. Data represent site means ( $\pm$  SE). Deer density estimate confidence intervals were excluded for clarity (but see Fig. 3-8).



**Figure 3-A2:** Scatterplots show native and exotic species richness in relation to estimated deer density or duration of time deer were excluded. Data represent site means ( $\pm$  SE) since deer density estimates were reported at the site-level. Deer density estimate confidence intervals were excluded for clarity (but see Fig. 3-8).

**Table 3-A1:** Correlation matrix used in landscape metric selection (DT = total developed cover; AG = total agricultural cover; PARM = perimeter-area ratio mean; CO = contagion; PR = patch richness; TF = total forest cover; TE = total patch edge).

	DT	AG	PARM	CO	PR	TF	TE
DT	1						
AG	0.2274972	1					
PARM	-0.1352633	0.37782675	1				
CO	-0.6553033	-0.6884474	-0.3007042	1			
PR	0.4047553	0.38065888	-0.0792681	-0.4950983	1		
TF	-0.7121886	-0.8158858	-0.1304968	0.8980562	-0.5420429	1	
TE	0.6140401	0.72366256	0.39384915	-0.9723101	0.49380321	-0.8724319	1

## **Epilogue**

In this dissertation, deer food plant preference was found to alter plant species composition in northeastern United States forest understories. Specifically, white-tailed deer selectivity reduced native plant abundance and species richness and facilitated increases in abundance of several invasive exotic plants. These field-based patterns were strongly linked to deer preference in controlled palatability trials. Despite some invasive exotic plants decreasing in the presence of deer, overall, deer increased the degree of plant invasion. When viewed from a landscape scale perspective, invasion patterns were strongly linked to native species richness and a suite of fragmentation metrics that characterize landscape structure and composition. Multiscalar processes drove plant invasion patterns. Top-level landscape-scale processes and bottom-level primary producer-consumer interactions were simultaneously important. What follows are additional perspectives, alternative methods, and potential applications for more efficient invasive plant management.

### **Relevance to ecological theory**

In the Northeastern United States, the success of exotic invasive plants is aided by their unpalatability (chemical or physical deterrents) and tolerance (rapid regrowth following losses to herbivory) to deer pressure. Contrary to my Chapter 1 hypotheses, I found that deer did not facilitate all exotic plants and, similarly, deer did not decrease all native plants. Deer increased the abundance of several species while decreasing the abundance of others. In Chapter 2, I demonstrated that the deer vs. no-deer patterns observed in Chapter 1 can be explained in large part by differences in palatability. These findings help contextualize previous research showing

that some exotic plants increase in the presence of deer (Knight et al. 2009, Eschtruth and Battles 2009, Kalisz et al. 2014) while others decrease (Rossell et al. 2007) or are unaffected (Bowers 1993). At the level of plant species-herbivore interactions, native and exotic plants responded similarly to deer herbivory. Some plant species have traits enabling their coexistence with deer, while others lack such traits. This could be explained by the lack of biochemical differences between native and exotic plants (Lind and Parker 2010). At the community scale, I found that deer did not affect the absolute abundance of exotic plants, but they significantly reduced native plant abundance, and increased community-wide invasion (exotic proportion of plot-level vegetation) (Chapter 1). Thus, at the community-level, native and exotic plants responded in separate ways to deer herbivory, shifting community composition in direct (native plant decline) and indirect (relative increase in exotic plants) fashions.

The exotic plant species occurring in a given location are typically a small subset (~one tenth) of the larger group of species initially introduced (Williamson and Fitter 1996). Many more exotic species are transported to novel territories than actually establish and persist. Thus while ample evidence exists for deer herbivory reducing native plant species more than exotic species (Wiegmann and Waller 2006), records of introduced exotic species failing to establish due to herbivory might not exist. Thus, researchers should be cautious in interpreting the strong decreasing effect of deer on native plant richness and abundance and the lack of an observable effect on exotic plants. This is particularly important because exotic plants have been found to be generally more palatable than native plants (Parker et al. 2006, Morrison and Hay 2011). Consequently, biotic resistance by native herbivores is likely to be important in limiting plant invasion (Parker et al. 2006), especially in non-fragmented landscapes (Chapter 3) but due to a lack of records such patterns might be overlooked.

