

THE EFFECT OF *CELASTRUS ORBICULATUS*, ORIENTAL BITTERSWEET, ON THE
HERBACEOUS LAYER ALONG A WESTERN NORTH CAROLINA CREEK

By

Jenny Rebecca Browder

A Thesis
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of
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Committee:

_____ Director

_____ Dean of the Graduate School

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Jenny Rebecca Browder

Director: Dr. Greg Adkison
Instructor of Biology
Biology Department

Committee Members: Dr. Katherine Mathews, Biology
Dr. Ron Davis, Geosciences and Natural Resources

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ABSTRACT

THE EFFECT OF *CELASTRUS ORBICULATUS*, ORIENTAL BITTERSWEET, ON THE HERBACEOUS LAYER ALONG A WESTERN NORTH CAROLINA CREEK

Jenny Rebecca Browder, M.S.

Western Carolina University (May 2011)

Director: Dr. Greg Adkison

Nonnative, invasive plants such as *Celastrus orbiculatus* Thunb. (Oriental bittersweet) threaten the biodiversity of areas they invade. I examine bittersweet's effect on the diversity, richness, and total abundance of the herbaceous layer of Dingle Creek in western North Carolina and its effect on the abundance of several native species found along Dingle Creek: *Phlox stolonifera*, *Viola sororia*, *Arisaema triphyllum*, and *Thelypteris noveboracensis*. I selected an area in this floodplain where bittersweet appeared to be encroaching but was not dominant to establish a transect of paired quadrats. A pair was defined as one quadrat with bittersweet and one quadrat without bittersweet. Abundance of all species in the herbaceous layer was measured as percent cover and as number of rooted shoots in each quadrat. I found that bittersweet is negatively affecting the community. Specifically, quadrats containing bittersweet had lower richness, diversity, and total abundance compared to quadrats without the invasive plant. Nearly a third of the species sampled were absent from quadrats with bittersweet. Also, one of the four populations I examined, *T. noveboracensis*, was less abundant in bittersweet quadrats relative to quadrats without bittersweet. These results, along with the abundance of young individuals of bittersweet in the floodplain and the dominance of bittersweet in areas where it has apparently been long established, all suggest that this species's highly developed morphological and physiological adaptations may allow it to eventually dominate this site.

INTRODUCTION

Invasive plants are one of the biggest threats to native species and to natural ecosystems in the United States (Levine et al. 2003; Zavaleta 2000). It has been estimated that 5,000 nonnative plant species have naturalized in the U.S., and these species represent almost a third of the entire plant population here (Morin 1995). Consequently, almost half of the threatened and endangered species of the Endangered Species Act are thought to be in peril as a result of invasive species (Wilcove et al. 1998). Escalating the problem of invasives are the growing human population, land development, and trade (Zheng et al. 2004).

The purpose of this study is to examine one of these invasives, *Celastrus orbiculatus* Thunb. (Oriental bittersweet), and its effect on the diversity, richness, and total abundance of the herbaceous layer of the riparian area of Dingle Creek. The study also examines the effect of bittersweet on the abundance of several typical floodplain species found along Dingle Creek. In this thesis, I discuss the general ecology of invasive plants, the specific case of bittersweet as an invasive, the encroachment of this plant in western North Carolina, and my research of its effect on the herbaceous layer along Dingle Creek in the Biltmore Forest.

Significance of the Herbaceous Layer

My study focuses on the herbaceous layer of the Dingle Creek riparian community. The herbaceous (herb) layer, ground vegetation, ground cover, or herb understory, has as many names as it does definitions. For my study, these terms are used to denote all vascular species that are less than, or equal to, 1.5m in height, including resident and transient species. Transients are included because they have dynamic interactions with the herb layer and are capable of altering both the tree layer (a term I use to encompass the canopy, sub canopy and understory layers of a forest) and the herbaceous layers' compositions (Gilliam & Roberts 2003).

The relationship between the herb and tree layers is dynamic and complex. It may be competitive, as both attempt to acquire minerals, water, and sunlight; it may be commensally facilitative, as one may provide the proper amount of shading necessary for the other; or it may be antagonistic, as one uses its neighbor to gain height. Most ecologists are aware of the tree layer's ability to inhibit the herb layer through the alteration of soil conditions and the obstruction of light availability, but the flipside of this relationship is not as well known. Following a disturbance, the herb layer is where a great deal of competition takes place. A forest's herbaceous layer affects the shrub layer, the sub-canopy layer, and the canopy layer by competing with their seedlings. Many herbaceous species are able to deter the growth of seedlings through shading and the hoarding of soil nutrients. In this way, the herbaceous layer is capable of contributing to the particular type of forest that re-establishes. (Gilliam 2007).

The herb layer is a greater contributor to forest biodiversity than any other plant layer (Gilliam 2007). High richness of non-tree vascular plants has a strong correlation with high richness of animal species (Ricketts et al. 1999). Gilliam (2007) evaluated data that had been collected on species richness of both the herb layer and tree layer from 28 different studies and found that the herb layer accounted for more than 80% of the total plant species richness of forest plant diversity. The studies he examined encompassed many different forest types in North America, including mixed hardwood, mixed conifer, white spruce, oak barren, northern hardwood and longleaf pine.

A forest's herbaceous layer affects the ecosystem processes, including flow of energy and cycling of nutrients (Gilliam 2007) and contributes abundantly to the net primary productivity, total net ecosystem carbon gain, and litter fall (Gilliam & Roberts 2003). In addition, C, P, K, and Mg concentrations are significantly higher on average in herbaceous foliage than in tree foliage (Gilliam & Roberts 2003). Some spring ephemerals are able to uptake N when tree foliage has not yet emerged thus freeing up these nutrients for use by trees. This process, termed

the vernal dam hypothesis (Rothstein 2000), demonstrates yet another way that the herb and tree layers are linked. Obviously, any disruption of the herbaceous layer by an invasive plant like bittersweet might jeopardize the biodiversity and functions of the forest in habitats such as Dingle Creek.

