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Investigating the ecology of native and non-native lianas

in

Central and Western New York

By

Scott G. Ward

A thesis submitted to the Department of Environmental Science and Ecology of The
College at Brockport, State University of New York in partial fulfillment of the
requirements for the degree of Master of Science

January 25, 2019

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By

Scott G. Ward

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ABSTRACT

Woody vines, also called lianas, are increasing in abundance in temperate forests of the Northeastern United States. Both native and invasive taxa can alter community trajectories and affect ecosystem function, but invasive taxa such as oriental bittersweet (*Celastrus orbiculatus*) and Asian wisterias (*Wisteria floribunda*; *Wisteria sinensis*), are particularly problematic. Questions remain regarding whether these lianas are passengers or drivers of ecological change where they occur. To analyze the effects of invasive lianas in Central and Western New York, I constructed a two-part study. In the first portion of my research, I performed a selective liana-removal experiment within two local forests that contain infestations of *C. orbiculatus* and *Wisteria floribunda*. Over three growing seasons, I measured the effect of lianas on native tree-growth by comparing trees that had no history of liana-infestation to trees that were either still infested or had lianas cut. The impacts of liana treatment varied according to the initial trunk size and species of infested tree, with some evidence for negative impacts in a situationally-dependent manner. Overall, while mature tree growth was not impacted by lianas to the extent I predicted, future impacts of lianas on forest succession may reveal their more dramatic effects. For the second portion of my research, I compared sites with plant communities that supported *C. orbiculatus* to those supporting its native congener, *C. scandens*, to analyze for possible landscape and community patterns that could help to explain the occurrence and abundance of both species. While landscape patterns and community structure were similar between *Celastrus* sites, those with the invasive *C. orbiculatus* tended to have higher dominance by exotics and lower floristic quality. These results suggest that the

encroachment of other exotics with *C. orbiculatus* into sites with *C. scandens* may be a symptom of underlying habitat disturbance. By quantifying conditions that may encourage the spread of invasive lianas and their impacts once present in plant communities, I highlight the challenge of regional conservation in a rapidly changing world.

GENERAL INTRODUCTION

Lianas are woody vines that utilize trees or other woody plants for structural support. Lianas possess higher leaf weight per stem ratios, which can make them superior competitors to trees (Putz 1984). Lianas can cause structural damage to their hosts, and increase competition for above- and below-ground resources (Lutz 1943; Campbell and Newberry 1993; Allen et al. 1997; Schnitzer et al. 2005), leading some to describe them as structural parasites (Stevens 1987). While lianas experience their greatest diversity in the tropics (Schnitzer 2005), they may be increasing in temperate areas where forest fragmentation provides ideal, edge-habitat where lianas can thrive. Because lianas can re-sprout vigorously after tree falls, they are able to thrive in plant communities that undergo both natural and human disturbance (Schnitzer et al. 2012).

The historically low diversity of lianas in temperate forests may also provide an open niche for invasive lianas to occupy (Leicht-Young and Pavlovic 2015). The numerous effects of invasive lianas in Eastern North America include their ability to smother trees and form dense monocultures, convert old fields into vine communities, delay successional trajectories of forests, and cause severe girdling and tree-mortality (Fike and Niering 1999; Trusty et al. 2007; Ladwig and Meiners 2010; Leicht-Young and Pavlovic 2015). Lianas have also been shown to increase competition with both tree seedlings and mature trees, which increases water stress and limits the growth and fecundity of trees (Stevens 1987; Pérez -Salicrup and Barker 2000; Toledo-Aceves and Swaine 2008; Kainer et al. 2014).

Perhaps no other invasive liana has spread so prolifically within native plant communities of the Eastern United States than oriental bittersweet (*Celastrus*

orbiculatus). Now present in thousands of sites across at least 25 states (DeiTredici 2014), *C. orbiculatus* has become ubiquitous within disturbed communities and is spreading into intact, mature forests (Pavlovic and Leicht-Young 2011).

Known to girdle and smother trees it grows on, oriental bittersweet has also been suggested to impact its native congener, American bittersweet (*Celastrus scandens*), which is now rare or endangered in parts of its range (Steward et al. 2003; NatureServe 2018). *Celastrus orbiculatus* has been shown to be reproductively and competitively superior to *C. scandens* by producing higher amounts of fruit and seed, allocating more resources to above-ground biomass, and interfering with the reproduction of *C. scandens* (Van Clef and Stiles 2001; Leicht-Young et al. 2007; Leicht-Young et al. 2011; Zaya et al. 2015). While studies have addressed the role that congeneric-competition may have played in the decline of *C. scandens*, further research is needed on the possible synergistic contribution of underlying habitat alterations.

Asian wisterias (*Wisteria spp.*) are also increasing in abundance within the Eastern United States, where they form dense monocultures and prohibit the abundance of native plants (Trusty et al. 2007). Remarkably, while dense populations of these lianas can be found throughout New York, little research exists on its impacts to native trees and how its effects may compare to other invasive lianas.

Vine removal experiments have often been employed to elucidate the role lianas play in tropical forests (Pérez-Salicrup and Barker 2000; Pérez-Salicrup 2001; Phillips et al. 2005; Ingwell et al. 2010), thus I aimed to determine if their effects were as important within temperate settings. I performed a selective vine-removal

experiment in two forests of Western New York that contained infestations of oriental bittersweet (*Celastrus orbiculatus*) and Japanese wisteria (*Wisteria floribunda*). In addition to its impacts on trees, because *C. orbiculatus* may be causing its native congener to decline, I sought to investigate the possible role that community and landscape patterns may play in the spread of *C. orbiculatus* into areas where *C. scandens* occurs. I analyzed these patterns using ordination techniques, Floristic Quality Analysis, and land-cover analyses. Both studies address two primary questions of invasion ecology: which conditions promote the establishment of invasive species into communities, and what impacts do invaders cause once present?

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Chapter 1: Quantifying the effects of invasive lianas on tree growth in Western New York

Introduction

Lianas are woody vines that utilize trees or other woody plants for support, sometimes causing a reduction in fitness of their hosts due to both exploitation and interference competition. Some have described lianas as structural parasites (Stevens 1987). Aboveground, exploitation competition occurs for light via liana-induced shading (Lutz 1943; Stevens 1987; Campbell and Newberry 1993), while belowground, liana roots increase competition with trees for nutrient and water acquisition (Dillenberg et al. 1993; Pérez-Salicrup and Barker 2000; Schnitzer et al. 2005). Lianas directly interfere with and reduce tree fitness through girdling, which can increase competition for space and cause structural damage through constriction of vessels and elements (Lutz 1943). Damage to trees can occur during severe weather events such as ice storms and hurricanes where lianas increase canopy loads (Siccama et al. 1976; Allen et al. 1997). The competitive effects and structural damage caused by lianas can severely reduce host fitness and ultimately cause tree mortality (Putz 1984, Ingwell et al. 2010, Leicht-Young and Pavlovic 2015).

Selective or experimental removal of lianas from individual trees or entire forest stands has been used to demonstrate the competitive effects of lianas on tree hosts. Removals from individual trees can decrease water stress and produce significant increases in tree host diameter growth and fecundity (Stevens 1987; Pérez-Salicrup and Barker 2000; Kainer et al. 2014). Controlled experiments on individuals have demonstrated the limiting effect lianas have on young tree growth and biomass

production due to both root and shoot competition (Dillenburg et al. 1993; Toledo-Aceves and Swaine 2008). Scaling up from individual trees, large-scale liana removal plots demonstrate significantly higher tree-seedling recruitment, enhanced sapling growth, and a doubling of mature tree growth (Grauel and Putz 2004; Campanello et al. 2012).

Impacts of lianas are perhaps most evident following disturbance within forested communities, revealing their role as initial passengers of ecological change. However, their role as possible drivers of change is also evident. For instance, within tree-fall and canopy gaps, lianas have the potential to suppress tree growth severely, limit seedling recruitment, and diminish overall tree regeneration (Schnitzer and Carson 2001; Schnitzer et al. 2005; Schnitzer and Carson 2010; Paul and Yavitt 2011). Lianas tolerate and often thrive amid disturbances such as fire and tree falls by sprouting vigorously from clonal stems and root sprouts (Schnitzer et al. 2012; Pavlovic et al. 2016). Growth characteristics such as wide vessels and sieve tubes, as well as greater leaf weight per stem ratios, make lianas superior competitors for resources compared to trees (Putz 1983; 1984). These characteristics, combined with their high level of plasticity, provide lianas with the capacity to persist in shaded understories and spread prolifically upon sudden increases in light (Ellsworth et al. 2004; Leicht and Silander 2006).

Most vine-removal experiments have occurred in tropical forests, where liana diversity and abundances are greater (Schnitzer 2005), but are their effects mirrored in temperate systems? Due to the historically low level of liana diversity in temperate forests, it is thought that exotic-invasive lianas can capitalize on this relatively open

niche within their introduced ranges (Leicht-Young and Pavlovic 2015). Oriental bittersweet (*Celastrus orbiculatus*) and Asian wisterias (*Wisteria floribunda*, *Wisteria sinensis*), occur in New York and have demonstrated both aggressive smothering and girdling potential across their widening ranges (Trusty et al. 2007; Leicht-Young and Pavlovic 2015). Both *Wisteria* species have demonstrated a wide array of environmental tolerances, vigorous growth potential, and the ability to form dense monocultures that prohibit the growth of native plants (Trusty et al 2007). *Celastrus orbiculatus* has acted similarly, via its “sit and wait” strategy, which allows individual vines to survive for extended periods of time in shade, until sudden increases in light allow for explosive growth (Greenberg et al. 2001). This strategy, combined with physiological advantages, provides *C. orbiculatus* with the necessary ecological ingredients to convert old fields and successional forests into novel vine communities, thereby diminishing herbaceous diversity and delaying community trajectories (Fike and Niering 1999; Silveri et al. 2001; Ladwig and Meiners 2010). Furthermore, control of this species is exacerbated by its capacity to allocate non-structural carbohydrates to re-sprouting after cutting and fire (Leicht-Young and Pavlovic 2015, Pavlovic et al. 2016) and even herbicide-treatment (Ward, personal observation).

Temperate Northeastern forests have experienced significant fragmentation, creating an abundance of induced edge habitat where lianas can proliferate. The ability for lianas to thrive in disturbed habitats provides very real implications for second-growth forests of Western New York, given the already present effects of deer overabundance, invasive insect pests, and edge effects in these types of forests (Côté et al. 2004; Harper et al. 2005; Gandhi and Herms 2010). Due to the paucity of liana

research across the temperate Northeast, I sought to investigate their possible effects within two Western New York forests that contain varying levels of both *Celastrus orbiculatus* and *Wisteria floribunda*. In these areas, I sought to determine to what extent these lianas affect their tree hosts through a vine-removal experiment. The purpose of this study was to determine if there were significant differences in growth responses of individual trees, comparing those with no history of vine infestation to trees receiving either cut or uncut treatments. Due to previous research, I expected four patterns. First, I expected that trees would show decreasing growth as vine infestations increased in severity. Second, I expected treatment to have an impact on tree growth, with control trees showing the largest growth response, trees with vines cut showing the second largest growth, and trees with vines still present showing the lowest growth response. Third, I expected larger, more canopy-dominant trees to show the greatest growth response overall, regardless of vine infestation or treatment. Lastly, I expected *C. orbiculatus* and *Wisteria* to cause similar impacts to host trees.

Methods

Study areas

I located two primary sites with varying levels of liana infestation in Mendon Ponds County Park, Honeoye Falls, NY (Fig. 1). The Quaker Pond site, the primary study area for *C. orbiculatus*, is a mixed deciduous forest, dominated by black and red oak (hereby lumped into *Quercus rubra*) and red cherry (*Prunus serotina*), interspersed with white pine (*Pinus strobus*), and planted stands of red pine (*Pinus resinosa*). This forest occurs along an expansive ridge with 8-60% slopes terminated along the eastern edge by marsh wetland. The predominant soil type is an Ontario-

Palmyra-Arkport complex, consisting of gravel and fine sand loams derived from glaciofluvial deposits (Web Soil Survey 2018). *Celastrus orbiculatus* occurs throughout the study area, with heavy concentrations along trails but also within forest interiors. Individual vines occupy all forest layers as both sprawlers and climbers, thereby growing on both understory trees and canopy-dominant individuals. Many lianas use saplings as “ladders”– initiating growth on younger trees and then climbing onto medium and large trees to reach canopy access (Leicht-Young and Pavlovic 2015; Ward, personal observation).