The small subset of species that are avoided by deer are also some of the most widespread exotics in the Northeastern US and they might be invasive precisely because they are

unpalatable (Chapter 2). Effective herbivore-deterrence via physical or chemical means is the mechanism underlying the plant invasion hypothesis of enemy release (Keane and Crawley 2002), i.e., where an invading species is successful in a novel range because it left behind natural enemies when it was transported from its native range. At the core of enemy release is an apparent competitive advantage but only where and when no similar enemies to those in the native range exist in the introduced range (i.e., the exotic range distribution). Preferential browsing of palatable species gives an indirect competitive advantage to unpalatable species (Holt 1977). Considering the herbivore preference–plant palatability range helps elucidate the opposing invasion hypotheses of enemy release and biotic resistance. Biotic resistance prevents or limits invader establishment via interactions in the native community occurring within the same trophic level as the invader or across trophic levels (Levine et al. 2004). For example, increasing native plant diversity was associated with reduced percentage exotic plant stem density in less fragmented landscapes in Chapter 3. Additionally, invaders that are palatable to abundant herbivores might be prevented from establishing via direct mortality. In contrast, relatively unpalatable plants that are not attacked by abundant herbivores in the introduced range will gain an indirect competitive advantage relative to palatable plants, evoking enemy release.

In deer preference trials, I found evidence for a preference-palatability gradient among the widespread and frequently occurring native and exotic species included in the experiment. For the invasive exotic plants studied, a fine line is apparent between herbivore tolerance to defoliation and plant-herbivore mutualisms. All of the invasive plants that were found to be palatable to deer possess fleshy fruits (Chapter 2), which are known to be animal-dispersed. Edible fruits evolved to attract animal-dispersers, who then consume the fruit and seeds contained therein. Then, perhaps a long distance away, animals excrete wastes as well as seeds, thus providing an animal-mediated dispersal mechanism (Myers et al. 2004). This mutualistic

exchange of food for dispersal of progeny is likely to be one of the most important mechanisms for plant colonization in primary succession as well as in early successional communities.

While birds are exceedingly important frugivorous dispersal agents (Richardson et al. 2000), deer are also known to disperse many invasive plants in the Northeastern US (Gill and Beardall 2001, Myers et al. 2004, Williams et al. 2008), including many of the invasive plants studied here (Chapters 1 and 2). For instance, 95% of viable seeds found in deer fecal pellets, collected in central New York State, were from 46 exotic plant species, including *Rosa multiflora* (Myers et al. 2004), a thorned vine/shrub, which was an indicator species of no-deer plots (showing that deer reduce its abundance) and which was largely palatable in deer preference trials (Chapter 2). White-tailed deer have been shown to spread even the unpalatable *Microstegium vimineum* via endozoochory (Williams et al. 2008). Even a small quantity of consumed biomass and the intentional or incidental consumption of seeds could result in seed dispersal and the establishment of new populations (Janzen 1984, Myers et al. 2004). Thus, being palatable and sustaining defoliation is a tolerable loss in exchange for propagule dispersal. Moreover, it emphasizes the various, and opposing, modes of animal-assisted plant invasion. My work lends support to both the enemy release and biotic resistance hypotheses. While some of the least palatable plants are also the most invasive, the palatable invasives appear to have anti-herbivore defenses or a mutualistic tolerance of herbivory to explain their invasiveness. Fleshy-fruited species are typically found in open habitats, thus their high abundance even in the face of high deer density, was not observed in this forest habitat-focused research. However, the high palatability of fleshy-fruited exotic species was strongly documented in Chapter 2. This means that research programs based only on one invader could provide evidence for either the enemy release or the biotic resistance hypothesis. However, my research suggests that one or the other of the enemy-based hypotheses of plant invasion can be supported depending on invader palatability to abundant herbivores in the system.

Primary producer-consumer relationships are important determinants of plant community assembly. In fact, a recent meta-analysis concluded that herbivore impact in oceanic systems was even more important than temperature in regulating plant richness and abundance (Poore et al. 2012). Additionally, the meta-analysis found that herbivore impact was determined by billion year-old anti-herbivore traits, indicating a strong phylogenetic signal. This finding is remarkable even for land-based plant communities, given that terrestrial life has oceanic origins, and suggests that herbivore coexistence traits might be even more important than environmental factors in facilitating high biodiversity.

In addition to exploring the community-level role of deer herbivory in plant invasion in Chapters 1 and 2, I explored the influence of a suite of landscape fragmentation metrics on regional plant invasion patterns in Chapter 3. For the extent of the Northeastern US region, landscape structure and composition were very important in explaining exotic plant abundance and the degree of plant community invasion. That patch richness was associated with increased exotic plant invasion is not surprising because more heterogeneous landscapes made up of more habitat types also support more species and, given the presence of exotic propagules, likely have more opportunities for invaders. For example, increased diversity of geologies (Anderson and Ferree 2010) and topographies (Crisfield 2012) leads to greater biodiversity.