Habitat Susceptibility

Some habitats appear to be more vulnerable to invasion than others. For example, all else being relatively equal, habitats that are richer in resources tend to be more susceptible to invasion (Maron & Marler 2007). Maron and Marler (2007) show experimentally that increased moisture increases invasibility of experimental plots. Given this apparent connection between resource availability and susceptibility to invasion, it is no surprise that disturbance tends to make habitats more susceptible to invasion. Disturbance can redistribute and free up resources that were previously being used (Silveri et al. 2001). Logging and development are two primary examples of this (Robertson et al. 1994; Silveri et al. 2001). Natural disturbances such as windstorms, wildfires, floods, and hurricanes may also provide a gateway through which invasives can enter and establish (Silveri et al. 2001).

Riparian areas are particularly susceptible to invasion (Lyon & Gross 2005). This can partially be attributed to floodwaters transporting propagules from a wide array of habitats along the watershed (Tickner et al. 2001; Brown & Peet 2003; Jansson et al. 2005). The establishment of incoming plant species may be facilitated as floodwaters make resources, such as space, light, and minerals available (Tickner et al. 2001; Brown and Peet 2003). The pool of colonizing species can be approximately 50% greater in riparian areas that experience hydrochory versus those that do not, even when accounting for the increased mortality rates due to the flooding (Jansson et al. 2005). A study that examined Southern Appalachian plant communities of riparian vs. upland habitats found richness, frequency, and cover of invasives to be much greater in riparian areas than upland areas (Brown and Peet 2003).

General Ecology of Invasive Plants

A small percentage of nonnative plants have traits that allow them to successfully invade new habitats (Gordon 1998). For example, invasive plants tend to grow rapidly and have high population growth rates (Mack et al. 2000; Hejda et al. 2009). Rapid individual growth means that these plants can quickly overtop and shade out native competitors. Combined with high rates of reproductive success and colonization, rapid individual growth also means that invasive species can quickly spread over a site and competitively exclude native species. In general, a nonnative species is likely to take over an area if it has a similar role as a native and is able to outcompete that native (Woods 1997; Gordon 1998), if its growth rate exceeds that of most natives (Gordon 1998) and if it more efficiently captures and uses available resources (Leicht-Young et al. 2007). A nonnative is also likely to successfully invade an area if it takes advantage of a niche that is not being occupied (Silveri et al. 2001) or possesses a unique trait that allows it to take advantage of the community's characteristics (Urgenson 2009).

Invasive plants also tend to have effective mechanisms of dispersal and colonization. Plants whose seeds are dispersed by wind, birds, mammals, and flying insects can potentially spread great distances with relative ease and thereby occur with high frequency in many locations. In contrast, plants whose seeds are dispersed by gravity or by insects that do not fly tend to disperse away from parent plants gradually. Within forest understories, species that cannot exceed heights of 1.5m (Gilliam & Roberts 2003) are often somewhat dispersal limited because they typically spread by invertebrates that do not fly. "Transient species," those species in the herb layer that may eventually emerge past the height of 1.5m and become part of another layer, tend to disperse more widely because they spread by wind, water, and vertebrates (Gilliam & Roberts 2003). Invasive plants affect community composition through both of these general paths. In other words, they often have dispersal mechanisms and growth rates that promote their spread, increasing the chance that they will colonize a particular site. Also, often they have traits

that allow them to compete successfully in a range of environmental conditions thereby altering environmental conditions to which native species might be specialized.

The most successful invaders are capable of altering resource availability, disturbance patterns (Gordon 1998), and ecosystem processes (Laungani & Knops 2009; Zavaleta 2000; Urgenson 2009; Reinhart et al. 2006), and they often do so in ways that favor their own needs. Several studies have examined the mechanisms by which invasives competitively exclude or reduce the growth of neighboring taxa (Levine et al. 2003). Of those mechanisms, the limitation of light appears to be the most common (Meekins & McCarthy 2000; Levine et al. 2003; Woods 1993; Wyckoff & Webb 1996) and is associated with decreasing species richness, diversity, and abundance (Antfingier et al. 1985). Monopolizing water is another mechanism used by invasives. African carrion flower (*Orbea variagata*) (Dunbar & Facelli 1999), common hottentot (*Carpobrotus edulis*) (D'Antonio & Mahall 1991), and cheatgrass (*Bromus tectorum*) (Melgoza et al. 1990) are all invasives that use this method. Additionally, invasives may influence disturbance regimes that support their regeneration (Reinhart et al. 2006; Mack 1996). Also, several methods of competition may be occurring simultaneously (Gentle & Duggin 1997; Busch & Smith 1995). Changes created by invasives impede the survival of plants lacking sufficient plasticity or genetic variation (Reinhart et al. 2006). Selection pressures created by the newly changed environment are then advantageous for the invasive (Vitousek 1990).

Commonly, plants in their native environments create negative plant-soil biota feedbacks that serve to regulate distribution of species and to increase diversity (Laungani & Knops 2009; Reinhart & Callaway 2006). When placed in foreign soils, these same plants, now considered nonnatives, create positive plant-soil biota feedbacks perpetuating their own population and inhibiting the growth of other species (Reinhart & Callaway 2006). These allelopathic traits allow them to literally hinder the growth of native plants by decreasing the growth, nutrient uptake, or germination of nearby plants (Pisula & Meiners 2010; van Ruijven et al. 2003; Gentle

