

Healthy forests to resist invasion: The role of resources, plant traits, and propagule
pressure

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Alexandra Gavin Lodge

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Dr. Peter B. Reich, Advisor

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Dedication

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Abstract

Invasive species are a global problem, dominating habitats, negatively impacting biodiversity, and changing ecosystem processes. There is no consensus regarding which nonnative species are likely to become invasive if introduced, nor which habitats are most susceptible to invasion. To investigate these questions, we studied the native and nonnative plants in 68 oak forest stands in Minnesota, USA. Nonnative plants possessed functional traits similar to those of some native species, suggesting that they exhibit similar growth strategies. These traits allow nonnatives and some natives to grow quickly in high resource environments. Among these same sites, we also examined whether there are characteristics of forests that make them more susceptible or resistant to a particularly pernicious invasive shrub, common buckthorn (*Rhamnus cathartica* L.). We found that buckthorn presence was best predicted by high propagule availability and site light levels, while buckthorn was more abundant in sites with higher soil fertility, lower resident plant diversity, and less leaf litter. Timber harvesting also affected buckthorn abundance, with more buckthorn in sites that were clearcut or unharvested than in those that were selection harvested. Management practices that minimize increases in light levels and soil disturbance or maintain or increase resident plant diversity (e.g., reduce deer populations) may help uninvaded forests resist buckthorn invasion, especially if local propagule pressure is also reduced.

Finally, we also investigated the below-ground effects of buckthorn by examining nutrient cycling across a natural gradient of buckthorn abundance along an invasion front.

Buckthorn appears to increase soil nitrogen, organic carbon, calcium, and pH through deposition of nutrient-rich leaf litter. Increases in soil fertility may lead to increased forest productivity and potentially facilitate further spread of buckthorn or other invasive species that may be better able than natives to take advantage of abundant resources. Overall, both the traits of invasive plants and the characteristics of receiving systems can play key roles in determining the success of nonnative species and the potential impacts they may have on native ecosystems.

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Introduction

Invasive species are a major driver of biodiversity loss around the globe. While much research has been conducted on invasion biology over the past 20 years, major questions still remain, including: which nonnative species are most likely to become invasive, and which habitats are most susceptible to invasion? Comparisons of plant functional traits are one method for predicting which newcomers are more likely to negatively impact ecosystems, and therefore allow managers to control them before they spread and become a problem. While many researchers have found nonnative plants to have more acquisitive traits than native plants that allow them to grow and reproduce quickly, there is no consensus and trait differences appear to vary across systems and species. When a nonnative species does establish and begin to impact native communities, it does not invade all habitats equally. While traits of the invading species are important in determining its success in various habitats, biotic and abiotic characteristics of resident communities can also play a role. Differences in resident plant diversity, varied availability of resources such as light or soil nutrients, and recent disturbance history could all make a given community more or less resistant to invasion. Additionally, while the above-ground impacts of many invasive plants on invaded communities have been well studied, much less is known about below-ground impacts, including potential ecosystem effects through changes in nutrient cycling. We explored these research topics through a field study of 68 mesic oak forest stands across central and southern Minnesota, as well as a closer examination of the impacts of the nonnative

shrub common buckthorn (*Rhamnus cathartica* L.) along an invasion front in central Minnesota.

Chapter 1 examined invasion from the perspective of arriving species. We investigated whether there are functional traits that allow some nonnative species to be successful in their invaded range. We compared trait values of native and nonnative plants at 68 oak forest stands in Minnesota using ordinations to examine multidimensional trait space, as well as relating community weighted mean trait values to the proportion of nonnative species present and site-level environmental conditions. We found few differences between trait spaces occupied by native and nonnative species, suggesting similar growth strategies. More nonnative species were observed in sites with community weighted mean trait values indicative of fast-growth strategies. These strategies were also more common in sites with higher light levels and greater nutrient availability. Overall, our results suggest that successful nonnative plants have functional traits similar to native plants. Additionally, more resource-rich sites may be more susceptible to invasion because both native and nonnative plants are more successful in these high-resource environments.

Chapter 2 investigated invasion from the perspective of receiving communities. We focused on one invasive shrub, common buckthorn (*Rhamnus cathartica* L.), that is especially problematic in oak forests of the Upper Midwest. We examined whether there are characteristics of those forests that make them more or less susceptible to invasion. Using a subset of the study sites examined in Chapter 1, we estimated buckthorn propagule availability surrounding the sites, measured environmental characteristics,

including soil and litter conditions, and surveyed the vegetation community. Overall, we found that buckthorn presence was best predicted by high propagule availability and site light levels, while buckthorn was more abundant in sites with higher soil fertility, lower resident plant diversity, and less leaf litter. Timber harvesting also affected buckthorn abundance, with more buckthorn in sites that were clearcut or unharvested than in those that were selection harvested. If land managers can limit increases in light levels (e.g., conduct selection harvests instead of clearcuts) and maintain or increase resident plant diversity (e.g., by reducing deer populations), while also working to reduce local buckthorn propagule pressure, they may be able to manage forests to better resist invasion by common buckthorn.

Chapter 3 investigated how buckthorn may be influencing below-ground processes, including nutrient cycling. We measured the annual influx of nutrients through leaf litterfall as well as nutrient pools and fluxes in the soil across two natural gradients of buckthorn abundance (invasion fronts). Buckthorn leaves and leaf litter contained more nitrogen and calcium than red maple or oak leaves, the dominant overstory species in this system. Additionally, more soil nitrogen, organic carbon, and calcium were present in sites with more abundant buckthorn. We observed limited impacts of buckthorn on net nitrogen mineralization, but did see changes in nutrient composition of soil microbes. Overall, buckthorn appears to increase soil nitrogen, organic carbon, calcium, and pH through deposition of nutrient-rich leaf litter. Such increases in apparent soil fertility due to buckthorn invasion could have substantial impacts on ecosystem functions such as forest productivity, pedogenesis, and nutrient export to groundwater and surface waters.

As a graduate student member of the Risk Analysis for Introduced Species and Genotypes Integrative Graduate Education and Research Traineeship (ISG-IGERT), my research also fits within a risk analysis framework. Risk assessment is a technical process used to determine the probability of an adverse event occurring and the consequences of that event. Risk assessment is encompassed within the wider framework of risk analysis, which includes communication of the risk assessment to stakeholders as well as risk management, or actions that could be taken to mitigate the risk (USEPA 1998). An ecological risk assessment has three main components: problem formulation, exposure and effects assessment, and risk characterization.

Problem formulation is the first stage in the process of ecological risk assessment, where stakeholders determine what entity they want to protect from a potential stressor. In the context of nonnative plant invasion, this entity could be a specific site of interest, a specific forest type, or a specific bird or plant species. Next, a specific attribute of that entity is selected as the assessment endpoint, or something about that entity that is at risk and that can be measured and monitored. Examples of quantifiable assessment endpoints could be the number of birds or an ecological service provided by a forest such as water quality.

The exposure assessment phase of the risk assessment process involves determining the likelihood that the entity of concern will be exposed to the potential stressor, including the duration and quantity of exposure. In the nonnative plant invasion context, this could involve comparing climatic conditions between the native range of potential invader and the conditions in the potential new range to see if they match. The

effects assessment focuses on determining whether or not that level of exposure will lead to harmful ecological effects, or whether and how the invader may harm the ecological entity of concern.

Finally, risk characterization combines the estimates of exposure and effects to determine an overall estimate of risk. This phase includes a description of the lines of evidence leading to the conclusions and interpretation of the significance of any adverse effects, as well as addressing the levels of uncertainty in the risk estimation. Following the completed risk assessment, the conclusions are communicated to stakeholders and further analysis can be done to determine risk management strategies, or actions that could reduce the probability of the adverse event, reduce the magnitude of damage if the adverse event occurs, or reduce uncertainty in the estimates.

The research presented in this dissertation mostly falls within the exposure and effects assessment part of the risk analysis framework, specifically chapters 2 and 3. The study of susceptibility of forest stands to invasion by common buckthorn described in Chapter 2 is examining the likelihood of exposure of those stands to the adverse event of buckthorn invasion. We investigate the characteristics of different forests that may make them more or less likely to be invaded and make some recommendations of management strategies that could reduce the risk of buckthorn invasion (risk management). In Chapter 3, we focus on the effects of buckthorn invasion. We examine what effects buckthorn may have on soil nutrient processing if it were to invade a forest.

CHAPTER 1

Invasive plants in Minnesota forests are “joining the locals”

Summary

Predicting which newly arrived species will successfully establish and become invasive is a problem that has vexed researchers for decades. Plant functional traits, as indicators of plant growth strategies, have been used to try to distinguish between plants that are nonnative but unlikely to cause harm and those that will likely negatively impact native ecosystems. Two contrasting hypotheses used to explain the success of certain nonnative species have both been supported in the literature. Under the “join the locals” hypothesis, successful invaders would be expected to share functional traits with resident species because they employ growth strategies that are successful under local environmental conditions. Alternatively, under the “try harder” hypothesis, successful invaders are expected to have functional traits different from native species in order to take advantage of unused niche space or resources and outcompete resident plants. We set out to examine these two opposing theories using native and nonnative plants observed in 68 oak forest stands of the Upper Midwest United States. We focused on a suite of traits related to plant establishment and growth that were available in trait databases or easy to measure, including specific leaf area (SLA), leaf carbon to nitrogen ratio (C:N), wood density, plant maximum height, mycorrhizal type, seed mass, and growth form. Using ordinations in multidimensional trait space, we found few differences between trait spaces occupied by native and nonnative species. Nonnative herbaceous and woody species occupied smaller areas of trait space than natives, but nonnative trait space was within the space occupied by natives, indicating similar growth strategies. We also calculated community weighted mean (CWM) trait values for each site and observed a

higher proportion of nonnative species in sites with higher woody species CWM SLA and lower CWM leaf C:N. Site-level light and soil pH were correlated with CWM trait values, with higher woody CWM SLA in sites with higher soil pH and lower CWM leaf C:N in sites with higher light levels. This indicates that acquisitive leaf traits were correlated with site resource availability. Overall, our results suggest that nonnative plants have functional traits similar to natives and are therefore “joining the locals”. Both native and nonnative species with acquisitive trait values are successful in sites with more available light and higher soil fertility, suggesting that such sites may be more susceptible to invasion.

Introduction

New invasive plants arrive in the United States each year while previously introduced species continue to expand their populations (Mack et al. 2000, Mack and Lonsdale 2001). However, only a small portion of the nonnative species that arrive in the U.S. actually become invasive, or cause ecological or economic harm or harm to human health (Vitousek et al. 1996, Williamson 1996, Clinton 1999). Many nonnative species that are introduced are unable to establish populations due to dispersal limitation, small number of propagules in the initial introduction, negative interactions with resident species, or other limitations of the new environment (Mack et al. 2000, Mack and Lonsdale 2001). Other species may at first appear to be harmless and not able to establish and spread, but after a period of time, or lag phase, may quickly increase in population and become a problem for land managers (Mack et al. 2000, Simberloff 2009, 2011).

In order to try keep track of which invasive plants are likely to become invasive, many states have “weed watch lists” or lists of early detection target species that are based on a variety of differing criteria that indicate those species that scientists, policymakers, and managers think may enter their state soon and are likely to cause harm (Daehler and Carino 2000, MNDNR 2015, USDA 2015b). Many researchers have tried to predict which nonnative species are likely to become problems (Reichard and Hamilton 1997, Richardson and Rejmánek 2004, Krivanek and Pysek 2006). Such predictions are often based on comparisons between climate and habitat in the new and native range, characteristics of the nonnative species, and/or whether a given species has been considered invasive elsewhere. Ideally, policymakers would have a list of clear criteria that classify a potential new species as invasive or simply nonnative. Many researchers have tried to identify universal rules of invasiveness, but there has been no consensus (Rejmánek and Richardson 1996, Richardson and Pysek 2006, Hawkes 2007, Tecco et al. 2010). Some researchers have suggested that such rules must be more specific, at least to the region, habitat type, or taxonomic or ecological grouping (Tecco et al. 2010, Pyšek et al. 2014).

One broad criterion used to predict whether a given plant species will become invasive is an examination of its functional traits. Functional traits are morphological, physiological, or phenological features of plants that directly or indirectly impact a plant’s growth, reproduction, or survival, and are useful as measureable proxies for examining whether species differ in their resource accumulation and reproductive strategies (Violle et al. 2007, Cleland 2011). Core traits that are often studied because

they are central to the lifecycle of plants include plant size (height), seed size (mass), and leaf structure (specific leaf area) (Grime 1979, Westoby 1998).

Research on plant traits and invasiveness dates back to the 1970s when Baker (1974) defined the characteristics of an ideal weed to include rapid growth, ability to germinate in a variety of conditions, high seed output and long seed viability, and multiple dispersal vectors. Since then, research has compared the traits of native and nonnative plants. Invasives are often thought to be faster growing and better competitors than natives, but that is not always the case. In meta-analyses, researchers have found nonnative plants to have higher values for fitness, size, specific leaf area, seed number, and growth rate while also having smaller seeds that disperse better (Leishman et al. 2007, van Kleunen et al. 2010a, Ordonez et al. 2010, Thompson and Davis 2011, Flores-Moreno et al. 2013, Ordonez and Olf 2013). In contrast, other studies have found no differences in trait values between native and nonnative species (Hawkes 2007, Ordonez et al. 2010, Flores-Moreno and Moles 2013). Overall, there is no clear consensus on trait differences between native and invasive plants, and it seems as though differences may vary across species and systems (Dawson et al. 2011).

A useful framework for thinking about invasiveness may be to look at two opposing theories of how given trait assemblages can allow or prevent a nonnative species from establishing in a new community. The first is “join the locals”, which follows the concept of habitat filtering (Keddy and Weiher 1999), where filters such as dispersal limitations or nutrient stress could reduce the range of growth strategies that could be successful in any given community (Daehler 2001, Leishman et al. 2007, Tecco

et al. 2010). Under this theory, successful invaders would have traits similar to the resident natives. Alternatively, the “try harder” framework follows the concept of limiting similarity (Keddy and Weiher 1999), whereby introduced species will more successfully establish in communities that lack species similar to them because they can tap into different resources or acquire the same resources in a different way (van Kleunen et al. 2010a, Tecco et al. 2010, Ordonez et al. 2010). While Tecco et al. (2010) referred to it as “try harder”, it could also be thought of as “try differently” – successful introduced species may possess trait values that are more extreme than (“try harder”), or simply different from (“try differently”), the resident species. This is also similar to Darwin’s naturalization hypothesis, in which invasives are more likely to be successful if they are less related to resident species (Richardson and Pysek 2006, Strauss et al. 2006).

We set out to examine these two opposing theories using native and nonnative plants in a single forest type – upland, mesic, oak-dominated forests of the Upper Midwest United States. We focused on traits that are correlated with life history strategies related to plant establishment and survival. Many other studies of traits and invasiveness examined many species across a wide range of habitats, defined at a coarse level (van Kleunen et al. 2010a, Ordonez et al. 2010, Richardson and Rejmánek 2011, Pyšek et al. 2014), or studied only one nonnative species within its new environment (Brym et al. 2011). We instead look in more detail at both herbaceous and woody nonnative and native plants in a single habitat, temperate forests, which have been less frequently studied than grasslands or tropical forests in the functional trait/invasion literature (Rejmánek and Richardson 1996, Daehler 2001, Krivanek and Pysek 2006, Dawson et al.

2011, but see Herron et al. 2007). Focusing on a single habitat type may provide more clarity and avoid the contradictory patterns often found in other studies conducted across larger, more heterogeneous areas.

Our objectives were to 1) Compare the average trait values of common native and nonnative plants in upper Midwestern forests to assess whether nonnative plants are similar to or different from native species; 2) Examine multiple traits simultaneously using multidimensional trait space to determine whether natives and nonnatives are occupying the same or different trait space; 3) Compare proportional abundance of nonnative species to community weighted mean trait values at a range of sites; and 4) Compare community weighted mean trait values across sites along gradients of environmental characteristics. Specifically, we expected that nonnative plants in upper Midwestern forests would be fast-growing and have more acquisitive (versus conservative, *sensu* Tecco et al. (2010)) trait values, for example, higher specific leaf area, lower leaf C:N ratio, and lower wood density. This assumption is common in much of the invasion biology literature, the idea that one reason invasive plants are successful is because they can grow and spread faster than native plants (Richardson and Pysek 2006, Catford et al. 2009, Lamarque et al. 2011, Moles et al. 2012). Additionally, we expected that nonnative plants would be grouped together in multidimensional trait space in an area unoccupied by native species, indicating that nonnative plants are “trying differently”, or possess growth and survival strategies that fill an unoccupied niche. Finally, we predicted that community weighted mean trait values would vary across

environmental gradients of light and soil pH and that proportionally more nonnative plants would be observed in sites with more conservative mean trait values.

Methods

Site selection and field survey

This study was conducted in the eastern broadleaf forest province of Minnesota, USA (MNDNR 2005). Sixty-eight sites were established in closed-canopy, dry-mesic to mesic, upland, red oak-dominated forests in central and southern Minnesota (figure 1). Sites were selected to minimize variation in forest type, but to allow for variation in environmental characteristics, such as light, through inclusion of forests with differing recent disturbance history. Eighteen of the sites had been harvested for timber within the previous ten years (13 selection harvests, 5 clearcuts), 12 sites had undergone invasive shrub removal at least once in the previous ten years, and the remaining 38 sites had not experienced any major disturbance in the previous decade. These sites were selected as part of another study (see Chapter 2), but were included in the present study because they allowed us to examine plant trait assemblages across gradients of light and soil fertility. These sites were located on public and private land, with the majority found in Minnesota State Parks, Forests, and Wildlife Management Areas. Candidate site locations were identified using GIS maps showing forest types on public lands as well as through recommendations by forest managers of sites that fit our criteria. All selected sites contained at least 40% red or pin oak (*Quercus rubra* or *Q. ellipsoidalis*) and total canopy cover of at least 75%. Other common canopy species included red and sugar maple (*Acer*

rubrum and *A. saccharum*), green ash (*Fraxinus pennsylvanica*), and American basswood (*Tilia americana*). Sites were located between 43.513236° and 46.123257° latitude and -94.358826° to -91.288147° longitude. Climate in this region is continental, with precipitation ranging from 70 to 90 cm per year and mean annual temperatures of 6.1 – 7.8 °C.

Once a suitable site was identified, 16 five-meter radius circular plots were established in a four by four grid in the first area of the site that we found with relatively homogenous topography within the approximately half-hectare plot area, and was also at least 40 m from the nearest forest edge. We identified all woody and herbaceous vegetation in each plot. Additionally, we measured the basal area of each woody species in each plot and estimated percent cover of each herbaceous species using the cover scale 1%, 3%, 5%, 10%, 20%, and continuing in increments of 10%. Plot data were combined at the site level and all analyses were conducted at the scale of the site. Taxonomy followed the *Flora of North America* (Flora of North America Editorial Committee 1993) and *Manual of vascular plants of northeastern United States and adjacent Canada* (Gleason and Cronquist 1991) and native or nonnative status was determined for all observed species based on the USDA Plants Database classification (USDA 2015a). Voucher specimens were deposited in the Herbarium of the J.F. Bell Museum of Natural History at the University of Minnesota.

Canopy openness was measured 1.4 m above the ground in the center of each plot using a densiometer. These values were averaged across plots within each site to get a site-level estimate of light availability. Three soil samples to a depth of 20 cm were

collected from three locations 2 m from the center of each plot (0°, 120°, and 240°) using a 2 cm diameter soil corer. Samples were composited at the site level and soil pH was measured using a Corning pH meter 240 with soils resuspended in a CaCl₂ solution. Plots were sampled during the summer of 2010, 2011, or 2012. Each plot was sampled once.

Trait data collection

For all of the herbaceous and woody species observed in the field, we sought the following functional trait values: specific leaf area (SLA, cm² g⁻¹), leaf carbon to nitrogen ratio, wood density (for woody species, mg mm⁻³), plant maximum height (m), mycorrhizal type, seed mass (mg), and growth form. SLA is positively related to potential relative growth rate and photosynthetic rate, as well as negatively related to leaf longevity and secondary compounds such as lignin (Reich et al. 1999, Westoby et al. 2002, Pérez-Harguindeguy et al. 2013). It is also associated with the leaf economics spectrum, or the tradeoff between fast or slow return on investment in leaf structures (Reich et al. 1999, Wright et al. 2004, Cornwell et al. 2006). Leaf nitrogen concentration is correlated with maximum photosynthetic rate and can vary significantly with soil nutrient availability (Pérez-Harguindeguy et al. 2013). Wood density and plant height are important to plant stability, defense, and hydraulics and are related to the balance between access to light and the cost of structural stability (Pérez-Harguindeguy et al. 2013, Ordonez 2014a). Mycorrhizal type is important for examining a species' nutrient uptake strategy based on its symbiotic associations with bacteria or fungi (Pérez-Harguindeguy et al. 2013). Seed mass is indicative of the tradeoff between producing a few large seeds, which contain

resources that can help seedlings establish, or many small seeds that can disperse more easily. Small seeds can also be buried deeper in the soil, allowing them to remain in the seed bank longer (Pérez-Harguindeguy et al. 2013).

Maximum plant height, seed mass, and wood density were obtained from the TRY plant trait database (Kattge et al. 2011). We averaged values for a given species-trait combination across TRY entries that were sourced from the eastern half of the United States, since many of these traits can vary regionally, and excluded non-field (i.e., greenhouse) trait measurements from the database. Maximum plant height was easily available in the TRY trait database, so we used those values instead of measuring actual plant height within our surveyed sites. Additionally, maximum height reflects the average character of a species and is related to other aspects of its biology. Plant height measured at any one site depends on individual plant age and growing conditions. We used the Kew database to fill in gaps in seed mass (Kew 2015), and online herbarium databases to fill in a few plant heights that were not found in TRY. Mycorrhizal type for all species was determined based on family relationships (Ian Dickie, personal communication). Growth form was determined based on observations from the survey sites. See appendices S1.A and S1.B for more information on the sources of trait values.

We measured leaf nitrogen and carbon content and SLA on leaves collected from our sites, since these have been shown to vary from site to site more than some of the other trait measurements (Pérez-Harguindeguy et al. 2013). We collected one leaf from 1 - 6 individuals of each species at 1 - 6 sites. Fully expanded young leaves were collected from sunny areas when possible. For species that are only found in the shaded understory,

shade leaves were collected. Leaves were stored in plastic bags in a cooler or refrigerator and processed within 8 hours. Leaves were scanned on an LI-3000 Leaf Area Meter (LI-COR, Lincoln, NE, USA), dried at 60°C for three days, and then weighed to calculate SLA. Dried leaves were then composited by species, ground using a SPEX CertiPrep 8000-D Mixer Mill (Metuchen, NJ, USA), and analyzed for carbon and nitrogen content using the combustion method (Pérez-Harguindeguy et al. 2013).

We measured wood density on a half-dozen shrub species that did not have entries in the TRY database. A four to six centimeter section of stem was cut near the base of the shrub. To quantify fresh wood volume, we used the water-displacement method, where each stem section was immersed in a water-filled beaker and weighed – the increase in mass on the scale was equal to the volume of the sample in cm³ (Pérez-Harguindeguy et al. 2013). Stems were then dried at 60°C for at least three days and weighed. Wood density was calculated by dividing dry mass by fresh volume.

Data analysis

Across all 68 sites, 339 species were identified (238 herbaceous species and 101 woody species). Of these, we were able to acquire trait data for all seven traits for 120 species (75 herbaceous, 45 woody, tables 1.1 and 1.2). These 120 species represented the dominant species at the sites and comprised about 70% percent of cover at each site, which is close to the 80% relative abundance recommended for trait sampling by Pérez-Harguindeguy et al. (2013). Of the 45 woody species, 4 were nonnative. Of the 75

herbaceous species, 7 were nonnative. These 120 species are used throughout the analyses.

Average trait values for native and nonnative species were compared using t-tests and Chi-square analyses in JMP pro version 11 (SAS Institute, Inc. Cary, NC, USA). Maximum plant height and seed mass were both log transformed to approximate normality.

Patterns in the multidimensional trait space between native and nonnative plants were examined using non-metric multidimensional scaling (NMS). All continuous trait variables were relativized by the maximum value prior to ordination in order to remove undue influence from traits measured using different units (Cornwell et al. 2006). The dissimilarity matrix was calculated using Bray-Curtis distance measures. NMS and statistical comparisons of the multidimensional trait space were conducted using the *vegan* package (Oksanen et al. 2015) in R version 3.1.2 (Team 2014). The *adonis* function, analogous to Permutational Multivariate Analysis of Variance (perMANOVA), was used to compare differences between mean trait space of native and nonnative species. Variance of the two groups was compared using the *betadisper* function.

Community weighted mean trait values for continuous traits were calculated for all species at each site using the Functional Diversity (FD) package in R (Laliberte and Legendre 2010, Laliberte et al. 2014). Trait values were weighted by herbaceous species percent cover and woody species basal area. Community weighted mean (CWM) is a measure of functional composition of a set of communities (Lavorel et al. 2008). In this study, CWM was calculated for each site so that functional composition could be

compared across sites. Multiple regression was used to compare the community weighted mean trait values at each site to the proportion of nonnative plants at each site, soil pH, and site mean light level.

Results

Single-trait comparisons

When all herbaceous and woody species were examined collectively, there were few differences in average trait values between native and nonnative species. Nonnative plants had significantly lower leaf C:N (16.1 ± 1.63 , mean \pm SE) than native species (19.7 ± 0.52 , $p < 0.05$), consistent with our hypothesis that nonnative species would have more acquisitive leaf trait values than natives. Contrary to our hypothesis, native and nonnative plants had similar maximum height, SLA, and seed mass. Additionally, nonnatives were no more likely to be woody than natives (Chi-square, $p > 0.1$).

Among only the 75 herbaceous species, there were no significant differences in average trait values between native and nonnative plants. Leaf C:N of nonnative herbaceous plants (14.9 ± 2.13) was lower than that of native plants (18.5 ± 0.68 , $p = 0.1087$), but only marginally. Nonnative and native herbaceous plants were equally likely to lack mycorrhizal associations (Chi-square, $p > 0.1$). There was no difference in maximum height, SLA, or seed mass.

Maximum plant height was the only trait that differed between native and nonnative woody plants. Nonnative woody plants ($0.46 \text{ m} \pm 0.22$) were significantly shorter than native plants ($1.0 \text{ m} \pm 0.07$, $p < 0.05$). This is likely because all of the

nonnative woody species sampled were shrubs (i.e., no nonnative trees). When the maximum height of only native shrubs was compared to that of nonnative shrubs, there was no difference in average height ($p = 0.56$). Leaf C:N of nonnative woody plants (18.2 ± 2.2) was lower than that of native plants (21.7 ± 0.69 , $p = 0.1451$), but not significantly. There were no significant differences in the SLA, seed mass, or wood density. Additionally, nonnative woody plants were not more likely to have ectomycorrhizal associations than native woody plants (Chi-square, $p > 0.1$).