The second study site within Mendon Ponds Park is located along the North Meadow Trail in the northeast portion of the park (Fig. 1). This site was historically used as a tree nursery and has since been abandoned, leaving rows of red oak (*Quercus rubra*) of varying size mixed with an assortment of ornamental tree species. Here, a significant patch of *Quercus rubra* is invaded by a prolific infestation of *Wisteria*. Vine individuals at the North Meadows site (herein NM) were observed twining from right to left (counterclockwise), which is a growth form distinct in Japanese wisteria (*W. floribunda*) (Trusty et al. 2007). However, it has been found that both Chinese (*W. sinensis*) and Japanese wisteria (*W. floribunda*) readily hybridize throughout their introduced ranges, making normally distinguishable morphological characters (such as twining direction) cryptic and unreliable (Trusty et al. 2007). Thus, vines at the NM site will herein be referred to as *Wisteria*. While *Wisteria* vines more densely cover host trees at the NM site, the infestation does not occur over as large of an area as *C. orbiculatus* at the Quaker Pond site.

Removal experiment

From 27 February 2016 to 20 May 2016, the diameter at breast height (DBH) (1.37 m from the ground) of a total 217 trees was measured to the nearest tenth of a cm at the North Meadows site (NM) and Quaker Pond site (QP) (Table 1). If trees had vine constrictions present at 1.37 m from the ground, the closest possible diameter measurement was taken free from any growth abnormalities (e.g., knots, stems, vine girdling). For trees < 8 cm DBH, stems were measured with calipers to the nearest thousandth of an inch at two adjacent points along the trunk at 1.37 m from the ground, and the average of the two measurements was taken. Only one caliper measurement could be taken for six trees < 8 cm DBH due to vine girdling. To re-measure trunk widths precisely at the same height, a small line of paint was sprayed onto the exact point of caliper placement.

For trees > 8 cm DBH, a standard DBH tape was initially used to measure individuals, eventually fitting them with dendrometer bands following the collar method described in Anemaet and Middleton (2013). First-year measurements for dendrometer bands have been shown to be species-dependent and have demonstrated varying levels of reliability (Fuller et al. 1988; Keeland and Sharitz 1993), especially for black cherry trees (Auchmoody 1976). Thus, installing bands one full growing season prior to measurements has been recommended for reliable results (Keeland and Sharitz 1993; Keeland and Young 2007). Due to the time constraints of my experiment, a period of five months was used before recording initial growth response.

Prior to vine removal, canopy position, initial DBH, and level of vine-infestation were noted for all trees. Canopy position was categorized as either

canopy-dominant or canopy-subdominant for larger trees, while all smaller trees fell within an “understory” canopy class. Level of vine-infestation was ranked from one (least infested) to five (most infested) on a per-tree basis according to the infestation size relative to tree-host size. For instance, if two trees contained vines of markedly different sizes, yet the vines were of similar infestation relative to individual tree size, then similar ranks were given.

Tree pairs were initially matched based on species and initial DBH, and then further arranged to account for canopy position and vine infestation. These pairs were then matched to one more individual of similar species and size characteristics that had no history of vine infestation to form triplicate groups. This grouping of triplicates accounted for differences between individual trees that would be matched experimentally. On 23 May 2016, one tree from each of these triplicates was chosen as the experimental treatment and had all living vine stems cut and stump-treated with herbicide. Therefore, I could compare growth rates between control trees (trees with no history of vine-infestation), treatment trees (trees with vines cut), and experimental-control trees (trees with vines uncut). Periodic cutting of re-sprouting vine stems was required throughout both growing seasons on trees that received the cut treatment despite initial herbicide use.

During each measurement period, caliper measurements were recorded to one thousandth of an inch (and later converted to centimeters for analyses) for all trees below a DBH of 8 cm. The larger size class of trees (DBH > 8 cm) had both DBH recorded to 0.1 cm and band measurements recorded with the same calipers used to measure smaller trees. Initial size of all trees was recorded in the Spring of 2016.

Subsequent measurements were collected (including band growth) in Fall 2016, Spring and Fall 2017, and once more in August 2018.

A sub-set of the small black cherry trees was selected for photosynthesis measurements. On a select number of days in the summers of 2016 and 2017, measurements were recorded using a LI-COR 6400 portable photosynthesis system to compare leaf performance within tree triplicates. Unfortunately, due to drought impacts in 2016, and logistical constraints in 2017, I was unable to collect a usable data set from these two years and thus could not make any valuable conclusions on the relationship of vine girdling to tree-host photosynthetic productivity.

Statistics

Trees were initially separated into two statistical categories based on whether their DBH was greater than (large class) or less than (small class) 8 cm. For trees in the smaller size class, growth response was measured as the difference in caliper measurements from initial sampling (Spring 2016) to the last sampling period (August 2018). The smaller size class contained 67 total trees from *Prunus serotina* and *Pinus strobus* (Table 1). For analyses, trees were divided into two groups according to species. These data failed the tests for normality in both species, thus, Kruskal-Wallis tests were performed to test for significant differences among treatment groups (control, cut, uncut).

For the larger size class, there were two final measurements for growth response: DBH and dendrometer band difference from Spring 2016 to August 2018. Only dendrometer band differences were used for analyses (except for band and DBH

correlation). For the larger size class, trees were placed into four groups: *Quercus rubra* (QP site), *Quercus rubra* (NM site), *Prunus serotina*, and a combined group for both pines (*P. strobus* and *P. resinosa*). *Quercus rubra* was divided based on *C. orbiculatus* infestations at the QP site and *Wisteria* infestations at the NM sites. Band measurement values had a constant value of 0.05 added to each for all trees within the four groups and were log-transformed to standardize data and account for values of zero. I performed four General Linear Models (GLM) for each of the four tree groups. Band growth was input as the response variable, initial DBH of individual trees was input as a covariate, and vine treatment and infestation size were input as fixed factors. An additional fixed factor of species was input into the *Pinus* model (based upon species of pine). Models were assessed with main effects of factors. GLM and post hoc analyses were performed in Minitab (version 18, Minitab inc., State College, PA).

Results

Smaller trees

Kruskal Wallis tests revealed that there was a significant difference between treatment groups for smaller trees of *Prunus serotina* ($P = 0.043$) but not for *Pinus strobus* ($P = 0.276$, Table 2). For *P. serotina*, the cut treatment group showed a greater growth response than the control group, and the uncut group showed little growth response overall, with the exception of two outliers (Fig. 2). While the control group for *P. strobus* appeared to have a wide range in caliper values (Fig. 2), overall, there was no significant effect observed between growth response and treatment type

(Table 2). For the smaller size class of both tree species, control and cut treatments did not consistently show greater growth responses than uncut treatments.

For the larger size class, individual trees tended to grow less with increasing vine infestation, although medium-sized vine infestations (1.5-3) still demonstrated high growth rates relative to the lowest infestation class (0-1.5) (Fig. 3). Generally, trees in the largest infestation size class (3-5) showed the lowest growth rates; however, oak trees with an initial DBH > 25-30 cm appeared to be less affected by greater vine infestations (dark circles, Fig. 3). For the larger size class of *Quercus* and *Prunus*, trees with control treatments and the lowest class of infestation size typically demonstrated greater growth rates (Fig. 4, Fig. 5). However, growth response often overlapped or did not differ drastically between treatments (e.g., cut and uncut treatments in *Quercus*) and infestation size (e.g., 1.5-3; 3-5 in *Prunus*, Fig. 4, Fig. 5). Overall, *Quercus* trees appeared to grow more than both *Prunus* and *Pinus* trees. While these data revealed that some pattern may have existed between treatment and infestation size with tree growth, statistical analyses showed that these factors did not consistently provide a significant effect.

General Linear Models revealed that initial DBH of trees had a significant effect on overall growth for *Quercus* trees at both sites ($P < 0.0001$); however, treatment and infestation size had no significant effect (Table 3). Few regenerating *Quercus* trees were observed at both sites, thus most oak individuals measured had higher initial DBH sizes than other tree species. Neither *C. orbiculatus* nor *Wisteria* caused significant effects to tree growth on *Quercus* trees. Both *Quercus* models at the QP and NM sites accounted for 43.8% and 37.8% of the variation in band growth,

respectively. Both initial DBH and treatment were found to explain the variation in growth for *Prunus* trees, while infestation size had no effect (Table 3). This model accounted for 39.6% of the total variation in band growth. For *Pinus*, initial DBH, tree species, and treatment had a significant effect on the growth of trees, with initial DBH and tree species having the most significant effects. *Pinus strobus* trees had a significantly higher growth rate than individuals of *Pinus resinosa*. The *Pinus* model accounted for 62.6% of the variation in band growth. Tukey's post-hoc tests for the *Pinus* model revealed that among the three treatments, control trees grew significantly more than cut and uncut groups and no significant difference was detected between cut and uncut groups.

Discussion

Of the 67 sapling or understory trees observed throughout this liana-removal study, *Prunus serotina* trees demonstrated significant growth differences based on treatment type, while *Pinus strobus* trees showed no significant patterns. Interestingly, while I hypothesized that control trees (trees with no history of vine infestation) would show superior growth rates to other treatments, black cherry trees that received cut treatments grew more than controls. This may have been due to an initial pulse in the growth of trees after pressures from vine-constriction were removed, although it is unclear if dead vine stems still present on trees could still impact growth. Effects of lianas in temperate forests may also depend upon each tree species' growing preferences, considering that shade-tolerant trees have been shown to be disproportionately affected by lianas in tropical forest gaps (Schnitzer and

Carson 2010). Overall this study demonstrated that *C. orbiculatus* can limit the growth of smaller *P. serotina* trees.

Only 14 individuals of smaller *Pinus strobus* trees were measured within this study; therefore, even minor measurement discrepancies could have affected results from treatment. Additionally, for small sample sizes, the Kruskal-Wallis statistic (H) may not follow a chi-squared distribution, and thus, results were interpreted with caution (McDonald 2009). Due to inherently softer wood, I expected that pines would show greater sensitivities to vine girdling compared to black cherries. It is unclear why the data did not support this assumption, although differing physiologies between the two species may have contributed. Softwood and hardwood trees have been shown to produce different types of reaction wood to account for gravitational pressures (Scurfield 1973). Similar phenomena may exist in trees that are girdled by vines, in which vessels and tracheids arrange in non-vertical orientation. While the goals of this study were not to evaluate the effect of vine girdling on tree physiology, future research may reveal underlying mechanisms of tree response under such forces. The effects of lianas on understory trees have been studied primarily in tropical areas (Schnitzer and Carson 2001; Grauel and Putz 2004; Schnitzer et al. 2005; Schnitzer and Carson 2010). Given that lianas can be abundant in regenerating temperate forests (Ladwig and Meiners 2010), further research is needed to investigate their specific impacts on understory trees, especially where liana infestations are extensive.

Although not all saplings responded equally to infestation by *C. orbiculatus*, many of the understory trees throughout my study area served as “ladders,” (Fig. 6) in

which vines gained canopy tree access by initially climbing up understory trees (Leicht-Young and Pavlovic 2015). Once vines reached the canopies of mature trees, they continued to girdle the saplings on which they originally ascended. This means that the next cohort of trees that would normally replace current canopy-dominant individuals will already have experienced damage from girdling (in addition to damage from deer browsing and antler rub). Looking ahead, forests with abundant *C. orbiculatus* in their understories are likely to experience significant alterations to forest composition through both natural disturbances such as canopy gap formation, as well as human-induced disturbances such as fragmentation (Pavlovic and Leicht-Young 2011; Leicht-Young and Pavlovic 2015).

This study indicated that invasive lianas may influence the growth of larger temperate trees. For instance, of the three tree groups, both *Prunus* and *Pinus* showed a significant difference between treatment types, while *Quercus* at both sites did not. Inherent differences may exist between *Prunus* and *Quercus* trees that cause dissimilar reactions to liana infestations. *Quercus rubra* growth has been shown to be impacted by *C. orbiculatus*, although this effect may not be apparent until more than a decade after initial infestation (Delisle and Parshall 2018). Furthermore, inherent differences in crown architecture may impact each hardwood's susceptibility to liana infestation, considering the crowns of *Quercus rubra* are known to be more spreading than the narrow crowns of *Prunus serotina* (Hosie 1969; Sander 1990). Differences in species' characteristics between pines may have also impacted results, given that *Pinus strobus* trees grew significantly more than individuals of *Pinus resinosa*. Although, competition for light may have been more influential on the growth of

individual *P. resinosa* trees, considering they tended to occur in denser stands than individuals of *P. strobus*. Furthermore, while treatment did have a significant impact on *Pinus* growth, there was no significant difference between cut and uncut treatments. Given more time, cut groups may demonstrate even higher growth rates compared to uncut groups, meaning that treating infested trees may be of long-term benefit to land managers. Future liana research should investigate the extent to which previously infested trees can recover after vine removal. The surprising resilience of trees that experience severe girdling begs the question of whether these trees could ever return to their original growth potential.