& Duggin 1997). For example, in an effort to explain why many invasives are competitively inferior in their native habitats but competitively superior in habitats they successfully invade, Callaway and Ridenour (2004) describe invasive species that release chemicals into the rhizosphere that weakly affect neighboring plants from the invasive's native habitat but strongly inhibit neighbors from invaded habitats since they lack previous experience in dealing with these "novel weapons". Sri Lankan privet (*Ligustrum robustum*) is able to prevent the regeneration of surrounding plants (Lavergne et al. 1999). To my knowledge, only one study has examined bittersweet's allelopathic capacities and more research is needed. Pisula & Meiners (2010) tested the allelopathic potential of ten co-occurring invasive species on the germination of one target species and ranked them on their relative strength. Based on the low inhibitory performance by both of the invasive shrubs examined (bittersweet and Japanese honeysuckle (*Lonicera japonica*)), they concluded that allelopathy by these lianas was unlikely to occur in the field. Some invasives may enrich the soil with nutrients (Hejda et al. 2009), creating specific environments in which only they are able to thrive (Leicht-Young et al. 2007; Reinhart & Callaway 2006; Truscott 2008). Vivrette & Muller's (1977) study of invader crystalline iceplant (*Mesembryanthemum crystallinum*) shows how the build up of salt under the plant prohibits the growth of other plants for years to come. Soil found beneath invasives generally has higher pH values, nutrient values, and nitrification rates than soil found under adjacent native plants (Laungani & Knops 2009; Ehrenfeld et al. 2001; Leicht-Young et al. 2009).

Clearly, much needs to be learned about the systemic interplay among these invaders, their targeted community, and other taxa sharing the same environment (Levine et al. 2003; Hejda et al. 2006; van Ruijven et al. 2003; Tickner et al. 2001; Hill & Silander 2001; Gentle & Duggin 1997). Fortunately, several studies over the past decade have begun exploring these systemic relationships. One study examining cape ivy (*Delairea odorata*) an invasive evergreen vine, found that the invader diminished diversity and richness of all forbs, grasses, and sedges, but not

ferns. It was proposed that the ferns' shade tolerance deemed it unaffected by cape ivy's smothering methods (Alvarez et al. 2002). Another study evaluating the impacts of Amur honeysuckle (*Lonicera maackii*) an invasive shrub, found it lowered species richness and abundance of the community. However, on a population level, 86% of the taxa were negatively affected, 10% were positively affected, and 4% showed neither positive nor negative effects. The variances in taxa response were attributed to the taxa's diverse life histories (Collier et al. 2002). Stinson et al.'s (2007) research on the invasion of garlic mustard (*Alliaria petiolata*) in a forest understory community found different taxa to vary in susceptibility.

A few studies have concluded that certain plant species may actually help prevent invasion. Hejda et al. (2009) found from their study of 13 invasive plants that native species vary in their ability to resist invasion, with some battling the invader more strongly than others. A study conducted in the Netherlands by Van Ruijven et al. (2003) found that particular plant species, oxeye daisy (*Leucanthemum vulgare*) and brown knapweed (*Centaurea jacea*), are able to resist invasion by native invaders. They suggest that research be conducted on these "suppressive species" to determine exactly how they reduce invasibility and if their resistance capabilities are effective with all plant invaders.

The bottom line is that invasives are capable of occupying the space, resources, and processes once controlled by natives (Urgenson 2009; Gordon 1998; Mack et al. 2000; Dukes and Mooney 2004; Vitousek 1990). As a result, roles that were formerly held by many species of a community are shifted into one or a few dominants. This shift changes an ecosystem's structure and functions (Urgenson et al. 2009; Hooper and Vitousek 1997; Chapin et al. 2000; Gordon 1998; Leicht-Young et al. 2009; Vitousek 1990). When an ecosystem's processes are changed, its goods are affected (Urgenson et al. 2009). This leads one to question what vital fundamentals invasives are really costing us. Though no decidedly fixed monetary value has been placed on specific ecosystem goods and services, it should be a point of great concern for humans, because

most of these products, such as clean water, fertile soil, nutrient cycling, and flood and waste management, are very important to our species (Vitousek 1990; Zavaleta 2000).

My research will provide information about one specific invader, bittersweet, and its effect on a riparian community and on common native taxa of that community.

Description and Identification of Bittersweet

Oriental bittersweet is a member of the *Celastraceae* family and is native to China, Japan, and Korea where it can be found primarily in lowland slopes or thickets (Zheng et al. 2004; Dreyer 1994). It is a deciduous, climbing, woody vine, also known as a liana. Its stems range from 5 to 13 cm at dbh (Dreyer 1994) and can reach heights of at least 30 m and girths of 18 cm (Leicht-Young et al. 2007). Its branches contain lenticels and are pale grey or brown, darkening as they mature. In addition to being an ornamental in its native land, its fruits are used for medicine, its bark for fiber, and its seeds for oil (Zheng et al. 2004).

Oriental bittersweet looks like and is sometimes confused with its congener, American bittersweet (*Celastrus scandens*), a native of the United States and Canada. American bittersweet is listed as endangered by the North Carolina Plant Conservation Board and is becoming even more rare as it hybridizes with and is outcompeted by the invasive (Pooler et al. 2002; Steward et al. 2003). One study suggests that this hybridization is threatening American bittersweet's genetic integrity (Pooler et al. 2002). In a variety of environmental conditions, the invasive is much more successful in reproduction, efficient in obtaining and using resources, and tolerant of a wide gradient of resource states. Oriental bittersweet is more shade tolerant than the native. A study that varied light transmittance between 0.8 and 6.4% found bittersweet to have a 90% survival rate compared with American bittersweet's 68% and a biomass that is almost three times greater (Leicht-Young et al. 2007). In an average forest understory bittersweet can grow 15 times greater than American bittersweet (Dukes et al. 2009). In studies with varying soil conditions from very dry to saturated, both species show a decrease in survival, but the native's mortality

rate is approximately three times greater than the invasive's (Leicht-Young et al. 2007; Woods 1997). The invasive's pollen is 67% viable compared to the native's 48%. Its seeds are also brighter and redder than the native's (Dreyer 1994). Germination rates of the invasive are double that of the native (Dreyer et al. 1987). When plots with Oriental bittersweet present are compared to plots of the same soil, location, and habitat type without it present, the plots with the invader are much higher in soil pH, potassium, calcium, and nitrogen levels and litter decomposition rates (Leicht-Young et al. 2009). This increase follows the pattern recognized for the majority of invasives.