In this work, the surrounding landscape influenced both exotic plants and deer density and some exotic plant invasion patterns depended on interactions between herbivory and the landscape attributes. In fragmented landscapes, deer and exotic plants have been known to be individually more abundant (Alverson et al. 1988, Vilà and Ibáñez 2011), however this is the first work to show that landscape fragmentation and deer density factors interact to facilitate exotic plant invasion. Increased resource availability in fragmented landscapes (e.g., light and anthropogenic eutrophication) might ultimately explain the increases in deer and exotic plant invasion, given that deer and invasive plants are typically more abundant in high-light, nutrient-

rich environments. Thus, local-scale herbivory, based on palatability, and landscape-scale fragmentation, driven by the expanding influence of humans, appear to be strongly regulating factors in exotic plant invasion.

Landscape structure provides a top-down constraint on deer abundance (Alverson et al. 1988). Non-fragmented landscapes support fewer deer and fragmented landscapes, which have greater developed cover and greater edge habitat (i.e., higher perimeter to area ratio), support more deer. The gradient in deer density across these landscapes helps explain differences observed in the plant communities, including plant invasion patterns. Deer prefer to forage in landscapes with greater edge habitat and less closed canopy habitat, areas where they have more intense effects on vegetation (Côté et al. 2004), particularly on native compared to exotic plants (Chapter 1), and where greater plant invasion was observed (Chapter 3). In addition to the top-down constraint of landscape configuration, the bottom-level factors operating at the level of plant-deer interactions investigated in Chapters 1 and 2 were important in understanding plant invasion at a local scale, showing that different foraging patterns are exhibited at different scales (Senft et al. 1987). At the community scale, deer selectively choose to eat plants or plant parts that are relatively more palatable, while avoiding unpalatable and/or highly defended ones. As a result of very small-scale decisions regarding which plants to consume or avoid, I found that deer can regulate which species are facilitated or inhibited in plant communities. Plant community composition and abundance at the patch scale represent the middle level in which top-level and bottom-level forces are revealed. In landscape ecology, hierarchy theory suggests that top-level forces constrain and bottom-level forces explain (Ahl and Allen 1996) and my research appears to support this theory. Landscape-scale factors and their effects on deer density constrain plant communities, while deer diet selection and plant traits explain the plant species-level increases and decreases observed across fenced and unfenced plots.

## **Limitations and alternative methods**

In Chapter 1, data from each site could have been analyzed individually. However, the goal of the research was to discern the overall effect of deer presence on exotic plants, while accounting for (and effectively ignoring) floristic variation between sites and across years. Using site as a random effect accomplished the research goal. Alternatively, a formal meta-analysis statistical approach could have been employed in this chapter. This would have involved determining the response ratio (e.g., log ratio) of exotic plant abundance or proportion in deer vs. no-deer plots. However, because I had the fortunate access to raw datasets, I was not limited to using treatment means from each site, which are relied upon in formal meta-analysis (Gurevitch and Hedges 1999, Hedges et al. 1999). Another goal of the research was preserving as much of the data as possible in its original form. Since ratios remove potentially important differences between plots (i.e., the same ratio could be a result of very different exotic abundance differences across plots), I decided against using formal meta-analysis techniques. Instead, I was able to explore deer effects on absolute exotic plant abundance as well as on the degree of plant community invasion (a relativized metric that took into consideration total plant abundance).

In Chapter 2, I used herbivore choice preference trials instead of no-choice trials. The primary goal in this research was determining the relative preference of exotic vs. native species, so representatives from both groups should be in each trial. Conducting no-choice trials and retaining the high number of species tested in tandem with choice trials would have been impossible given the short seasonal timeframe for a set of trials. Even in the two-week timeframe implemented, plant phenology changed from the first to the last trial, thus approximately two weeks appeared to be the maximum time within which to conduct all trials for a season. At minimum, 15 additional trial days would have been required to test no-choice preference of each species because 15 species were included in preference testing, let alone the need for replication.