Multiple-trait comparisons

When all 120 herbaceous and woody species were ordinated in a trait space composed of seven traits, a two-dimensional ordination was found (stress = 0.1069). Important traits included growth form (tree (*TreeY*), shrub (*ShrubY*), etc.), mycorrhizal type (arbuscular mycorrhizal (*MycorAM*), ectomycorrhizal (*MycorEC*), non-mycorrhizal (*MycorN*)), seedmass, plant height, and SLA. When native status (*NativeY*) was overlaid onto the trait space, it was very weakly correlated with ordination axes (figure 1.2, top panel). When all 120 species were examined simultaneously, the multidimensional trait space occupied by the nonnative species was located within the trait space occupied by the native species (fig 1.3). The trait space occupied by all native species and all nonnative species was not significantly different ($p > 0.1$, table 1.3). The dispersion, or variance, of the trait space occupied by native herbaceous and woody plants also did not differ from the space occupied by nonnative plants ($p = 0.54$). Similarly, the average

distance across multidimensional trait space from each species to its native/nonnative group centroid did not differ.

The patterns observed in the trait space of native and nonnative herbaceous species are similar to those observed when all herbaceous and woody species were combined. The trait space occupied by native and nonnative herbaceous species overlapped (figure 1.4) and was not significantly different ($p > 0.1$). Additionally, the variance of the trait space occupied by native and nonnative herbaceous species did not differ significantly ($p > 0.1$).

The pattern of trait space occupied by native and nonnative woody plants is different from that observed in herbaceous and all species combined. The nonnative woody plants appear to be grouped closely together in the ordination (figure 1.5). While the trait space occupied by nonnative woody plants is still located within the larger space occupied by native woody plants, analysis with perMANOVA showed that these trait spaces differed ($p < 0.05$, table 1.4). Additionally, the variance of the traits of nonnative species was significantly smaller than that of native woody plants ($p < 0.05$, table 1.5).

Community weighted mean traits

The proportional abundance of nonnative species was significantly greater in sites with higher community weighted mean woody plant leaf SLA values and lower leaf C:N ratios ($p = 0.0429$, $p = 0.0804$, respectively; figure 1.6), or sites with mean trait values indicative of more acquisitive resource strategies. Abundance of nonnative species was not correlated with any other site mean trait. This is contrary to our hypothesis that more

nonnative species would be observed in sites with resident species with conservative mean trait values.

The community weighted mean trait values for herbaceous plants were not correlated with the site environmental characteristics of light or soil pH, however some of the traits of woody species were related to environmental characteristics. Soil pH was positively correlated with woody plant CWM maximum height (figure 1.7a, $p < 0.05$) and woody plant CWM SLA (figure 1.7b, $p < 0.05$). Community weighted mean wood density and leaf C:N ratio were both negatively correlated with soil pH (figure 1.7c and 1.7d, $p < 0.05$). Community weighted mean wood density and leaf C:N were also lower in sites with more open canopies (figure 1.8a, $p < 0.001$; figure 1.8b $p < 0.01$, respectively). No other mean traits were associated with site light levels.

Discussion

In general, we found few differences in traits between native and nonnative herbaceous and woody species. These results lend support to the “join the locals” hypothesis, suggesting that in our study system, nonnative plants are successful because they share traits similar to those of resident plants and are therefore able thrive under local environmental conditions (Tecco et al. 2010). This also provides support to the idea that not all successful invaders are super-plants – some may be successful simply by following the same strategies as successful native species (Flores-Moreno and Moles 2013) – although there may be a tendency toward nonnative plants having greater leaf nitrogen than natives (Tecco et al. 2010, Kurokawa et al. 2010).

However, it is possible that there are other traits that we did not examine that could separate nonnatives from natives, such as phenology or dispersal mechanism (Wolkovich and Cleland 2011, Brym et al. 2011). For example, studies of autumn olive (*Elaeagnus umbellata*) and common buckthorn (*Rhamnus cathartica* L.) have shown that these invasive shrubs have a distinctive phenology, leafing out earlier and holding their leaves longer than native shrub species (Harrington et al. 1989, Knight et al. 2007, Brym et al. 2011, Fridley 2012). These species may be taking advantage of an unoccupied temporal niche. Dispersal syndrome may also be important for determining success of nonnative species, with successfully establishing nonnative species more likely to have seeds dispersed by wind or birds (Lake and Leishman 2004). Even though we did not detect a trait difference in SLA between natives and nonnatives (and only a marginal difference between leaf C:N), it is possible that nonnative plants may be successful due to more extreme trait values on unmeasured trait axes such as leaf phenology or dispersal syndrome.

While woody nonnative plants had trait values similar to those of natives, there was far less variability in their location within the multidimensional trait space. This suggests that nonnatives were more similar to each other in traits than the natives are to each other. A small sample size bias correction was used in this analysis, but the very small number of nonnative woody species (4) as compared to the number of native woody species (41), may limit the applicability of this result. If this grouping of nonnatives had occurred in an open area of native trait space, it would suggest that these nonnatives are located in an unoccupied niche space and that this system is more

susceptible to woody invaders with a specific range of traits. However, there were native species located in the same small area of multidimensional trait space where the nonnatives were grouped, indicating that they have not moved into an unoccupied niche, but simply possess traits similar to those of natives. Ordonez et al. (2010) observed that nonnatives clustered toward the edge of at least one dimension of trait space, and it appears as though the woody species in our study do cluster toward an axis of shorter maximum height. However, this is likely due to the lack of nonnative tree species present in our data set. There are only a small number of nonnative woody species currently found in Minnesota forests, and very few of those species are trees (MNDNR 2015). Additionally, van Kleunen et al. (2010) observed greater differences between traits of invasives and native species than between invasives and noninvasive nonnatives. There were a limited number of nonnative plants in our study, and some of those are not considered to be invasive, so this could have weakened the signal of any trait differences that may be present.

Environmental characteristics such as light and soil nutrients did affect which ranges of trait values were prominent in a given site in our system. Sites with higher soil pH, and therefore likely more nutrients available to plants, had higher community weighted mean values for woody species SLA and plant height. These sites, as well as those with more open canopies, also had lower mean woody density and leaf C:N of woody plants. With greater nutrient availability and more light, it would be expected that the most successful species in these environments would be able to grow quickly. They would put more resources toward growing large, thin leaves, high in nitrogen to

photosynthesize rapidly, as well as quickly put on less dense wood. This has ramifications for invasion because sites with higher CWM SLA and lower leaf C:N of woody species also contained a greater proportion of nonnative plants. This suggests that sites that are good for native plants are also good for nonnative plants, and that both natives and nonnatives may therefore be more successful in sites with higher light levels and more available nutrients. Thompson and Davis (2011) suggest that winners and losers among plant species are not due to native or invasive status, but are instead due to the possession of traits that are successful in human-dominated landscapes that are disturbed and nutrient-enriched. Van Kleunen et al. (2010) also observed no difference in trait values between those of invasives and natives that were invasive in other regions, again suggesting that both native and nonnative species could possess the same traits that make them successful in more disturbed habitats.

Conclusion

Overall, a better ability to predict which species may become invasive would help managers to target newly arrived species before they become a problem (Ordonez 2014b). In order to be successful in a new environment, nonnative plants need to have similar traits to resident native species to pass through environmental filters. However, certain nonnatives may be even more successful if they differ from natives in one or two key traits that provide them with a competitive advantage over the resident species. Our results suggest that nonnative species with many functional traits similar to those of resident native species may be more likely to successfully establish in forests of the

Upper Midwest. However, some of these nonnative species do differ in some unmeasured traits, including phenology and dispersal syndrome (e.g., common buckthorn; Knight et al. 2007). It is possible that these differences in traits not examined in the current study allow certain nonnatives to successfully establish, spread, and become invasive.

Additionally, sites that have higher light levels and greater soil fertility may be more susceptible to invasion because they are sites where both ruderal native and nonnative plants can grow and spread quickly. Land managers may want to monitor such sites more frequently to catch new invasions early, when it is still possible to control them. While plant functional traits can play a part in predicting invasion success of nonnative plants, they will likely not be sufficient for nonnative/invasive categorization. Incorporation of environmental conditions in both the native and potential new range, as well as estimation of propagule pressure and other large-scale drivers must be incorporated alongside trait considerations in order to better predict nonnative plant establishment (Pyšek et al. 2014).

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Table 1.1. List of 45 woody plants for which traits were collected with native or nonnative status.

Species	Native?
Acer negundo	Yes
Acer rubrum	Yes
Acer saccharum	Yes
Acer saccharinum	Yes
Berberis thunbergii	No
Betula papyrifera	Yes
Carya cordiformis	Yes
Celastrus scandens	Yes
Celtis occidentalis	Yes
Cornus alternifolia	Yes
Cornus racemosa	Yes
Corylus americana	Yes
Diervilla lonicera	Yes
Frangula alnus	No
Fraxinus americana	Yes
Fraxinus nigra	Yes
Fraxinus pennsylvanica	Yes
Juglans nigra	Yes
Lonicera dioica	Yes
Lonicera spp.	No
Menispermum canadense	Yes
Ostrya virginiana	Yes
Parthenocissus quinquefolia	Yes
Parthenocissus vitacea	Yes
Populus tremuloides	Yes
Prunus serotina	Yes
Prunus virginiana	Yes
Quercus alba	Yes
Quercus ellipsoidalis	Yes
Quercus macrocarpa	Yes
Quercus rubra	Yes
Rhamnus cathartica	No
Rhus glabra	Yes
Ribes cynosbati	Yes

Ribes missouriense	Yes
Rubus allegheniensis	Yes
Rubus idaeus	Yes
Rubus occidentalis	Yes
Sambucus canadensis var. canadensis	Yes
Sambucus racemosa	Yes
Smilax tamnoides	Yes
Staphylea trifolia	Yes
Tilia americana	Yes
Ulmus americana	Yes
Ulmus rubra	Yes
Vaccinium angustifolium	Yes
Viburnum lentago	Yes
Viburnum opulus	Yes
Viburnum rafinesquianum	Yes
Vitis riparia	Yes
Zanthoxylum americanum	Yes

Table 1.2. List of 75 herbaceous plants for which traits were collected with native or nonnative status.

Species	Native?
<i>Actaea rubra</i>	Yes
<i>Adiantum pedatum</i>	Yes
<i>Agrimonia striata</i>	Yes
<i>Alliaria petiolata</i>	No
<i>Ambrosia artemisiifolia</i>	Yes
<i>Ambrosia trifida</i>	Yes
<i>Amphicarpaea bracteata</i>	Yes
<i>Anemone acutiloba</i>	Yes
<i>Aquilegia canadensis</i>	Yes
<i>Aralia nudicaulis</i>	Yes
<i>Aralia racemosa</i>	Yes
<i>Arctium minus</i>	No
<i>Arisaema triphyllum</i>	Yes
<i>Asarum canadense</i>	Yes
<i>Asclepias exaltata</i>	Yes
<i>Athyrium filix-femina</i> var. <i>angustum</i>	Yes
<i>Botrychium virginianum</i>	Yes
<i>Carex blanda</i>	Yes
<i>Carex gracillima</i>	Yes
<i>Carex normalis</i>	Yes
<i>Carex pedunculata</i>	Yes
<i>Carex pensylvanica</i>	Yes
<i>Carex rosea</i>	Yes
<i>Caulophyllum thalictroides</i>	Yes
<i>Chenopodium album</i>	No
<i>Cirsium arvense</i>	No
<i>Cryptotaenia canadensis</i>	Yes
<i>Desmodium glutinosum</i>	Yes
<i>Dioscorea villosa</i>	Yes
<i>Dryopteris carthusiana</i>	Yes
<i>Echinocystis lobata</i>	Yes
<i>Elymus hystrix</i>	Yes
<i>Eurybia macrophylla</i>	Yes
<i>Eutrochium purpureum</i>	Yes

<i>Festuca subverticillata</i>	Yes
<i>Fragaria virginiana</i>	Yes
<i>Galeopsis tetrahit</i>	Yes
<i>Galium boreale</i>	Yes
<i>Geranium maculatum</i>	Yes
<i>Geum canadense</i>	Yes
<i>Glechoma hederacea</i>	No
<i>Hackelia virginiana</i>	Yes
<i>Impatiens capensis</i>	Yes
<i>Laportea canadensis</i>	Yes
<i>Lysimachia borealis</i>	Yes
<i>Maianthemum canadense</i>	Yes
<i>Melilotus alba</i>	No
<i>Mitella nuda</i>	Yes
<i>Oryzopsis asperifolia</i>	Yes
<i>Osmorhiza claytonii</i>	Yes
<i>Osmorhiza longistylis</i>	Yes
<i>Osmunda claytoniana</i>	Yes
<i>Oxalis stricta</i>	Yes
<i>Phryma leptostachya</i>	Yes
<i>Pilea pumila</i>	Yes
<i>Piptatherum racemosum</i>	Yes
<i>Plantago rugelii</i>	Yes
<i>Polygonatum biflorum</i>	Yes
<i>Polygonatum pubescens</i>	Yes
<i>Prenanthes alba</i>	Yes
<i>Ranunculus abortivus</i>	Yes
<i>Sanguinaria canadensis</i>	Yes
<i>Sanicula gregaria</i>	Yes
<i>Scrophularia lanceolata</i>	Yes
<i>Smilax ecirrhata</i>	Yes
<i>Solidago canadensis</i>	Yes
<i>Solidago flexicaulis</i>	Yes
<i>Solidago gigantea</i>	Yes
<i>Sonchus oleraceus</i>	Yes
<i>Streptopus lanceolatus</i>	Yes
<i>Symphyotrichum cordifolium</i>	Yes
<i>Symphyotrichum lateriflorum</i>	Yes
<i>Taraxacum officinale</i>	No

Thalictrum dioicum	Yes
Thalictrum thalictroides	Yes
Trillium grandiflorum	Yes
Triosteum perfoliatum	Yes
Uvularia grandiflora	Yes
Verbascum thapsus	Yes
Veronicastrum virginicum	Yes
Viola pubescens	Yes
Viola sororia	Yes

Table 1.3. Permutational multivariate analysis of variance results comparing the multidimensional trait space occupied by herbaceous and woody native plants to the trait space occupied by nonnative plants.

	DF	Sums of Squares	Mean Squares	F Value	R²	Prob > F
Native [Y]	1	0.149	0.14896	1.2006	0.01007	0.2977
Residuals	118	14.641	0.12407	0.98993		
Total	119	14.790		1.00000		

Table 1.4. Permutational multivariate analysis of variance results comparing trait space occupied by native woody plants to that of nonnative woody plants.

	DF	Sums of Squares	Mean Squares	F Value	R²	Prob > F
Native [Y]	1	0.2650	0.265039	3.6433	0.07811	0.03197
Residuals	43	3.1281	0.072746	0.92189		
Total	44	3.3931		1.00000		

Table 1.5. ANOVA results comparing the distances of each species in trait space to its group centroid, with the two groups as native woody plants and nonnative woody plants. Bias due to small sample size has been corrected (Stier et al. 2013).

	DF	Sums of Squares	Mean Squares	F value	Prob > F
Groups	1	0.17884	0.17884	10.554	0.002253
Residuals	43	0.72867	0.016946		

Figure 1.1. Map of Minnesota displaying locations of study sites (points).

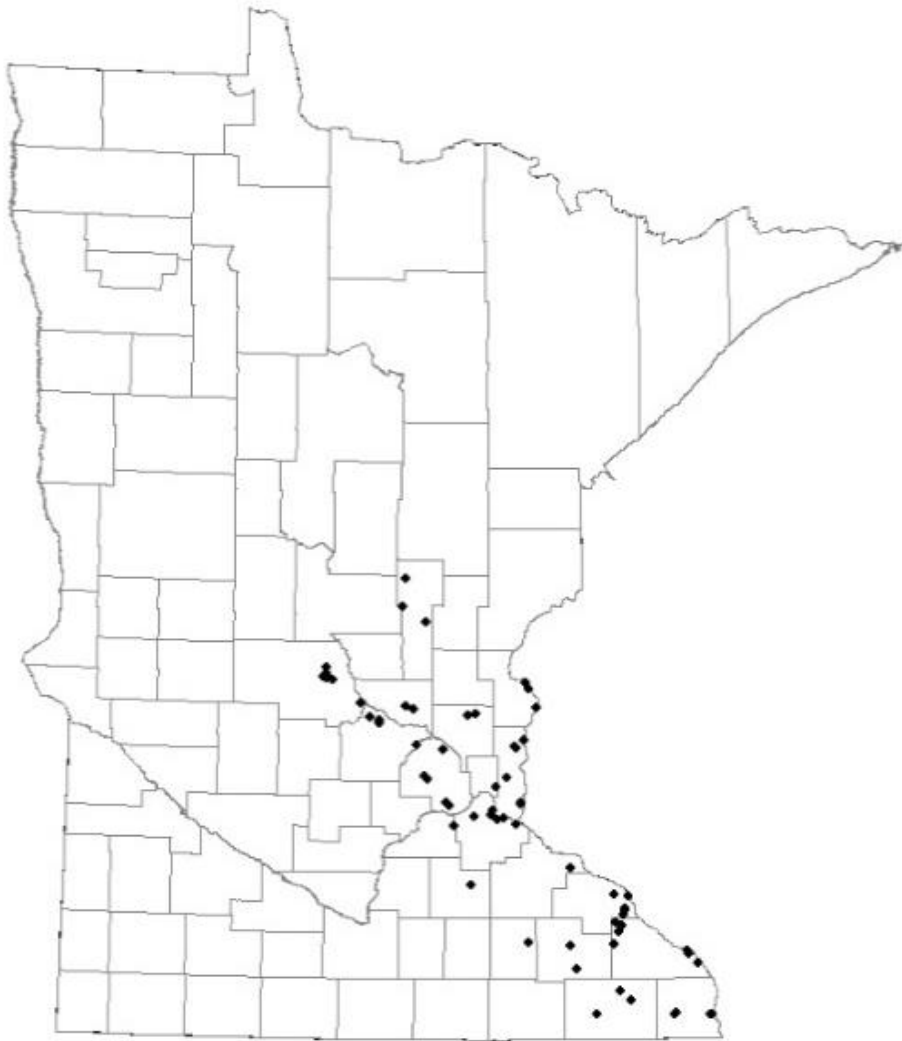


Figure 1.2. Non-metric multidimensional scaling ordination of trait space occupied by 120 herbaceous and woody species. Length of vector lines indicates the strength of the relationship between a given trait and an ordination axis. The top panel includes vectors for all trait variables examined. The bottom panel shows only the most significant traits. Stress = 0.1069.

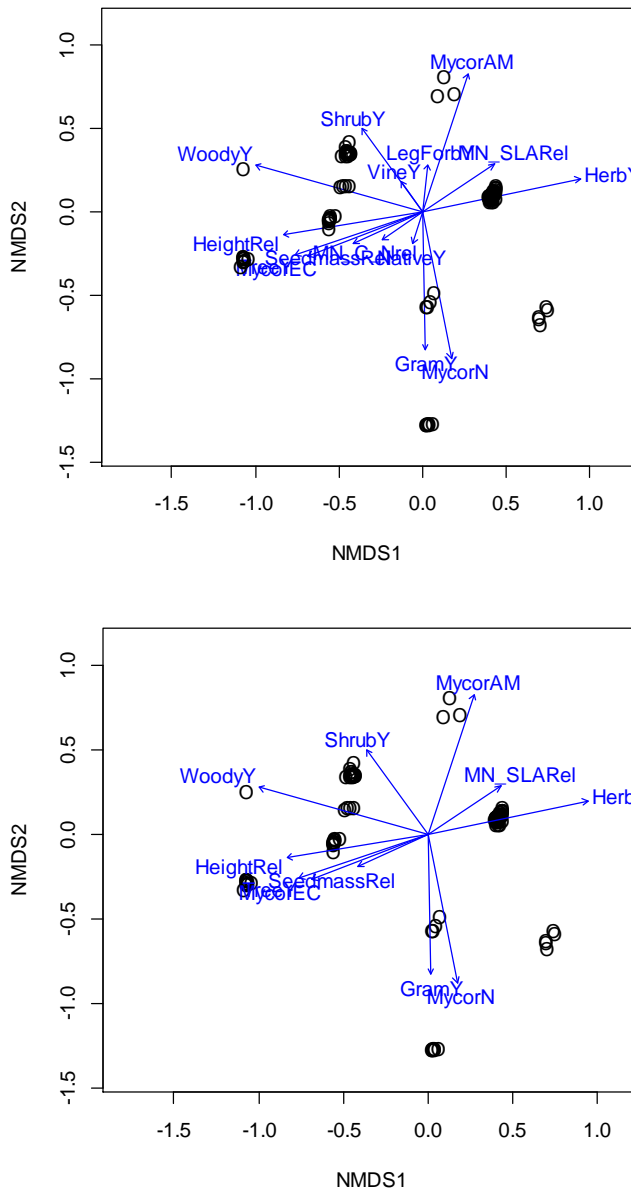


Figure 1.3. Non-metric multidimensional scaling ordination of the trait space occupied by native and nonnative herbaceous and woody plants. Shaded polygons indicate convex hulls of the trait space occupied by native plants (dark gray) and nonnative plants (light gray). Stress = 0.1069.

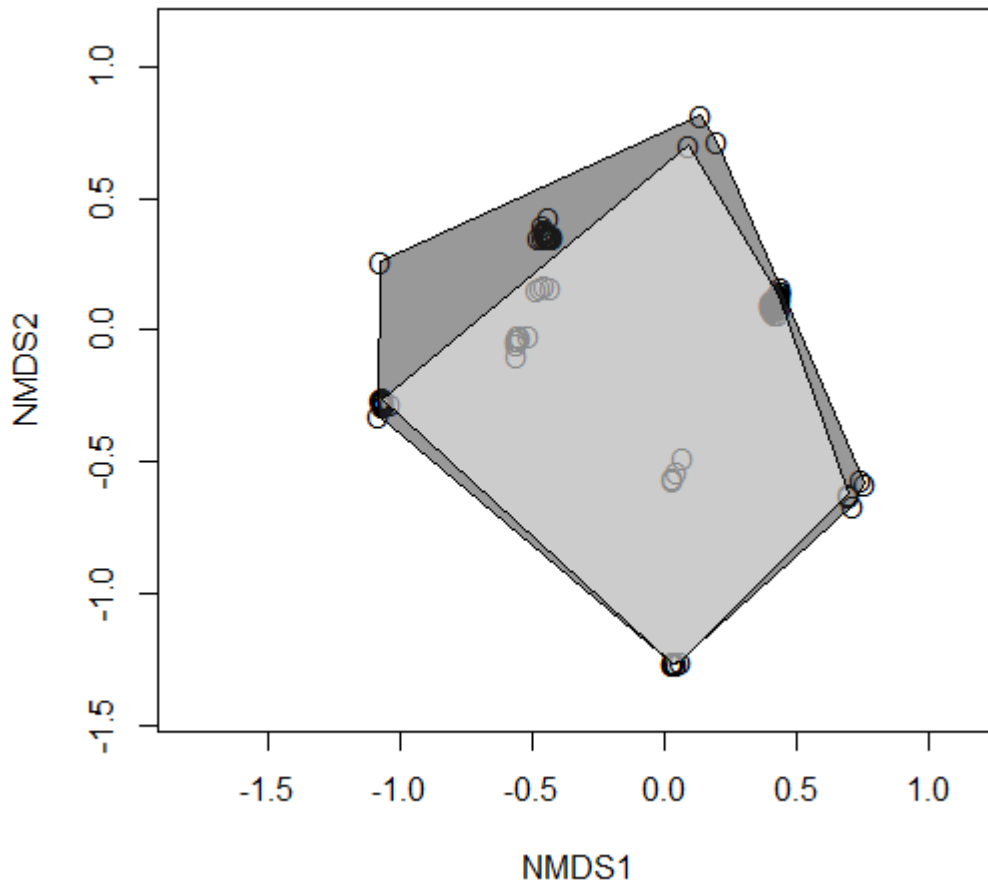


Figure 1.4. Non-metric multidimensional scaling ordination of the trait space occupied by native and nonnative herbaceous plants. Top panel: Vector arrows indicate the traits that are most significant. Bottom panel: Convex hulls separately outline the trait space of native (dark gray) and nonnative (light gray) herbaceous plants. Stress = 0.0435.

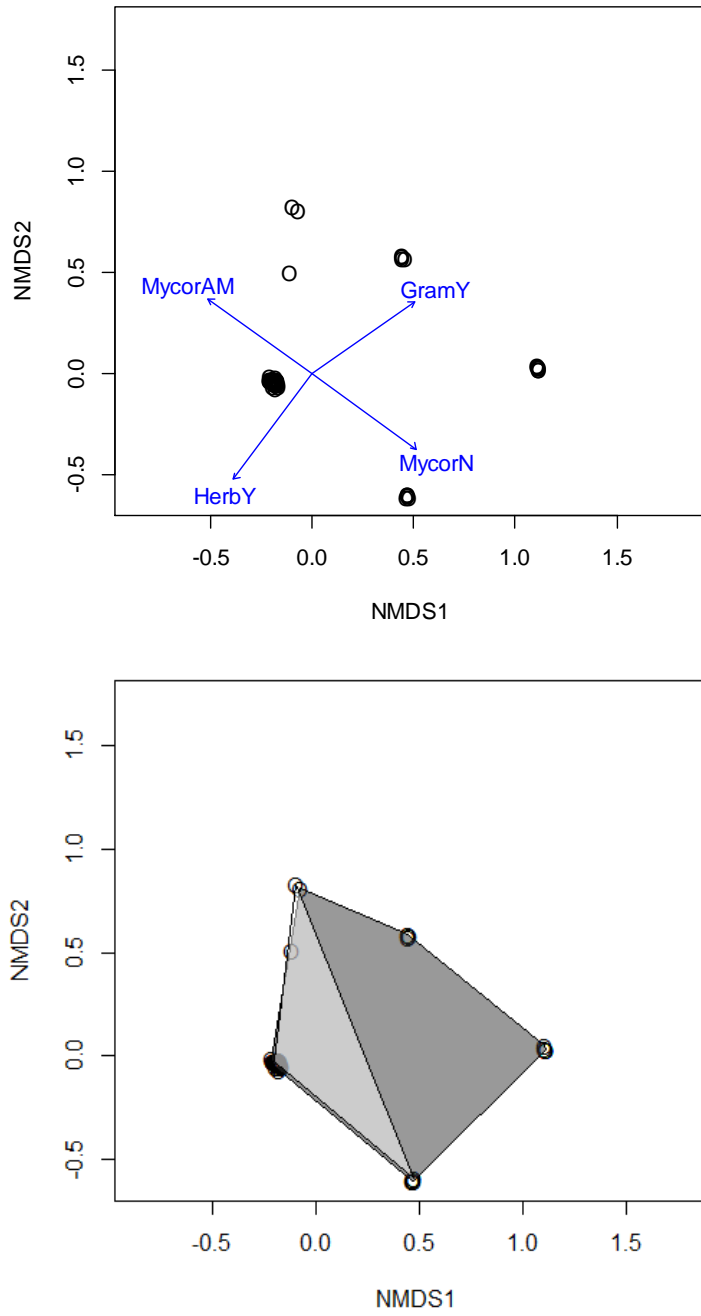


Figure 1.5. Non-metric multidimensional scaling ordination of trait space occupied by native and nonnative woody plants. Top panel: Vector arrows indicate the traits that are most significant. Bottom panel: Convex hulls separately outline the trait space of native (dark gray) and nonnative (light gray) woody plants. Note: Light gray polygon is too small to see on this figure; it is located on top of the right-most group of points. Stress = 0.0574.