Oriental bittersweet's light green to yellow flowers appear from May to June (Zheng et al. 2004) and are functionally dioecious (Dreyer et al. 1987; Williams & Timmins 2003). Its fruits are yellow-orange globose capsules ranging from 8-10mm in diameter (Zheng et al. 2004) that are produced from functionally female plants (Dreyer et al. 1987). When ripe, the ovary wall breaks open exposing three to six bright red, plump seeds (Dreyer et al. 1987) that are 4-5mm in length and 2.5-3 mm in diameter (Zheng et al. 2004).

Oriental bittersweet has axillary cymes with three to seven green flowers and fruit, and a vegetative bud. It may produce flowers all along its stem, unlike American bittersweet, which has just one terminal panicle inflorescence. This is the most reliable characteristic to use for distinguishing the two species, but can only be applied to female flowers since male flowers do not follow these distinct patterns (Dreyer et al. 1987; Dreyer 1994). Its leaves are broadly obovate, orbicular, or oblong, 5-13 cm long and 3-9 cm wide. They have toothed margins, an apiculate apex, and a broadly cuneate or nearly obtuse base (Zheng et al. 2004). Its buds and leaves emerge in the Southern Appalachian region in early April, ahead of most summer plants. Its vines break dormancy and elongate their stems at least a month and a half earlier than the trees of the region (McNab & Loftis 2002). Its leaves may remain green for at least a month after the first frost (Tibbetts & Ewers 2000).

Oriental bittersweet has the capacity to grow 3 m every year (McNab & Loftis 2002; Patterson 1974; Silveri et al. 2001). Its early and rapid growth gives it a height advantage that makes the reestablishment of the herb and tree layers more difficult (McNab & Loftis 2002; Patterson 1974; Silveri et al. 2001). During autumn some understory seedlings experience freezing at their buds but compensate for their loss by allocating growth to the roots (McNab & Loftis 2002; Patterson 1975).

Three known fungal species that occur in bittersweet's native land help to keep it in check: *Microsphaera celastri*, *Amazonia celastri*, and *Uncinula sengokui* (the latter of which is host specific). Also, there are six known arthropod species that prey on bittersweet: *Plinachtus bicoloripes*, *Aphis clerodendri*, *Trioza celastrae*, *Yponomeuta sociatus*, *Hypothenemus eruditus*, and *Unaspis euonymi* (Zheng et al. 2004). The last two are native in North America. Generally, local pests and pathogens target invasives less than natives.

Dispersal, Range, and Preferred Habitat of Bittersweet

Dispersal of the species results from birds dining on and then defecating its abundant seeds during the winter and from pollination by hymenopterous insects, primarily bees (Williams & Timmins 2003). A strong correlation between bittersweet's presence and scarification of the litter layer (Silveri et al. 2002; McNab & Loftis 2002) could suggest that other animals may be dispersing the plant. Primary distribution of this plant has been by humans as a garden or dried ornamental (Chornesky & Randall 2003; McNab & Meeker 1987; Dreyer et al. 1987). The plant spreads vegetatively by root sprouting, the phenomenon of shoots emerging from a below ground root (Dreyer et al. 1987).

Being a liana is another great advantage of bittersweet. Like most lianas (Silveri et al. 2001), bittersweet is opportunistic for sites that have experienced disturbance, especially in the canopy and soil (McNab & Loftis 2002). Its vines have spine-like protuberances that burrow into the bark of its hosts (Silveri et al. 2001). As the vines climb or grow over their host, they girdle

its stems and trunk inhibiting nutrient and water flow, smother it preventing air and sun access as they leaf out, outcompete it for other vital resources, and add extra weight (Dreyer et al. 1987; Williams & Timmins 2003).

Oriental bittersweet grows in a wide range of habitats. A topic with a more succinct description would be habitats that bittersweet does not prefer. The liana is full sun tolerant and shade tolerant (Leicht-Young et al. 2007; Ellsworth et al. 2004). It has the capacity, through complex modifications of leaf morphology and physiology, to lower its growth rate in low light conditions, while increasing its survival (Woods 1997; Ellsworth et al. 2004). Therefore, it is able to survive in the forest understory, growing slowly, and then flourish if forests are thinned or harvested (Ellsworth et al. 2004). Its seeds can germinate in the dark and survive as seedlings in extremely low light intensity for prolonged periods of time (McNab & Loftis 2002; Patterson 1975; Patterson 1974; Silveri et al. 2001; Dreyer et al. 1987).

There are conflicting data about whether or not sunlight plays a role in the plant's abundance. Where light availability was thought to be a major factor contributing to bittersweet's positive response to disturbance, some studies have found there to be no correlation between light availability and the abundance of the plant (McNab & Loftis 2002). Yet others found abundance of irradiance to greatly increase its presence. A study by Leicht-Young et al. (2007) warns of bittersweet's tolerance of low light and its ability to thrive in areas such as forest edges or gaps where light is accessible, permitting this plant to dominate two widely diverse habitats. These contradictory findings demonstrate the high plasticity this invasive possesses.

Oriental bittersweet's capacity to surpass natives in a wide array of environmental conditions has been documented time and time again (Leicht-Young et al. 2007). Its adaptable nature gives it a competitive edge that makes it superior to most native vegetation, including its native congener, American bittersweet (McNab & Loftis 2002; Dreyer et al. 1987; Leicht-Young et al. 2007). It is prolific in mesic (Leicht-Young et al. 2007) to abundantly moist (McNab &

Loftis 2002) soil conditions including those associated with concave topography (McNab & Loftis 2002), which is a water collecting curvature on landscapes with relief.