Ultimately, the single most significant predictor of growth for both hardwoods (*Quercus*, *Prunus*) and softwoods (*Pinus*) was the initial size of trees. Similar findings have been noted in temperate forests, in which canopy dominance better determined tree growth than size of liana infestation (Ladwig and Meiners 2009). This means that the implications of liana infestations are perhaps less concerning for canopy-dominant trees, where light is less of a limiting factor. While initial DBH was more important than liana infestation for all tree species, my study provided preliminary evidence that the heaviest class of vine infestation (3 to 5) may disproportionately affect different tree species, although statistics did not support this pattern.

It is unknown if smaller vines in larger trees act more epiphytic than structurally parasitic, especially if they do not cause substantial girdling or canopy smothering. After all, lianas employ numerous climbing techniques (Putz 1984); thus, each may impact their hosts in different ways. Both liana taxa researched in this study

were stem-twiners; however, both did not appear to cause demonstrable impacts from girdling on large *Quercus* trees at either site. Girdling impacts are likely severe on young *Quercus* trees given that girdling effects are evident on saplings of other hardwoods present at the site (e.g., *Carya glabra*).

Although neither liana species caused statistically significant impacts to *Quercus* trees at either site, infestation size was shown to be less impactful to *Quercus* trees at the QP site, which were infested with *C. orbiculatus*. This may be attributed to differences in liana and host tree biology or differing site characteristics and land-use histories. *Quercus* trees were arranged much more densely at the NM site compared to the QP site due to its historical use as a tree nursery. This condensed arrangement could have increased competition for sunlight and nutrients, further complicating my ability to isolate effects from lianas. Given that forest pathogens, insect outbreaks, drought, and invasive species all have the potential to alter ecological processes in temperate forests (Ayres and Lombardero 2000; Bréda et al. 2006; Webster et al. 2006), it will likely be difficult to isolate singular impacts to trees from lianas unless more controlled experiments occur.

Little to no research has quantified vine girdling on phloem and xylem transport, despite structural damage being noted for years (Lutz 1943). Unfortunately, logistical and drought constraints affected my capacity to compare photosynthetic capabilities of girdled vs. non-girdled trees, although further research in this regard may be warranted. While water pressure has been shown to differ in liana-infested trees (Pérez-Salicrup and Barker 2000), phloem transport may be markedly difficult to measure without damage to phloem turgor (Ryan and Asao 2013). While trees have

been observed growing under extreme cases of girdling, it is unknown to what extent they are affected from a physiological and biological perspective.

This study supports previous research that has shown liana impacts to be subtler on a shorter time scale, given that it could take more than a decade for *C. orbiculatus* to impact mature tree growth (Delisle and Parshall 2018). Much of the research involving liana-removal experiments has taken place in large tropical plots over long periods of time (e.g., 10 or more years) (Phillips et al. 2005; Ingwell et al. 2010). Thus, perhaps the short duration of this study limited my findings, although short term liana-removals (e.g., four years) in temperate settings have previously indicated a significant effect on temperate hardwood tree growth (Whigham 1984). Nonetheless, the relationship between tree growth suppression and liana infestation has been clearly documented in tropical forests (Dewalt et al. 2000; Ingwell et al. 2010; Schnitzer and Carson 2010) and thus warrants more research in temperate regions where lianas are increasing in abundance (Leicht-Young and Pavlovic 2015).

It is possible that liana impacts may be subtler in temperate forests; however, my research indicated that larger trees were more often impacted than not. Ladwig and Meiners (2009) reported that lianas were less important than canopy position in determining tree growth across a nine-year period in New Jersey. Liana research in temperate forests may also differ compared to tropical forests due to the levels of vine abundances that are typical. For instance, much of the tropical liana research occurs in “liana forests,” where large contiguous forests contain extremely high liana densities (Pérez-Salicrup 2001) and often undergo pronounced dry and wet seasons (Schnitzer 2005). These systems are markedly different from my area of study in

which forests are not hyper-seasonal and liana densities are often lower. Hence, while there are likely to be some mirrored effects, comparisons between lianas in tropical and temperate forests should be addressed with caution.

An additional problem that may have impacted my study results is the differential settling times of dendrometer bands, or band slack (Auchmoody 1976; Keeland and Sharitz 1993). Overall, band growth and DBH measurements were found to be strongly correlated ($R^2 = 0.72$), but differences in bark structure between black cherry and red oak trees may have altered initial band expansion rates. Pines showed low relative growth rates compared to hardwoods and perhaps required more time for bands to settle. Despite issues related to initial band slack and differences in species' bark characteristics, dendrometer bands typically offer relatively reliable precision on smaller times scales (Keeland and Sharitz 1993; Keeland and Young 2007). Additionally, caliper measurements may have provided inconsistent levels of precision that were necessary to account for minute growth differences in both smaller *P. strobus* and *P. serotina* trees. In cut and uncut trees, certain individuals could only receive one caliper measurement due to the presence of girdling vine stems. Conversely, control trees consistently received two equally spaced caliper readings; therefore, sapling stem width may have been more accurate in controls. Furthermore, it is unclear if tree measurements at, above, or below the point of girdling provide a reliable account of actual tree growth. It is also possible that measuring stem width at breast height only partially represented overall growth in understory individuals. Perhaps sapling height or newest shoot length would have provided clearer insights into understory tree responses to vine treatments. Forest

Inventory Analysis (FIA) design does not require measuring protocols for saplings other than rapid DBH measurements, but this may be due to time constraints of sampling (Bechtold and Patterson 2005).

While invasive lianas have become prolific within the upland areas of Mendon Ponds Park and many other forested areas in the region, it is important to consider their overall relevance. Disturbed forests, such as those at Mendon Ponds Park, already experience numerous stressors. For instance, while oaks comprise a major portion of the canopy within the park, an overwhelming deer abundance limits their regeneration through over-browsing and antler rub. Additionally, while allelopathic impacts have been noted for *C. orbiculatus* (Ladwig et al. 2012), it is unknown if other prolific invasive plants in the area of study, such as pale swallowwort (*Vincetoxicum rossicum*), impact tree seedling regeneration. Of the saplings that survive past browse height, many are already being used as liana ladders and are severely girdled.

Multiple trees of varying sizes showed evidence of infestation from forest mites and insects, such as black cherry finger gall (*Eriophyes cerasicrumena*), pine bark adelgid (*Pineus strobi*), and Eastern tent caterpillar (*Malacosoma americanum*). Additionally, some invasive insects (e.g., gypsy moth, emerald ash borer) could possibly alter future forest dynamics within the park given their demonstrable effects on forests in the Northeastern United States (Davidson et al. 1999; Herms and McCullough 2014). Lastly, management of these issues within the park is either absent or severely limited. In fact, my experimental removal of vines was probably the first concerted control effort ever to occur on a large scale within the park. So,

while invasive lianas should be of serious concern to those interested in forest preservation in temperate areas, their proliferation in some cases may merely reflect underlying forces related to fragmentation, disturbance, and poor management. In the coming decades, managers of forests must seriously consider how they will handle the growing abundance of invasive lianas in their natural areas, given the immense pressure that these areas already face from both natural and human-influenced changes.

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Tables

Table 1. Summary of individual trees measured for vine-removal experiment at North Meadows site (NM) and Quaker Pond site (QP) in Mendon Ponds Park based upon species and size.

Species	NM site		QP site	
	< 8 cm	> 8 cm	< 8 cm	> 8 cm
<i>Quercus rubra</i>	-	42	-	28
<i>Prunus serotina</i>	53	56	-	-
<i>Pinus strobus</i>	14	14	-	-
<i>Pinus resinosa</i>	-	10	-	-
Total	67	122	-	28

Table 2. Kruskal Wallis tests for *Prunus serotina* and *Pinus strobus* trees less than 8 cm DBH between three treatment types. Bolded numbers denote statistical significance.

<i>Prunus serotina</i>					<i>Pinus strobus</i>				
Treatment	N	Median	Mean Rank	Z-value	N	Median	Mean Rank	Z-value	
Control	17	0	24.7	-0.73	4	1.8375	10	1.41	
Cut	18	0.72888	33.9	2.33	5	0.2205	5.6	-1.27	
Uncut	18	0	22.3	-1.61	5	0.735	7.4	-0.07	
Overall	53		27		14		7.5		

Method	DF	H-value	P-value	DF	H-value	P-value
Not adjusted for ties	2	5.65	0.059	2	2.46	0.292
Adjusted for ties	2	6.31	0.043	2	2.58	0.276

Table 3. General linear model results for four groups of trees above a DBH of 8 cm in vine-removal experiment: *Quercus rubra* (QP site), *Quercus rubra* (NM site), *Prunus serotina*, and *Pinus* (*P. strobus* and *P. resinosa* grouped together). *Quercus* trees at QP site were infested with *Celastrus orbiculatus*; *Quercus* trees at NM site were infested with *Wisteria*. Four separate GLM analyses were performed for each tree group. GLM results explained 43.8%, 37.8%, 62.6%, and 39.6% of the variation in band growth (adjusted R²) for *Quercus* (QP site), *Quercus* (NM site), *Pinus*, and *Prunus* groups, respectively. Initial DBH was input as a covariate. Treatment consisted of three levels (control, cut, uncut). Infestation size consisted of three levels of vine infestation grouped into three categories of increasing size (0-1.5, 1.5-3, 3-5) (see methods). Bolded numbers denote statistical significance.

Quercus (QP site)						Quercus (NM site)				
Source	DF	Adj SS	Adj MS	F-Value	P-Value	DF	Adj SS	Adj MS	F-Value	P-Value
Initial DBH	1	1.36806	1.36806	33.76	< 0.0001	1	0.46426	0.46426	17.41	< 0.0001
Treatment	2	0.00317	0.00158	0.04	0.962	2	0.00557	0.002783	0.1	0.901
Infestation size	2	0.03123	0.01561	0.39	0.683	2	0.08834	0.04417	1.66	0.214
Error	36	1.45868	0.04052			22	0.5865	0.026659		
Lack-of-Fit						21	0.56704	0.027002	1.39	0.594
Pure Error						1	0.01946	0.019459		
Total	41	2.95625				27	1.1567			
Pinus						Prunus				
Source	DF	Adj SS	Adj MS	F-Value	P-Value	DF	Adj SS	Adj MS	F-Value	P-Value
Initial DBH	1	0.145884	0.145884	20.73	< 0.0001	1	0.78056	0.78056	24.04	< 0.0001
Treatment	2	0.088505	0.044253	6.29	0.009	2	0.26954	0.13477	4.15	0.021
Infestation size	2	0.005228	0.002614	0.37	0.695	2	0.08329	0.04165	1.28	0.286
Species	1	0.145725	0.145725	20.71	< 0.0001					
Error	17	0.119625	0.007037			50	1.62361	0.03247		
Lack-of-Fit	16	0.11659	0.007287	2.4	0.472					
Pure Error	1	0.003035	0.003035							
Total	23	0.432481				55	2.95565			

Figures

Figure 1. Location of vine-removal experiment in Mendon Ponds Park, Honeoye Falls, New York. Black triangles indicate location of individual trees. Lower three sections (triangles) were primary study area; section in Northeast portion of map (circles) refers to *Wisteria* infestation along the North Meadows Trail.