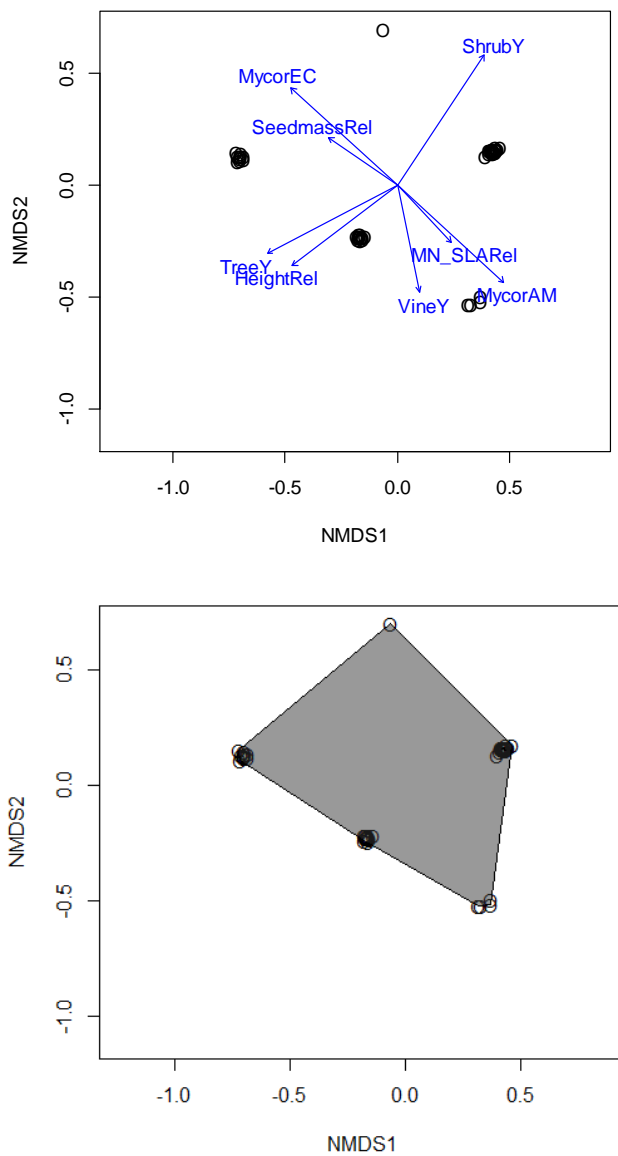


Figure 1.6. Relationships between community weighted mean trait values and the proportion of nonnative species in each site. Top panel: Correlation between the community weighted mean value for woody species SLA and the proportion of nonnative plants in each site ($R^2 = 0.06$, $p < 0.05$). Bottom panel: Correlation between the community weighted mean value for woody species leaf C:N ratio and the proportion of nonnative plants in each site ($R^2 = 0.05$, $p = 0.0804$).

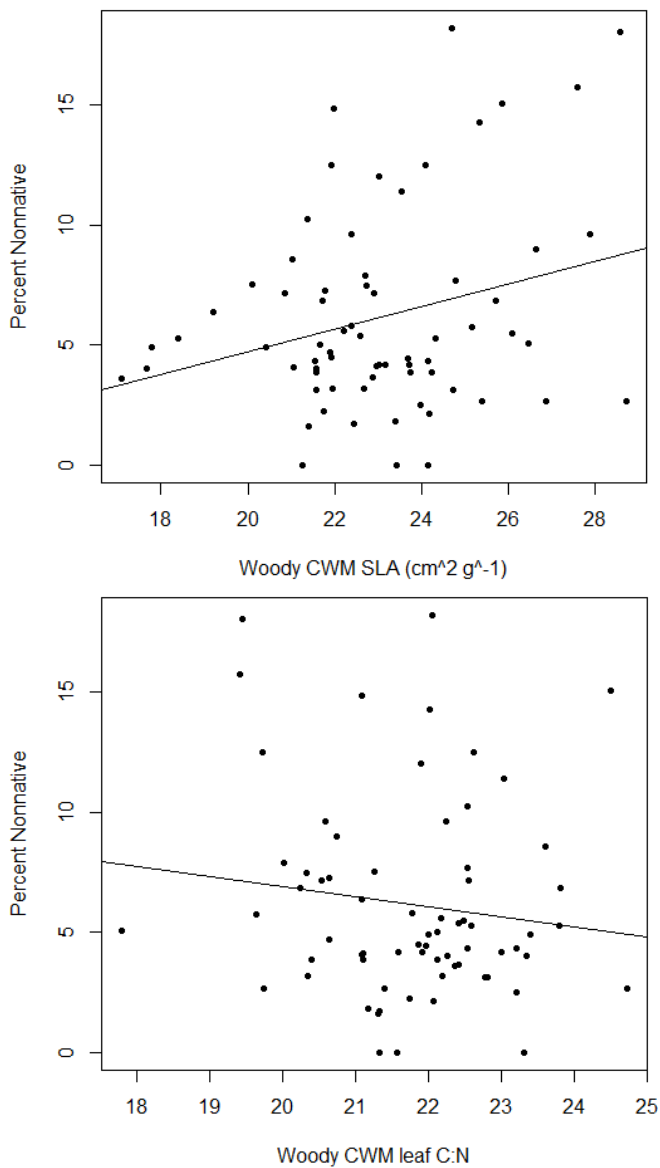


Figure 1.7. Relationships between soil pH at 68 forest sites and various community weighted mean trait values for woody species. a) CWM maximum plant height, $R^2 = 0.09$, $p = 0.0124$; b) CWM SLA, $R^2 = 0.10$, $p = 0.0096$; c) CWM wood density, $R^2 = 0.06$, $p = 0.0448$; d) CWM leaf C:N, $R^2 = 0.26$, $p < 0.0001$.

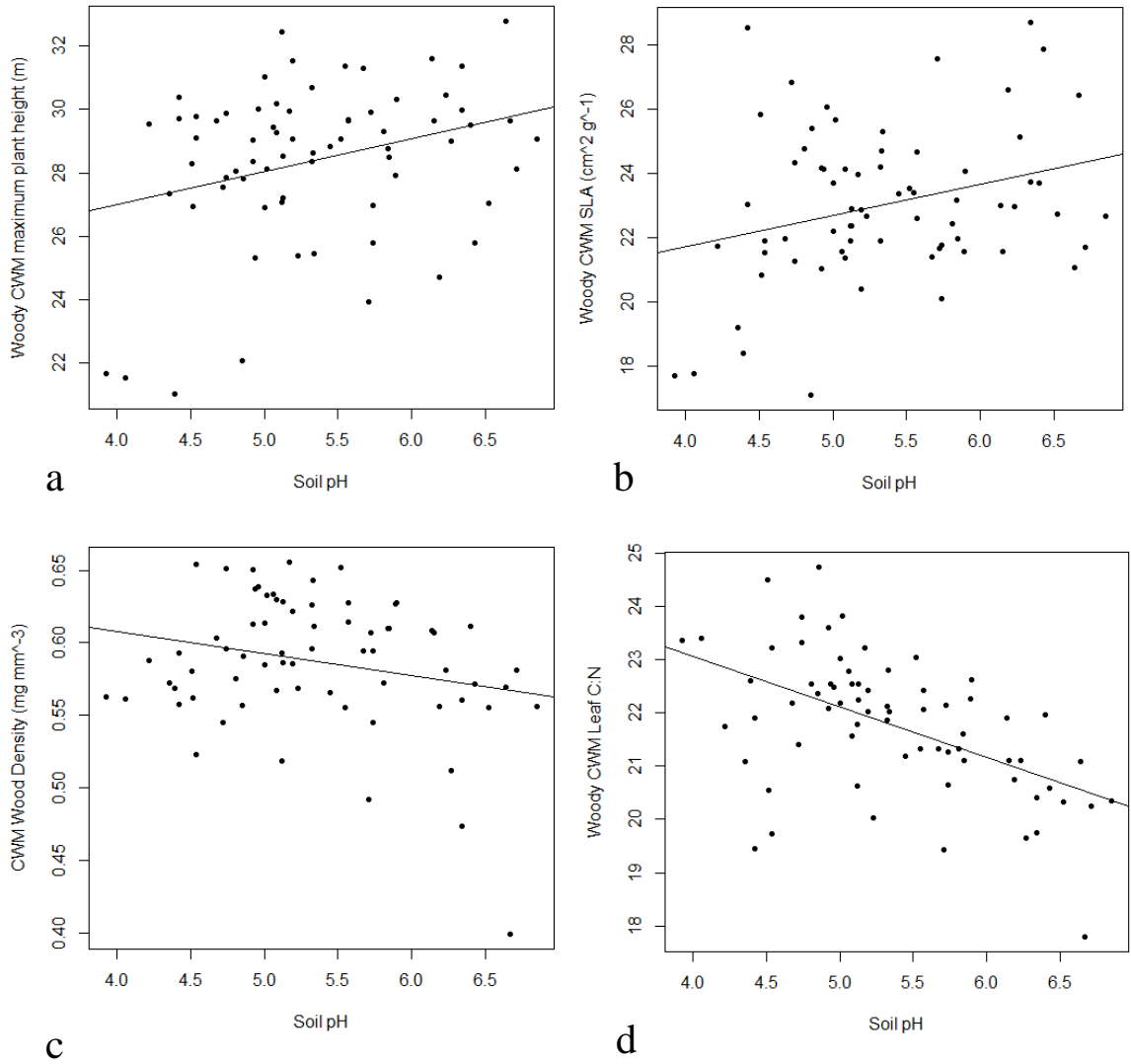
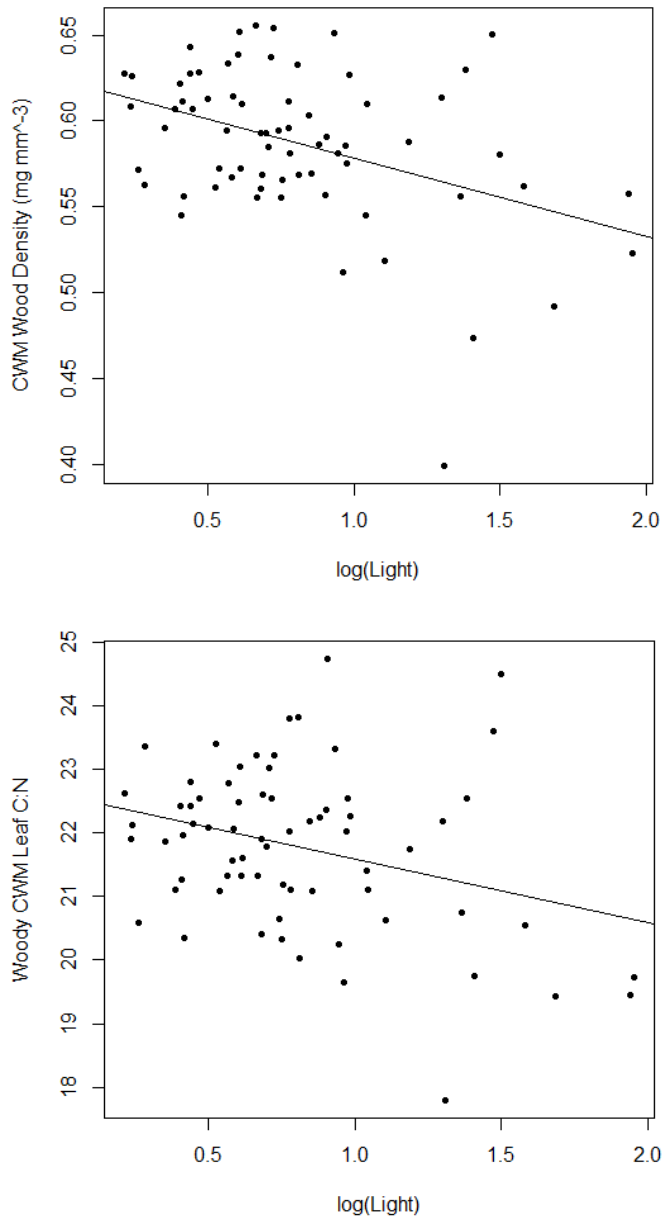


Figure 1.8. Relationships between light level at 68 forest sites and various community weighted mean trait values for woody species. Top panel: CWM woody density, $R^2 = 0.16$, $p = 0.0006$; Bottom panel: CWM leaf C:N, $R^2 = 0.15$, $p = 0.0012$.



CHAPTER 2

**Propagule availability and resident plant diversity are important considerations for
managing forests to minimize buckthorn invasion**

Summary

Nonnative invasive plants are a major threat to global biodiversity yet there is a lack of universal theories of invasibility regarding either the susceptibility of an area to invasion or the capacity of a taxon to invade. Resident plant diversity, abiotic site characteristics such as light levels and soil fertility, and disturbance history may all affect the susceptibility of a given site to invasion. The objective of this study was to examine patterns of invasion by a nonnative shrub, common buckthorn (*Rhamnus cathartica* L.), in North American temperate deciduous forests and relate buckthorn presence and abundance to disturbance history and environmental characteristics. We surveyed 56 oak-dominated stands, 18 of which had been harvested for timber within the previous decade. We identified all species present and also measured a series of environmental characteristics, including canopy openness, soil pH, soil nutrient concentrations, percent bare soil, litter depth, and slope. Additionally, we estimated local buckthorn propagule availability using a driving survey and measured proxy variables for propagule availability using GIS map layers. We combined all site-level characteristics into logistic and multiple regression models to determine the drivers of community invasibility. Results showed that buckthorn presence was best predicted by propagule availability and site light levels. Timber harvesting was not a significant predictor of initial buckthorn invasion. However, sites that were selection harvested contained less buckthorn than those that were clearcut or unharvested. This could have been due to changes in resident plant diversity or other site characteristics following harvesting, or due in part to the tendency to use this harvest method on large, interior forest stands. Buckthorn abundance

was greater in sites with high light, high soil pH, and low leaf litter. Sites with high resident plant diversity that were located far from forest edges contained less buckthorn. While propagule availability was an important predictor of buckthorn presence, it was not retained in the model explaining buckthorn abundance. We propose that some habitats are more resistant to invasion due to their light levels, soil and seedbed conditions, and resident plant diversity, some of which may be amenable to management actions that could help sites resist new invasions. Overall, our results suggest that some quantification of local propagule pressure is crucial prior to any management activities and selection harvests may encourage less buckthorn spread than clearcuts. Resident plant diversity may also serve as biotic resistance to invasion. Management strategies that reduce local propagule pressure, increase resident plant diversity, and minimize disturbances that could increase light levels and expose bare soil may help forests to resist buckthorn invasion.

Introduction

Invasive plants are a major driver of biodiversity loss around the globe (Vitousek et al. 1996, Wilcove et al. 1998, Secretariat of the Convention on Biological Diversity 2009). While much research has been conducted on invasion biology over the past 20 years, questions still remain as to why invasive species are present in one area and not in seemingly similar areas nearby. There is also a lack of universal theories of invasibility, regarding either the susceptibility of an area to invasion or the capacity of taxa to invade (Johnstone 1986, Davis et al. 2001). A variety of theories have been suggested for

different systems, including Darwin's naturalization hypothesis (Darwin 1859, Rejmánek and Richardson 1996, Daehler 2001), the fluctuating resource availability hypothesis (Davis et al. 2000, Moles et al. 2012), and the biotic resistance hypothesis (Elton 1958, Levine and D'Antonio 1999; see review in Richardson and Pysek 2006). These hypotheses are based on the functional traits and taxonomy of invading species, anthropogenic or natural disturbances that could change resource availability in the receiving system, as well as diversity and abundance of the resident species. It is likely that all of these different factors play a role in successful invasions and that the importance of each factor varies with invader and invaded system (Richardson and Pysek 2006).

Invasive plants are often fast-growing, shade-intolerant, pioneer species (van Kleunen et al. 2010b, Ordonez et al. 2010), but closed-canopy forests are also vulnerable to invasion (Martin and Marks 2006, Martin et al. 2009). Meta-analysis showed that northern temperate forests may be especially vulnerable to decreases in biodiversity following invasion as compared to tropical forests and aquatic systems (Murphy and Romanuk 2014). Common buckthorn (*Rhamnus cathartica* L.) is one of the most widespread forest invaders in the United States (USDA 2015a). Introduced from Europe as an ornamental shrub in the early 1800s, it has since established and begun to dominate the understory of many forests, especially in the Upper Midwest United States (Knight et al. 2007, Kurylo et al. 2007, Mascaro and Schnitzer 2007, Kurylo and Endress 2012). Buckthorn has a high reproductive rate (Archibold et al. 1997) and forms dense patches in the understory of forests (Knight et al. 2007), completely shading out native herbs and

tree seedlings (Fagan and Peart 2004, Frappier et al. 2004, Schulte et al. 2011, Klionsky et al. 2011) and changing forest soil properties (Heneghan et al. 2006).

However, even when an invasive plant such as buckthorn is present in a region, it does not invade all areas or habitats equally (Lonsdale 1999). A number of abiotic and biotic filters exist that can enable or prevent introduced species from establishing in a given site. Biotic filters, also called biotic resistance (Elton 1958), include competition for resources, pathogens, and predation (reviewed in Levine et al. 2004). Abiotic filters include climate, soil nutrient and moisture levels (Alpert et al. 2000, Thomsen et al. 2006, Cleland et al. 2013), light levels (Knight et al. 2008), and seedbed conditions (Wilson and Arthur 2013, Mattingly and Orrock 2013).

These biotic and abiotic characteristics of forests often change following disturbance, which can sometimes lead to an increase in the presence or abundance of invasive species (Gray et al. 1987, Alpert et al. 2000, Davis et al. 2000). Canopy gaps formed through individual tree falls or larger-scale blowdowns increase light levels on the forest floor and sometimes also decrease competition for water and nutrients. Insect defoliation and pathogens can also create canopy gaps that could allow invasive plants to increase in abundance (Eschtruth and Battles 2014). Fire can damage resident species, opening space for colonization and changing nitrogen availability (Keeley 2001). While natural disturbances can change conditions to facilitate invasion by exotic plants, some forest management activities can also lead to similar changes. Forests can be managed to improve or maintain wildlife habitat, trails may be maintained for recreational uses, and trees harvested for economical purposes or to maintain or improve forest health.

Timber harvesting is often an important element of forest management activities and can lead to many changes in biotic and abiotic forest characteristics. Timber harvesting also changes the light levels reaching the forest floor by creating canopy gaps. This can either directly increase light available to emerging invader seedlings, or change resident species diversity and cover by increasing light available to pioneer resident species (Bailey et al. 1998, Zenner and Berger 2008). Timber harvesting can change seedbed conditions by compacting the soil along roads and skid trails or exposing bare mineral soil by disturbing the leaf litter (Battles et al. 2001, Silveri et al. 2001, Zenner and Berger 2008). These conditions can sometimes increase invasion by ruderal nonnative species (Bailey et al. 1998, Battles et al. 2001, Silveri et al. 2001), some of which may have been introduced on logging equipment (Buckley et al. 2003). However, different intensities of harvesting (e.g. clearcut versus selection harvest) can result in a range of abiotic and biotic condition changes, and therefore have varying effects on invasion success (Huebner and Tobin 2006, Burke et al. 2008, Lee and Thompson 2012). Additionally, several studies have found that despite changes in environmental characteristics due to harvesting, this anthropogenic disturbance does not necessarily increase exotic plant invasion (Stapanian et al. 1998, Kern et al. 2006).

We propose that some forests are more resistant to invasion due to their biotic and abiotic characteristics, some of which may be amenable to management actions that could help forests to resist new invasions. In a previously published study (Whitfeld et al. 2013), we examined the abiotic and biotic characteristics that affected common buckthorn abundance in 24 oak forests without recent disturbance or management in

central Minnesota. We found that sites with higher phylogenetic diversity contained less buckthorn and that canopy openness and bare mineral soil were both positively correlated with buckthorn. The current study expands upon this work by examining an additional 32 sites, including 18 that experienced recent anthropogenic disturbance (timber harvesting). We also improved estimates of propagule pressure and conducted more thorough soil analyses. This allowed us to test whether timber harvesting increases susceptibility to buckthorn invasion, while also providing a more comprehensive examination of the importance of propagule availability and abiotic site conditions than the preliminary study.

The objective of this study was to examine patterns of buckthorn invasion in cold temperate deciduous forests and relate buckthorn presence and abundance to disturbance history and environmental characteristics. We expected that buckthorn propagule availability in the surrounding area would be a strong predictor of buckthorn distribution. While difficult to quantify (Richardson and Pysek 2006, Eschtruth and Battles 2011), propagule pressure has been found to be an important predictor of invader presence and abundance (Gray et al. 1987, Tilman 1997, Colautti et al. 2006, Thomsen et al. 2006, Eschtruth and Battles 2009, Simberloff 2009). Many studies use quantitative surrogates to estimate propagule pressure (Richardson and Pysek 2006), including the number of visitors to a park, who may transport seeds (Lonsdale and Lane 1994, Allen et al. 2008); human population density; distance to or density of trails, roads, or rivers, which can all serve as direct conduits for propagule inputs or indirectly via human traffic or bird habitat (von der Lippe and Kowarik 2007, Allen et al. 2008, Gorchov et al. 2014); and habitat

fragmentation. We used multiple methods to estimate propagule availability, including an on-the-ground estimate of mature, seed-producing buckthorn in the area around each research site and GIS measures of local and regional features that are likely to contain mature buckthorn or serve as conduits for seed introduction. Studies of invasibility are often confounded by not accounting for propagule pressure – only once propagule pressure has been accounted for can we tease apart a site’s current level of invasion from its susceptibility to invasion (Lonsdale 1999, Eschtruth and Battles 2011).

A number of factors are likely to be important for the success or failure of buckthorn establishment. Due to buckthorn’s affinity for germinating on bare mineral soil (Knight et al. 2007), whether the exposed soil is due to invasive earthworm feeding (Bohlen et al. 2004, Frelich et al. 2006), timber harvesting or other human disturbances (trail construction, etc.), or other causes, we expected that sites with more exposed soil and less leaf litter would be more susceptible to buckthorn invasion. While buckthorn is able to grow in closed-canopy forests, sites with greater light availability to the understory are expected to contain more buckthorn as it grows more quickly (and reproduces at greater rates) when it is located in higher-light forest edge or gap environments (Gourley and Howell 1984, Knight et al. 2007, Kurylo et al. 2007). We also expected that sites with higher resident plant diversity would better resist buckthorn invasion. High diversity communities (whether measured through plant richness, functional, or phylogenetic diversity) are thought to more fully utilize available resources and therefore limit access to resources to new invaders (Knops et al. 1999, Kennedy et al. 2002, Fargione and Tilman 2005). However, if resources are plentiful, invasive plants are

often more successful at establishing (Stohlgren et al. 1999, Levine and D'Antonio 1999, Davis et al. 2000, Howard et al. 2004, Huebner et al. 2009), and we expected buckthorn would follow this trend and be able to grow more quickly under high nutrient, moist conditions (Kurylo et al. 2007).

Since timber harvesting increases light levels, disturbs seedbed conditions, and potentially introduces invasive plant seeds, we expected that sites that had been harvested within the past decade would contain more buckthorn than those that had experienced no major disturbance during that time. Overall, we aimed to gain a better understanding of the relative importance of biotic and abiotic site characteristics and propagule availability in affecting forest susceptibility to buckthorn invasion. This information may help land managers prioritize monitoring efforts toward forests more susceptible to new invasions and also suggest management techniques that may enable forests to better resist invasions.

Methods

Site selection

This study was conducted in the eastern broadleaf forest province of central and southern Minnesota, USA, (MNDNR 2005) during the summers of 2010, 2011, and 2012. Criteria for site selection included closed-canopy red or pin oak-dominated forest that had either been harvested for timber within the previous ten years or had not experienced any major disturbance in the previous ten years. Fifty-six study sites were established in dry-mesic to mesic, red or pin oak-dominated hardwood forests (figure

2.1). Eighteen of these sites had been harvested for timber within the previous ten years, while the remaining 38 sites had experienced no major disturbance in the past decade. Of the 18 harvested sites, 13 were selection harvests while 5 were clearcut harvests. These sites were located on public and private forestland, with the majority found in Minnesota State Parks, State Forests, and Wildlife Management Areas. Candidate site locations were identified using GIS maps and recommendations from forest managers. All selected sites contained a minimum of 40% basal area of red or pin oak (*Quercus rubra* or *Q. ellipsoidalis*) and at least 75% total canopy cover. Other common overstory species included red and sugar maple (*Acer rubrum* and *A. saccharum*), green ash (*Fraxinus pensylvanica*), and American basswood (*Tilia americana*). This forest type was selected because it is common in Minnesota and is frequently invaded by common buckthorn (MNDNR 2005, Schulte et al. 2011). Sites were located between 43.513236° and 46.123257° latitude and -94.358826° to -91.288147° longitude. Climate in this region is continental, with precipitation ranging from 70 – 90 cm per year and mean annual temperatures of 6.1 - 7.8 °C. Since we were interested in how site characteristics affect invasion success by buckthorn (not vice-versa) we sampled sites with few large, seed-producing buckthorn.

Data collection

Once a suitable site was identified, 16 five-meter radius circular plots were established in a four by four grid in the first area of the site that we found with relatively

homogenous topography within the approximately half-hectare plot area. All plots were at least 40m from the nearest forest edge.