Origin and Arrival of Bittersweet

Eastern Asia is a main source of plants used for horticulture, agriculture, and the prevention of soil erosion in the United States (Ding et al. 2006); so it is not surprising that many of our invasive plants—including bittersweet—come from that part of the world. Of the 58 invasive plants in Illinois for example, 24 species are native to eastern Asia or China (Ding et al. 2006). The United States has exported many invasive plants to China as well (specific numbers are unknown). Examples include annual ragweed (*Ambrosia artemisiifolia*) and great ragweed (*Ambrosia trifida*). Both were introduced in the '30s and have naturalized in at least ten provinces (Ding et al. 2006). Invasive smooth cordgrass (*Spartina alterniflora*), native to gulf coasts of the United States, was introduced to China to prevent erosion in the '60s (Ding et al. 2006). As a result of our similar environments, we have many common invasives from other continents such as water hyacinth (*Eichhornia crassipes*) and alligator weed (*Alternanthera philoxeroides*) (Ding et al. 2006).

The time of bittersweet's entry to North America is unclear. Though the consensus is that it was brought here for horticultural purposes (Albright et al. 2009; Miller 2003; Patterson 1973), the cited year of its arrival varies greatly. Albright et al. (2009) and Miller (2003) state that it was first introduced into the United States as an ornamental in 1736. Patterson (1973) reports that it came to North America in the 1860s and was first admired publicly by the Arnold Arboretum at Harvard University. Collections dating back to 1910 document its naturalization in northeastern North America (Steward et al. 2003). It has naturalized in at least 21 midwestern and eastern states, including North Carolina (Patterson 1974; Albright et al. 2009).

Bittersweet in Western North Carolina

Regionally, studies indicate that bittersweet is “concentrated in areas south of Asheville, North Carolina, where it has been documented as far back as 1895” (Albright et al. 2009; Merriam 2003; McNab & Meeker 1987). McNab and Loftis (2002) report its presence in 39% of the plots sampled at Bent Creek Experimental Forest, just south of Asheville. National Biological Information Infrastructure data (2009) indicate that bittersweet occurs in roughly a tenth of sampling sites (on public lands) in the southern Appalachians, with the greatest concentration in western North Carolina.

It is conventionally stated that bittersweet was first introduced to southern Asheville where it was cultivated on a homestead as an ornamental. It supposedly spread throughout the area when the construction of the Blue Ridge Parkway (beginning in the 1930s) ran through that homestead (McNab & Meeker 1987, Merriam 2003).

Interestingly, the Biltmore Estate may have helped in the early establishment of this invasive plant, both locally and nationally, through the work of its nursery. The concept of invasive plants was unheard of at the founding of the nursery in the late 1800s; and it was the trend of the times for nurseries of North America and Europe to grow and sell any plant that could possibly be obtained (Alexander 2007). Especially prestigious were the collections of fast growing ornamentals from foreign lands. Landscape architect Frederick Law Olmsted recommended to Vanderbilt that, “To obtain them (trees, shrubs, and vines) in quantity of a desirable planting size will take several years. Some can best be propagated on the ground; some obtained as small seedlings in Europe or from Japan and advanced on the Estate” (Alexander 2007).

In the first ten years of the nursery’s establishment, plants were cultivated almost solely for the Biltmore Estate (Alexander 2007). Then, from around 1898 until 1916, shipments of seeds and plants of an extensive range of plants (4,430 species total) were made to over 200

clients primarily located in the eastern half of the United States. Customers included but were not limited to individual estate owners, botanical gardens, arboretums, universities, experiment stations, landscape architects, hospitals, resorts, parks, schools, and nurseries.

The *Celastrus* vines, *C. orbiculatus* and *C. scandens*, were noted in the Biltmore Nursery catalog (Alexander 1912) to be “extremely hardy and very effective for covering walls, rocks or trellis work, or for climbing trees and lattice” (Alexander 1912). Oriental bittersweet was described as “splendid for decorating.” Today, the Biltmore Estate spends a lot of time and money controlling oriental bittersweet and other invasives first planted on the property by Olmsted (Parker Andes 2010 interview). Thus there is an ironic element of Biltmore’s botanical legacy whereby the Biltmore Nursery may have played a prominent role in the introduction and spread of the invasive Oriental bittersweet.

Encroachment of Bittersweet

Historical references of bittersweet note its ability to encroach and spread abundantly. Nash (1919) writes of the “vigorous high-climbing shrub” and states that it (*Celastrus articulatus*, a former name) was growing on several trees behind the Museum building of the New York Botanical Garden: “It was of accidental occurrence there, and perhaps originated from seed carried by birds from the large specimen in the viticetum but a short distance to the east” (Nash 1919). Records of harvesting a mountainous terrain in North Carolina in 1985 observe an unsubstantial presence of bittersweet (McNab & Loftis 2002) where a 2002 inventory of the same site notes bittersweet’s presence on 77 of the 198, 314m² plots (McNab & Loftis 2002). In a study conducted over four decades in a Central Hardwoods Forest region of southern New England, researchers were expecting the sites to follow typical succession patterns for post agricultural fields, forming an herbaceous community that eventually lead to the establishment of a forest community. They instead found that forty years of forest growth had resulted in a forest dominated by bittersweet. The 41 herbaceous species that were documented in 1954 had

dwindled to just seven in 1992 (Fike & Niering 1999). They report that bittersweet was able to dominate the habitat, change shrub stratum, facilitate northern fox grape's (*Vitis labrusca*), ability to gain height and cause destruction, arrest forest development, and decrease species diversity and richness.

To what degree bittersweet will spread is hard to predict, but it is forecasted to be part of our ecosystems for quite some time (Albright et al. 2009; McNab & Loftis 2002). Certain environmental events that may exacerbate bittersweet's spread are climate change and the dying off of the hemlocks. Albright et al. (2009) suggest that future deaths of hemlocks, *Tsuga spp.*, may provide large disturbed areas for opportunistic invaders such as bittersweet. If future climate conditions involve warmer temperatures and increased winter precipitation, the spread of bittersweet could also be greatly accelerated (Dukes 2009; McNab & Loftis 2002; Tibbetts & Ewers 2000).