I decided the biggest gains in understanding relative deer preference for a large suite of species could be achieved by including all species of interest in every trial. Another alternative approach would have been to conduct preference trials during winter. Only woody species would have been candidates for those trials, but still this could have increased understanding of the broader picture of relative deer preferences for the suite of species. The reason winter trials were not conducted was because the focus of preference trials was on the leafy biomass common among all plant habits (from grasses and ferns to shrubs and trees) and which was quantified in the regional plant censuses used for analysis in Chapters 1 and 3.

In Chapter 3, many variables could have been included in analyses beyond herbivore presence, native plant diversity, and landscape structure and composition metrics. I decided against including a suite of plot-scale environmental factors, because much previous research has focused on the role of environmental gradients in plant invasion (Nord et al. 2010, Averill et al. 2010, 2011). Environmental variation likely influenced the plant invasion patterns observed across the region in this work. However, less attention has been given to the roles of high deer numbers and landscape structure and composition in plant invasion and thus I intended to focus my research on these less studied, but seemingly highly important plant invasion factors. Importantly, ecosystem-level environments are affected by both deer (Heckel et al. 2010) and landscape fragmentation (Kupfer et al. 2006), thus associated patch-scale environmental covariation might have been inherently accounted for by using those variables.

Alternative statistical approaches could have been taken in Chapter 3, such as using partial least squares regression, which identifies relevant variables and their magnitudes of influence in complex phenomena (Carrascal et al. 2009), or path analysis, which predicts direct and indirect effects among a suite of variables (Wootton 1994). However, the Random Forests approach was used because it does not assume linearity, can handle small n large p problems, is efficient in handling many predictor variables, and avoids overfitting the models. Mixed models

were used because they accounted for the random effects of plot pair and site, as well as enabled detection of interactions among variables. To my knowledge, neither partial least squares nor path analysis can account for random effects. Random Forests cannot account for random effects either, thus error in resulting models cannot be attributed to known hierarchical structure in the data. Another downside is that although Random Forests accounts for interactions without requiring model specification, these are not explicit in statistical output. An alternative to Random Forests is the highly cited cforest package for R statistical software, which is based on a modification of the random forest algorithms that aims to reduce bias in variable selection (Strobl et al. 2007), although it appears to have similar issues with identifying interactions. Random Forests might be biased when potential predictor variables vary in their scale of measurement or number of categories, thus in future work aiming to determine the relative importance of multiple predictor variables, cforest might be a useful tool.

### **Potential applications**

Based on this work, using limited resources to control invasive exotic plants that are facilitated by deer seems likely to be ineffective. Since landscape configuration ultimately and high deer density proximately appear to increase these species, controlling them will not solve the overarching problems driven by anthropogenic alterations and would not be expected to increase native plant diversity. In this scenario, the invasive plants appear to be passengers of ecological change (MacDougall and Turkington 2005) and eliminating them will not reverse the damage issued by top-level forces. Instead, other invaders would likely take their place unless additional management activities are instituted, such as planting unpalatable native species, excluding deer with fencing, or increasing hunting to reduce deer populations.

In the face of high deer pressure, less palatable species should be preferentially planted. Lists of unpalatable species are available from local extension agencies (e.g., Perdomo et al. 2004) and many gardening retailers signify ‘deer-resistance’ on labels. Fencing to exclude deer is also an option, though requires an initial investment in fencing materials, as well as long-term maintenance. There appears to be a trade-off in fencing costs and maintenance required; the sturdier, and therefore more expensive the fencing, the less upkeep is required. Fencing should be at least 2 m in height to prevent deer jumping over the fences. Alternatively, two adjacent shorter (e.g., 1.3 m) fences can also provide successful deer exclusion. Fences can also be shorter when they exclude deer from a relatively small area (e.g., <math>9\text{ m}^2</math>), into which they are unable or unlikely to jump. Electric fences can also be effective and, especially when solar-powered, can be low-cost alternatives to traditional fencing.

Reducing deer numbers, especially in fragmented landscapes where deer densities are higher, would likely increase native species diversity and reduce the degree of exotic plant invasion in those areas. Successful deer reduction programs have been instituted by hiring professional sharpshooters, including at Catocin Mountain Park, MD. However, deer management is difficult and controversial and voices from many perspectives have been involved in the debate over the past century (Leopold 1933, Leopold et al. 1947, Alverson et al. 1988, Sterba 2012, Cerulli 2014). Repeated population reductions year after year are typically necessary, since deer move across the landscape widely. Hunters, farmers, home- and landowners, gardeners, landscapers, motor vehicle drivers, insurance company stakeholders (due to vehicle collisions), gun control advocates and opponents, animal rights activists, and ecologists are all interested in deer management regulations. Abundant deer reduce plant biomass in agricultural crops and ornamental plantings and cause many vehicular accidents. Specifically, white-tailed deer can cause major biomass losses in soybean, corn, and cover crops (pers. comm. with G. Roth). Additionally, cars are thought to kill more white-tailed deer than hunters in many