Within each of the 16 five-meter radius circular plots at each site, we identified and measured the diameter at breast height (dbh) of all woody plants >1.4 m tall. Within one-meter radius circular plots centered in each five-meter plot, we identified all herbaceous and woody plants, estimated percent cover of herbaceous plants, and counted stems of woody plants <1.4 m tall. Percent cover was visually estimated using a cover scale of 1%, 3%, 5%, 10%, 20%, continuing in increments of 10%. Taxonomy followed the *Flora of North America* (Flora of North America Editorial Committee 1993) and *Manual of vascular plants of northeastern United States and adjacent Canada* (Gleason and Cronquist 1991). Invasive or native status was determined for all observed species based on the USDA Plants Database classification (USDA 2015a). Voucher specimens were deposited in the Herbarium of the J.F. Bell Museum of Natural History at the University of Minnesota. We used Phylomatic (Webb and Donoghue 2005) to estimate a backbone phylogenetic hypothesis for all species surveyed based on a published supertree (APG 2009) (Appendix S2.A). We then calculated the mean pair-wise phylogenetic distance (MPD) for each site using R (R Development Core Team 2009). This metric gives a measure of phylogenetic diversity by accounting for the pair-wise phylogenetic distance between all species in a sample (Webb 2000). Details of our phylogenetic analysis methods can be found in Whitfeld et al. (2013).

Canopy openness (as an estimate of light levels) was measured using a densiometer held in the center of each five-meter plot, 1.4 m above the ground. Slope and

aspect of each plot were recorded at the same location (by using a clinometer and compass, respectively). Soil samples were collected to a depth of 20 cm at three locations (0°, 120°, and 240°) approximately 2 m from plot center using a 2 cm diameter soil corer. These samples were air dried and composited across all 16 plots to create a site-level soil sample. Soil pH was measured using a Corning pH meter 240 with soils resuspended in a CaCl₂ solution. Soil texture was measured using the hydrometer method (Gee and Bauder 1986). These measurements were used to estimate plant-available nutrient levels and soil water holding capacity, respectively. In addition, samples were sent to the University of Minnesota Soil Analysis Laboratory for determination of nutrient concentrations of nitrogen, carbon, potassium, calcium, and magnesium. Depth of the leaf litter layer and duff (partially decomposed organic matter) were measured at the three soil sampling locations within each plot. Percent bare ground was visually estimated on a ten-percent increment scale within a 1 m² square frame at two locations within each plot (120° and 240°). We also assessed invasive earthworm species presence and density at the site scale by using the Invasive Earthworm Rapid Assessment Tool (Loss et al. 2013).

To estimate buckthorn propagule pressure, we counted mature buckthorn stems growing along roadways adjacent to our study sites whose seeds could be expected to be carried into the sites by birds. In the summer of 2011, we conducted a driving survey of buckthorn plants >1 m tall on each side of the road at a speed of approximately 20 mph. Driving surveys were intended to sample as close to study sites as possible – typically 8 - 35 km of roadway were surveyed in a loop surrounding each study site. If two study sites were located close together (i.e., in the same forest property), one set of road survey data

was applied to both sites. The smallest loops were an average of 0.6 km from the surveyed site while the largest loops were up to 5.1 km from the sites. These distances are well within the home range for birds known to eat buckthorn fruit (Lindsey 1939, Minderman et al. 2010). In addition to conducting continuous driving surveys, we also stopped the car every 1.6 km and recorded separate point counts of all buckthorn >1 m tall visible along an approximately 30 m transect on each side of the road. Continuous driving surveys and point counts were highly correlated across the 22 sites surveyed in 2011 ($R^2 = 0.8779$, $p < 0.0001$), so only the faster, easier, and safer method of point counts was used for all sites surveyed in 2012. In order to account for the variety of land cover throughout the study area, the distance of surveyed road that was not directly abutted by agriculture (i.e., plowed land where buckthorn would not be allowed to grow; fence lines and uncultivated agricultural field edges were included in the road surveys) was measured using Farm Services Administration (FSA) color orthophotos (DNR 2004) in ArcGIS (ESRI 2012). The buckthorn point count total divided by the number of kilometers of roadway without agriculture (mean buckthorn per countable kilometer) was used in analyses as an estimate of landscape-level propagule availability for each site.

Using GIS mapping software, we calculated a number of different variables for each site that may be useful proxies for propagule pressure. These variables included forest stand area, perimeter, and perimeter to area ratio (stand was defined as a contiguous piece of forest based on aerial photographs); distance from site to nearest forest edge, road, and populated area (defined as more than four buildings grouped together); density of roads within a 1 km-radius circular buffer around each site; and

distance to a point directly between the centers of the large cities of Minneapolis and St. Paul. The Minneapolis-St. Paul variable was measured because this is the largest metropolitan area in the surveyed region and is presumed to be one of the regional epicenters of buckthorn introduction, as well as a proxy for how urban a site was based on how close to it was to the metropolitan area. Other smaller cities were present in the survey region, but distance to these was not calculated to limit complexity. Road measurements were made using the DNR major roads layer (DNR 2012), while FSA orthophotos (DNR 2004) were used to measure forest stand and populated area characteristics. In other studies, many of these variables were used as proxies for propagule pressure due to their indication of human presence, disturbance, and other factors – such as high-light edge environments – that may be more likely to contain mature invasive plants that could be releasing seeds into the site (Lonsdale and Lane 1994, von der Lippe and Kowarik 2007, Christen and Matlack 2008, Mortensen et al. 2009, Flory and Clay 2009).

Data analysis

Many biotic and abiotic factors were measured at each site. However, many of these variables were correlated, so only some variables were included in modeling (Appendix S2.B). All of the soil characteristics were highly correlated, therefore soil pH was selected a priori to be the only soil variable entered into the regression models, since soil pH can serve as an indicator of soil fertility. Shannon Diversity Indices for herbaceous and woody species were selected a priori to enter in the regression models

because this measure accounts for both number of species (richness) and evenness. The phylogenetic diversity estimates for herbaceous and woody species, based on species presence and separately weighted by abundance, were surprisingly not highly correlated with each other, however some of these variables were correlated with species richness and Shannon Diversity values. Herbaceous and woody mean pair-wise phylogenetic distance (MPD) based on species presence/absence (not weighted by abundance) was also entered into regressions. The MPD of woody species, weighted by abundance (stem count), was also selected a priori, while the MPD of herbaceous species weighted by percent cover was excluded due to strong correlation with Shannon Diversity Index. Percent bare soil and litter depth were each significantly correlated with date of survey, so the residuals of each of these after accounting for their relationship with Julian day were used. Regarding all of the propagule pressure-related variables, stand area, perimeter, and perimeter-area ratio were all strongly correlated, so stand perimeter to area ratio was selected a priori because it incorporated multiple variables. Driving point count and stems per countable kilometer (driving count with kilometers of agriculture removed) were highly correlated, so the latter was selected for inclusion. Distance from each site to the nearest forest edge, nearest road, nearest city/town, and road density were not strongly correlated, so distance from each site to nearest forest edge was selected a priori because it was most biologically relevant to buckthorn (i.e., buckthorn is most likely to be found along forest edges). Finally, canopy openness as an estimate of light level was also entered into the models, as well as whether a site had been harvested for timber within the past decade. Throughout all analyses, the number of buckthorn stems was used

as the response variable. Variables were log transformed to approximate normality when necessary.

Diversity, abiotic site characteristics, propagule availability, and harvest history (variables specified above) were entered into a logistic regression model to predict site-level buckthorn presence or absence. The same variables were combined in a general linear model to predict site-level buckthorn abundance, defined as the total number of stems in all plots at each site. Only the 46 sites that contained buckthorn were included in the general linear model. In order to meet the assumption of normality, stem counts at these 46 sites were log-transformed. The best-fit models were chosen based on the minimum Akaike information criteria (AICc) score. All analyses were performed using JMP Pro (SAS Institute, Inc. 2012).

Site characteristics including diversity, abiotic site characteristics, and propagule availability were compared between harvested and unharvested sites, between clearcut and selection harvested sites, and between clearcut, selection harvested, and undisturbed sites using Students t-tests and Analysis of Variance (ANOVA), followed by post-hoc Tukey's HSD tests.

Results

Across all sites, we observed 313 species of trees, shrubs, vines, and herbaceous plants. For individual sites, herbaceous species richness ranged from 13-63, while woody species richness ranged from 11-40. The most common invasive species included buckthorn (46 sites), *Lonicera spp.* (exotic honeysuckle, 29 sites), *Arctium minus*

(common burdock, 12 sites), and *Alliaria petiolata* (garlic mustard, 8 sites). Buckthorn was also by far the most abundant invasive plant at the plot scale. In the 46 sites where buckthorn was present, there was an average of 2,701 buckthorn stems per hectare (standard error = 731) and buckthorn basal area ranged from 0.0000125 to 3.82 m² per hectare. Additional summary information on site characteristics is shown in Appendices S2.C and S2.D.

Buckthorn presence and absence

Estimates of propagule availability and light levels provided the best-fit logistic regression model predicting buckthorn presence. This model included driving survey point counts, stand perimeter to area ratio, and light levels ($R^2 = 0.60$, $p < 0.0001$, table 2.1). Buckthorn was more likely to be present in sites with greater nearby buckthorn abundance based on driving surveys, higher stand perimeter to area ratio, and greater light levels. Timber harvest was not a significant predictor of buckthorn presence in the best-fit model.

Buckthorn abundance

Disturbance history (i.e. timber harvest), soil characteristics, resident plant phylogenetic diversity, and light levels were all significant predictors in the best-fit multiple regression model predicting buckthorn abundance in the 46 sites where buckthorn was observed. More buckthorn stems were observed in sites with higher soil pH, lower resident plant phylogenetic diversity, less leaf litter, more light, located closer

to forest edges, and in sites that had not been harvested for timber recently ($R^2 = 0.64$, $p < 0.0001$; table 2.2). No interaction terms were found to be significant predictors of buckthorn abundance when two-way interactions between all six significant predictors were included in the model. While proxies for propagule pressure such as the driving survey point count had a univariate correlation with buckthorn abundance ($R^2 = 0.23$, $p = 0.0007$), these variables were not retained in the best-fit model predicting buckthorn abundance.

While this analysis excluded sites that did not contain buckthorn, when all sites were binned into no/low/moderate/high abundance of buckthorn, the mean site attribute values found to be significant predictors of buckthorn abundance followed the same trends as buckthorn-free sites, with the exception of light availability (table 2.3). This result suggests that these relationships extend across all levels of buckthorn abundance. Light availability increased from sites without buckthorn to sites with moderate buckthorn, then was much lower in high-buckthorn sites. Sites without buckthorn were more likely to be located in closed-canopy forests without many canopy gaps, while sites with moderate buckthorn had more open canopies. Low light availability in the high-buckthorn sites may be caused by shading by the dense buckthorn shrub layer, even if the canopy may have been more open.

Surveyed sites that experienced timber harvest differed in some characteristics from sites that had not experienced this disturbance. Some of these differences may be due directly to harvesting, while others may be due to the locations of public lands with recent timber harvests within central and southeastern Minnesota. Harvested sites were

located significantly farther from the Twin Cities metropolitan area ($p = 0.0004$), in larger tracts of forests ($p = 0.0468$), had smaller stand perimeter to area ratios ($p = 0.0187$), contained fewer mature buckthorn stems on the roadways surrounding the sites ($p = 0.0221$), had higher light levels ($p < 0.0001$), and less exposed mineral soil ($p = 0.0238$). Harvested sites also contained higher percent cover of herbaceous plants ($p = 0.0008$) and higher herbaceous species diversity ($p = 0.0003$). Harvested sites contained more native species (selection harvest: 68.5 ± 3.8 ; clearcut: 65.2 ± 6.1) than unharvested sites (48.7 ± 2.2 ; $p < 0.0001$). They also contained higher richness of nonnative species than unharvested sites ($p < 0.0001$), with this trend mostly due to the significantly higher number of nonnative species recorded in clearcut stands (8.6 ± 0.93) than those that were selection harvested (3.9 ± 0.58) or unharvested (2.8 ± 0.34). Harvested sites did not differ from unharvested sites in their distance to forest edges, nearest road, nearest town or city, nor in their soil pH, woody species diversity, phylogenetic diversity, or leaf litter depth (all $p > 0.1$).

However, the type of timber harvest also influenced buckthorn success. Sites that were clearcut contained significantly more buckthorn than selection harvest sites ($p = 0.0303$, figure 2.2). In addition, the canopy at these sites was significantly more open ($p = 0.0141$, figure 2.3), as would be expected following removal of the canopy trees. Clearcut sites were also located farther from populated areas than selection harvest sites ($p = 0.0042$). The vast majority of other measured/observed characteristics did not differ between selection harvest sites and clearcut sites. These characteristics included stand area, perimeter, and perimeter to area ratio; distance to the Twin Cities, nearest forest

edge, and nearest road; number of mature buckthorn counted in the driving survey; pH, bare soil, and litter depth; herbaceous plant cover; and Shannon and phylogenetic diversity.

Discussion

Invasive plants can cause ecological and economic harm on public and private lands, and interfere with successful implementation of forest management. Understanding what characteristics of forests may make them more susceptible to invasion may suggest management practices that could reduce site invasibility, or at least give managers insights into which sites may be more susceptible and therefore would benefit most from frequent monitoring to catch new invasions. Our study examined abiotic and biotic characteristics of forests, while accounting for local propagule pressure, to determine which factors most influenced invasion by common buckthorn.

As expected, local propagule pressure is very important to predicting buckthorn presence in a given forest stand. This was indicated not only by the inclusion of the driving survey stem counts in the logistic regression model, but also the stand perimeter to area ratio. The amount of buckthorn seeds nearby may be critical for determining whether buckthorn has an opportunity to invade. Forest stands with more forest edges, and less forest interior, harbor more microsites suitable for buckthorn growth and reproduction (Gourley and Howell 1984). Even if a forest tract of interest is located deep in the interior of a larger forest parcel, if that parcel is highly dissected, it is more likely to support buckthorn along its margins, which could lead to seed transport into the forest

interior. Similar results regarding the importance of stand shape have been found with other invasive species (Honnay et al. 2002, Bartuszevige et al. 2006, Ohlemuller et al. 2006). Forests with higher light levels also were more likely to have buckthorn present, likely due to the invader's preference for intermediate light levels – those that would be found in large forest gaps (Gourley and Howell 1984, Knight et al. 2007).

While propagule availability appears to be most important for determining presence or absence of buckthorn, biotic and abiotic site characteristics tend to play a more important role in affecting abundance of buckthorn stems. Sites with higher resident plant phylogenetic diversity were more resistant to buckthorn invasion, echoing the findings of Whitfeld et al. (2013). Communities with higher diversity may more completely utilize available resources and serve as a barrier to invasion (Davis et al. 2000, Cadotte et al. 2009, Gerhold et al. 2011) or at least as a constraint on abundance of invaders (Levine et al. 2004). Sites with higher pH appeared more susceptible to buckthorn invasion. This is supported by earlier findings that invasive plants often are more successful in high-nutrient habitats (Howard et al. 2004, Gurevitch et al. 2008) and that buckthorn is limited on acidic soils, such as those found in coniferous forests (Gourley 1985, Kurylo et al. 2007). However, buckthorn has also been shown to increase soil pH (Heneghan et al. 2002, 2004, 2006, Iannone et al. 2015). The observational nature of the current study prevented us from teasing apart whether buckthorn preferred microsites with higher soil pH or whether presence of buckthorn increased soil pH.

Seedbed conditions appear to influence buckthorn abundance once it is present in an area due to its affinity for germination on bare mineral soil (Bisikwa 2005). In the

present study, we found sites with a thicker leaf layer contained less buckthorn, while Whitfeld et al.(2013) observed more buckthorn in sites with more bare soil. These two variables, litter depth and bare soil, are well correlated and suggest the importance of exposed mineral soil for buckthorn establishment. In previously glaciated regions of the Upper Midwest, European earthworms are changing the structure of the forest floor by consuming leaf litter (Hale et al. 2006, Frelich et al. 2006). It is possible that earthworms are facilitating the spread of buckthorn by consuming leaf litter and improving seedbed conditions for buckthorn germination (Whitfeld et al. 2014, Roth et al. 2014).

Our multiple regression model indicated that sites with recent timber harvest were less invasible by buckthorn than unharvested sites. While harvesting was not a significant predictor of buckthorn presence, when only sites with buckthorn present were examined, those that had been harvested contained less buckthorn. This could suggest that harvesting may slow the spread or reduce the abundance of buckthorn, at least in the short term. Following a clearcut harvest, when the canopy is removed and abundant light is allowed to reach the forest floor, native and nonnative early successional plant species respond by growing quickly and forming dense herbaceous and shrub layers. This dense vegetation could potentially compete with young buckthorn seedlings, shading them and reducing growth and survival, potentially limiting the abundance of buckthorn. However, over time, trees will again form a canopy that will reduce understory light levels, reducing or eliminating shade-intolerant species. If some buckthorn seedlings were able to persist among the dense early-successional species, many of these saplings are likely to continue to survive in the shaded environment of the tree canopy. Therefore, while

buckthorn abundance may be reduced by competing vegetation soon after harvesting, over time it may still be present and continue to spread in regenerating forest stands.

Since this was an observational study, we located sites where harvest treatments were implemented and almost all of our harvested sites were located outside of the Twin Cities metropolitan area. It is probable that the Twin Cities were one of the initial regional introduction points for buckthorn, and may have served as the epicenter from which the initial invasion spread. Our driving survey counts of mature buckthorn are negatively (but weakly) correlated with distance to the Twin Cities (R^2 0.1469, $p = 0.0036$), indicating that propagule pressure is higher closer to the metro area and lower where our harvest sites were located. The studied forests were all second-growth forests that were logged and/or grazed in the early 1900's and allowed to reestablish (Bachmann 1965). Moles et al. (2012) suggest that disturbance itself does not inherently make a forest more invasible but a change in the disturbance regime could increase invasibility. Within our study, it is possible that selection harvests are mimicking small-scale wind disturbance events, an element in the historic disturbance regime for these forests (although fire was also historically present; Abrams 1992, Andersen et al. 1996), and therefore are not increasing the invasibility of the stands.

Selection harvesting is often used in higher-quality, interior forest stands in order to maintain or improve habitat for migratory birds. Many neotropical migrants suffer less predation and parasitism in larger, contiguous, intact forests than in forests fragmented by agriculture or even-age forest management, such as clearcutting (Robinson 1995, Knutson et al. 2004). The small canopy gaps formed by single tree or group selection

harvesting are often frequented by insectivorous forest birds due to the high quantity of insects attracted by a denser shrub layer and abundant foliage (Ewart and Hamas 1995). Selection harvests also maintain a mature tree canopy, which is favorable to many forest bird species (Thompson et al. 1995). These migratory birds are mainly insect-eating and therefore are unlikely to consume or transport buckthorn seeds into harvest sites.

Even after we accounted for propagule pressure and other factors, we still observed lower buckthorn abundance in harvested sites. When we separated harvest sites into clearcuts and selection harvests, we observed that sites that had been clearcut contained more buckthorn than selection harvest sites. This may have been due in part to the higher light levels in clearcut stands. A similar pattern was observed with a related invasive shrub, *Frangula alnus*, with the highest levels of invasion in clearcut stands, followed by selection harvest, and unharvested stands (Lee and Thompson 2012). However, that study was conducted in an area where the studied species was well-established and widespread, whereas our study was located across a larger area with more variable local propagule availability. Other researchers have also observed more invasive plants, along with more weedy generalist native plants, in stands following commercial clearcut than in stands with less intensive harvesting (Battles et al. 2001, Burke et al. 2008, Olson et al. 2011).

Overall, our results support previous findings of Whitfeld et al. (2013) regarding the influence of phylogenetic diversity, canopy openness, and bare soil on buckthorn abundance, while also highlighting the importance of propagule availability for new and spreading invasions. In order for buckthorn control efforts to be successful, they should

be conducted in coordination with surrounding landowners to reduce the propagule availability in the area. When propagule pressure is accounted for, abiotic and biotic site characteristics such as light, leaf litter depth, and resident plant diversity play a role in site invasibility. Management techniques that limit large increases in light availability (e.g., selection harvests rather than clearcuts), maintain or increase resident plant diversity (e.g., manage deer populations), and limit the spread of invasive earthworms that consume leaf litter can all contribute to maintaining forests more resistant to buckthorn invasion.

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Table 2.1. Results of best-fit logistic regression model for buckthorn presence in 56 surveyed sites. The complete model included stand perimeter to area ratio (*Perimeter:area*), number of buckthorn stems counted in driving survey of nearby roads (*Driving count*), and site light levels (*Light*). The best-fit model was chosen based on minimum AICc score (total $R^2 = 0.60$).

Term	Estimate	Standard Error	Chi Square	Prob > Chi Square
<i>Intercept</i>	-18.947	8.267	5.25	0.0219*
<i>Perimeter:area</i>	18.402	7.729	5.67	0.0173*
<i>Driving count</i>	5.856	2.536	5.33	0.0209*
<i>Light</i>	4.411	2.392	3.40	0.0652

Table 2.2. Results of best-fit multiple regression for buckthorn abundance (stems) in 46 surveyed sites where *R. cathartica* was present. *Harvest*: Factor variable indicating whether site was harvested or not; reference level is harvested. *Edge*: distance to nearest forest edge. *Phylogenetic diversity*: Mean phylogenetic distance between all pairs of species present in the site. The best-fit model was chosen based on minimum AICc score (total $R^2 = 0.64$).

Term	Estimate	Standard Error	t Ratio	Probability > t
<i>Intercept</i>	10.390	4.374	2.38	0.0224*
<i>Harvest</i>	0.567	0.151	3.75	0.0006**
<i>Edge</i>	-0.745	0.358	-2.08	0.0437*
<i>Soil pH</i>	0.596	0.161	3.70	0.0006**
<i>Light</i>	1.100	0.355	3.10	0.0035*
<i>Phylogenetic Diversity</i>	-0.052	0.016	-3.29	0.0021*
<i>Litter Depth</i>	-0.490	0.162	-3.03	0.0042*

Table 2.3. Mean values for a number of site characteristics, averaged across all plots within each site, averaged by buckthorn abundance (none to high). *N* = number of sites; *Phylogenetic Diversity* = Mean pair-wise phylogenetic distance for all herbaceous and woody species present in each site; *Driving Survey Stems per km* = average number of mature buckthorn stems counted in roadside survey, with agricultural land excluded.

Buckthorn Stem Class	N	Distance to Edge (km)	pH	Canopy Openness	Phylogenetic Diversity	Litter Depth (mm)	Perimeter to Area Ratio	Driving Survey Stems per km
<i>None</i>	10	0.2887	5.07	9.613	270.203	12	4.601	1.109
<i>Low</i>	25	0.1439	5.19	12.104	267.063	11	8.638	3.208
<i>Moderate</i>	11	0.1129	5.47	16.716	265.408	7	8.480	8.461
<i>High</i>	10	0.1368	5.64	8.100	262.196	5	9.776	7.146

Figure 2.1. Map of Minnesota displaying locations of study sites (points).

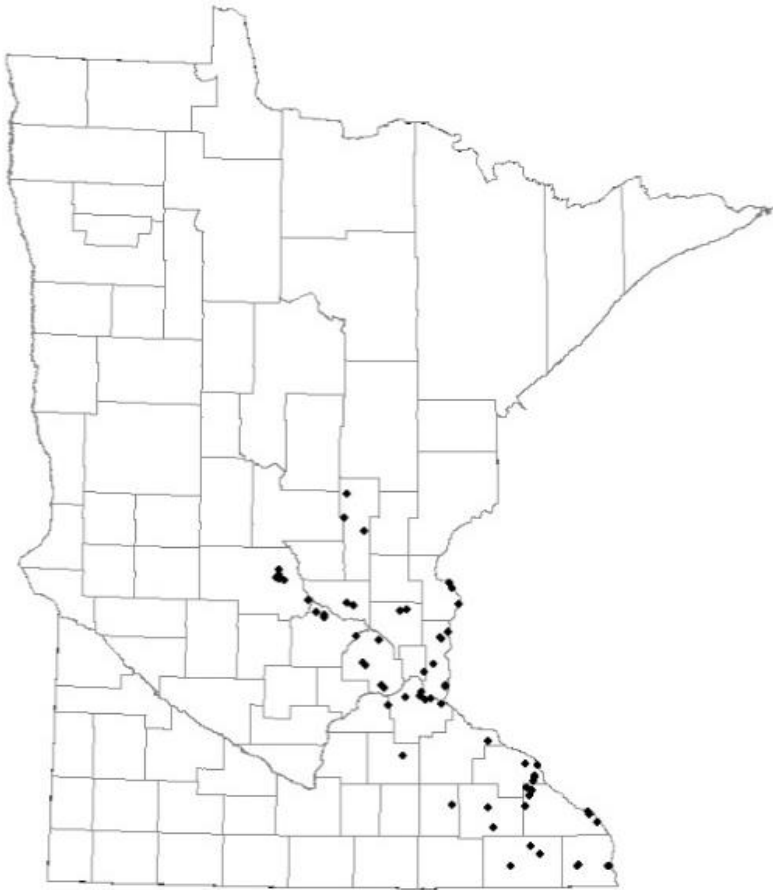


Figure 2.2. Abundance of buckthorn observed in sites where buckthorn was present that had experienced clearcut (N = 5), selection harvest (N = 9), or no recent disturbance (N = 32). Error bars are standard error. Letters indicate significant different between means ($p < 0.05$).