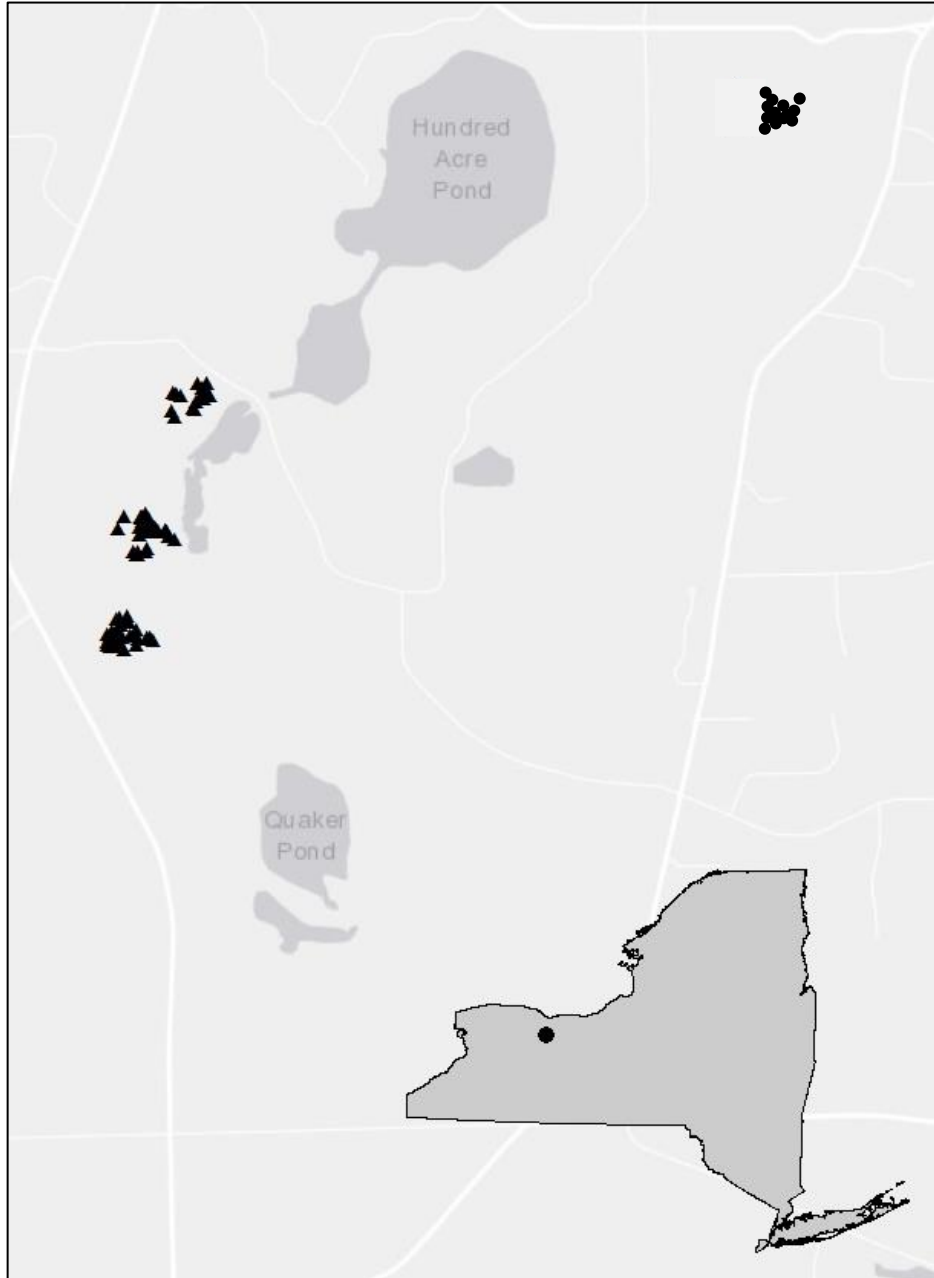


Figure 2. Caliper difference (cm) in 53 *Prunus serotina* and 14 *Pinus strobus* trees less than 8 cm DBH. Trees received tree treatments (control, cut, uncut). Control trees had no history of vine infestation. Cut trees had vines removed. Uncut trees had vines still present.

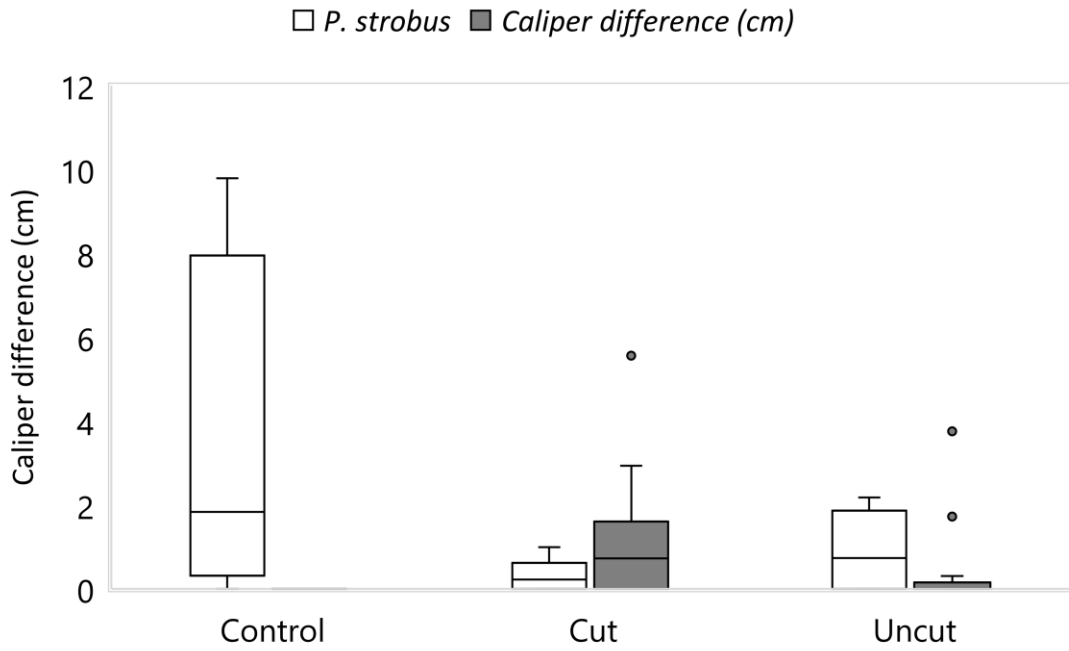


Figure 3. Dendrometer band growth (cm) of four tree species exceeding an initial DBH of 8 cm with differing levels of vine infestation classes (0 to 1.5, 1.5 to 3, 3 to 5). Shapes represent four tree species (see legend). Shading of shapes represent vine infestation class (darker shading refers to increasing level of infestation severity).

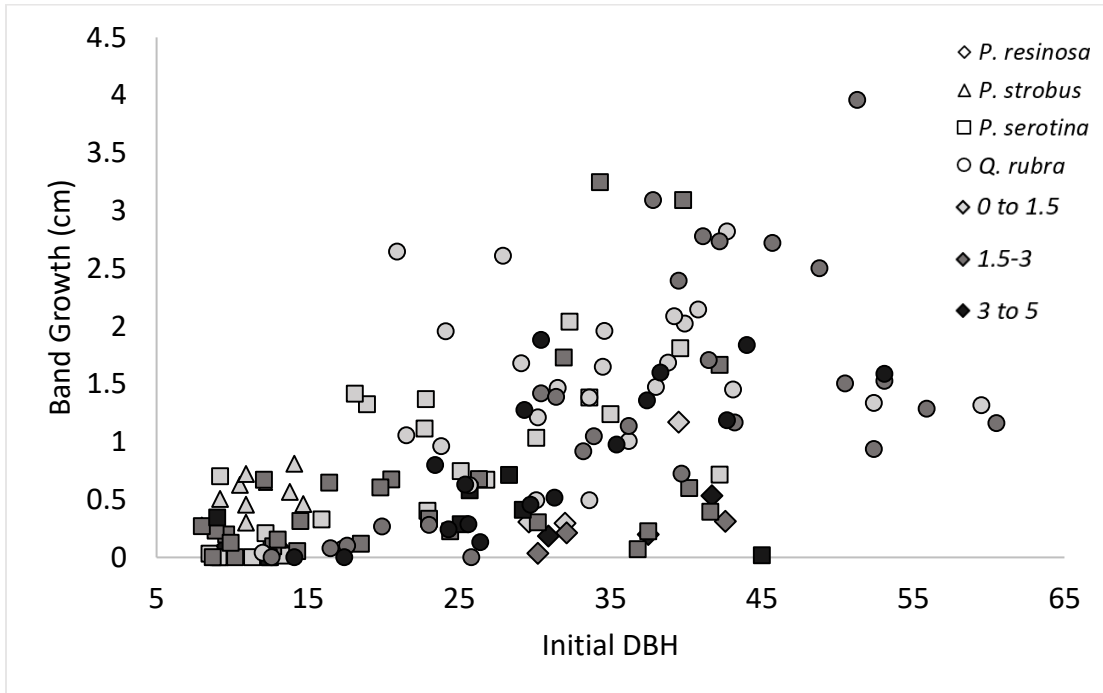


Figure 4. Tree band growth (log) of *Quercus rubra* at Quaker Pond site (*Quercus* QP), *Q. rubra* at North Meadows site (*Quercus* NM), *Prunus serotina* (Prunus), and *Pinus serotina* and *Pinus strobus* (Pinus) according to vine treatment (control, cut, uncut).

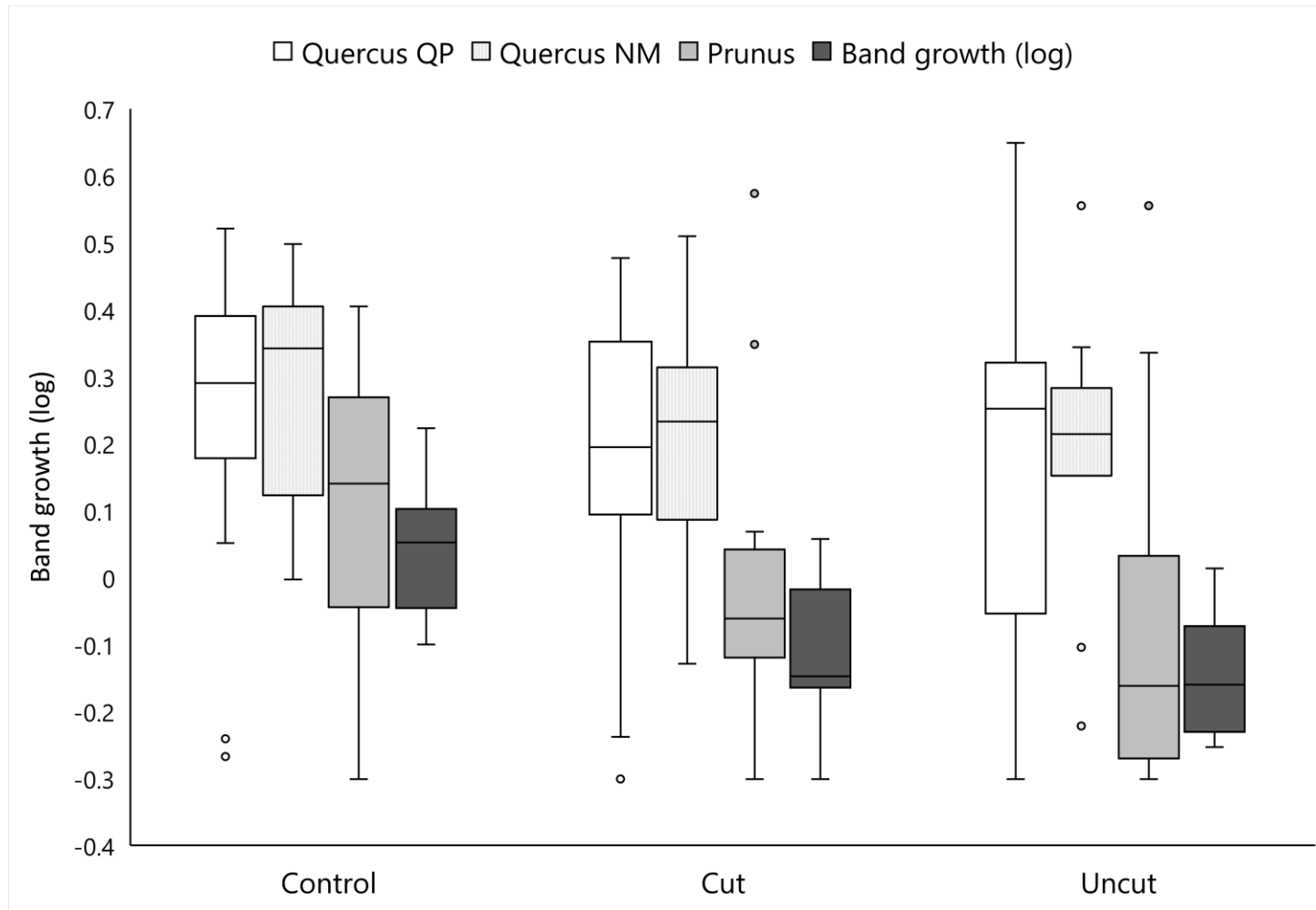


Figure 5. Tree band growth (log) of *Quercus rubra* at Quaker Pond site (Quercus QP), North Meadows site (Quercus NM), *Prunus serotina* (Prunus), and *Pinus serotina* and *Pinus strobus* (Pinus) according to vine infestation class (0 to 1.5, 1.5 to 3, 3 to 5).