Eastern US states. However, hunters are likely the most vocal group of all interested parties and, unfortunately, many of them strongly advocate for low numbers of issued hunting permits to keep deer numbers high and hunting relatively easy. Major social changes would need to occur to convince stakeholders of the importance of smaller deer herds.

Changing landscape structure and composition in order to lower plant community invasion and promote native diversity in forest understories would be challenging in that it would require major changes in social perspective and in altering land use (e.g., increasing non-crop habitat) (Egan and Mortensen 2012). Joint management with deer reductions would appear to offer the most benefits.

### **Do plant invasions have a silver lining?**

Although plant invasions are associated with long lists of negative impacts on native plant and animal assemblages, invading plants also offer ecosystem services. Invaded communities can facilitate native birds via fleshy fruit provisioning and native plants via seed dispersal (Gleditsch and Carlo 2011), floral service provisioning, soil stabilization, and being able to establish and grow where and when native plants are incapable. Plant invaders could be well suited for providing ecosystem services in the face of extreme anthropogenic alterations, including Earth's rapidly changing climate.

Humans have so drastically altered landscape and environmental conditions that the majority of natural area plant communities are novel in one way or another. Expecting native plant communities to remain static when the conditions regulating species composition and abundance are so different from those under which they previously evolved, *sensu* a no-analog future (Fox 2007), is unwise. Weed management in natural areas, based on trying to mimic past floristic censuses, is naïve. Plant assemblages arise in response to the constantly changing

filters/rules of community assembly. Interestingly, the degree to which plant communities have changed in the face of human disturbance provides important insight into how anthropogenic activities alter community assembly trajectories. Perhaps any plants that are capable of persisting in the novel conditions humans have created should be welcomed and accepted, even if it means temporarily lower diversity and altered ecosystems. Although plants certainly have effects of their own on other plants, animals, and microbes and on system material cycling, they are unlikely to be the ultimate drivers of ecological change (MacDougall and Turkington 2005, Didham et al. 2005). Humans have become the ultimate drivers of ecological change on Earth. Instead of placing blame on plants, consider that weedy and invasive plants might be playing important roles in ecosystem service provisioning particularly where native plants have been reduced in abundance, for example by habitat loss and fragmentation and high deer densities.

Previously, ecologists have questioned the categorization of species by native/exotic status (Davis et al. 2011). Davis and colleagues (2011) suggested that ecologists and the public “embrace the fact of ‘novel ecosystems’”, consider both the uses and harms of invaders, and focus on species’ functions rather than origin. Many other highly regarded ecologists view such perspectives as attacks on the field of invasion ecology, maintaining that non-native species can have severe impacts that might not be manifested for decades (Simberloff 2011, on behalf of 141 signatories). However, in the system I studied, the drivers causing severe changes to forest understory communities do not appear to be the non-native plant species but instead native deer and human activity. Thus, vegetation patterns need be considered in the context of indirect drivers, multiple interacting trophic levels, and hierarchical phenomena. Species’ services, such as persistence despite heavy herbivore pressure and fragmented habitats, rather than their area of origin appear highly important in rapidly changing systems.

Weedy, invasive species, i.e., early successional plants, play an important role in quickly tying up available resources. Invaded systems have been shown to have greater productivity and

decomposition than uninvaded systems (Hooper et al. 2012). Additionally, invasive plants are more efficient in acquiring limiting resources than natives (Suding et al 2004; Funk and Vitousek 2007), so the fact that invaded communities have higher primary productivity (Liao et al. 2007) is not surprising. Invaded systems, regardless of habitat type (forests, grasslands, and wetlands) also have higher root and shoot carbon stocks and higher plant and soil nitrogen concentrations (Liao et al. 2007). If invasive plants are faster at acquiring abundant resources and are more productive than non-invasive plants, ecologists could view invaders as providing valuable ecosystem services. During the switch from an uninvaded community characterized as resource-poor to another state characterized as resource-rich (e.g., due to anthropogenic eutrophication), a system might be able to maintain functionality or biological robustness with the aid of invasions (Kitano 2007). Drastic changes might not result from perturbations if the system is open to colonization by species which are able to persist in the face of the altered conditions and which can help compensate for lost native species.