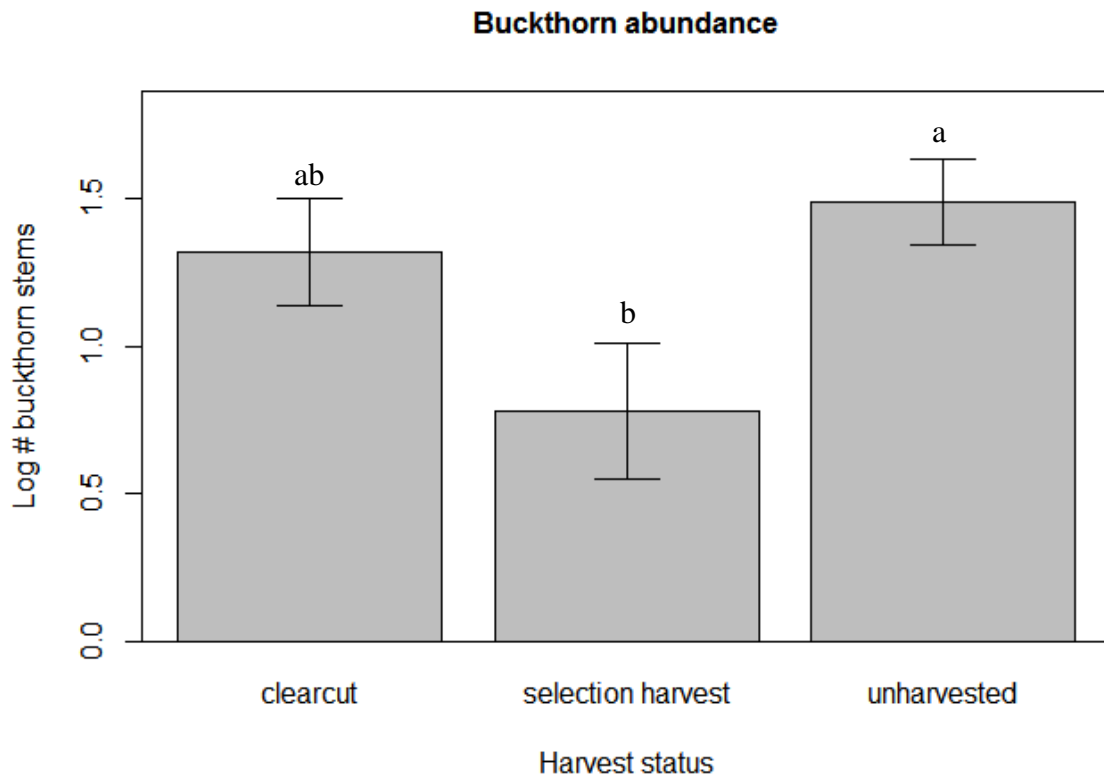
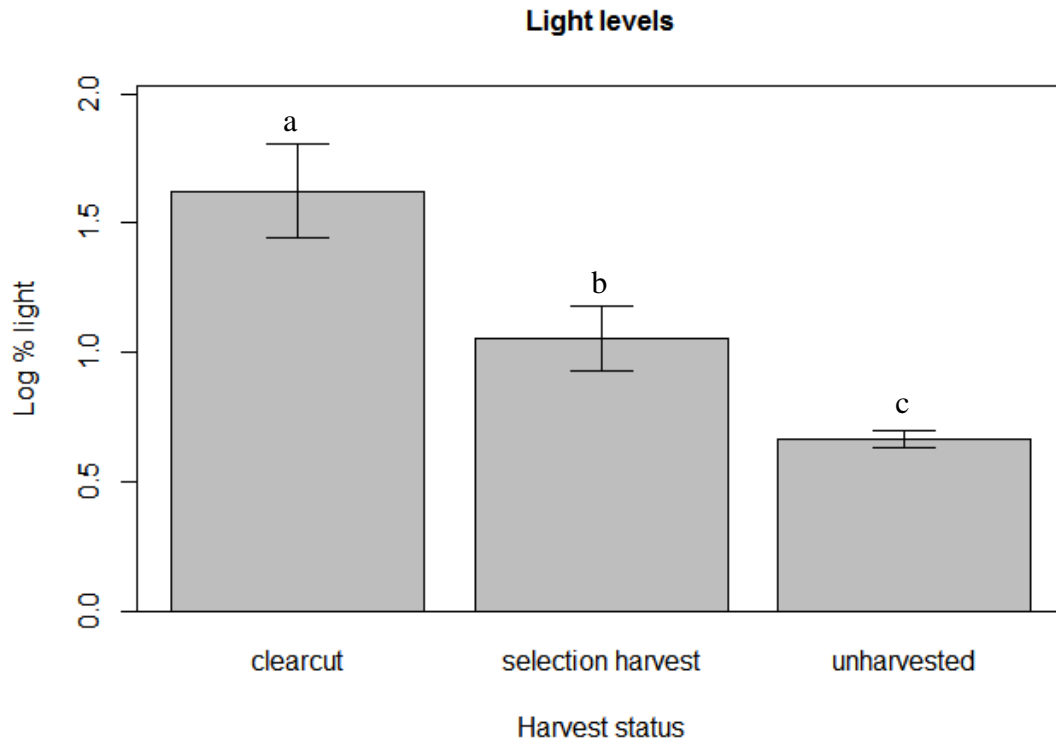


Figure 2.3. Light levels observed in sites that had experienced clearcut (N = 5), selection harvest (N = 9), or no recent disturbance (N = 32). Error bars are standard error. Letters indicate significant different between means ($p < 0.05$).



CHAPTER 3

Unseen changes: Invasive common buckthorn's influence on nutrient cycling in northern temperate forests

Summary

Common buckthorn (*Rhamnus cathartica* L.) is a pernicious invasive shrub in North American temperate forests. While many of the negative effects of common buckthorn on native plants and animals have been studied, less is known about its effects on soil nutrient pools and processes. Our study explored the potential impacts of buckthorn on soil nutrients by examining nutrient cycling across a natural gradient of buckthorn density representing an invasion front where its abundance resulted from migration rather than underlying soil-site factors. Focal elements included nitrogen, phosphorus, base cations (e.g., calcium), and carbon. We quantified nutrient inputs from leaf litterfall, rates of net nitrogen mineralization in soil, and the size of soil nutrient pools, including microbial biomass. We then assessed whether variance in these aspects of nutrient cycling was related to buckthorn abundance. Compared with maple or oak, buckthorn leaves and leaf litter contained at least 48% higher concentrations of nitrogen and calcium, but similar concentrations of phosphorus. We observed positive correlations between buckthorn abundance and total nitrogen, organic carbon, and calcium in soil. Soil pH also increased with buckthorn abundance. Conversely, there were no apparent effects of buckthorn on phosphorus concentration in soil. Contrary to our expectations, net nitrogen mineralization in the winter was lower where buckthorn was abundant and nitrogen mineralization in other seasons was not correlated with buckthorn abundance. We also observed changes in the nutrient composition of soil microbes in the spring across the buckthorn abundance gradient. Overall, buckthorn appears to increase soil nitrogen, organic carbon, and pH through deposition of nutrient-rich leaf litter. Such

increases in apparent soil fertility due to buckthorn invasion could have substantial impacts on ecosystem functions such as forest productivity, pedogenesis, and nutrient export to groundwater and surface waters.

Introduction

Invasive plants can impact ecosystems by changing ecosystem processes such as nutrient cycling (Ehrenfeld 2003, 2010, Castro-Díez et al. 2014). This can be caused by a nonnative newcomer fixing nitrogen (N) (Stock et al. 1995) or disrupting N-fixing activities of resident plants via allelopathy (Wardle et al. 1994). Invasive plants can also impact nutrient cycling by depositing leaf litter with different biochemical composition as compared to native plants, with potential consequences for microbial communities, litter decomposition rates, rates of nutrient mineralization in litter and soil, and storage of organic and inorganic nutrients in soil (Ehrenfeld et al. 2001, Mitchell et al. 2011, Poulette and Arthur 2012, Bajpai 2013, Schuster and Dukes 2014). For example, if invasive plants have higher concentrations of nutrients in leaf litter and/or lower concentrations of phenolic compounds, including tannins and lignin, plant invasion could result in increased rates of litter decomposition and nutrient mineralization (Liao et al. 2008, Ehrenfeld 2010) and enhanced stabilization of organic matter in soil (Tamura and Tharayil 2014). Such changes are expected based on stoichiometric controls on the microbial processes that regulate litter decomposition, nutrient mineralization, and soil organic matter stabilization (Parton et al. 2007, Manzoni et al. 2008, 2012, Cotrufo et al. 2013). In addition, plant invasion could result in altered nutrient cycles if invasive plants

have a novel phenology with respect to the uptake of water and nutrients or senescence of leaves and roots (Ehrenfeld 2003). Such alterations in nutrient cycling can have important impacts on nutrient use by native plants, native and invasive plant productivity, recruitment of native and nonnative seedlings, and nutrient exports to aquatic systems.

In this study we evaluated the potential effects of common buckthorn (*Rhamnus cathartica* L.) on nutrient cycling in temperate forests of North America. Common buckthorn is a shrub or small tree introduced to North America from Europe and Asia in the 1800's as an ornamental and medicinal plant (Kurylo and Endress 2012). It can grow in a wide variety of habitats, including open areas, woodlands, forest interiors, anthropogenic areas, and wetlands (Kurylo et al. 2007). It has spread across much of the eastern deciduous forest of the United States, where it can form dense stands that shade the forest floor and are difficult for humans and wildlife to walk through (Knight et al. 2007). Indeed, common buckthorn is now present in 33 U.S. states (USDA 2015a). Common buckthorn has been shown to have pervasive effects on temperate forests ecosystems. For example, the presence of common buckthorn has been associated with a decrease in the flowering of native herbs and regeneration of native trees as well as changes in bird and mammal behavior (Schmidt and Whelan 1999, Fagan and Peart 2004, Frappier et al. 2004, Knight et al. 2007, Kliensky et al. 2011, Vernon et al. 2014). Common buckthorn is also associated with European earthworm invasion (Heneghan et al. 2007, Heimpel et al. 2010).

Some studies suggest that common buckthorn might alter nutrient cycling. Comparing soil properties of forest stands with and without common buckthorn,

Heneghan et al. (2004, 2006) reported that buckthorn presence is associated with higher percent nitrogen (N), percent carbon (C), and pH in soil, with variable apparent effects of buckthorn on inorganic N availability in soil. In a similar study, Knight et al. (2006) observed that plots near mature buckthorn trees had higher soil nitrate availability, higher rates of net N mineralization in soil, and elevated leaf N in buckthorn seedlings. Presently, the impacts of common buckthorn on nutrient cycling in temperate forests are not well known, partly due to the limited number of studies. Further, previous studies have focused on a limited number of plant nutrients, nutrient pools, and nutrient fluxes and failed to evaluate the role of potentially confounding factors (e.g. pre-existing variability in soil texture and soil fertility).

The unique chemical composition of buckthorn leaf litter could play a strong role in determining the impact of common buckthorn on nutrient cycling. Buckthorn leaf litter is high in N and decomposes quickly relative to the native woody plants with which buckthorn co-occurs (Harrington et al. 1989, Heneghan et al. 2002, 2006, Knight et al. 2007). Such high-nutrient litter could change the availability of nutrients in oak- or maple-dominated eastern forests, where buckthorn is now abundant. However, previous studies have not quantified and reported the annual flux of N and other nutrients from buckthorn leaf litter to soils. Further, we are unaware of any study that reports the concentration of base cations (e.g. calcium) in buckthorn leaf litter and only one that examines calcium in soils beneath buckthorn (Iannone et al. 2015). Unpublished analyses of the nutrient content of buckthorn leaves in Wisconsin, U.S.A., (Harrington et al. 1989) suggest that buckthorn leaves might have high concentrations of base cations as

compared to co-occurring woody plants (Reich unpublished data). Collectively, these knowledge gaps hinder the understanding of the scope and mechanisms of altered nutrient cycling in the presence of buckthorn.

This phenology of common buckthorn could also lead to differences in the magnitude and timing of nutrient fluxes in invaded forests. Common buckthorn has an extended leaf phenology, leafing out earlier in the spring than native trees and shrubs and holding its leaves later into the fall than the natives (Harrington et al. 1989, Knight et al. 2007, Fridley 2012). In forest stands where buckthorn is abundant, this unique leaf phenology likely has consequences for both nutrient uptake and the return of nutrients to the soil via leaf litterfall.

Our study aimed to further explore these potential impacts of buckthorn on soil nutrients by examining nutrient cycling across a natural gradient of buckthorn density. In a temperate forest in the northern United States, we quantified nutrient inputs from leaf litterfall, rates of net N mineralization in soil, and the size of soil nutrient pools, including microbial biomass. Then we assessed whether variance in these aspects of nutrient cycling were related to buckthorn density across a gradient ranging from no buckthorn present to dense buckthorn stands with mature buckthorn individuals. More specifically, for N, calcium (Ca), and phosphorus (P) we measured the size of both the soil nutrient pools and the annual nutrient flux in leaf litterfall. In addition, we measured a suite of other ecosystem properties, including soil texture, soil organic carbon, soil pH, soil bulk density, and root biomass. Consequently, this study is, to our knowledge, more comprehensive than prior studies and aims to provide a broader assessment of the impact

of buckthorn invasion on nutrient cycling in temperate forests. As part of this broader aim, we also tested three specific hypotheses. The high N content of buckthorn leaf litter would result in at least two changes in nutrient cycling as buckthorn density increased: 1) increased N mineralization rates in soil, and 2) increased total C and N in mineral soils. Additionally, we expected that buckthorn leaves and leaf litter would have relatively high Ca content, which could be associated with an increase in soil pH and soil Ca concentrations (Reich et al. 2005).

Methods

Site description

This study was conducted at the Lee and Rose Warner Nature Center located in Marine-on-Saint-Croix, Minnesota, about 50 km northeast of St. Paul, Minnesota (45.172626°, -92.831987°). Climate is continental with 30-year normal mean temperatures of -9.6 °C in January and 22.1 °C in July. Mean annual precipitation is 830 mm, about 70% of which occurs between the months of May and October. This 280-hectare property is topographically variable, mainly consisting of upland forests, with areas of lowland forests, wetlands, and prairie. Slopes are typically less than 20°. We focused on upland areas characterized by mesic, deciduous forest dominated by red and white oaks (*Quercus rubra* and *Q. alba*; typically > 80 years old) and red maple (*Acer rubrum*; typically < 50 years old). Sporadic black cherry (*Prunus serotina*) and basswood (*Tilia americana*) are also present in the canopy. The forest is heavily invaded by

European earthworms and the studied areas ranked as a 5 on the Invasive Earthworm Rapid Assessment Tool (Loss et al. 2013).

Common buckthorn has been present at the site for about 30 years and the staff members have monitored its spread over the last decade (Ron Lawrenz, personal communication). There were 32 annual tree rings counted on a stem cross-section of one of the largest buckthorn in the area. Moreover, buckthorn invasion fronts are visible in multiple locations at the site. These are areas where one can see clear spatial gradients of buckthorn abundance where large, older buckthorn is growing in dense stands that gradually grade to an understory characterized by small, sparse, young buckthorn. Thus, both knowledge of site history and spatial patterns of buckthorn abundance, age, and size indicate that in these areas buckthorn presence or absence is not strictly soil-related: hence this invasion front provides a useful model system to examine effects of the nonnative species, similar to other studies of nonnative species effects on ecosystems along invasion fronts (Lederer et al. 2006, Hale et al. 2006, Lankau et al. 2009). Sampling for determination of vegetation and soil properties occurred between June of 2012 and May of 2013.

Plot setup and vegetation survey

We studied 28 plots located along two different natural gradients of buckthorn abundance; 12 plots were located along a gradient of buckthorn abundance on sandy soils (45-62% sand) and 16 plots were located nearby (~300 m distant) along a similar buckthorn gradient on silty soils (2%-22% sand, 53%-71% silt). On the silty soils, 4 of

the plots were located in areas where the land managers had manually removed buckthorn using weed wrenches to uproot large stems and hand-pulling small stems either three (two plots) or six years (two plots) prior to sampling for this study. Buckthorn reinvaded these plots and is now found in low to moderate densities (1400-2400 stems/ha). Throughout the study area, the organic soil horizon consisted largely of recognizable leaf litter and sporadic coarse woody debris, without development of humified horizons (i.e., an O_i horizon was present but O_e and O_a horizons were not apparent), due to European earthworm invasion (Frelich et al. 2006). We attempted to minimize variability among plots with respect to slope (4 - 16 degrees), elevation (285 - 374 m), and characteristics of the tree canopy, including tree species composition (see below) and understory light availability (e.g., we avoided canopy gaps associated with canopy tree mortality).

Each plot was 6 m in radius, with a 1.5 m radius circular subplot in the center. Within the 6 m radius plot, we identified all woody plants taller than breast height (1.4 m) and measured their diameters at breast height. Within the 1.5 m radius subplot, we also identified all woody plants smaller than breast height. Buckthorn density ranged from 0 to 294 stems per 6 m-radius plot (0 - 25,000 stems/ha), with buckthorn basal area ranging from 0 to 185.277 cm^2 per plot (0 - 1.638 m^2/ha). Overstory composition was similar across plots, with average red maple basal area of 6.4 m^2/ha (se = 0.97) and average oak species (both red and white oak) basal area of 26.2 m^2/ha (se = 3.67).

Sampling, processing, and analysis of soil properties

Soil texture and all measures of nutrient pools and fluxes were made in the 1.5 m subplot located in the center of each plot. With one exception (see below), all soil sampling was focused on the upper 20 cm of mineral soil using a 2 cm diameter soil corer. At least three soil samples per plot were collected for each sampling event and all soil properties were measured at the plot-scale by compositing the replicate samples within each plot (see Appendix S3.A for more detail on the timing of soil sampling events). Soil texture was measured using the hydrometer method (Gee and Bauder 1986) on two independent sets of soil samples, one collected in June and the other in July of 2012. Soil texture measurements were averaged between the two samples. For the purposes of expressing soil nutrient pools in units of ground area, bulk density of the soil fraction < 2 mm was measured using the measured volume of soil cores and the dry weight of sieved soil. Gravimetric soil moisture was measured on sieved soil for each sampling period. Total organic C, total N, exchangeable cations, total and extractable P, and soil pH were estimated using standard methods from a single sampling event in July of 2012. Briefly, total organic C and total N were estimated by combustion and quantification of CO₂ and N₂ using a VarioMAX C/N analyzer (Elementar, Inc.). Exchangeable cations were measured by extraction with ammonium acetate and quantification with ICP-AES. Total P was estimated using microwave digestion with a vanadate-molybdate reagent followed by ICP-AES. Bray-extractable P was measured by extraction with HCl and NH₄F followed by quantification with colorimetry. Soil pH was

estimated in a 1:1 (v/v) suspension of soil and water. All nutrient analyses were performed by the University of Minnesota Research Analytical Laboratory.

Net N mineralization and the abundance of inorganic N in soil were measured at successive time periods from summer of 2012 through spring of 2013 (Appendix S3.A). Each sampling event corresponded approximately with the seasons, including a summer sampling period (July 2012), a fall (November 2012) sampling period, an overwinter sampling period (November through April), and a spring sampling period (May 2013). We used a time series of soil core samples and *in situ* soil incubations to estimate both extractable ammonium (NH_4) and nitrate (NO_3) in soil as well as rates of net N mineralization (Raison et al. 1987, Binkley and Hart 1989). Briefly, for each sampling event, three 2 cm diameter soil cores were removed from each plot and three PVC tubes (5 cm diameter, with a tapered end to minimize compaction) were placed in each plot and capped with white plastic. The three removed soil cores were composited, sieved (2 mm) and extracted with 1 M KCl. Nitrate and ammonium concentrations in KCl extracts were then measured on an Alpkem autoanalyzer. After ~30 days (or 130 days for the overwinter samples), the PVC tubes were removed and then composited by plot, sieved, and extracted as described above. Net N mineralization rates were estimated by subtracting the total inorganic N (ammonium- and nitrate-N) in the soil cores from that in the field-incubated PVC tubes.

We also measured inorganic N availability using ion-exchange resin bags that were deployed and harvested coincident with the PVC tubes used to estimate net N mineralization. The resins (14.8 mg, Dowex Marathon MR-3) were placed in acid-

washed nylon bags. For each time period and at three locations within each plot, one resin bag was buried at approximately 10 cm depth in the soil. A narrow shovel was used to create a slit in the soil approximately 45 degrees relative to the soil surface, the resin bags were placed near the bottom of the slit, and the slit was pushed closed. After collection, the resin bags were rinsed in deionized water, air-dried and then frozen until extraction with 1 M KCl. Extracts were analyzed for nitrate and ammonium as described above.

We also measured C and N in microbial biomass in spring, summer, and fall using the chloroform-fumigation technique (Brookes et al. 1985, Vance et al. 1987). For each time period, using a composite soil sample for each plot after sieving to 2 mm, one aliquot of soil was immediately extracted using 0.5 M K₂SO₄ and another aliquot was fumigated with chloroform for 40 hours prior to extraction with 0.5 M K₂SO₄. Dissolved organic C and N were measured using a Shimadzu TOC/TDN analyzer and microbial C and N were estimated as the difference in dissolved C and N between the fumigated and non-fumigated samples. Due to equipment malfunctions, for the summer time period the microbial biomass C and N were measured on the top 15 cm of soil as opposed to the top 20 cm of soil. Root biomass was also measured after sieving (2 mm) and hand picking soil collected in July 2012 from the top 15 cm of soil.

Nonnative earthworms were sampled at two locations within each plot in July and November 2012 and July and September 2013. The liquid mustard solution extraction method was used (Lawrence and Bowers 2002). At each sampling location, 40 g of ground yellow mustard powder dissolved in four liters of water was slowly poured into a

35 cm by 35 cm metal frame. As earthworms emerged, they were collected and placed in containers containing 95% ethanol. For more details on earthworm sampling, see Roth et al. (in prep).

Green leaf and leaf litter collection and processing

In early September 2012, we collected leaves from buckthorn and red maple from all plots where one or both species were present and had branches low enough to reach with pole pruners. These two species were selected because they were the most common in the understory and lower canopy. We collected up to five leaves from a given individual from up to three individuals per species per plot. All leaves were composited by species and plot, then oven-dried (60 °C), weighed, and ground.

In early September of 2012 we also installed two 10-gallon pots, with diameter of approximately 50 cm, in each plot to collect leaf litterfall throughout the fall season. One pot, i.e., litter trap, was placed in the center of each plot and one litter trap was placed 1.5 m away to the north of plot center. Every two weeks between September 7 and December 3, we collected all leaves that had fallen into each litter trap. Pots were 42 cm tall, so buckthorn litter may be slightly underrepresented because some plants were shorter than the pot walls. We sorted the litter to species prior to oven-drying (60 °C) and weighing. After grinding, green leaf tissue and leaf litter were analyzed for concentrations of C, N, P, and cations including Ca. The C and N analyses were performed as described above, while P and cations were estimated following dry-ashing and acid-digestion using ICP-AES.

Following Aerts (1996), for buckthorn and maple we estimated resorption of N and P as the difference between N and P concentrations of green leaves and leaf litter in each plot (normalized to the concentration of N and P in green leaves). The flux of N via leaf litterfall for each plant species in each plot was calculated by multiplying the total grams of leaf litter of each species in a plot by the leaf litter N concentration of that species in the same plot. The total flux of N in leaf litterfall was calculated for each plot by summing these species-level leaf litter fluxes.

Data analysis

Green leaf and leaf litter nutrient concentrations were compared across species by using analysis of variance (ANOVA). We used simple and multiple regression to examine the influence of buckthorn abundance and other factors on nutrient pools and fluxes and other ecosystem properties (e.g. soil moisture and root biomass) in each sampled season. Percent sand was included as a covariate in the model when relevant to account for potential effects of soil texture on nutrient pools and fluxes. Data were log-transformed when necessary to approximate normality. Buckthorn basal area was used as the measure of buckthorn abundance because it was normally distributed following a log base ten plus 0.001 transformation, while the distribution of buckthorn stem counts remained skewed even after transformations. In a few instances (e.g. for total soil N), we used an information-theoretic approach to compare models with different combinations of potential predictor variables in order to identify which predictors were most useful in

explaining variability in nutrient pools and fluxes and to assess the independence of various predictor variables.

Results

Leaves and leaf litter

Both green leaves and leaf litter of buckthorn contained higher nutrient concentrations than maple leaves and litter from maple and oak, respectively. Compared to maple leaves of similar-sized individuals with canopies in similar understory positions, green buckthorn leaves contained higher concentrations of N and Ca (88% and 138% higher, respectively; $p < 0.0001$), 7.5% lower concentrations of C ($p < 0.0001$), and similar concentrations of P ($p = 0.66$; figure 3.1, left column). Green buckthorn leaves also contained higher concentrations of many other elements, including aluminum (Al), potassium (K), magnesium (Mg), and sodium (Na) than green maple leaves ($p < 0.05$; Appendix S3.B).

Buckthorn leaf litter nutrient concentrations followed the same patterns, with significantly more N and Ca than maple litter (48% and 180% higher, respectively; $p < 0.0001$) and oak litter (11% and 178% higher, respectively; $p < 0.0001$), as well as about 10% lower percent C ($p < 0.0001$) and comparable P levels ($p = 0.09$; figure 3.1, right column). Buckthorn leaf litter was also higher in Al, K, and Na (Appendix S3.C). When the N concentrations of leaf litter and green leaves were compared, buckthorn appeared to resorb less of its leaf N in the fall than maple trees (36% resorption vs. 52% resorption; p

< 0.0001; Figure 3.2). Buckthorn also appeared to resorb marginally less P than maple (74% resorption vs. 87% resorption, respectively, $p = 0.07$; figure 3.2).

When nutrient concentrations of green buckthorn leaves were compared among plots along the gradient of buckthorn abundance, leaf Ca concentrations were positively correlated with buckthorn abundance while leaf P was marginally negatively correlated with buckthorn abundance ($p = 0.08$, figure 3.3). There was no relationship between buckthorn leaf N concentration and buckthorn density. Additionally, nutrient concentrations of green maple leaves were not correlated with buckthorn abundance.

When leaf litter nutrient concentrations were compared among plots along the gradient of buckthorn abundance, both maple and oak litter had higher percent N when collected from plots with higher buckthorn abundance ($p < 0.05$, figure 3.4a & b). Buckthorn litter followed the same positive trend for N, but the relationship was not statistically significant ($p = 0.45$; figure 3.4c). The community weighted average litter N concentration was also significantly greater in plots with higher buckthorn abundance (data not shown). P concentrations of maple leaf litter were positively correlated with buckthorn abundance ($p < 0.05$, figure 3.4a). This trend was the same for buckthorn litter, but it was not significant ($p = 0.64$). For all of the focal plant species, concentrations of Ca, Mg, Al, and Na in leaf litter were not correlated with buckthorn density.

Plots with abundant buckthorn did not differ in total leaf litterfall from those with less buckthorn ($R^2 = 0.002$, $p = 0.84$). This result is consistent even when the basal area of canopy trees (oaks and maples) is included in the model as covariates. However, the total influx of N via leaf litterfall was positively correlated with buckthorn basal area ($p <$

0.05, figure 3.5a). The annual flux of N in leaf litter increased from $\sim 3.5 \text{ g m}^{-2}$ where buckthorn density was low to $\sim 4.5 \text{ g m}^{-2}$ where buckthorn density was high. Total Ca and potassium in leaf litterfall were also greater in high buckthorn plots ($p < 0.05$, $p < 0.01$, respectively; figure 3.5c & d). The flux of P in leaf litterfall followed the same trend, but the relationship was not significant ($p = 0.19$, figure 3.5b).

Roots

Fine root ($< 1 \text{ mm}$ diameter) biomass was positively correlated with buckthorn abundance ($p < 0.05$; figure 3.6a). There were up to 100 g more fine roots per m^2 in plots with high buckthorn abundance than in plots with sparse buckthorn. Coarse root ($> 1 \text{ mm}$ diameter) density followed the same trend ($p = 0.12$). While fine roots increased with buckthorn abundance, fine roots were negatively correlated with summer nonnative earthworm (*Lumbricus* spp.) biomass ($p = 0.054$). Root concentrations of K increased with buckthorn density ($p < 0.05$; figure 3.6e), while Ca, C, N, and P concentrations in roots did not vary across the buckthorn abundance gradient ($p > 0.05$, figure 3.6b, c, and d).