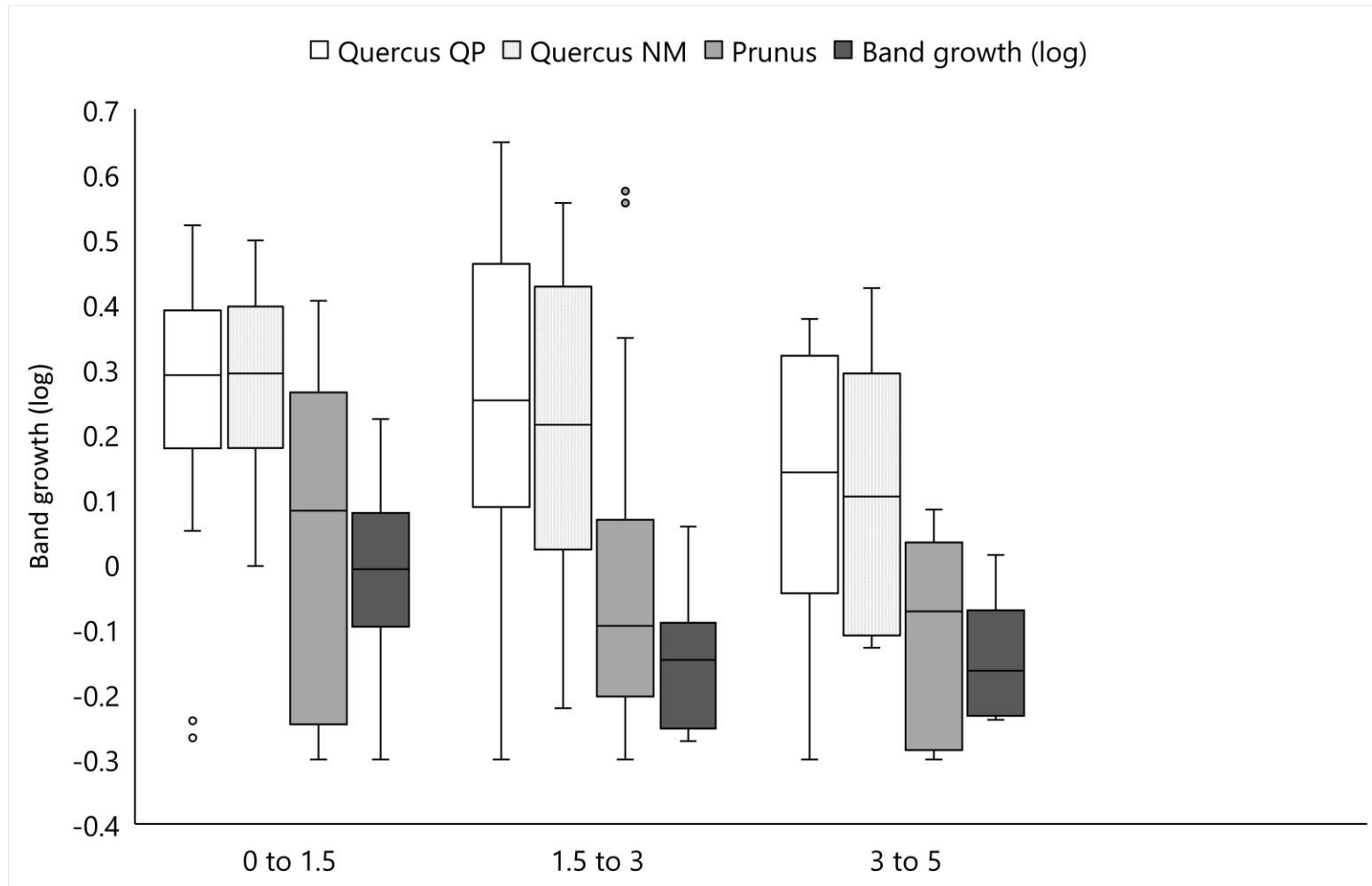


Figure 6. Girdling of *Acer saccharum* (left) by *Celastrus orbiculatus*. It is unclear if altered wood structure on tree hosts is analogous to reaction wood, in which vessels and tracheids re-orient according to gravitational pressure. Liana “ladder” (right) in which *C. orbiculatus* initially uses an understory *P. serotina* individual to reach canopy-dominant trees.



Chapter 2: Community and landscape comparisons between *Celastrus scandens* and its invasive congener, *C. orbiculatus*, in Central and Western New York

Introduction

Invasive species are one of the most significant contributors to global change through their impacts to the communities and ecosystems they invade. Invasive plants, in particular, have been shown to alter nutrient cycles, soil characteristics, and disturbance regimes drastically (Hejda et al. 2009; Ehrenfeld 2010; Pyšek et al. 2012) and contribute greatly to biotic homogenization and native plant reduction (Vitousek et al. 1997; Vilà et al. 2011).

The potential impact of invasive plants depends on both the invasive species' traits and the characteristics of the communities they invade. In some instances, invaders act as passengers of ecological change, merely taking advantage of altered environmental conditions that weaken competitive factors of communities (MacDougall and Turkington 2005). Conversely, invaders may act as drivers of change by competing with native species and causing their decline, regardless of prior conditions (MacDougall and Turkington 2005). More recently, this discussion has become more nuanced, as some species fail to align distinctly with either category. Some invaders may be “back-seat drivers”— species that benefit from ecosystem disruption but also contribute to native species decline (Bauer 2012).

Woody vines, also called lianas, are increasing in temperate regions in both fragmented forests and forest interiors and have the potential to respond to and enact change within ecosystems (Londré and Schnitzer 2006; Pavlovic and Leicht-Young

2011). Lianas respond to disturbances such as fire and treefalls through prolific re-sprouting (Schnitzer et al. 2012; Yorke et al. 2013; Pavlovic et al. 2016) yet also disrupt ecosystem processes by altering forest succession and causing tree mortality (Grauel and Putz 2004; Schnitzer and Carson 2010; Leicht-Young and Pavlovic 2015). In temperate regions, some exotic lianas (e.g. *Lonicera japonica*) tend to colonize areas as passengers of disturbance (Lemke et al. 2011) although other species can potentially drive change within both previously disturbed and intact forest communities (Pavlovic and Leicht-Young 2011). One example of an invasive liana that seizes upon instances of disturbance and influences communities within intact habitats is oriental bittersweet (*Celastrus orbiculatus*).

Introduced into the United States in 1874 (Del Tredici 2014), *C. orbiculatus* began to naturalize in the Northeast by the early 1900s (Patterson 1973) and is now prevalent in at least 25 states across the Eastern and Midwestern United States (Leicht-Young et al. 2007b; Del Tredici 2014). While *C. orbiculatus* has been shown to be present in some areas as a passenger of natural and human disturbances (Pavlovic et al. 2016; Hoosein and Robinson 2018), it can alter ecological processes by smothering and girdling trees, invading old-growth forests, and delaying forest succession (Ladwig and Meiners 2010; Pavlovic and Leicht-Young 2011; Leicht-Young and Pavlovic 2015). Furthermore, *C. orbiculatus* may be present in mature and old-growth forests, where disturbance is infrequent (Pavlovic and Leicht-Young 2011).

While *C. orbiculatus* is concerning in its own regard, it has generated alarm within the botanical community due to impacts to its native congener, American

bittersweet (*Celastrus scandens*), within their concurrent range. The prolific spread and reproductive vigor of invasive *C. orbiculatus* is associated with the decline of its native congener (Steward et al. 2003), which is now listed as vulnerable, endangered, or extirpated throughout much of its range (NatureServe 2018). Compared to its native congener, *C. orbiculatus* demonstrates higher germination rates, increased seed longevity, superior pollen and seed viability, and greater fruit and seed production (Dreyer et al. 1987; Van Clef and Stiles 2001; Pooler et al. 2002; Leicht-Young et al. 2007a; Zaya et al. 2015). *Celastrus orbiculatus* also has the capacity to out-compete its native congener by allocating more resources to aboveground biomass and show higher survivorship during early growth stages (Leicht and Silander 2006; Leicht-Young et al. 2011). Furthermore, while hybrid swarm has likely not played a factor in the spread of *C. orbiculatus* or *Celastrus* hybrids, unidirectional pollen flow has likely caused *C. scandens* to waste reproductive effort (Zaya et al. 2015), thereby impacting its success by limiting recruitment.

Factors beyond competition, such as habitat loss and degradation, may also be causing *C. scandens* to decline throughout its range (Leicht-Young et al. 2007a; Zaya et al. 2015). Although both congeners have been shown, at times, to occupy similar habitats (Leicht-Young et al. 2007b), differences in habitat preferences may also limit where the species now occur. For instance, *C. orbiculatus* has been shown to grow more successfully across a wider spectrum of soil moisture and light conditions, enabling it to occupy a broader niche of mesic, forested habitats than *C. scandens* (Leicht-Young et al. 2007a; Pavlovic and Leicht-Young 2011). Further evidence suggests that *C. scandens* may preferentially grow in habitats with specific soil

characteristics (e.g., higher pH, higher sand content), lower liana richness, and greater availability of sunlight compared to *C. orbiculatus* (Leicht-Young et al. 2007a; Pavlovic and Leicht-Young 2011). Thus, while it may have some habitat preference, *C. scandens* may also mirror the status of other rare species across the region that relied on once-open habitat in a now more forested landscape (Leicht 2005; Leicht-Young et al. 2007a). Consequently, because the decline of native species often reflects underlying synergistic impacts from exotics and habitat change (Gurevitch and Padilla 2004), habitat and landscape conditions may be important considerations in the ecology of the native *Celastrus*.

One challenge of native plant conservation is anticipating the quality of habitat that certain species require to maintain populations and persist over time. Floristic Quality Assessment (FQA) is one method used to distinguish between high- and low-quality habitats. FQA utilizes Coefficients of Conservatism, or C-values, which relate to all native plant species in a region. These C-values correspond to an individual plant species' fidelity to specific habitat types, natural disturbance regimes, and habitat qualities, which can be used to predict the C-values of species they co-occur with in communities (Matthews et al. 2015). Communities with higher scoring plant species (C value= 7-10) typically correspond to higher quality habitats (Taft et al. 1997); therefore, FQA may be useful in indicating the quality of sites that certain species require to persist (Swink and Wilhelm 1994; Taft et al. 1997; Rooney and Rogers 2002). In addition to FQA indices, land-cover analyses may also be useful when considering the role of human landscape alterations on native plants. While these methods have been used to assess the role of landscape modifications on the

spread of the invasive *C. orbiculatus* (Lundgren et al. 2004; Mosher et al. 2009; Merow 2011), there has been little use when considering landscape changes on *C. scandens*. Additionally, while landscape analyses have been used extensively to assess habitat quality for such taxa as birds, insects, and mammals (Moilanen and Hanski 1998; Cardillo et al. 1999; Gottschalk et al. 2005), they may also be effective for considering habitat quality for plant species of increasing rarity.

My goal was to evaluate if the native and invasive *Celastrus* persist in similar habitat types based on landscape and community composition variables. I located six sites in Central and Western New York that supported populations of both *Celastrus* congeners. At these sites, I evaluated landscape conditions, *Celastrus* abundance, and measured associated plant communities of each *Celastrus* species to test for differences in community structure. Given the current spread of *C. orbiculatus* and decline of *C. scandens*, I expected the invasive *C. orbiculatus* to achieve higher population densities. Given that both species often co-occur within a wide range of disturbed habitat types, I anticipated little differences in plant community structure or FQA based on *Celastrus* species.

Methods

In the growing seasons of 2016 and 2017, I located sites that supported populations of *Celastrus scandens* in Western and Central New York (Fig. 1). At each site, I located the most proximal occurrence of *Celastrus orbiculatus*. This formed one “geographically-linked” pair. Each pair were always in direct proximity except for Site 4 (Finger Lakes National Forest), in which populations were approximately 5,000 meters (3.1 miles) apart. In total, eight populations of *C.*

scandens were studied, of which six were found with co-occurring *C. orbiculatus*, thus only six were used in analyses.