The important point is that bittersweet represents a clear and present danger to our forest community. Albright et al. (2009) warn land managers to prepare for its expanding impact. It has high pollen and seed viability; its seeds are extremely attractive to birds and it can persist under a dense coverage until the opportunity for growth presents itself; it can girdle and diminish the size of established trees (Fike & Niering 1999) and collapse forest canopies. Thus it has traits that make it successful as an invader and it likely will strengthen over the long term as it entrenches itself in the regional landscape.

Objective

Several works have expressed the need for research examining the relationships between invasive and invaded communities (Stinson et al. 2007; Tickner et al. 2001; Alvarez & Cushman 2002; Levine et al. 2003; Hejda et al. 2009), and more specifically between invasive and particular native species (Tickner et al. 2001; Truscott et al. 2008; Urgenson et al. 2009; Alvarez & Cushman 2002; Collier et al. 2002; Stinson et al. 2007; Levine 2003).

I examined whether bittersweet affects species diversity, richness, and total abundance of the herbaceous community along Dingle Creek in Buncombe County, western North Carolina. I also tested whether the presence of bittersweet affects the abundance of several native species typical of floodplains in western North Carolina. These species include phlox (*Phlox stolonifera*), common blue violet (*Viola sororia*), New York fern (*Thelypteris noveboracensis*), and Jack-in-the-pulpit (*Arisaema triphyllum*).

The hypothesis that bittersweet reduces diversity, richness, and total abundance of the herbaceous community would be supported if plots with bittersweet are less diverse, less rich, and less productive than plots without bittersweet. Similarly, the hypothesis that bittersweet hinders the growth of typical floodplain species would be supported if these plants are less abundant in plots with bittersweet than in plots without bittersweet.

The Biltmore Estate and Forest

I was particularly interested in conducting research on the Biltmore Estate because of its rich history in addition to its special relevance for bittersweet. Lurking on the estate grounds are fabled spirits from the beginnings of professional forest management and nature conservation; and this forest is hallowed as the birthplace of American forestry. All of the historical information in this subsection is from Alexander's book (2007) and his paper entitled "Biltmore Estate's Forestry Legacy" (2003). The Blue Ridge Mountains in the Asheville area became popular in the late 1880s as a health resort for people with common illnesses of the time. The mountain air and moderate temperatures attracted people like George Vanderbilt who would come to vacation with his mother who had malaria (Alexander 2003; Alexander 2007).

Vanderbilt hired Frederick Law Olmsted, Sr., to be his landscape architect in 1888. Olmsted had designed the grounds of the United States Capitol in Washington, D.C. and Central Park in New York City and would later be considered America's "Father of Landscape Architecture." Olmsted reviewed the property and found it to be in an extremely depleted

condition. The settlers in that area had been poor and had to use every resource they had available. Land was overgrazed by livestock and cleared with the use of fire. Shallowly planted and unrotated crops were placed on steep terrain increasing erosion. The landscape, along with unsustainable agricultural practices, made long term farming not lucrative, so clear cutting became a way of survival. Biltmore forest became a primary timber supplier with several sawmills (Alexander 2003; Alexander 2007).

Olmsted still had hope for the land. He envisioned a park-like setting surrounding Vanderbilt's home, with gardens, a nursery and arboretum, a botanical library and herbarium, a working forest and game preserve. In a short working paper entitled "Project Of Operations For Improving The Forest of Biltmore," (1889) he proposed novel, methodical management for both growth and diversity for the forest, while also accounting for beauty (Alexander 2003; Alexander 2007).

Gifford Pinchot was hired in 1892 to be Olmsted's consulting forester. His three goals were "profitable production, a nearly constant annual yield, and an improvement in the condition of the forest" (Pinchot 1893; Alexander 2003; Alexander 2007). He wrote the "Biltmore Working Plan" (1892), the first report to introduce forest management as a noteworthy concept in America (Pinchot 1893; Alexander 2003). After launching his management plan, he left Biltmore in 1895 to become the original chief of the U.S. Forest Service.

Dr. Alwin Schenck expanded upon the continuing vision in 1895 with his own ideas of sustainable forestry, converting depleted lands into healthy forests. He established the Biltmore Forest School in 1898, which was the country's first such entity. It operated on the Biltmore grounds from 1898 to 1909 and produced the initial generation of the nation's professional foresters (Alexander 2003; Alexander 2007).

After George Vanderbilt died in 1909, 86,000 of the 125,000 acres were sold to the federal government becoming the nation's first national forest on the east coast, the Pisgah

National Forest. The Cradle of Forestry was established in 1968 by Congress to honor the beginning of forest conservation in the United States (Alexander 2003; Alexander 2007).

The Biltmore Estate is truly the birthplace of conservation in the U.S. and it provides an inspiring locale for my research.

METHODS

Study Area

Dingle Creek is located in the southeastern corner of the Biltmore Estate and flows westward into the French Broad River (Figure 1). This riparian habitat has a dense herbaceous layer that includes many species of trees, ferns, and wildflowers. It is home to several invasive species including oriental bittersweet (*Celastrus orbiculatus*), autumn olive (*Eleagnus umbellata*), Japanese honeysuckle (*Lonicera japonica*), Chinese privet (*Ligustrum sinense*), Nepalese browntop (*Microstegium vimineum*), and multiflora rose (*Rosa multiflora*).

Streams can affect the ecological functions of not only their specific locale, but of the collective riparian system (Edward 2003). I used Hruby's (2009) guidelines for assessing ecological functions of riparian areas to estimate Dingle Creek's ecological services. Under these guidelines, the presence of particular physical structures in riparian areas, referred to as indicators, signifies the occurrence of certain ecological processes. Dingle Creek possesses many of these indicators.