Soils

Buckthorn abundance impacted a variety of soil characteristics. Soil bulk density was negatively correlated with buckthorn basal area ($p < 0.05$; figure 3.7a). Soil pH was positively correlated with buckthorn abundance, even after accounting for soil texture ($p < 0.001$, figure 3.7b). As compared to plots with small or sparse buckthorn, soil pH was

roughly half a pH unit higher in plots with abundant buckthorn. The amount of exchangeable Ca and Na in soil was also much greater in high-buckthorn plots ($p < 0.01$; figure 3.7d), while exchangeable K and Mg were not correlated with buckthorn abundance ($p > 0.1$). Soil exchangeable Ca was as much as twice as high in plots with dense buckthorn as in those with sparse buckthorn. Total soil N and soil N:P were positively correlated with buckthorn abundance ($p < 0.001$ and $p < 0.01$, respectively; figure 3.7c), but Bray P and total P in the soil were not ($p > 0.05$, figure 3.7e). Soil moisture in the upper 20 cm of soil was negatively correlated with buckthorn basal area in October and November ($p < 0.05$), but was not correlated with buckthorn abundance in any other sampling period ($p > 0.1$).

The best-fit multiple regression model, based on minimum AIC score, of total soil N included percent sand and the percent of total leaf litterfall attributed to buckthorn litter ($R^2 = 0.57$, $p < 0.0001$; table 3.1, Model 1). Neither the total leaf litter N flux nor soil pH were retained in the best-fit model. Notably, when the total leaf litter N flux was added to the model, the percent of total leaf litterfall attributed to buckthorn remained a significant predictor in the model (table 3.1, Model 2). This suggests that there may be other effects of buckthorn on soil N, beyond its impact on total N inputs. Based on the best-fit regression model, total soil N increased by 0.65 standard deviations with every one standard deviation increase in the percent of total leaf litterfall attributed to buckthorn litter.

There were not strong or consistent trends across the buckthorn gradient for rates of net N mineralization or the abundance of inorganic and dissolved organic N in soil,

regardless of the sampling period. Neither soil ammonium nor nitrate concentrations varied with buckthorn abundance in any sampling period, and the same was true for ammonium and nitrate accumulation on ion-exchange resins ($p > 0.05$). Net N mineralization did not vary with buckthorn abundance in the summer or fall, but decreased significantly with buckthorn abundance in the winter, with $\sim 1 \text{ g m}^{-2}$ lower net N mineralized during the course of the *in situ* incubation in plots with abundant buckthorn ($p < 0.01$, figure 3.8a-c).

The ratio of C to N in microbial biomass was negatively correlated with buckthorn abundance in the spring, when microbial C:N ratio decreased significantly with buckthorn abundance, but did not vary with buckthorn abundance in the summer or fall sampling ($p < 0.001$, figure 3.8d-f).

Effects of buckthorn removal

There was generally no evidence that the nutrient cycling properties of plots where dense buckthorn had been manually removed were different than expectations based on their more moderate buckthorn density at the time of sampling; i.e. the triangular and circular symbols in figures 3.4 – 3.8, indicating buckthorn removal plots, did not consistently deviate in a positive or negative manner from model predictions based on their buckthorn density at the time of sampling. Additionally, when buckthorn removal status (“buckthorn removed” or “unmanaged”) was added as a discrete variable to the statistical models, the removal variable was not statistically significant ($p > 0.05$).

Discussion

Our results suggest the presence and abundance of the invasive woody shrub *Rhamnus cathartica* L. (common buckthorn) could have pervasive and marked impacts on nutrient cycling in northern temperate forests of North America. As buckthorn abundance increased along two invasion fronts in Minnesota, USA, we observed increasing concentrations of organic C, N, and exchangeable base cations (e.g., Ca and K) in soil, increasing fluxes of N and other nutrients to soil via leaf litterfall, as well as higher soil pH. These altered patterns of nutrient cycling are likely due to a combination of different ways buckthorn might alter biogeochemical dynamics in this system. Potential effects include: i) the deposition of buckthorn's high-nutrient leaf litter, ii) the unique phenology of buckthorn's physiological activities, and iii) the impacts of buckthorn presence and abundance on the nutrient uptake and use by co-occurring native trees (as reflected in characteristics of native species' leaf litter).

Buckthorn typically leafs out earlier than native shrubs and trees in the spring and also retains its leaves later into the fall (Harrington et al. 1989, Fridley 2012). This unique phenology could result in increased nutrient uptake and retention during times when other woody plants are less active, explaining the general increase in forest nutrient pools and fluxes that is apparent along gradients of buckthorn abundance. To evaluate this would require detailed quantification of pools and fluxes of available elements across numerous short time periods in the spring in plots with differing abundances of buckthorn; this was well beyond the scope of the present study.

Buckthorn also tends to drop its leaves while they are still green (Brown et al. 1985); this may be visually indicative of lower rates of N resorption by buckthorn as compared to co-occurring native shrubs and trees (which we documented for the first time in this study). Moreover, even with similar resorption rates, the higher N concentrations in green leaves would result in more N-rich litter. In our study, maple and oak leaf litter also had higher N concentrations in plots with more buckthorn. This could be evidence that, as a consequence of buckthorn invasion, nutrient uptake and/or resorption by co-occurring trees is altered, or some transfer of N from buckthorn litter to litter from neighboring plant species via microbial activity occurs within a couple weeks of leaf senescence. Regardless of the underlying cause of this pattern, this result shows the potential of buckthorn to have important consequences on the nutrient content and productivity of co-occurring trees as well as detrital chemistry and thus the decomposition of leaf litter and subsequent recycling and retention of litter-derived nutrients. The positive correlation between pH and buckthorn abundance may be due to buckthorn rapidly taking up any available nitrate and increasing hydrogen concentrations in the soil (Imas et al. 1997), as well as through slow enrichment of the soil with cation-rich Ca from the higher leaf and litter Ca of buckthorn (see below).

Our results regarding soil properties are generally consistent with those of previous studies. For example, Heneghan et al. (2004, 2006) also observed higher soil pH and total soil N in plots containing buckthorn. However, these and other previous studies (Knight 2006, Iannone et al. 2015) compared plots with and without buckthorn, but did not address the role of other factors that could differ among plots. Our use of spatially

localized gradients of buckthorn abundance, combined with the use of covariates such as soil texture, provides more substantial evidence that buckthorn invasion is likely causing these changes in soil characteristics (as opposed to the alternative explanation that buckthorn tends to be abundant in microsites that differed with respect to nutrient cycling prior to invasion).

Our study is also novel in two other aspects. First, we report that buckthorn leaves and leaf litter can contain much higher concentrations of not only N, but also of base cations as compared to co-occurring native species (red oak, white oak, and red maple in our study). Increased retention of base cations in soil and plant tissues due to buckthorn presence and activity, coupled with potentially increased retention of inorganic N, likely provide an explanation for observations that soil pH is higher in forest plots with abundant buckthorn. Second, the positive relationship between buckthorn abundance and the annual flux of nutrients through leaf litterfall provides a potential explanation for the impacts of buckthorn invasion on soil nutrient pools. This relationship also demonstrates that, despite being much smaller in stature and productivity than co-occurring tree species (e.g., buckthorn leaf litter accounted for between 5 – 9% of total leaf litterfall in most “dense” buckthorn plots, with 18% buckthorn litter in one plot), buckthorn invasion can have substantial impacts on the magnitude of annual nutrient fluxes from leaves to soil.

Given evidence that buckthorn invasion coincides with invasion by nonnative earthworms (Heneghan et al. 2007, Madritch and Lindroth 2008, Heimpel et al. 2010), some of the relationships reported here could reflect earthworm effects in addition to, or in conjunction with, effects of buckthorn presence and abundance. Indeed, across the

buckthorn gradient that we sampled, the abundance of invasive earthworms was positively correlated with buckthorn abundance (Roth et al. in prep). However, with one exception, regression analyses suggest that earthworm abundance did not explain variation in nutrient cycling or ecosystem properties beyond that which could be explained by buckthorn abundance alone. In other words, when *Lumbricus* spp. biomass was included with buckthorn abundance as a covariate in models of the various nutrient pools and fluxes or other ecosystem properties, it was not a significant predictor of anything except fine root biomass – while fine roots increased with buckthorn density, fine roots decreased with earthworm biomass. However, invasive earthworms in similar forests have been shown to decrease available soil N and Ca through immobilization and leaching (Hale et al. 2005, Resner et al. 2014). Our results suggest that buckthorn is increasing soil N and Ca, suggesting that buckthorn may be counteracting some of the impacts of the concurrent invasive species. Further research is necessary to better tease apart the magnitude of impacts on soil nutrients by both earthworms and buckthorn.

Contrary to our expectations, and inconsistent with effects on total N pools, we saw minimal effects of buckthorn abundance on net N mineralization rates and the abundance of inorganic N in soils. Instead of an expected increase in net N mineralization in plots with increasing buckthorn abundance, net N mineralization was unrelated overall and decreased with buckthorn abundance during our winter sampling period. Perhaps the lower soil moisture in plots with more buckthorn in the fall translated into decreased microbial activity and a corresponding decrease in winter net N mineralization. Such a decrease in fall soil moisture could be the result of increased water uptake and

evapotranspiration, as might occur due to the greater density of fine roots under buckthorn and buckthorn's unique phenology that results in an extended period of potential activity in fall (Harrington et al. 1989, Fridley 2012). This decrease in N mineralization rates under dense buckthorn is similar to that found by Heneghan et al. (2006) at one of their forested sites, although there was no difference in net N mineralization rate between plots where buckthorn was present and absent at their other research site. N mineralization is a dynamic process that is sensitive to many factors that can differ between studies, sites, plots, and seasons (e.g., soil moisture, soil texture, plant and soil community composition; Liao et al. 2008). We suggest the inconsistent relationships between buckthorn abundance and net N mineralization rates across studies likely reflects a dependence of this relationship on seasonally and inter-annually varying environmental conditions, such that additional studies are needed to further characterize buckthorn effects on N mineralization and inorganic N availability. For example, our study occurred during and after a relatively dry and hot summer and this likely constrained the nature of buckthorn impacts on N mineralization and inorganic N availability.

We observed changes in the microbial biomass C to N ratios in the spring sampling period. A pulse of buckthorn litter decomposition in the spring may result in transfer of a substantial amount of high "quality" litter into the soil, potentially favoring a soil food web dominated by bacteria over fungi. Bacteria have a lower C:N ratio than fungi, so we could be detecting a shift in soil community (Wardle et al. 2005). Buckthorn and other invasive plant species have been shown to have distinct effects on microbial

community structure and function (Kourtev et al. 2002, Heneghan et al. 2004, Liao et al. 2008, Stokdyk and Herrman 2014). Changes in microbial community composition can have ramifications for future plant growth (i.e., legacy effects) - both nonnative *Berberis* sp. and native *Viburnum* spp. grew better in soils that had been preconditioned with *Berberis* sp. litter and maintained their altered microbial community over time (Elgersma et al. 2012). Mature buckthorn also facilitated buckthorn seedling growth, possibly through its effects on soil biota (Knight 2006).

We found no evidence for legacy effects of buckthorn 3 and 6 years after manual removal. The plots where buckthorn had been removed did not vary in soil nutrients from what would be expected based on their current moderate buckthorn levels, as opposed to their historical very high buckthorn levels. One possible explanation is that much of the additional C and nutrients in soils of dense buckthorn plots is bound in organic matter pools that are not especially stable, such as particulate organic matter. In contrast, Heneghan et al. (2004) observed differences in soil pH, soil total N and C, and microbial communities in plots under buckthorn. They suggested these effects may persist following buckthorn removal, although buckthorn legacy effects might differ across sites with different environmental conditions, including soil types. Larkin et al. (2014) examined slightly different characteristics, but found that forests where buckthorn had been removed showed recovery in some ecosystem properties, including soil CO₂ efflux, abundance of particulate organic matter, and erosion.

Conclusions

Collectively, our study and others document that there is strong potential for buckthorn to increase soil fertility in temperate forests of North America. If buckthorn is increasing pools of C, N, and nutrient cations in soil or tissues of co-occurring plant species, perhaps buckthorn could, over time, have an overall positive effect on forest productivity. Additionally, the effect of buckthorn on N to P ratios in soil, which reflects the lack of buckthorn effects on P, suggests that buckthorn could also potentially impact productivity or community composition by altering the outcome of competition among plants and soil organisms with different stoichiometric requirements. Although a general increase in productivity due to buckthorn invasion seems likely, it is more uncertain which plant species would benefit most from enhanced nutrient availability. Previous studies suggest that buckthorn itself or other nonnative species may benefit at the expense of some native species (Davis et al. 2000, Gilliam 2006, Funk and Vitousek 2007, Liao et al. 2008, Ehrenfeld 2010, Huebner et al. 2014). Over the long term, buckthorn invasion is another stressor, along with high deer populations and a changing climate, that may change the structure of Midwestern forests (Frelich and Reich 2010, Fisichelli et al. 2012).

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Table 3.1. Best-fit multiple regression model explaining total soil N (“Model 1”) and model containing total leaf litter N flux (“Model 2”). Cell values report standardized beta coefficient for each predictor when present in the model. Bold value indicate significant predictors.

	% Sand	Buckthorn leaf litter (% of total)	Total leaf litter N flux	AICc Score	R ²
Model 1:	-0.62	0.65		299.59	0.57
Model 2:	-0.65	0.75	-0.19	300.81	0.60

Figure 3.1. Nutrient content of green leaves (left column) of maple (*Acer rubrum*) and buckthorn (*Rhamnus cathartica*) and nutrient content of leaf litter (right column) from buckthorn, oak (*Quercus* spp.), and maple collected from 28 plots.

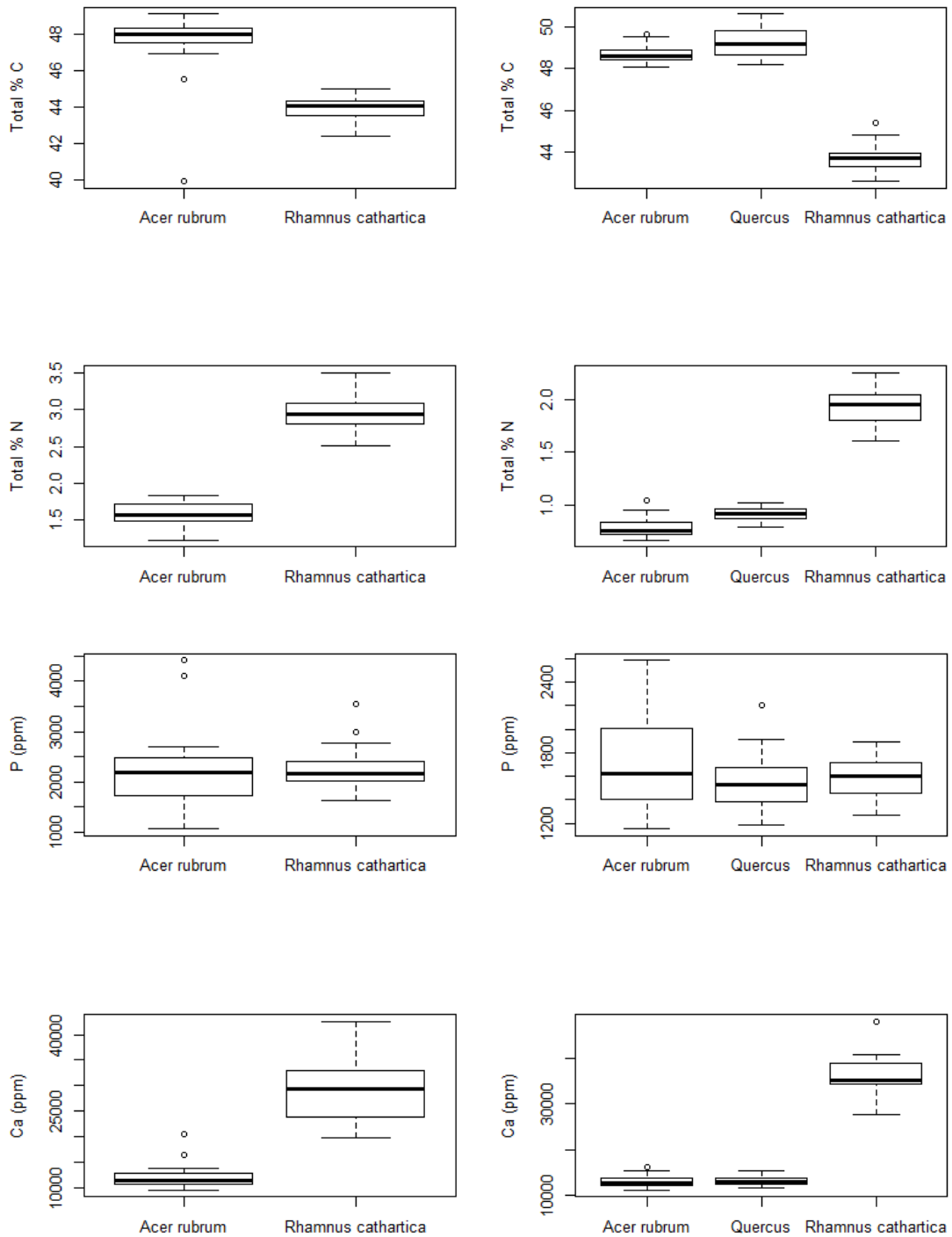


Figure 3.2. Percent difference in N concentration (left, $p < 0.0001$) and P concentration (right, $p = 0.07$) between green leaves and fallen leaf litter of buckthorn (*R. cathartica*) and red maple (*A. rubrum*). This value represents the percentage of N and P that is retranslocated by each species prior to leaf senescence.

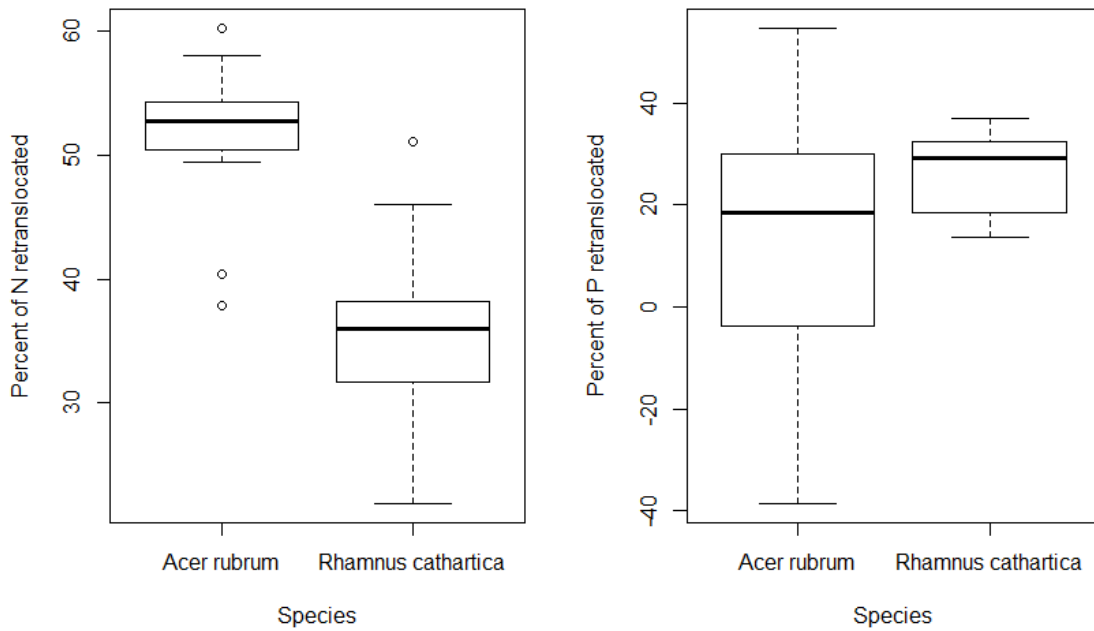


Figure 3.3. Leverage plots of Ca, P, and N concentrations in green buckthorn (*R. cathartica*) leaves collected across a gradient of buckthorn abundance, after accounting for the significant influence of percent sand. a) Ca concentration: R^2 (of full model containing buckthorn basal area and percent sand as predictors) = 0.76, $p = 0.0013$; b) P concentration: $R^2 = 0.15$, $p = 0.08$; c) N concentration: $R^2 = 0.06$, $p = 0.29$.

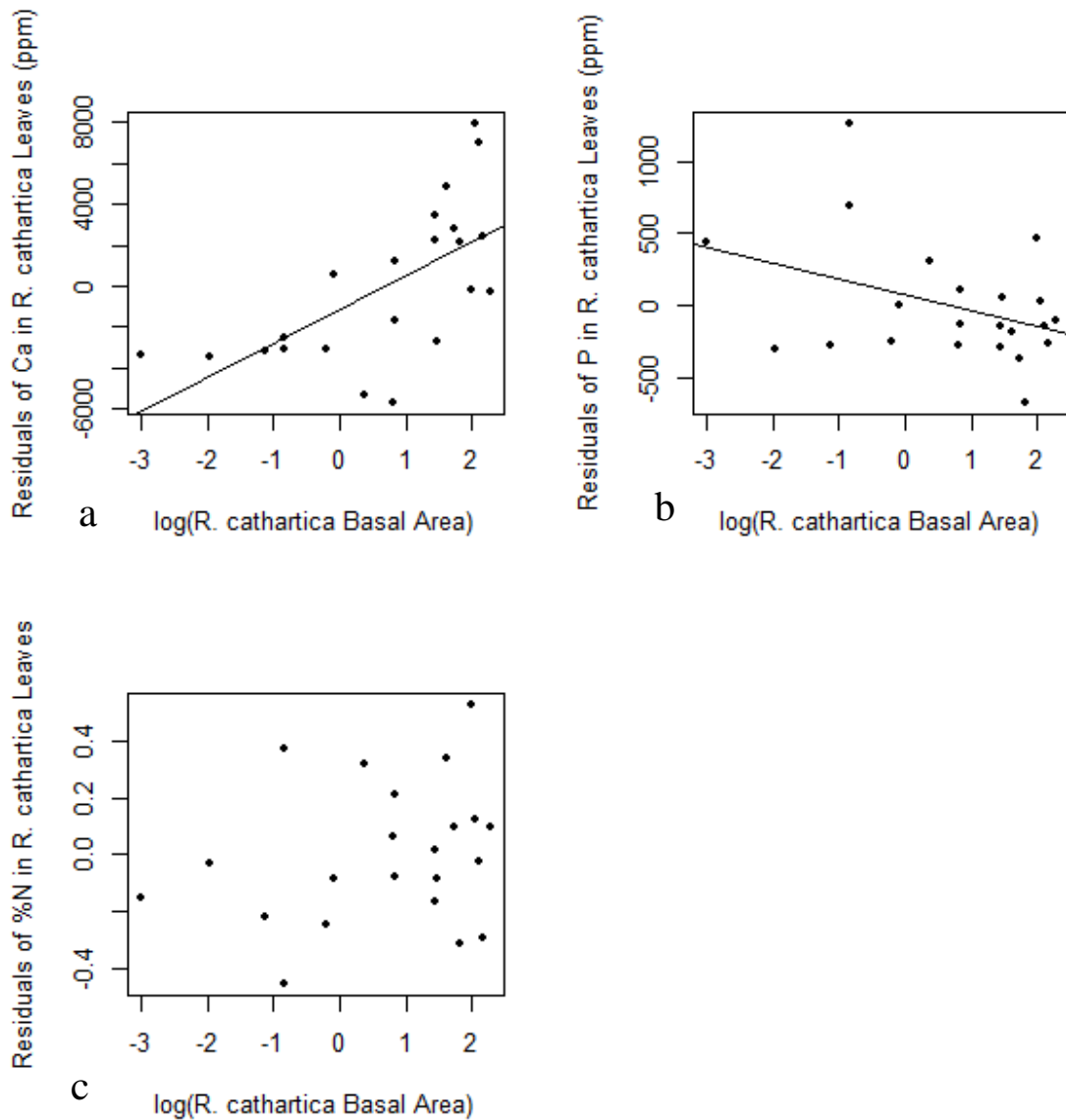


Figure 3.4. Biplots of N and P concentrations in maple (a: $R^2 = 0.18$, $p < 0.05$; b: $R^2 = 0.22$, $p < 0.05$, respectively), oak (c: $R^2 = 0.16$, $p < 0.05$; d: $R^2 = 0.04$, $p = 0.28$), and buckthorn (e: $R^2 = 0.03$, $p = 0.45$; f: $R^2 = 0.01$, $p = 0.64$) leaf litter collected across a gradient of buckthorn abundance. Triangles and circles represent plots where buckthorn was removed 3 or 6 years prior to sampling, respectively.