Vegetation sampling

At each *Celastrus* location within a paired site, a rectangular 100-150 m² plot was laid out and the diameters of all woody plants with a DBH \geq 3 cm were identified and measured as the tree layer. Basal area in f²/acre was calculated based on these data to account for differing plot sizes (Virtual Cruiser Test 2018), and later converted to metric (m²/hectare).

In each plot, three to four 10-15-meter-long transects were laid out parallel to one another, and 2.82-m-diameter shrub plots were placed at each 5-meter interval along each transect (Fig. 2). In each shrub plot, all woody plants with a DBH of $<$ 3 cm and a height $>$ 0.5 m were identified. The number of stems was counted of each woody plant, and if the plant was between a height of 0.5 and 2 meters, percent cover was estimated in the 2.82-m wide plot. If the shrub plots fell on the edge of a trail, the plot was halved. Lastly, within the shrub plots, 1-m² quadrats were placed in which all herbaceous plants were identified to the lowest possible taxonomic level and identified for percent cover. This also included all stems that did not exceed 0.5 m in height of saplings, shrubs, and lianas.

This plot design was based on a hybrid method of forest inventory analyses described in Johnson et al. (2008) but scaled down in plot size to allow for a greater number of sampling opportunities across the entire region of study. Furthermore, this hybrid method accounted for discrepancies in the Forest Inventory Analysis (FIA)

and University of Wisconsin Plant Ecology Laboratory (PEL) forest inventory methodologies in which understory and herbaceous layers are possibly under-sampled (Johnson et al. 2008). Plant species were identified using Gleason and Cronquist (1991), and nomenclature was updated using Weldy et al. (2018).

GIS methods

LandSAT cover classes were calculated using 2011 LandSAT data in which a 16-class land-cover classification scheme was determined for all domestic territory within the United States (Homer et al. 2015). Two sites (CSC6 and COR6) bordered the Niagara River, which dissects Canadian and American territory; thus, land-cover use was only quantified for the land present on domestic territory. For all sites, 13 total land-cover types were determined from three radial buffer sizes: 100, 500, and 2000 meters. Two categories, open water and shoreline, were removed due to their irrelevance within the study, thus leaving 11 total LandSAT classes.

Statistics

A Principal Components Analysis (PCA) was performed using the percentage cover value of each LandSAT classification type per site in IBM SPSS Statistics (version 24, IBM Corp., Armonk, NY). PCA is a useful tool for relating different kinds of environmental data to community data (McCune and Grace 2002). I performed PCAs on the three buffer sizes (100, 500, 2000 m). The PCA for 2000 meter buffers indicated the strongest relationships in three total components. The three 2000m PCA components were then converted into synthetic variables for each of the 12 *Celastrus* locations for further analyses.

Community structure

To analyze community structure across the 12 sites I used Nonmetric Multidimensional Scaling (nMDS) with Sorenson distance on herb-layer frequency of occurrences (McCune and Grace 2002). As sites varied in size, only herb data for the first nine quadrats sampled per site were used in analyses. Before ordination, I removed species that occurred in less than five total quadrats within the 9-quadrat herb samples across all 12 sites. Ordinations were performed in PC-ORD using the ‘slow and thorough’ approach (version 5.0, MjM Software Design, Gleneden Beach, OR). A three-axis solution was achieved for frequency of occurrence community data after 89 iterations with a total stress of 7.32. Axes 1, 2, and 3 accounted for 28.7%, 71.7%, and 90.8%, respectively, of the cumulative variation in species. Only axes 1 and 2 are presented for simplicity. Shrub cover and LandSAT PCA variables were overlaid as a biplot, with only shrub species and LandSAT vectors greater than a R value of 0.3 presented. An Analysis of Similarity (ANOSIM) test calculated significant differences between *Celastrus* pairs using PRIMER (version 6, PRIMER-e, Quest Research Limited, Auckland, New Zealand).

FQA metrics

To compare floristic integrity between *Celastrus* pairs, each site received a rating based upon eight FQA indices (Table 1). These indices were calculated by using community cover data from each population in which all plant species were assigned a C-value. C-values (Coefficients of Conservatism) correspond to a native species’ fidelity to specific habitat types and its tolerance to natural and anthropogenic disturbance. Values range from 0 to 10, with lower values

corresponding to ruderal species with little fidelity to high-quality natural areas and higher values corresponding to relict species that tolerate little degradation or anthropogenic disturbance. All non-native species receive a value of zero, although there has been some debate on whether exotics should be scored negative relative to native ruderals (Taft et al. 1997). I chose to use the initial data set of C-values that covers the entirety of New York State (NEIWPC 2011; Bried et al. 2012).

FQA indices were calculated from the first nine herb quadrats and shrub plots sampled per site and were calculated separately for herb vs. layers. I chose to omit FQI and FQI native indices from my analyses (Table 1); however, I kept Mean C and Cover-weighted Mean C, and utilized modifications of FQI (e.g. Cover-weighted FQI, Adjusted FQI). FQI equations are still presented in Table 1. While species richness and sample size have demonstrated influence on FQI, Mean C has demonstrated robustness to these influences (Matthews 2003; Bourdaghs et al. 2006). FQI has also demonstrated inferior performance to modified FQI abundance-weighted indices (Miller and Wardrop 2006; Rocchio 2007; Bourdaghs 2012). While Cover-weighted FQI, and Cover-weighted FQI native may be weak indicators of human disturbance (Rocchio 2007), I calculated these to evaluate the possible effect of dominant species on overall floristic integrity at each site. Furthermore, Adjusted FQI has demonstrated utility in indicating human disturbance (Miller and Wardrop 2006). While much of the research concerning FQA has explored the suitability of using various indices under differing ecological circumstances, the purpose of this paper was merely to use them as proxies for disturbance and floristic integrity at my research sites.

Final FQA scores were log-transformed to account for drastic numerical differences in rating scale across indices (e.g., Mean C vs. Adjusted FQI). The 12 populations were then placed into two groups, Oriental (O) and American (A), so that each group consisted of six ratings. Paired t-tests were performed on each of the eight indices between each O/A grouping. Sequential Bonferonni corrections were calculated for each pair from the derived P value to adjust for probability values in multiple statistical tests (Rice 1989). However, when multiple significant results are achieved with relatively large p-values, these are more likely to represent actual significance or biological importance than not, despite the problem of multiple comparisons (Moran 2003).

Results

Site Characteristics

Basal area and herb-layer richness were not consistently greater in *C. orbiculatus* plots compared to *C. scandens*; however, cover of *Celastrus* and % exotic richness tended to be greater (Table 3). Both cover of *Celastrus* and % exotic richness were greater at sites 1-4, in which *C. orbiculatus* was more abundant than *C. scandens* within pairs. Sites 5 and 6 had similar cover of *Celastrus* congeners, and % exotic richness was similar for site 6 within pairs. The high basal area value for CORB5 was influenced by the presence of a large individual tree of *Populus deltoides* within the plot. Site 6 (Niagara Gorge) had the lowest basal area results.

Land cover

The four dominant land-cover groupings across sites were cultivated land (crops; pasture); developed (low to medium intensity; open space), forest (deciduous; evergreen; mixed); and as a small percentage, wetland (palustrine forested and shrub) (Table 3; Table 5). Overall, sites tended to show similar land cover within pairs, with minor exceptions. For instance, because site-4 pairs were spaced apart slightly more than other site pairs, cultivated and forested land covers differed. Forest cover at sites 2 and 4 was greater for communities with *C. orbiculatus* compared to sites with the native *C. scandens*, in which cultivated land covers were greater. Some of the cultivated land cover for site 1 corresponds to natural grassland (Rush Oak Openings).

Principal Components Analyses revealed three distinct axes based upon 11 land-cover types in 2,000-meter buffers. PCA1 indicated a strong positive relationship with developed and urban land and weak negative relationships with cultivated land (pasture; cultivated crops). PCA2 indicated a strong association with forest cover (deciduous, evergreen, and mixed) and weak relationships with cultivated land and shrub wetlands. PCA3 correlated with palustrine forested wetland cover and only slightly with shrub wetlands. Overall, the three components pointed to a separation based on both developed or undeveloped land, and the nature of the less developed land. The spread of sites with *C. scandens* across a matrix of varying land-cover dominance was evident.

Community structure

Final ordination plots revealed that *Celastrus* populations were more closely grouped based upon site location than on whether the site supported either *C.*

orbiculatus or *C. scandens* (Fig. 3). ANOSIM tests revealed no significant differences in community composition between *Celastrus* site type (Global R = -0.044, p = 0.064). Sites 1, 4, and 5 clustered based upon their shared habitat characteristics (moderately disturbed edges in open habitat, old fields and successional forests). Sites 2 and 3 plotted in proximity to one another, as they were both along less disturbed trail edges in dry-mesic to wet-mesic conditions within a mixed forest landscape. Site 6 was distinct from all other sites, likely due to its unique habitat within the Niagara Gorge; however, there were no species that correlated strongly to this pair's location in ordination space.

Axis 1 was strongly positively correlated with *Prunus avium* and *Cornus racemosa* (Fig. 3) and had weaker associations ($R < 0.3$) with *Fraxinus americana*, *Fragaria virginiana*, *Melilotus albus*, and *Rosa multiflora*. Axis 1 was strongly negatively correlated with *Lindera benzoin* and *Cornus alternifolia* (Fig. 3) and had weaker associations ($R < 0.3$) with *Carpinus caroliniana*, *Mainthemum canadense*, *Carex blanda*, and *Prunus serotina*. Axis 2 had positive associations with *Solidago flexicaulis*, *Toxicodendron radicans*, and *Galium odoratum* and negative associations with *Fraxinus americana*, *Solidago canadensis*, and *Rosa multiflora*, although no species correlated strongly.

FQA

Celastrus orbiculatus sites consistently scored lower than *C. scandens* sites across all eight indices for both herb and shrub layers. Within the herb layer, four of the eight indices showed statistically significant differences between site pairs, with Cover-weighted Mean C and Cover-weighted FQI showing significant differences

after sequential Bonferonni correction (0.086 and 0.053, respectively, Table 2). Within the shrub layer, five of the eight indices showed statistically significant differences, and two indices (Mean C native and Cover-weighted FQI native) approached significance. Adjusted FQI and Adjusted cover-weighted FQI showed statistically significant differences between site pairs after sequential Bonferonni correction (0.004 and 0.006, respectively).

Scores varied between site pairs and within layers at each site depending on the index used. For instance, both Cover-weighted FQI and Cover-weighted FQI native scored lower within the shrub layer for both congeners; however, Adjusted cover-weighted FQI scored higher. Additionally, statistical differences between pairs weakened when accounting for native-only indices. For instance, Mean C, Cover-weighted Mean C, and Cover-weighted FQI were initially significant between site pairs in both herb and shrub layers. When accounting for only native species in these same three indices, weaker and statistically insignificant differences were found. Thus, the inclusion of exotics affected the overall score of each initial index. Adjusted cover-weighted FQI, which is a native-only index, was found to be significantly different between pairs in the shrub layer and thus indicated that *C. scandens* was found at sites where native shrubs were a more dominant component to the community. Conversely, Adjusted cover-weighted FQI revealed the more exotic shrub dominance at sites with *C. orbiculatus*.

Discussion

The native *Celastrus scandens* may grow in certain habitats that provide refugia from threats to its persistence; however, many smaller scattered populations

are likely vulnerable to changes in habitat quality and competition by *C. orbiculatus* and other invasive plant species. Four of the six populations of *C. scandens* were found at sites that lacked unique habitat characteristics and had moderately low quality. However, the unique habitat characteristics of the two other populations imply that *C. scandens* may persist on the landscape if management is targeted towards specific habitat conditions.

Both species are found at sites embedded in a matrix of urban, agricultural, and developed land-cover, indicating the potential for competition and displacement of the native *Celastrus* by its invasive congener. It was not surprising to find the native *Celastrus* in this context given that it can often be found in open fields, along shrub and forest edges, and adjacent to agricultural areas (Leicht-Young et al. 2007a; Ward, personal observation). The especially high cover of developed land surrounding the Niagara Gorge did offer an interesting perspective on the persistence of *C. scandens* in urbanized areas, given that it is thought to be in decline in at least one large metropolitan area (Steward et al. 2003). Although, it is thought that the decline of *C. scandens* may be highest in areas where *C. orbiculatus* has had extensive time to invade (Dreyer et al. 1987, Steward et al. 2003, Leicht 2005), and the history of *C. orbiculatus* invasion in the Buffalo/Niagara Falls area was not quantified in this study. Furthermore, habitat within the gorge, where *C. scandens* grows, may provide refugia-like conditions in an otherwise urbanized landscape.