Dingle Creek is a primary stream channel. A portion (approximately 300m x 55m) of its floodplain falls within the Biltmore Estate. It consists primarily of woody vegetation, with patches of wetland habitat interspersed. This physical layout has been linked with an area's potential to offer the hydrological services of allocating surface water, dispersing and slowing floodwaters, and maintaining the water table, all of which lessen the effects of floods on areas downstream (Edward 2003).

Pockets of sediment erosion and deposition are present along Dingle Creek, assisting in the removal of toxins and in nutrient and sediment cycling. Current human-driven increases in nitrogen levels (Laungani & Knops 2009; Vitousek et al. 1997) make this service critical. Dingle

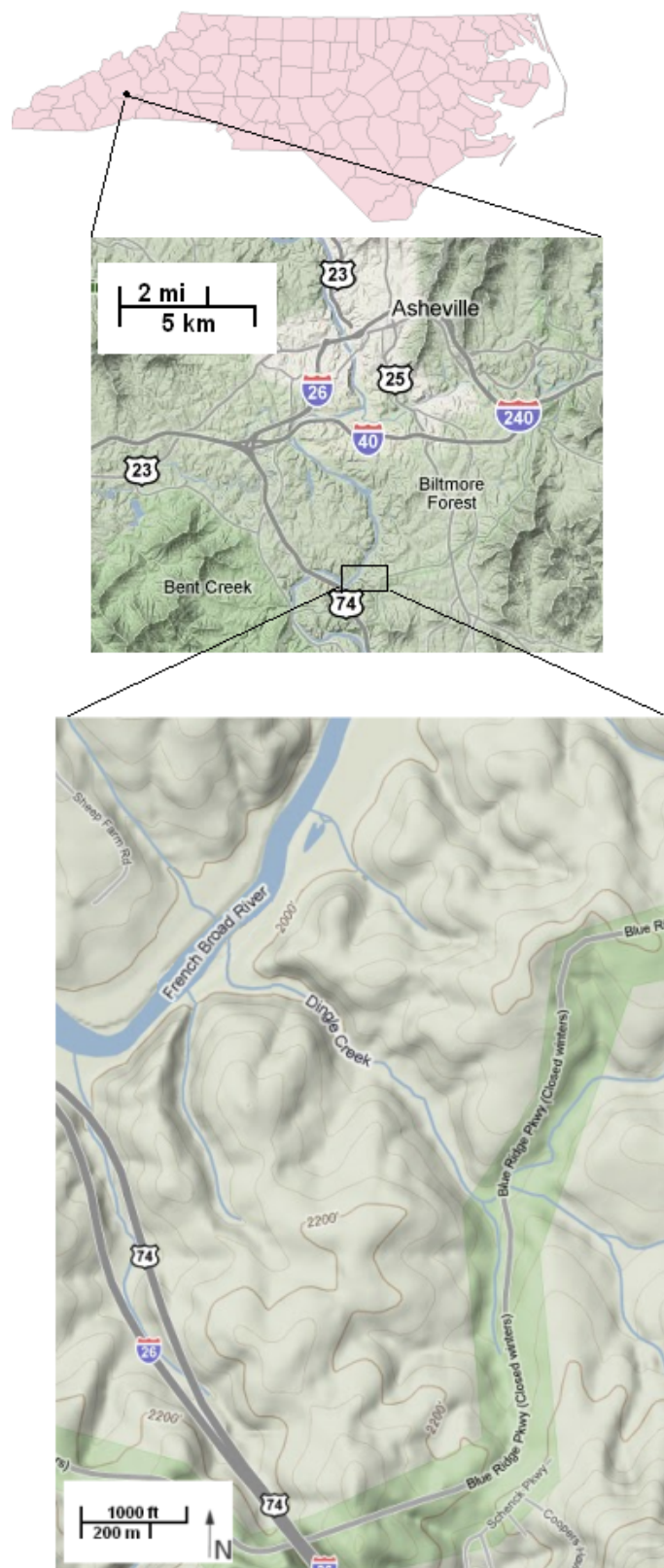


Figure 1. Location of study site.

Creek has many large trees such as black gum, white pine, and sycamore. Riparian zones that contain large trees have been found to support the habitats and food webs of terrestrial and aquatic organisms (Hruby 2009; Edward 2003). Dingle Creek is a vital and important place for both the Biltmore Estate and the Pisgah forest, not only for the environmental services it provides, but also for the beauty and serenity it offers to visitors.

Sampling Design

Oriental bittersweet has already encroached upon much of the landscape in the Dingle Creek area, with particularly strong presence in the areas within 3m from the creek and within 5m from the upland dirt road that is approximately 60 m from the creek. The vines in this creek side corridor and in the roadside corridor are rampant and large, indicating that this invasion has been ongoing for decades. However bittersweet is not dominant in the area between these corridors, where relatively young bittersweet vines and shoots and the occasional large vine share space with many other plants.

I selected an area in this floodplain where bittersweet appeared to be encroaching but was not dominant. A 5m wide transect starting 5m from Dingle Creek's northern bank was laid parallel to the creek for 290m (Figure 2). Twenty-five pairs of 1m x 1m quadrats were flagged within the 5m x 290m transect. The pairs were located within each 10m span of the 5m x 290m transect. One quadrat of the pair contained bittersweet and one did not contain bittersweet. A complete randomized design was not possible because each quadrat pair needed to meet specific criteria. First, every quadrat was located at least 1m from any tree greater than 13cm in diameter and at least ½ m from any shrub greater than 13cm in diameter. Second, to exclude plants not in the herbaceous layer, no quadrat included any plant greater than 1.5m in height or with a basal area greater than 13cm in diameter (other than bittersweet). Third, each quadrat pair within these 5m x 10m blocks was as similar to each other in microhabitat as possible.