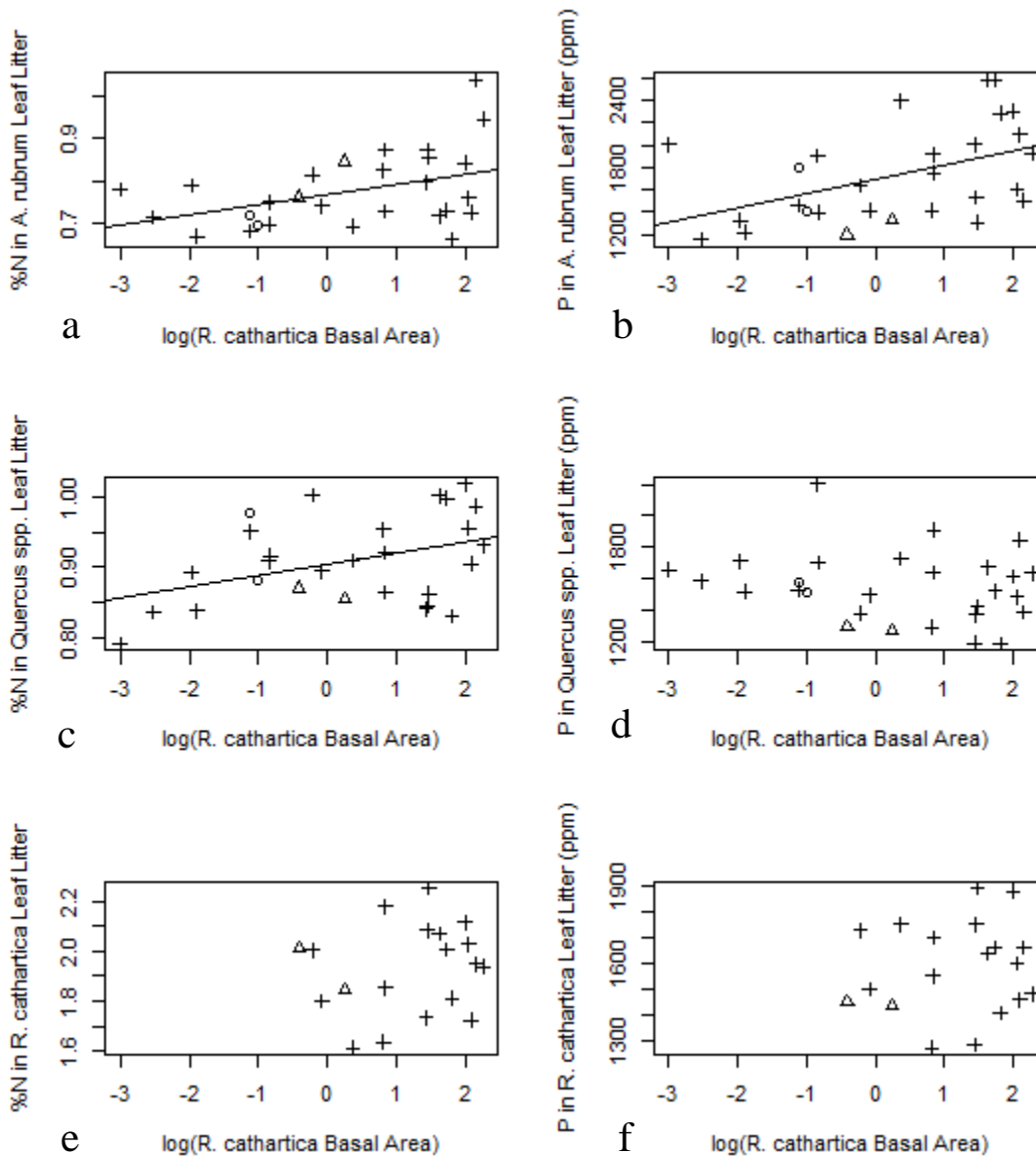


Figure 3.5. Biplots of total leaf litter nutrient concentrations across a gradient of buckthorn abundance. a) N: $R^2 = 0.19$, $p < 0.05$; b) P: $R^2 = 0.07$, $p = 0.19$; c) Ca: $R^2 = 0.21$, $p < 0.05$; d) K: $R^2 = 0.40$, $p < 0.001$. Triangles and circles represent plots where buckthorn was removed 3 or 6 years prior to sampling, respectively.

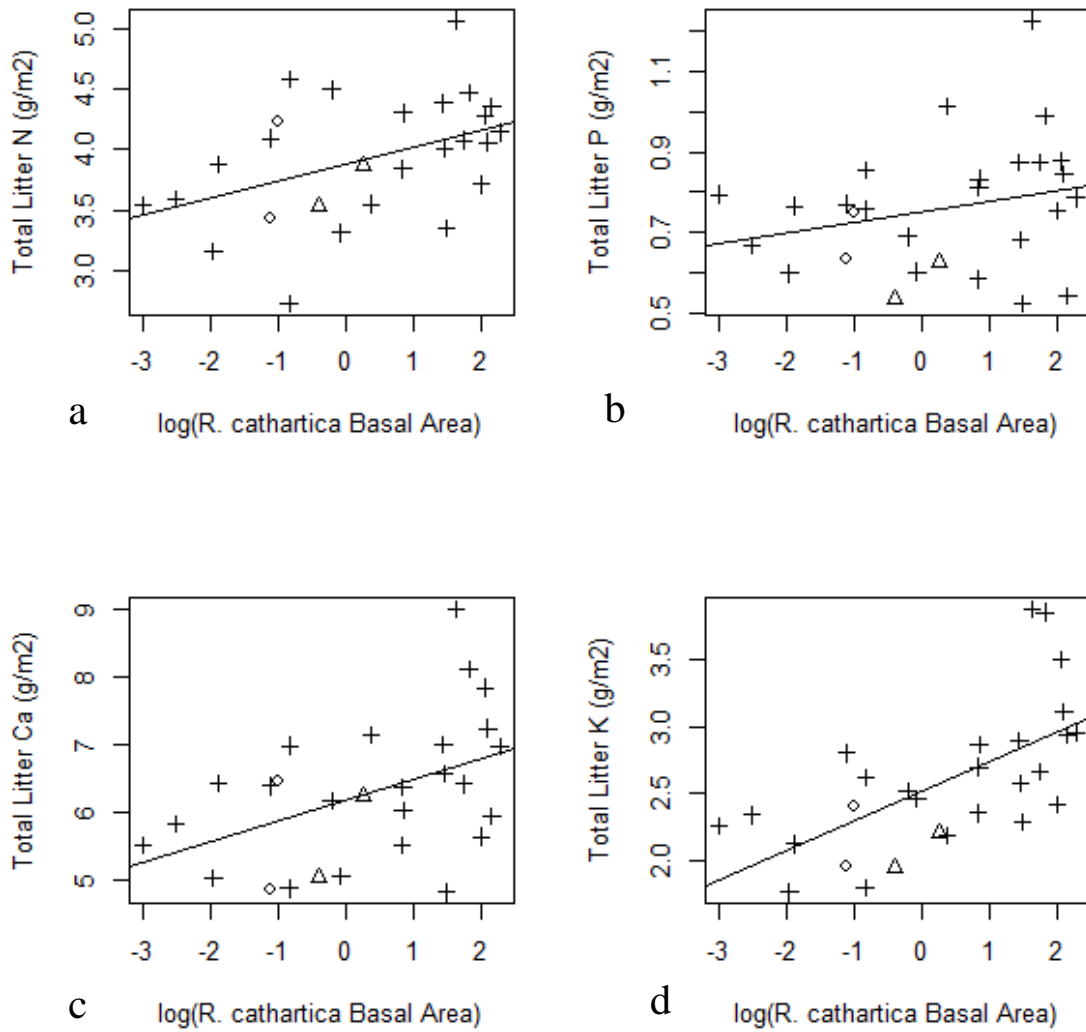


Figure 3.6. a) The relationship between fine root biomass (< 1 mm) and buckthorn basal area, $R^2 = 0.21$, $p < 0.05$; b-d) Nutrient concentrations of plant roots collected from plots spread across a gradient of buckthorn abundance after accounting for soil type. b) N: $R^2 = 0.06$, $p = 0.20$; c) P: $R^2 = 0.01$, $p = 0.57$; d) Ca: $R^2 = 0.12$, $p = 0.10$; e) K: $R^2 = 0.41$, $p < 0.001$ (full model includes % sand). Triangles and circles represent plots where buckthorn was removed 3 or 6 years prior to sampling, respectively.

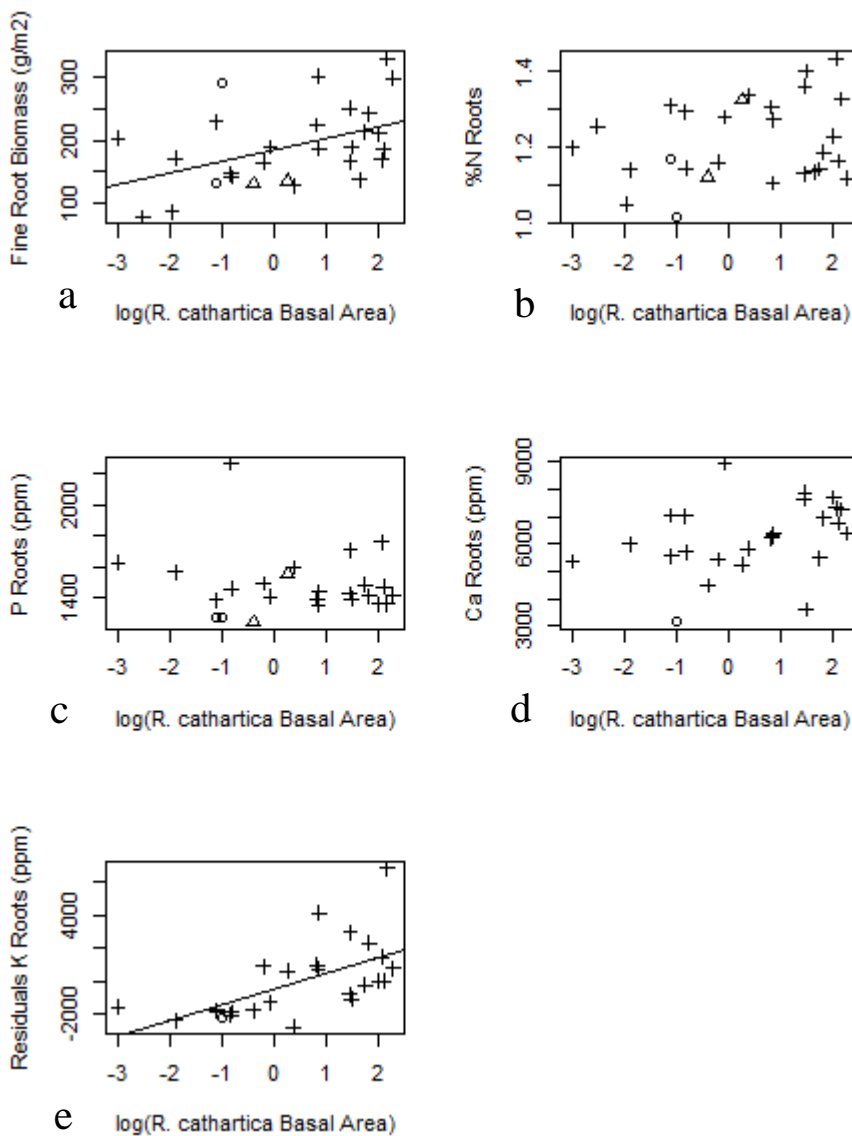


Figure 3.7. Plots displaying soil nutrient levels across a gradient of buckthorn abundance, after accounting for the influence of % sand when necessary. a) Bulk density: $R^2 = 0.16$, $p < 0.05$; b) pH: $R^2 = 0.24$, $p < 0.01$; c) Total N: $R^2 = 0.55$, $p < 0.001$ (full model included % sand); d) Ca: $R^2 = 0.33$, $p < 0.01$ (full model included % sand); e) P: $R^2 = 0.02$, $p = 0.42$. Triangles and circles represent plots where buckthorn was removed 3 or 6 years prior to sampling, respectively.

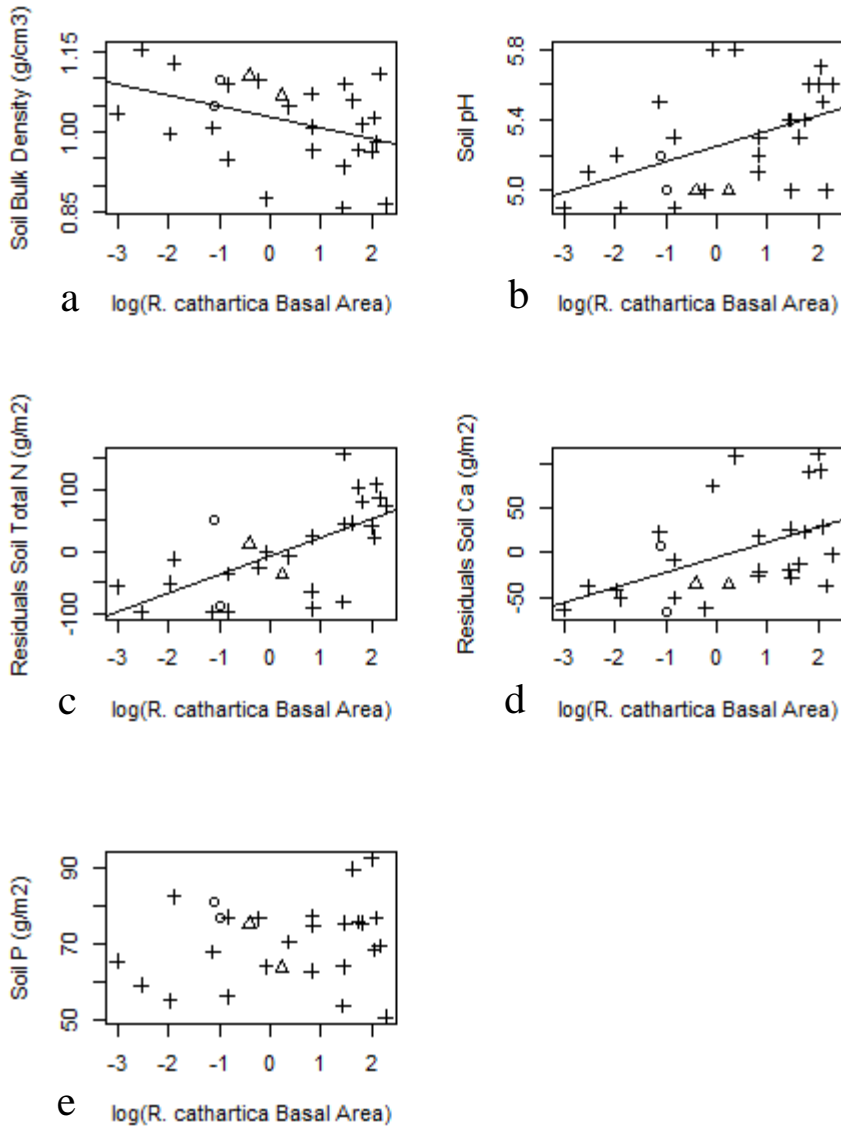
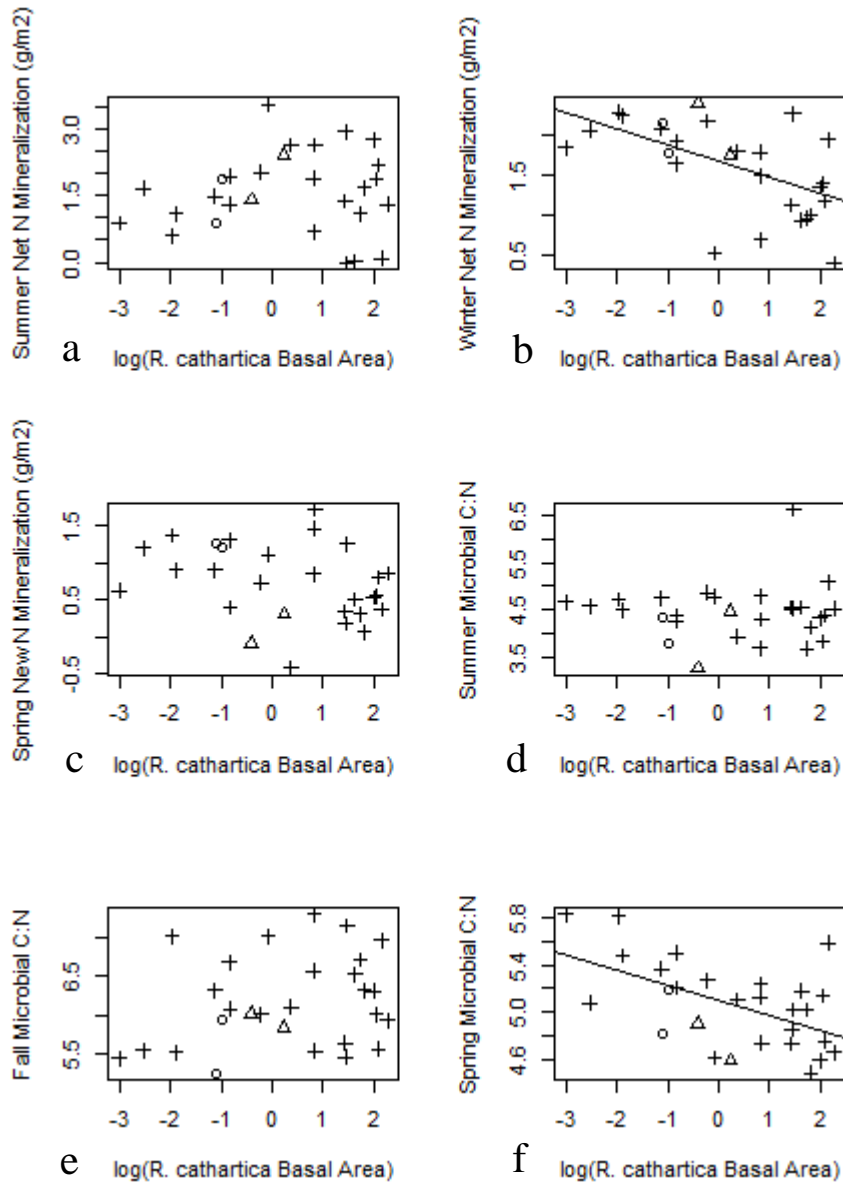


Figure 3.8. Biplots of net N mineralization and microbial C:N ratio across a gradient of buckthorn abundance in three seasons. a) Summer net Nmin: $R^2 = 0.01$, $p = 0.72$; b) Winter net Nmin: $R^2 = 0.29$, $p < 0.01$; c) Spring net Nmin: $R^2 = 0.09$, $p = 0.11$; d) Summer microbial C:N: $R^2 = 0.00$, $p = 0.92$; e) Fall microbial C:N: $R^2 = 0.06$, $p = 0.21$; f) Spring microbial C:N: $R^2 = 0.30$, $p < 0.01$. Triangles and circles represent plots where buckthorn was removed 3 or 6 years prior to sampling, respectively.



Conclusion

The characteristics of invading species and the characteristics of receiving communities both play important roles in determining the success of nonnative species. Plant functional traits may explain, in part, why certain nonnative species become invasive. Overall, our results suggest that nonnative plants are using similar growth strategies to those used by natives in deciduous forests of the Upper Midwest. These strategies are focused on growing and acquiring resources quickly, and are more prevalent in sites with high resources, where these strategies can be most effective. These results were echoed in our study focusing on receiving communities and a single problem invader, common buckthorn. Sites with higher light and higher nutrient availability had more abundant buckthorn. However, we did observe evidence of biotic resistance – sites with more diverse resident plant communities appeared more resistant to buckthorn invasion. This suggests that even though both native and nonnative species may be more successful in high resource environments, the diversity of the resident community may provide some resistance to invasion.

Ultimately, it is only after controlling for local propagule availability that the other environmental characteristics became important predictors of buckthorn presence and abundance. This suggests that land managers must be cognizant of local propagule pressure and consider propagule management in the area in order to adequately help their site resist invasion. While controlling buckthorn is difficult once it establishes, it may be worth the effort and expense to try to prevent buckthorn from spreading into uninvaded

forests due to its potential to affect nutrient cycling. Increases in soil fertility due to deposition of buckthorn's nutrient-rich leaves may lead to increases in forest productivity. Such increases in available resources are likely to benefit both native and nonnative plants, and may allow for increased spread and dominance of invasive plants that are better able to take advantage of these conditions.

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Appendix S1.A. Table of measured plant traits, variable type, and source(s) of trait data.

Trait	Data Type	Data Source(s)
<i>Specific leaf area</i>	Continuous (cm ² g ⁻¹)	Measured in field in MN
<i>Maximum plant height</i>	Continuous (m)	TRY database; Missouri Botanic Garden; University of Connecticut Plant Database
<i>Wood density</i>	Continuous (mg mm ⁻³ ; for woody species only)	TRY database; measured 20 species in the field in MN
<i>Leaf C:N</i>	Continuous	Measured in field in MN
<i>Plant growth form</i>	Nominal (tree, shrub, woody vine, forb, nitrogen-fixing forb, graminoid)	Measured in field in MN
<i>Mycorrhizal type</i>	Nominal (arbuscular mycorrhizal, ectomycorrhizal, no mycorrhizal association)	Determined based on family relationships by Ian Dickie
<i>Native/nonnative status</i>	Binary (native/nonnative)	USDA Plants Database
<i>Seed mass</i>	Continuous (mg)	TRY database; Kew database

Appendix S1.B. List of species with sources of each trait value. *MN* = Author measured in the field at sites in Minnesota; *TRY database* = value averaged from species entry in TRY Plant Trait Database (Kattge et al. 2011); *avg genus in TRY* = value averaged from species in same genus in TRY Plant Trait Database (Kattge et al. 2011); *CT Botanic Society* = <http://www.ct-botanical-society.org/>; *MO Botanic Garden* = <http://www.missouribotanicalgarden.org/>; *MN Wildflowers* = <https://www.minnesotawildflowers.info/>; *UCT Horticulture Department* = <http://hort.uconn.edu/>; *Amy Zanne* = personal communication; *Harmon et al.* = Harmon et al. (2008); *Ian Dickie* = personal communication; *USDA Plants* = USDA (2015a); *Kew database* = Kew (2015); *Prairie Moon* = Prairie Moon Nursery, <https://www.prairiemoon.com>.

Species	Specific leaf area	Maximum Plant Height	Wood density	Leaf C:N	Growth Form	Mycorrhizal type	Native Status	Seed Mass
<i>Acer negundo</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Acer rubrum</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Acer saccharinum</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Acer saccharum</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Actaea rubra</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Adiantum pedatum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Agrimonia striata</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Alliaria petiolata</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Ambrosia artemisiifolia</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Ambrosia trifida</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Amphicarpaea bracteata</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Anemone acutiloba</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Aquilegia canadensis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Aralia nudicaulis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Aralia racemosa</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Arctium minus</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Arisaema triphyllum</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Asarum canadense</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Asclepias exaltata</i>	MN	CT Botanic Society	n/a	MN	MN	Ian Dickie	USDA	TRY database

<i>Athyrium filix-femina</i> var. <i>angustum</i>	MN	MO Botanic Garden	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Berberis thunbergii</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Betula papyrifera</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Botrychium virginianum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Carex blanda</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Carex gracillima</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Carex normalis</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Carex pedunculata</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	avg genus in TRY
<i>Carex pensylvanica</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Carex rosea</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Carya cordiformis</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Caulophyllum thalictroides</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Celastrus scandens</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Celtis occidentalis</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Chenopodium album</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Cirsium arvense</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Cornus alternifolia</i>	MN	TRY database	Harmon et al.	MN	MN	Ian Dickie	USDA	TRY database
<i>Cornus racemosa</i>	MN	TRY database	Harmon et al.	MN	MN	Ian Dickie	USDA	TRY database
<i>Corylus americana</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Cryptotaenia canadensis</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Desmodium glutinosum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Diervilla lonicera</i>	MN	avg genus in TRY	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Dioscorea villosa</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Dryopteris carthusiana</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Echinocystis lobata</i>	MN	MN Wildflowers	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Elymus hystrix</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon

<i>Eurybia macrophylla</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Eutrochium purpureum</i>	MN	MO Botanic Garden	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Festuca subverticillata</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Fragaria virginiana</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Frangula alnus</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Fraxinus americana</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Fraxinus nigra</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Fraxinus pennsylvanica</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Galeopsis tetrahit</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Galium boreale</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Geranium maculatum</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Geum canadense</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Glechoma hederacea</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Hackelia virginiana</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Impatiens capensis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Juglans nigra</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Laportea canadensis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Lonicera dioica</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Lonicera</i> spp. (nonnative)	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Lysimachia borealis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Maianthemum canadense</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Melilotus alba</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Menispermum canadense</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Mitella nuda</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Oryzopsis asperifolia</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Osmorhiza claytonii</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon

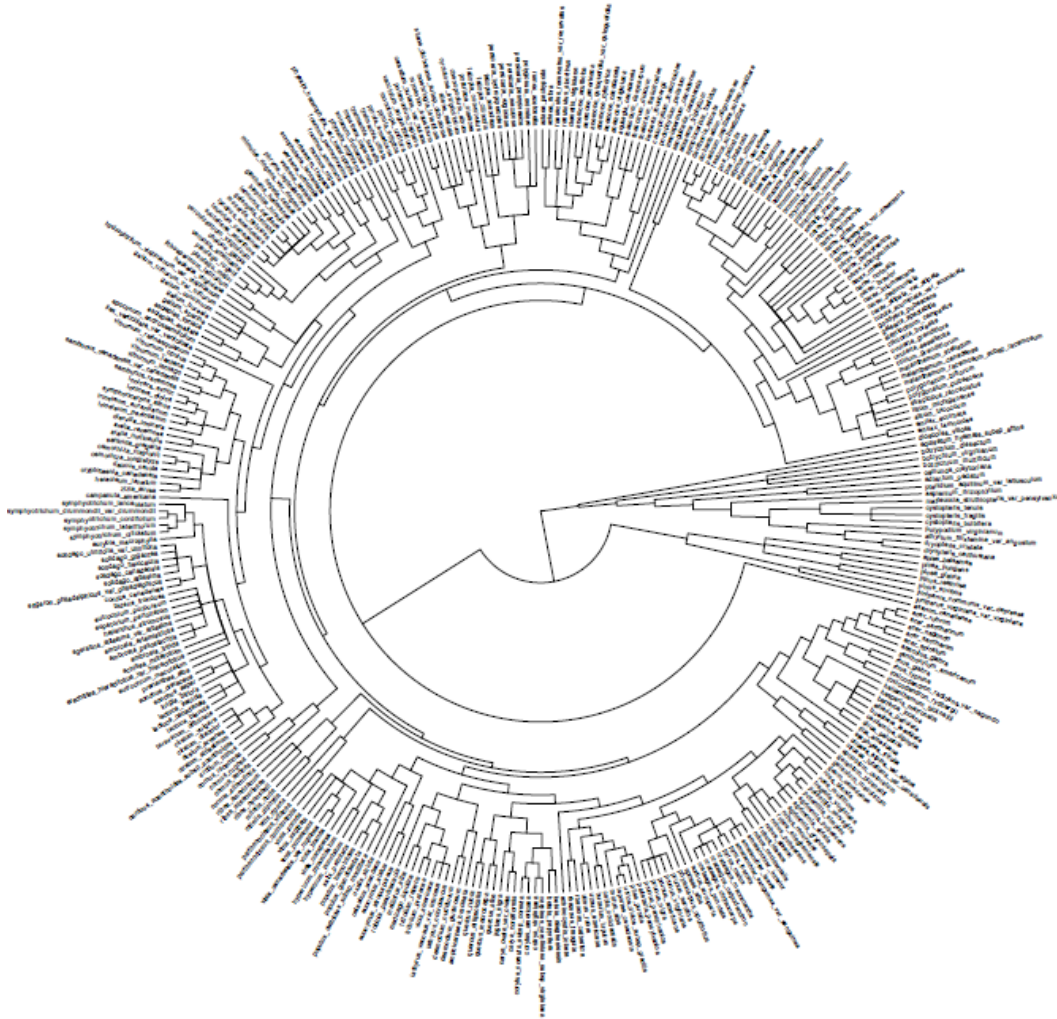
<i>Osmorhiza longistylis</i>	MN	CT Botanic Society	n/a	MN	MN	Ian Dickie	USDA	Kew database
<i>Osmunda claytoniana</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Ostrya virginiana</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Oxalis stricta</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Parthenocissus quinquefolia</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Parthenocissus vitacea</i>	MN	avg genus in TRY	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Phryma leptostachya</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Pilea pumila</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Piptatherum racemosum</i>	MN	gardening.eu	n/a	MN	MN	Ian Dickie	USDA	avg genus in TRY
<i>Plantago rugelii</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Polygonatum biflorum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Polygonatum pubescens</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	avg genus in TRY
<i>Populus tremuloides</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Prenanthes alba</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Prunus serotina</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Prunus virginiana</i>	MN	TRY database	Harmon et al.	MN	MN	Ian Dickie	USDA	TRY database
<i>Quercus alba</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Quercus ellipsoidalis</i>	MN	TRY database	Harmon et al.	MN	MN	Ian Dickie	USDA	TRY database
<i>Quercus macrocarpa</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Quercus rubra</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Ranunculus abortivus</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Rhamnus cathartica</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Rhus glabra</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Ribes cynosbati</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Ribes missouriense</i>	MN	avg genus in TRY	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Rubus allegheniensis</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database

<i>Rubus idaeus</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Rubus occidentalis</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Sambucus canadensis</i> var. <i>canadensis</i>	MN	U-CT Horticulture Dept.	MN	MN	MN	Ian Dickie	USDA	Kew database
<i>Sambucus racemosa</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Sanguinaria canadensis</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Sanicula gregaria</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Scrophularia lanceolata</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Smilax ecirrhata</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Smilax tamnoides</i>	MN	avg genus in TRY	TRY database	MN	MN	Ian Dickie	USDA	avg genus in TRY
<i>Solidago canadensis</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Solidago flexicaulis</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Solidago gigantea</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Sonchus oleraceus</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Staphylea trifolia</i>	MN	MO Botanic Garden	TRY database	MN	MN	Ian Dickie	USDA	Kew database
<i>Streptopus lanceolatus</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	avg genus in TRY
<i>Symphyotrichum cordifolium</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Symphyotrichum lateriflorum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Taraxacum officinale</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Thalictrum dioicum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Thalictrum thalictroides</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Tilia americana</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Trillium grandiflorum</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Triosteum perfoliatum</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Ulmus americana</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Ulmus rubra</i>	MN	TRY database	Amy Zanne	MN	MN	Ian Dickie	USDA	TRY database
<i>Uvularia grandiflora</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Kew database

<i>Vaccinium angustifolium</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Verbascum thapsus</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Veronicastrum virginicum</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Viburnum lentago</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Viburnum opulus</i>	MN	TRY database	TRY database	MN	MN	Ian Dickie	USDA	TRY database
<i>Viburnum rafinesquianum</i>	MN	avg genus in TRY	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Viola pubescens</i>	MN	TRY database	n/a	MN	MN	Ian Dickie	USDA	TRY database
<i>Viola sororia</i>	MN	avg genus in TRY	n/a	MN	MN	Ian Dickie	USDA	Prairie Moon
<i>Vitis riparia</i>	MN	avg genus in TRY	MN	MN	MN	Ian Dickie	USDA	TRY database
<i>Zanthoxylum americanum</i>	MN	TRY database	MN	MN	MN	Ian Dickie	USDA	TRY database

APPENDIX 2. Supplementary information for Chapter 2.