Despite heavily urbanized conditions at one site, evidence showed that *C. scandens* tended to grow in areas with high cover of agricultural land. This implies that certain characteristics of the edge habitat found in agricultural areas provide

some inherent value for the growth of the native *Celastrus* (e.g., high sunlight, nutrient enhancement). Higher agricultural cover with less urban development could be one reason why *C. scandens* is still somewhat common in Western New York compared to downstate in the New York City metropolitan area, where the species has seen precipitous declines (Steward et al. 2003). One challenge of land-cover analyses is distinguishing differences at certain buffer-size scales (e.g. 500, 2000 meter level). Additionally, *Celastrus* pairs at some sites were often so close that substantial overlap at the 2,000 meter level may have meant land cover was relatively indistinguishable. After all, land-cover analyses come with an inherent level of inaccuracy, and have faced scrutiny from scale and resolution issues (Shao and Wu 2008). One surprise of my land-cover analyses was that the invasive *Celastrus* was not shown to consistently occur within a more-forested context than its native congener, given that it has been shown to tolerate more mesic, forested conditions (Leicht-Young et al. 2007a; Pavlovic and Leicht-Young 2011) and invade mature, intact forests (Pavlovic and Leicht-Young 2011). This may have also been due to buffer-overlap, although in most cases, basal area calculations did not indicate especially high tree cover for sites with *C. orbiculatus*.

Plant communities supporting each *Celastrus* congener represented substantial overlap in ordination structure, which is potentially problematic for the native *C. scandens*. Additionally, the differing community types in which *C. scandens* occurred further aligned with prior evidence of the vine species' broad ecological tolerances (Leicht 2005; Leicht-Young et al. 2007a; Zaya et al. 2015). Given evidence suggesting there is little preventing the invasion of *C. orbiculatus* into sites with *C.*

scandens, and that they already so often occur together (Ward, personal observation; Zaya et al. 2015), it seems possible that their niche overlap will further complicate the regional status of *C. scandens*, although possible habitat preferences between the congeners is discussed below. My study also provided evidence that *C. orbiculatus* tended to be more abundant than *C. scandens* within site pairs, further implicating its more dominant role in the areas it invades.

The abundance of *C. scandens* at site 6 illustrates the species' predilection for open, calcareous sites, as the Niagara Gorge is typified by calcareous shoreline outcrop (New York Natural Heritage Program 2017). This was the case at site 1 as well (Rush Oak Openings), which is influenced by calcareous, dolomitic substrates and supports numerous small patches of *C. scandens* along thicket edges with high sunlight availability. Furthermore, *C. scandens* readily occurs on limestone alvars in Northern New York (B. Gilman, personal communication; Ward, personal observation). These habitats contain strong calcareous influences, periodic natural disturbances and stressors (e.g., fire, drought), and open areas with abundant sunlight and low tree cover. This supports previous evidence that the native *Celastrus* may be abundant in more specialized habitat with higher pH, lower canopy cover, and differing soil structure (e.g., higher sand content) compared to its invasive congener (Pavlovic and Leicht-Young 2011). This suggests areas managed for drier, more-open habitat may provide suitable habitat for *C. scandens*. Owing to this, the presence of drought-stressed vines of *C. orbiculatus* growing in full sun on exposed rock at site 6 (Ward, personal observation) supports evidence reported by Leicht-Young et al. (2007a) that its success may be limited in open, xeric sites. Conversely, *C. scandens*

has shown higher mortality rates in wetter and more shaded conditions compared to *C. orbiculatus* (Leicht-Young et al. 2007a). While my study showed that *C. scandens* can persist in a wide variety of habitats, further research is needed to explore if certain environmental factors promote its abundance, given its prolific growth in open, calcareous habitats.

Conservation of species that require open or early successional habitat is complicated given that maintenance of this habitat requires some level of disturbance to maintain vegetation structure. Disturbances (e.g., mowing, grazing, fire), in some cases, may provide habitat-refugia for more shade intolerant species like *C. scandens*. After all, the disappearance of once-open landscapes highlights a regional conservation challenge for a number of rare plant species that have experienced alarming rates of extirpations in recent decades. Refugia-like conditions for shade-intolerant species have been previously demonstrated in utility rights-of-way in human-dominated or forested landscapes (Smallidge et al. 1996); however, these areas unfortunately also provide opportunities for exotic plants to proliferate (Rubino et al. 2002). The precipitous decline of *C. scandens* in parts of its range raise questions about the relationship of its regional status to habitat disturbances. After all, moderate to highly conservative species may be more sensitive to anthropogenic habitat-disturbance (Taft et al. 1997). The varying conservatism scores of *C. scandens* throughout its range (e.g., higher in Northeastern states vs. Midwestern states) appear justified, despite issues in scoring long-lived woody taxa (Matthews et al. 2015). *Celastrus scandens* may be more sensitive to extirpation in Northeastern states, given that the region has experienced a longer history of invasion by *C. orbiculatus*

compared to Midwestern states (Patterson 1973; Steward et al. 2003) and now offers less open habitat that *C. scandens* favors. FQA results suggest *C. orbiculatus* clearly takes advantage of areas with poor floristic quality (e.g., Adjusted FQI scores of 20-25), which correlate to increased human disturbance (Miller and Wardrop 2006). Additionally, by using an assortment of FQA indices in my study, I offer multiple floristic perspectives on the role that exotics and disturbance might play at sites with *C. orbiculatus*. Although the use of exotics in certain indices has been a criticism of FQA, these indices have demonstrated reliability (Cohen et al. 2004; Kutcher and Forrester 2018), and in other cases, excluding exotics has not been shown to cause any demonstrable impact on FQA performance (Bourdagh et al. 2006; Miller and Wardrop 2006).

While *C. scandens* did not necessarily grow in communities with especially high floristic quality, these areas had greater representation by native, woody species, and consistently showed higher floristic quality than sites supporting *C. orbiculatus*. This did not support my initial anticipations that both congeners would occur in areas with similar floristic quality, and suggests that there may be a threshold of exotic shrub-layer abundance for the native *C. scandens*, which would be consistent with matrix-species ratings in FQA theory (Taft et al. 1997). Thus, suitable habitat for *C. scandens* may not only include various soil and light characteristics, but may also require a more native shrub component. Interestingly, while much research has highlighted competition of *C. scandens* with *C. orbiculatus*, few studies have concentrated on possible interactions with exotic shrub species-of-concern (e.g. *Lonicera spp.*, *Rosa multiflora*); however, studies have demonstrated the competitive

effects of exotic shrubs with other native woody taxa (Gorchov and Trisel 2003; Fagan and Peart 2004; Frappier et al. 2004).

In the case of *C. scandens*, its regional status is complicated, given that in cases where it may be relegated to edge-habitat, encroachment of *C. orbiculatus* can contribute to increased competition, pollen-swamping, and subsequent decreased reproductive success (Leicht 2005, Leicht-Young et al. 2007b, Leicht-Young et al. 2011; Zaya et al. 2013; Zaya et al. 2015). Furthermore, bird-generated seed dispersal and commercial and residential development have been shown to favor the spread of *C. orbiculatus* (Mosher et al. 2009; Merow et al. 2011), and proximity to *C. orbiculatus* appears to impact the likelihood that *C. scandens* will hybridize (Zaya et al. 2013). This makes conservation of *C. scandens* complicated; however, declining species rarely afford simplistic management strategies.

Regional implications

Minimal steps can be taken to preserve remaining populations of *C. scandens* in New York, especially if trail-widening impacts where it occurs are minimized and stewards are taught how to distinguish between *Celastrus* congeners (Leicht-Young and Pavlovic 2007b). It is not uncommon to see populations of *C. scandens* significantly damaged by trail-widening (Ward, personal observation). Interestingly, at Mendon Ponds Park in Western New York, *C. scandens* was once listed as frequent within thickets and open woods (Goodwin 1942), where now only its invasive congener can be found amidst a depauperate flora (Ward, personal observation). Close by, at Rush Oak Openings, numerous populations of *C. scandens* can still be found growing and reproducing. While beyond the scope of this research, it is worth

mentioning that these two natural areas have undergone significantly different management regimes. Thus, in some cases, land-use history and management practices may be implicit in the decline of *C. scandens*. Those interested in increasing regional out-planting efforts could collect and propagate wild seed, although efforts should emphasize limiting over-collection in areas where *C. scandens* is endangered. Additionally, nurseries could promote the sale of *C. scandens*, although concerted efforts should be made to distribute material of non-hybrid origin (see Zaya et al. 2017).

Future research should highlight the possible contributing role of successional and land-conversion processes in the decline of *C. scandens*, in which site conditions are compared between historical and extant occurrences. Throughout this study, numerous sites with previously unreported populations of *C. scandens* were found by scouting in late fall to early winter when the brightly colored fruit and yellow foliage stood out from surrounding vegetation. Thus, botanists and ecologists interested in monitoring for *C. scandens* within their region could concentrate scouting efforts at a similar time, while also monitoring for encroachment of *C. orbiculatus* into areas where *C. scandens* is found.

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Tables

Table 1. Floristic Quality Analysis (FQA) indices used in analyses of six paired sites of plant communities with *Celastrus orbiculatus* and *Celastrus scandens* in Central and Western New York. Table based off Rocchio (2007) and Miller and Wardrop (2006). Asterisk denotes index not used in analyses. C_j = C-value of all species (native and non-native); C_i = C-value of only native species; N_{all} = total species richness (native and non-native); N_n = total native species richness; MC_{all} = Mean cover/all species; MC_n = Mean cover/native species; TC_{all} = total mean cover all species; TC_n = total mean cover native species.

Index	Description	Equation
Mean C	Average C-value of all plants	$\bar{C} = \sum C_j \div N_{all}$
Mean C native	Average C-value of only native plants	$\bar{C}_n = \sum C_i \div N_n$
Cover weighted Mean C	Sum of each species C-value multiplied by its cover values, then divided by the sum of cover values for all species	$\bar{C}_{cover} = (\sum C_j * MC_{all}) \div TC_{all}$
Cover weighted Mean C native	Sum of each native species C-value multiplied by its cover values, then divided by the sum of cover values for native species	$\bar{C}_{n cover} = (\sum C_n * MC_n) \div TC_n$
FQI*	Mean C of all plants multiplied by the square-root of all species richness	$I_{all} = \bar{C} * \sqrt{N_{all}}$
FQI native*	Mean C of native plants multiplied by the square-root of native species richness	$I_n = \bar{C}_n * \sqrt{N_n}$
Cover weighted FQI	Cover-weighted Mean C for all species multiplied by the square-root of all species richness	$FQI_{all cover} = \bar{C}_{cover} * \sqrt{N_{all}}$
Cover weighted FQI native	Cover-weighted Mean C for native plants multiplied by the square-root of native species richness	$FQI_{n cover} = \bar{C}_{n cover} * \sqrt{N_n}$
Adjusted FQI	Mean C of native plants divided by 10 multiplied by square-root of native plants divided by the square-root of number of all plants then multiplied by 100	$I' = \left(\frac{\bar{C}_n}{10} * \frac{\sqrt{N_n}}{\sqrt{N_{all}}} \right) * 100$
Adjusted cover-weighted FQI	Cover-weighted Mean C for native plants divided by 10 multiplied by square-root of native plants divided by the square-root of number of all plants then multiplied by 100	$I'_{cover} = \left(\frac{\bar{C}_{n cover}}{10} * \frac{\sqrt{N_n}}{\sqrt{N_{all}}} \right) * 100$

Table 2. Paired T tests of FQA index values comparing six paired sites of plant communities with *Celastrus orbiculatus* (O) and *Celastrus scandens* (A) in Central and Western New York. Indices were calculated for Herb and Shrub layers (see sampling methods). Original mean presented from metric. Paired t-tests were performed on log-transformed FQA data. Bolded numbers refer to tests with initial statistical significance. An asterisk denotes significance after sequential Bonferonni correction. Adjusted FQI and Adjusted cover-weighted FQI only use native species. Equations for metrics are listed in Table 1.