Interestingly, across much of Earth's surface, humans have reduced biodiversity with limited diversity agricultural systems. Farmers aim to minimize interspecific competition in crop fields. However, progress has been made toward regenerative agriculture, which places high value on covering soil and increasing species diversity in cropping systems (Pearson 2007, Groff 2008). Nonetheless, while monodominance is traditionally highly valued in agricultural systems and much time and energy is spent keeping it that way, in natural systems the near monodominance inherent in plant invasions carries negative connotations and is associated with undesirable effects, namely declines in biodiversity (Hooper et al. 2012). Much time and energy is spent trying to reverse invasion patterns and regain diversity. Perhaps this is a paradox and a challenge that epitomizes modern multifunctional landscape management.

Ecologists are perfectly situated to help advance broader perspectives and foster holistic approaches to modern land management problems (Naeem 2002). Considering potential

ecosystem services of invasive plants seems just as important as considering ecosystem disservices. Focusing on the conservation of ecosystem functions and services is an alternative application of ecological principles instead of trying to eliminate invasive exotic plants simply because they are non-native and associated with ecosystem change. Weedy and invasive plants appear to provide the valuable services of stabilizing resources and increasing productivity.

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## Kristine M. Averill Curriculum Vita

### PEER-REVIEWED PUBLICATIONS AND THESES

- Averill KM, A DiTommaso, CL Mohler, and LR Milbrath (2011) Survival, growth, and fecundity of the invasive swallow-worts (*Vincetoxicum* spp.) in New York State. *Invasive Plant Science and Management* 4: 198-206
- Averill KM, A DiTommaso, CL Mohler, & LR Milbrath (2010) Establishment of the invasive perennial *Vincetoxicum rossicum* across a disturbance gradient in New York State, USA. *Plant Ecology* 211: 65-77
- Blanchard ML, JN Barney, KM Averill, CL Mohler, & A DiTommaso (2010) Does polyembryony confer a competitive advantage to the invasive vine *Vincetoxicum rossicum* (Apocynaceae)? *American Journal of Botany* 97(2): 251-260
- Averill KM (2009) *Vincetoxicum* spp. biology and ecology in New York State: Establishment success, vegetative expansion, and physiology of two invasive perennial vines in the Apocynaceae. MS Thesis, Cornell University, Ithaca, NY. 123 pp
- Averill KM, A DiTommaso, & SH Morris (2008) Response of pale swallow-wort (*Vincetoxicum rossicum*) to triclopyr application and clipping. *Invasive Plant Science and Management* 1(2): 196-206
- Averill KM & A DiTommaso (2007) Wild parsnip (*Pastinaca sativa* L.): A troublesome species of increasing concern. *Weed Technology* 21(1): 279-287
- Averill KM (2005) Nutritional and consumer preference tests of 'Liberty' apples grown under organic and integrated fruit production systems. BS Honors Thesis, Cornell Univ, Ithaca, NY. 35 pp

### SELECTED AWARDS AND HONORS

- Northeastern Weed Science Society (NEWSS) 1st Place Graduate Student Oral Paper Presentation (2012)
- NEWSS Robert D. Sweet Outstanding Graduate Student Award (2011)
- Cornell University MacDonald & Musgrave Graduate Student Award for Excellence, Dept. of Crop and Soil Sciences (2008)
- NEWSS 1st Place Graduate Team, Collegiate Weed Science Contest (2006)
- Cornell University Ring Memorial Award for Excellence in Plant Sciences (2005)

### SELECTED SERVICES

- Peer reviewer for one or more of the following journals per year: *Biological Invasions*, *Canadian Journal of Botany*, *Canadian Journal of Plant Science*, *Ecology Letters*, *Invasive Plant Science and Management*, *Plant Ecology*, and *Weed Research* (2006–2013)
- Penn State Ecology Graduate Student Representative for the Ecology Program Committee (2011)
- Penn State Ecology Program Spring 2012 Seminar Series: *Saving a Changing World: Ecology in the Public Eye* Coordinator (2011–2012)
- Northeastern Weed Science Society Nominating Committee (2011–2012)
- Governor's Invasive Species Council Meeting, Harrisburg, PA, presentation on *Invasive Plants and Deer Research* (2011)
- Penn State Ecology Graduate Student Representative for the Andersen Award Committee (2010–2011)