Appendix S2.A. Phylogeny and R code of 313 woody and herbaceous species from 56 survey plots located in oak dominated mesic forests in southern Minnesota. Phylogeny was generated in Phylomatic (Webb and Donoghue 2005) with subsequent resolution of terminal branches based on published phylogenetic analyses (Alice and Campbell 1999, Aliscioni *et al.* 2012, Ballard *et al.* 1998, Barker *et al.* 2001, Bayer and Starr 1998, Bendiksby *et al.* 2011, Brunsfeld *et al.* 1994, Cai *et al.* 2009, Catalan *et al.* 1997, Clement and Donoghue 2011, Downie *et al.* 2000, FNA 1993+, Hadiyah *et al.* 2008, Hamzeh *et al.* 2006, Harbaugh *et al.* 2010, Hoot *et al.* 1994, Jacobs *et al.* 2010, Jeandroz *et al.* 1997, Kadereit *et al.* 2008, Kim *et al.* 2004, Nadot *et al.* 2000, Potter *et al.* 2007, Renner *et al.* 2008, Scheen *et al.* 2010, Smith *et al.* 2006, Sun and Downie 2010, Tank *et al.* 2006, Vaezi and Brouillet 2009, Xiang *et al.* 2006, Yen and Olmstead 2000). Branch lengths represent millions of years estimated using the branch length adjustment algorithm (Webb *et al.* 2009). For more detail on phylogeny, see Whitfeld *et al.* (2013).



```

#nexus
begin trees;
tree healthyforests = [&r]
((((abies_balsamea,picea_glauca,(pinus_resinosa,pinus_strobus)),(juniperus_communis_
var_depressa,juniperus_virginiana_var_virginiana)),(asarum_canadense,((((((((((((acer_r
ubrum,acer_negundo),(acer_saccharum,acer_spicatum)),aesculus_glabra)sapindaceae,zan
thoxylum_americanum),(rhus_glabra,rhus_typhina),toxicodendron_rydbergii)sapindale
s,((alliaria_petiolata,boechera_laevigata,cardamine_diphylla)brassicaceae,(dirca_palustris
,tilia_americana))),((circaea_alpina_var_alpina,circaea_lutetiana_var_canadensis),epilob
ium_coloratum)onagraceae,(geranium_bicknellii,geranium_maculatum)geraniaceae)),((((
((geum_canadense,(rosa_blanda,((fragaria_virginiana,(potentilla_norvegica,potentilla_si
mplex)),(agrimonia_pubescens,agrimonia_striata))),((rubus_recurvans,rubus_allegheNie
nsis),rubus_pubescens,rubus_steelei),(rubus_idaeus,rubus_occidentalis))),((((amelanchie
r_interior,amelanchier_laevis,amelanchier_sanguinea_var_sanguinea),pyrus_malus,(crata
egus_chrysocarpa,crataegus_punctata)),sorbus_aucuparia,spiraea_alba),(physocarpus_op
ulifolius,(prunus_serotina,prunus_virginiana)))rosaceae,(((parietaria_pensylvanica,(pile
a_pumila,(urtica_dioica_subsp_gracilis,laportea_canadensis)))urticaceae,celtis_occidenta
lis),(ulmus_americanus,ulmus_rubra)),(rhamnus_cathartica,rhamnus_frangula)rhamnaceae
))rosales,(((betula_alleganiensis,betula_papyrifera),(carpinus_caroliniana_subsp_virgi
niana,ostrya_virginiana),(corylus_americanus,corylus_cornuta_subsp_cornuta)))betulacea
e,((carya_cordiformis,carya_ovata_var_ovata),juglans_nigra)juglandaceae,((quercus_alb
a,quercus_macrocarpa),(quercus_ellipsoidalis,quercus_rubra))),((amphicarpaea_bracteat
a,(desmodium_glutinosum,desmodium_nudiflorum)),((((lathyrus_ochroleucus,lathyrus_v
enosus_var_intonsus,vicia_americanus),(trifolium_pratense,trifolium_repens)),(medicago_
lupulina,melilotus_alba)),robinia_pseudoacacia)fabaceae,(celastrus_scandens,(oxalis_st
ricta,(((populus_deltoides_subsp_monilifera,(populus_grandidentata,populus_tremuloide
s)),salix_petiolaris)salicaceae,(viola_conspersa,((viola_blanda,viola_canadensis_var_rug
ulosa),viola_pubescens),viola_sagittata,viola_sororia))))),((parthenocissus_quinquefolia,
parthenocissus_vitacea),vitis_riparia)vitaceae,((mitella_diphylla,mitella_nuda)saxifragac
eae,(ribes_cynosbati,ribes_missouriense)),((((arctium_minus,(carduus_acanthoides_su
bsp_acanthoides),(cirsium_altissimum,cirsium_arvense,cirsium_discolor,cirsium_vulgare)
)),((taraxacum_officinale,(lactuca_canadensis,lactuca_serriola),krigia_biflora,sonchus_ol
eraceus,prenanthes_alba),(eutrochium_maculatum,erechites_hieracifolius_var_hieracifol
ius,achillea_millefolium,((ageratina_altissima_var_altissima,Helianthus_strumosus),biden
s_froncosa)),(conyza_canadensis,erigeron_philadelphicus_var_philadelphicus),(solidago_
altissima,solidago_canadensis,solidago_flexicaulis,solidago_gigantea,solidago_ulmifoli
a_var_ulmifolia),(eurybia_macrophylla,(((symphyotrichum_ciliolatum,symphyotrichum
_lateriflorum),(symphyotrichum_cordifolium,symphyotrichum_drummondii_var_drumm
ondii)),symphyotrichum_lanceolatum))))))asteraceae,(((zizia_aurea,heracleum_lanatum),
cryptotaenia_canadensis,osmorhiza_claytonii,sanicula_gregaria)apiaceae,(aralia_nudicaul
is,aralia_racemosa)),((diervilla_lonicera,(triosteum_perfoliatum,triosteum_aurantiacum),
(symphoricarpos_albus,(lonicera_dioica,lonicera_exotic))))),((sambucus_racemosa,((vibun
um_lentago,viburnum_lantana),(viburnum_opulus,viburnum_rafinesquianum)))adoxace
ae)dipsacales,ilex_verticillata_var_verticillata)

```

,(((apocynum_androsaemifolium,(asclepias_exaltata,asclepias_syriaca))apocynaceae,(galium_aparine,galium_boreale,galium_concinnum,galium_triflorum_var_triflorum)rubiaceae)gentianales,(hydrophyllum_virginianum_var_virginianum,(hackelia_virginiana,lithospermum_latifolium))boraginaceae,((((((plantago_major,plantago_rugelii),veronica_american),chelone_glabra),veronicastrum_virginicum),((((scutellaria_lateriflora,lycopus_americanus,(glechoma_hederacea,galeopsis_tetrahit),nepeta_cataria)lamiaceae,(mimulus_ringens_var_ringens,phryma_leptostachya)),(verbena_hastata,verbena_urticifolia)),(scrophularia_lanceolata,verbascum_thapsus))),((fraxinus_nigra,(fraxinus_american),fraxinus_pennsylvanica))oleaceae),solanum_dulcamara))),((impatiens_capensis,(((lysimachia_borealis,lysimachia_ciliata),((pyrola_american),pyrola_elliptica),monotropa_uniflora),vaccinium_angustifolium)ericaceae),polemonium_reptans))ericales),((cornus_alternifolia,(cornus_septica,(cornus_rugosa,cornus_racemosa)))cornaceae)asterid,(((cerastium_nutans_var_nutans,myosoton_aquaticum),moehringia_lateriflora),((fallopia_cilinodis,fallopia_scandens),(persicaria_maculosa,persicaria_virginiana,persicaria_hydropiperoides))polygonaceae)caryophyllales),((((actaea_pachypoda,actaea_rubra),((ranunculus_abortivus,ranunculus_recurvatus_var_recurvatus),((anemone_acutiloba,anemone_american),anemone_quinquefolia_var_quinquefolia,(anemone_cylindrica,anemone_virginiana))))))ranunculaceae,(aquilegia_canadensis,(thalictrum_dioicum,thalictrum_thalictroides)),((berberis_thunbergii,caulophyllum_thalictroides),podophyllum_peltatum)berberidaceae),menispermum_canadense),sanguinaria_canadensis)ranunculales,((arisaema_triphyllum,symplocarpus_foetidus)araceae,((((((((phalaris_arundinacea,festuca_subverticillata,cinna_arundinacea,leersia_virginica),(poa_palustris,poa_pratensis)),(elymus_hystrix,elymus_virginicus)),(bromus_kalmii,bromus_latiiglumis)),(oryzopsis_asperifolia,piptatherum_racemosum)),brachyelytrum_erectum),setaria_pumila)poaceae,(((carex_blanda,carex_albursina,carex_leptonervia),carex_grisea,carex_deweyana_var_deweyana,carex_hirtifolia,(carex_gracillima,(carex_pennsylvanica,(((carex_sparganioides,carex_rosea),(carex_normalis,carex_brevior)),carex_intumescens))),carex_pedunculata,carex_stipata_var_stipata)cyperaceae,luzula_acuminata_var_acuminata))poales,goodyera_pubescens),(((clintonia_borealis,(uvularia_grandiflora,uvularia_sessilifolia)),trillium_grandiflorum),(((maianthemum_canadense,maianthemum_racemosum_subsp_racemosum),(polygonatum_biflorum,polygonatum_pubescens),strep-topus_lanceolatus,lilium_michiganense),(smilax_ecirrhata,smilax_tamnoides))))),dioscorea_villosa))))),((botrychium_virginianum,botrychium_multifidum),(osmunda_claytoniana,((adiantum_pedatum,pteridium_aquilinum_var_latiusculum),((cystopteris_tenuis,cystopteris_fragilis),(athyrium_filixfemina_var_angustum,(dryopteris_cristata,dryopteris_carthusiana))))))euphyllophyte;

end;

Appendix S2.B. Correlation coefficients between stem counts of common buckthorn and predictor variables from 46 sites where buckthorn was present. Variables that were retained for the stepwise regressions after dropping highly correlated variables are in bold. *MPD* = mean pair-wise phylogenetic distance

Predictor variable	Correlation coefficient <i>r</i>
<i>Stand characteristics</i>	
Stand area (km ²)	0.014
Stand perimeter (km)	0.087
Stand perimeter to area ratio	0.144
Distance to nearest road (km)	0.002
Distance to nearest forest edge (km)	0.248
Distance to populated area (km)	0.181
Road length in 1km radius (m)	0.011
# buckthorn per km in driving survey	0.421
# buckthorn in driving survey per non-agricultural km	0.455
<i>Soil characteristics</i>	
Percent sand	0.066
Percent clay	0.143
Percent silt	0.134
pH	0.326
Soil K (ppm)	0.161
Soil Na (ppm)	0.117
Soil Ca (ppm)	0.230
Soil Mg (ppm)	0.241
Percent total organic carbon	0.139
Percent soil nitrogen	0.143
Average litter depth (cm)	0.520
Average percent bare soil	0.319
Earthworm rating (1-5)	0.136
<i>Diversity estimates</i>	
Herbaceous Shannon Diversity Index	0.323
Woody Shannon Diversity Index	0.045
Abundance-weighted MPD (herbaceous)	0.323
MPD of herbaceous species based on presence/absence	0.199
Basal area-weighted MPD (woody)	0.078
Stem count-weighted MPD (woody)	0.421
MPD of woody species based on presence/absence	0.011
MPD of herbaceous & woody species based on	0.383

presence/absence	
Herb richness	0.257
Woody richness	0.157
Average herbaceous cover per plot	0.331
<i>Light measurement</i>	
Site average canopy openness	0.171

Appendix S2.C. Average, median, minimum, and maximum values of characteristics of 38 sites that had not been harvested in the previous decade. *MPD* = mean pair-wise phylogenetic distance.

Predictor variable	Mean	Median	Minimum	Maximum
<i>Stand characteristics</i>				
Stand area (km ²)	2.50	1.45	0.08	12.14
Stand perimeter (km)	15.26	9.86	1.40	64.28
Stand perimeter to area ratio	9.06	8.00	2.03	18.46
Distance to nearest road (km)	0.38	0.29	0.08	1.28
Distance to nearest forest edge (km)	0.17	0.11	0.04	0.77
Distance to populated area (km)	1.97	1.33	0.13	6.13
Road length in 1km radius (m)	5.21	3.49	0.00	25.40
# buckthorn per km in driving survey	3.76	2.22	0.00	17.41
# buckthorn in driving survey per non-agricultural km	5.98	4.76	0.00	28.39
<i>Soil characteristics</i>				
Percent sand	52.47	57.25	10.43	89.45
Percent clay	13.94	12.33	5.91	31.83
Percent silt	33.58	30.85	4.64	67.97
pH	5.31	5.19	4.06	6.85
Soil K (ppm)	94.10	83.24	43.02	212.40
Soil Na (ppm)	7.90	8.28	0.00	14.15
Soil Ca (ppm)	1344.19	1194.35	132.64	4096.70
Soil Mg (ppm)	244.43	175.56	35.93	1040.00
Percent total organic carbon	1.79	1.65	0.72	4.21
Percent soil nitrogen	0.13	0.12	0.04	0.35
Average litter depth (mm)	9.55	7.55	1.77	27.29
Average percent bare soil	22.31	20.16	0	91.88
Earthworm rating (1-5)	4.45	5	2	5
<i>Diversity estimates</i>				
Herbaceous Shannon Diversity Index	0.97	0.99	0.38	1.29
Woody Shannon Diversity Index	0.87	0.88	0.31	1.57
Abundance-weighted MPD (herbaceous)	222.06	224.96	95.14	268.20
MPD of herbaceous species based on presence/absence	276.68	278.13	260.62	292.08
Basal area-weighted MPD (woody)	116.07	113.98	43.45	199.53
Stem count-weighted MPD (woody)	150.04	153.97	73.59	208.11
MPD of woody species based on presence/absence	233.74	233.67	215.99	247.80
MPD of herbaceous & woody species	266.82	266.85	254.99	281.19

based on presence/absence				
Herb richness	27.47	28	13	47
Woody richness	24.00	24	11	36
Average herbaceous cover per plot	26.87	22.88	5.92	62.78
<i>Light measurement</i>				
Site average canopy openness	4.97	4.37	1.64	9.59
<i>Vegetation measurements:</i>				
Total # woody stems in 1m plots per site	572.92	416.5	63	3153
Average # woody stems per 1m plot	35.81	26.03	3.94	197.06
Total basal area (m ² /ha)	35.04	34.33	20.31	48.48
Buckthorn basal area (m ² /ha)	0.34	0.01	0	3.82
Buckthorn stems per ha	2813.90	167.11	0	27939.65

Appendix S2.D. Average, median, minimum, and maximum values of characteristics of 18 sites that had been harvested in the previous decade. *MPD* = mean pair-wise phylogenetic distance.

Predictor variable	Mean	Median	Minimum	Maximum
<i>Stand characteristics</i>				
Stand area (km ²)	3.72	3.03	0.49	12.55
Stand perimeter (km)	18.22	15.46	4.58	52.48
Stand perimeter to area ratio	6.04	6.21	3.25	9.40
Distance to nearest road (km)	0.41	0.37	0.05	1.19
Distance to nearest forest edge (km)	0.16	0.12	0.04	0.47
Distance to populated area (km)	3.04	1.38	0.24	11.65
Road length in 1km radius (m)	3.21	3.08	0.00	11.91
# buckthorn per km in driving survey	1.28	0.77	0.00	5.31
# buckthorn in driving survey per non-agricultural km	3.35	1.83	0.00	19.28
<i>Soil characteristics</i>				
Percent sand	41.84	37.27	11.22	89.34
Percent clay	15.99	17.29	3.93	23.59
Percent silt	42.16	46.18	5.57	66.15
pH	5.29	5.05	4.22	6.67
Soil K (ppm)	103.55	78.91	59.27	224.66
Soil Na (ppm)	8.68	8.80	2.16	16.63
Soil Ca (ppm)	1516.13	1103.00	305.45	3632.10
Soil Mg (ppm)	274.05	188.60	44.45	764.12
Percent total organic carbon	2.08	1.78	0.67	3.98
Percent soil nitrogen	0.16	0.13	0.07	0.30
Average litter depth (mm)	8.65	8.28	0.42	15.21
Average percent bare soil	15.27	7.66	0	54.69
Earthworm rating (1-5)	3.94	4	2	5
<i>Diversity estimates</i>				
Herbaceous Shannon Diversity Index	1.21	1.22	0.79	1.56
Woody Shannon Diversity Index	1.12	0.86	0.51	3.44
Abundance-weighted MPD (herbaceous)	221.72	228.55	85.62	257.58
MPD of herbaceous species based on presence/absence	273.58	273.42	256.85	292.40
Basal area-weighted MPD (woody)	125.08	125.04	67.94	189.54
Stem count-weighted MPD (woody)	170.60	175.64	117.80	227.86

MPD of woody species based on presence/absence	233.89	235.11	214.38	247.46
MPD of herbaceous & woody species based on presence/absence	263.05	262.80	250.42	274.27
Herb richness	43.39	46	23	63
Woody richness	29.39	31.5	15	40
Average herbaceous cover per plot (%)	50.20	21.80	11.88	116.33
<u>Light measurement</u>				
Site average canopy openness	26.37	20.11	1.73	89.75
<u>Vegetation measurements:</u>				
Total # woody stems in 1m plots per site	783.56	705.50	98	2351
Average # woody stems per 1m plot	48.97	44.09	6.125	146.94
Total basal area (m ² /ha)	18.89	20.05	0.50	40.68
Buckthorn basal area (m ² /ha)	0.05	8.55 E-05	0	0.55
Buckthorn stems per ha	614.96	31.83	0	6047.89

APPENDIX 3. Supplementary information for Chapter 3.

Appendix S3.A. Timing of soil sampling events.

In situ net N mineralization incubation tubes:

Sampling period	Installation date*	Removal date
Summer	7/5/12 ^{bc}	8/2/12 ^{ab}
Winter	11/26/12 ^b	4/29/13
Spring	5/6/13 ^b	6/3/13

* Initial soil cores were collected on PVC tube installation days.

^a Bulk density calculated on these soil samples

^b Soil moisture and microbial C and N were measured on these soil samples

^c Total organic C, total N, exchangeable cations, total and extractable P, soil texture, and soil pH were measured on this sample

Resin bags:

Sampling period	Installation date	Removal date
Summer	7/5/12	8/2/12
Fall	10/2/12	11/13/12
Winter	11/14/12	4/29/13
Spring	5/6/13	6/3/13

Appendix S3.B. Table of mean nutrient concentrations in green leaves of common buckthorn (*Rhamnus cathartica* L.) and red maple (*Acer rubrum*).

Nutrient and species	Mean	Standard deviation	Number of plots
Al (ppm) buckthorn	151.43	61.66	22
Al (ppm) maple	66.60	15.29	19
B (ppm) buckthorn	64.99	6.26	22
B (ppm) maple	43.29	8.13	19
Ca (ppm) buckthorn	29322.73	5807.16	22
Ca (ppm) maple	12346.54	2584.77	19
Cd (ppm) buckthorn	0.19	0.05	22
Cd (ppm) maple	0.33	0.10	19
Cr (ppm) buckthorn	7.47	6.94	22
Cr (ppm) maple	2.79	1.10	19
Cu (ppm) buckthorn	4.81	0.77	22
Cu (ppm) maple	5.31	1.63	19
Fe (ppm) buckthorn	229.35	94.78	22
Fe (ppm) maple	103.30	19.55	19
K (ppm) buckthorn	29670.91	1964.64	22
K (ppm) maple	8755.32	2068.35	19
Mg (ppm) buckthorn	3039.89	370.83	22
Mg (ppm) maple	2481.67	991.98	19
Mn (ppm) buckthorn	130.14	38.99	22
Mn (ppm) maple	542.66	245.79	19
Mo (ppm) buckthorn	1.76	0.98	22
Mo (ppm) maple	0.60	0.29	18
Na (ppm) buckthorn	124.59	25.70	22
Na (ppm) maple	62.31	13.72	19
Ni (ppm) buckthorn	2.17	1.45	22
Ni (ppm) maple	1.29	0.53	19
P (ppm) buckthorn	2297.90	421.67	22
P (ppm) maple	2205.46	873.19	19
Pb (ppm) buckthorn	1.26	0.59	22
Pb (ppm) maple	0.55	0.26	17
Total C (%) buckthorn	43.97	0.62	22
Total C (%) maple	47.51	1.99	19
Total N (%) buckthorn	2.97	0.24	22
Total N (%) maple	1.57	0.15	19
Zn (ppm) buckthorn	17.52	1.88	22

Zn (ppm) maple	35.68	12.66	19
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Appendix S3.C. Table of mean nutrient concentrations in leaf litter of common buckthorn (*Rhamnus cathartica* L.), red maple (*Acer rubrum*), and oak (*Quercus alba* and *Q. rubra*).

Nutrient and species	Mean	Standard deviation	Number of plots
Al (ppm) buckthorn	250.54	42.49	19
Al (ppm) maple	73.08	12.20	28
Al (ppm) oak	71.40	8.77	26
B (ppm) buckthorn	59.86	4.61	19
B (ppm) maple	43.96	4.32	28
B (ppm) oak	66.80	5.38	26
Ca (ppm) buckthorn	36242.74	4642.94	19
Ca (ppm) maple	12950.16	1189.57	28
Ca (ppm) oak	13061.41	1035.93	28
Cd (ppm) buckthorn	0.27	0.05	19
Cd (ppm) maple	0.35	0.09	28
Cd (ppm) oak	0.18	0.03	26
Cr (ppm) buckthorn	6.38	2.38	19
Cr (ppm) maple	1.49	0.47	28
Cr (ppm) oak	2.06	0.50	26
Cu (ppm) buckthorn	4.74	0.51	19
Cu (ppm) maple	4.65	0.75	28
Cu (ppm) oak	2.82	0.48	26
Fe (ppm) buckthorn	382.44	130.84	19
Fe (ppm) maple	108.68	24.93	28
Fe (ppm) oak	79.59	12.27	26
K (ppm) buckthorn	20006.11	1734.97	19
K (ppm) maple	5674.98	846.59	28
K (ppm) oak	4735.57	552.42	28
Mg (ppm) buckthorn	3319.95	413.07	19
Mg (ppm) maple	2569.16	324.68	28
Mg (ppm) oak	1597.65	321.70	28
Mn (ppm) buckthorn	214.31	65.31	19
Mn (ppm) maple	708.53	235.81	28
Mn (ppm) oak	913.73	157.21	28
Mo (ppm) buckthorn	1.85	1.05	19
Mo (ppm) maple	0.70	0.22	24
Mo (ppm) oak	0.67	0.29	22
Na (ppm) buckthorn	143.74	21.99	19

Na (ppm) maple	53.00	7.13	28
Na (ppm) oak	57.02	7.33	26
Ni (ppm) buckthorn	1.93	1.19	19
Ni (ppm) maple	1.15	0.44	28
Ni (ppm) oak	3.07	1.02	26
P (ppm) buckthorn	1586.41	180.88	19
P (ppm) maple	1729.45	426.93	28
P (ppm) oak	1547.44	224.94	28
Pb (ppm) buckthorn	1.27	0.30	19
Pb (ppm) maple	0.54	0.18	23
Pb (ppm) oak	0.51	0.22	21
Total C (%) buckthorn	43.74	0.65	19
Total C (%) maple	48.69	0.40	28
Total C (%) oak	49.25	0.75	28
Total N (%) buckthorn	1.92	0.18	19
Total N (%) maple	0.77	0.08	28
Total N (%) oak	0.90	0.06	28
Zn (ppm) buckthorn	22.28	4.75	19
Zn (ppm) maple	36.10	5.46	28
Zn (ppm) oak	22.88	7.86	26