Metric	HERB				SHRUB		
	Site type	Mean \pm SD	t	P	Mean \pm SD	t	P
Mean C	O	2.01 \pm 0.568	-3.17	0.025	1.6 \pm 0.617	-3.7	0.014
	A	2.8 \pm 0.434			3.02 \pm 0.606		
Mean C native	O	3.35 \pm 0.409	-1.59	0.172	3.25 \pm 0.79	-2.4	0.063
	A	3.65 \pm 0.258			4.08 \pm 0.522		
Cover weighted Mean C	O	1.02 \pm 0.415	-5.23	0.003*	0.87 \pm 0.629	-3.4	0.02
	A	2.94 \pm 0.993			2.78 \pm 1.131		
Cover weighted Mean C native	O	3.09 \pm 0.542	-2.14	0.086	3.32 \pm 0.955	-1.5	0.196
	A	3.75 \pm 0.791			4.02 \pm 1.052		
Cover weighted FQI	O	4.42 \pm 1.63	-4.48	0.007*	2.55 \pm 2.142	-3.4	0.02
	A	13.91 \pm 5.781			9.15 \pm 4.228		
Cover weighted FQI native	O	10.42 \pm 2.497	-2.53	0.053	6.86 \pm 2.987	-2.5	0.053
	A	15.56 \pm 4.515			11.43 \pm 3.869		
Adjusted FQI	O	25.84 \pm 5.196	-2.77	0.039	23.55 \pm 7.442	-5	0.004*
	A	31.86 \pm 3.694			47.7 \pm 6.411		
Adjusted cover-weighted FQI	O	23.74 \pm 5.08	-1.58	0.174	24.02 \pm 7.833	-4.5	0.006*
	A	30.94 \pm 10.502			46.99 \pm 12.518		

Table 3. Cover values of *Celastrus* (with standard error) in the shrub layer (see methods) at 12 plots across six site pairs in Central and Western New York. Cover of *C. orbiculatus* corresponds to CORB sites; cover of *C. scandens* corresponds to CSC sites. Site 2 did not have *C. scandens* present within shrub layer. Refer to Table 4 for site location names. Herb richness, % exotic richness, % exotic shrub cover (average) and BA (basal area of tree layer in m²/hectare) presented per site. Forest refers to combined forest cover types (deciduous, evergreen, mixed). Developed refers to three levels of development intensity and urban/recreational land cover. Cultivated includes cropland and pasture cover at each site. Refer to Table 5 for full list of uncombined LandsAT cover percentages.

Site	<i>Celastrus</i> cover	Herb richness	% exotic richness	% exotic shrub cover	BA (m ² /hectare)	Forest	Developed/Urban	Cultivated
CORB1	21.78 ± 8.471	26	29.7%	12.89%	7.51	49.8%	0.8%	48.6%
CORB2	1.72 ± 1.034	13	31.6%	16.07%	1.52	48.9%	0.1%	42.2%
CORB3	15.56 ± 3.875	9	43.8%	19.13%	1.98	32.4%	2.5%	59.2%
CORB4	55 ± 10.851	6	60.0%	24.59%	5.74	84.2%	0.0%	15.8%
CORB5	1.78 ± 1.097	8	50.0%	9.51%	35.90	20.7%	14.8%	64.0%
CORB6	11.11 ± 5.198	12	29.4%	19.2%	0.21	22.2%	74.0%	3.8%
CSC1	1.56 ± 0.564	20	28.6%	13.65%	6.10	50.1%	0.8%	48.4%
CSC2	0 ± 0	30	14.3%	25%	14.84	43.9%	0.1%	47.1%
CSC3	1.67 ± 1.571	12	20.0%	8.17%	13.20	32.8%	2.4%	58.6%
CSC4	4.11 ± 1.478	20	35.5%	10.13%	6.52	58.0%	0.0%	41.7%
CSC5	4.44 ± 2.049	14	22.2%	11.5%	3.98	20.8%	10.7%	67.9%
CSC6	12 ± 1.819	11	21.4%	3%	0.34	23.1%	73.6%	3.3%

Table 4. Site codes and location names of six paired sites of plant communities with *Celastrus orbiculatus* and *Celastrus scandens* in Central and Western New York used in study. Community type based upon Edinger et al. (2014). Communities with an asterisk occur over calcareous substrates (limestone and dolomite). *C. scandens* grows along the edges of the openings at Rush Oak Openings, in shrub thickets.

Site #	Site codes	Site names	Ecological community type
1	COR1/CSC1	Rush Oak Openings	Oak opening*
2	COR2/CSC2	Iroquois National Wildlife Refuge	Beech-maple mesic forest
3	COR3/CSC3	Montezuma National Wildlife Refuge	Successional Forest
4	COR4/CSC4	Finger Lakes National Forest	Pastureland/Old field
5	COR5/CSC5	Wilson Tuscarora State Park	Successional Forest
6	COR6/CSC6	Whirlpool State Park (Niagara Gorge)	Calcareous shoreline outcrop*

Table 5. Percent cover of each LandSAT cover classification present at *Celastrus* sites. Open water and shoreline were removed.

Site	Cultivated crops	Pasture	Developed				Urban and Recreational	Deciduous Forest	Evergreen Forest	Mixed Forest	Palustrine	
			Developed (low)	Developed (medium)	(Open Space)	Forested Wetland					Shrub Wetland	
COR1	13.2%	35.5%	0.0%	0.4%	0.2%	0.2%	43.7%	0.3%	5.8%	0.6%	0.2%	
COR2	10.0%	32.2%	0.0%	0.1%	0.1%	0.0%	39.4%	0.0%	9.5%	7.6%	0.5%	
COR3	15.9%	43.4%	0.0%	1.6%	0.6%	0.3%	29.8%	0.0%	2.6%	3.5%	2.3%	
COR4	0.1%	15.7%	0.0%	0.0%	0.0%	0.0%	58.6%	2.6%	23.0%	0.0%	0.0%	
COR5	20.9%	43.2%	2.1%	0.6%	9.7%	2.4%	15.7%	0.2%	4.8%	0.3%	0.2%	
COR6	3.2%	0.6%	17.0%	14.2%	34.8%	7.9%	16.3%	0.2%	5.7%	0.0%	0.0%	
CSC1	12.8%	35.6%	0.0%	0.4%	0.2%	0.2%	44.0%	0.2%	5.8%	0.5%	0.1%	
CSC2	11.8%	35.3%	0.0%	0.0%	0.1%	0.0%	35.5%	0.1%	8.2%	8.4%	0.4%	
CSC3	16.0%	42.6%	0.0%	1.5%	0.6%	0.3%	30.1%	0.0%	2.7%	3.7%	2.5%	
CSC4	0.9%	40.7%	0.0%	0.0%	0.0%	0.0%	41.2%	1.8%	15.0%	0.3%	0.0%	
CSC5	20.9%	47.0%	1.1%	0.6%	7.2%	1.8%	15.7%	0.2%	5.0%	0.3%	0.2%	
CSC6	2.7%	0.6%	14.7%	13.7%	37.5%	7.7%	16.6%	0.3%	6.2%	0.0%	0.0%	

Figures

Figure 1. Sampling locations of paired *Celastrus* populations in Central and Western New York. Asterisks refer to two *C. scandens* sites initially sampled but not included within analyses due to lack of congener.

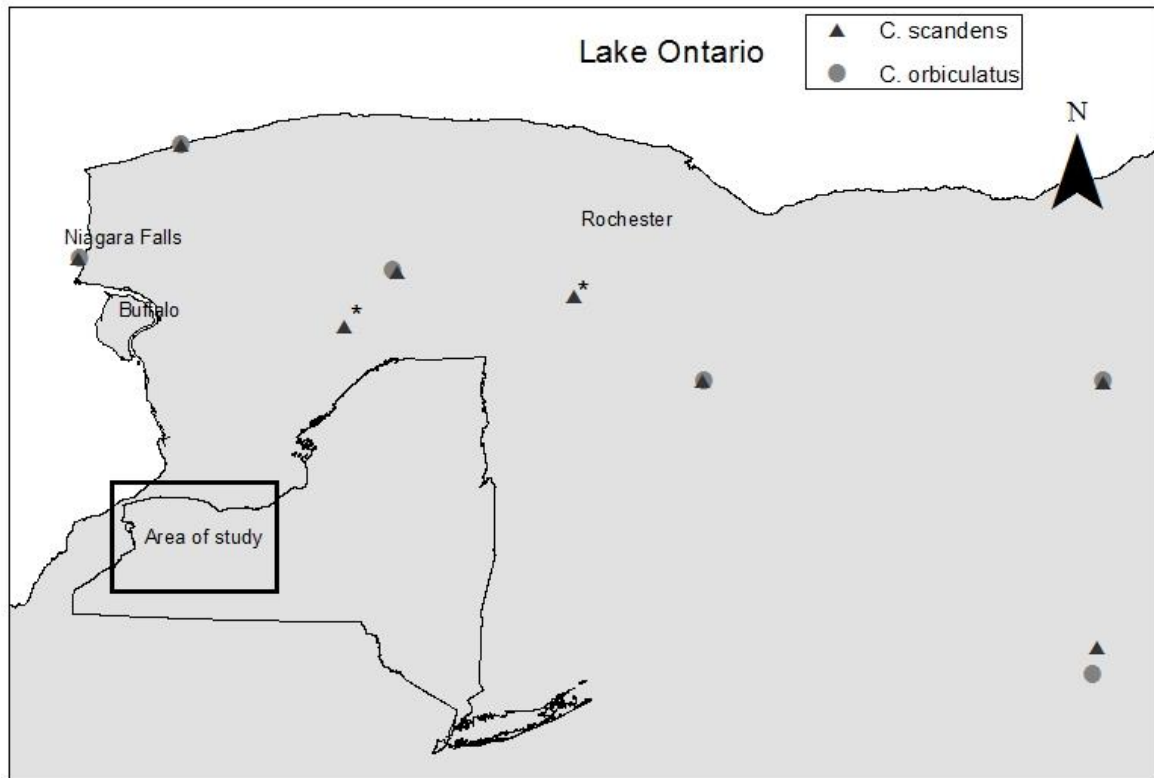


Figure 2. Sample plot design. Sample layers are indicated by shape and color.

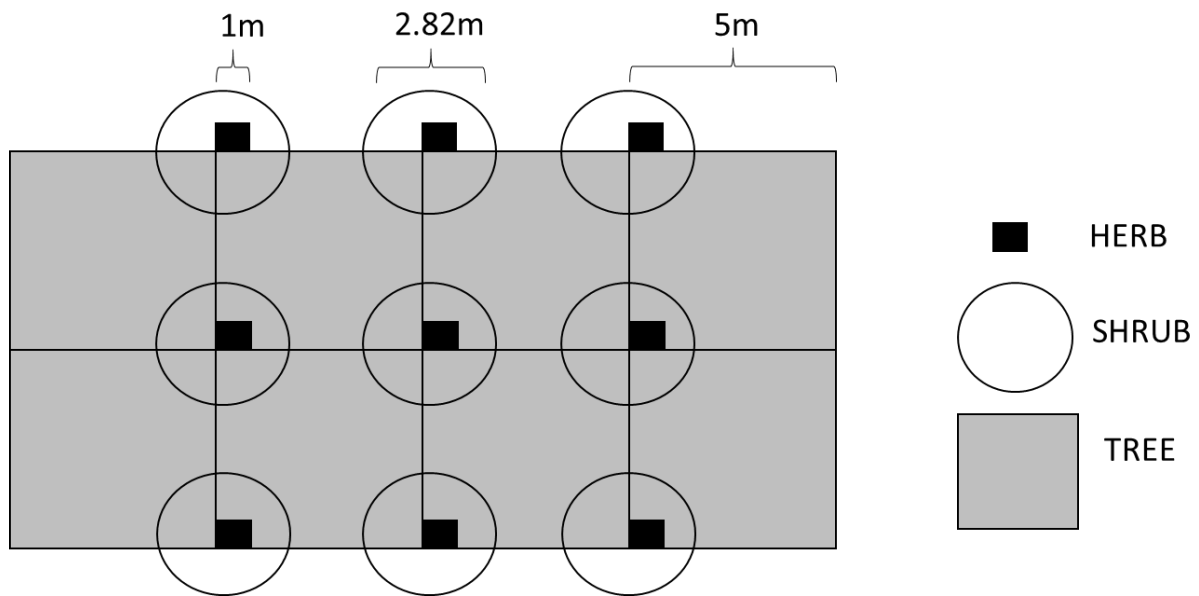


Figure 3. nMDS ordination with Sorenson (Bray-Curtis) distance of paired sites of *Celastrus* populations. Only axes 1 and 2 are presented, which account for 28.7% and 43.0% of the variance in floristic composition, respectively. Shaded circles refer to *C. orbiculatus* (CELORB) populations and open triangles refer to *C. scandens* (CELSCA) populations. Vectors represent land-cover PCA axes and shrub cover values from biplot with $r^2 > 0.3$. Refer to Table 4 for location names.