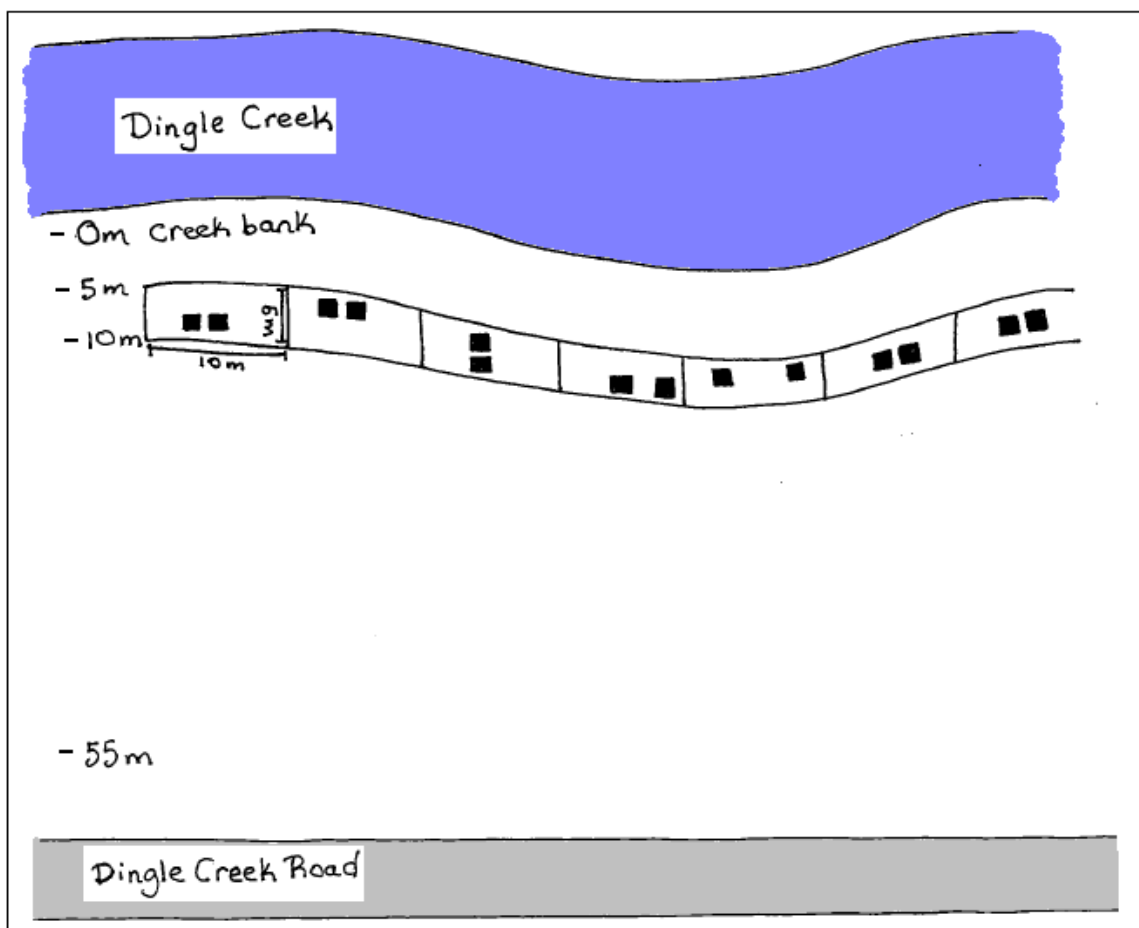


Figure 2. Layout of sampling transect in the Dingle Creek floodplain. This sketch shows seven of the 25 pairs of 1m x 1m quadrats flagged within each 5m x 10m plot. The 5m wide transect was placed 5m from the bank of Dingle Creek and ran parallel to the creek in the floodplain for 290m.

Starting upstream at the 5m marker, I walked away from (perpendicular to) the stream, to the 10m boundary, making a path back and forth within the 5m wide belt transect. Once bittersweet was encountered, a flag was placed to indicate the location for a “with” bittersweet quadrat. To locate the “without” bittersweet member of the paired quadrats, I looked first on either side (in the same meter distance from the creek), then above and below the previously flagged “with” bittersweet area, all while staying within the transect boundaries. If there was not

a pair in close proximity that met all the criteria, I followed the aforementioned methodical pathway, back and forth, heading downstream, until one was encountered. One meter by one meter patches without bittersweet were somewhat difficult to find in this transect. If a “without” bittersweet quadrat was not found, I started over at the beginning of that particular 10m section of transect and proceeded in the back and forth pathway until one was found.

I concentrated on the shoots of bittersweet that were less than 3.8 cm (1.5 in.) basal area because I was particularly interested in exploring if the young shoots have an impact on the herbaceous understory. These shoots were immersed in the herbaceous understory community, whereas the larger bittersweet vines appeared to be surrounded by an almost barren barrier from the understory growth, though they were in tight proximity to vines like fox grape (*Vitis labrusca*) and various trees.

Interestingly, bittersweet’s ability to provide the structural support for the native vine, *V. labrusca* has been reported (Fike & Niering 1999). These co-occurring vines (McNab & Meeker 1987; Tibbetts & Ewers 2000; Fike & Niering 1999) may form a facilitative relationship compounding their destructive effects. By setting plots 1 meter away from trees (which are generally where the large vines of *V. labrusca* and bittersweet are found), I avoided the larger bittersweet vines and therefore did not get the opportunity to confirm Fike and Niering’s results. However, I observed this frequent intertwining of bittersweet and *V. labrusca* and concur that when coupled, they appear to be much larger in size than when alone.

Data Collection and Analysis

Abundance was measured for every species in every quadrat as the number of rooted shoots and as percent cover. Bittersweet's size was measured as basal area (cm). Species richness was measured by counting the total number of species present in each quadrat. Species diversity (i.e., richness accounting for the relative abundance of each species) in each quadrat was

calculated using the Shannon-Wiener diversity index. These data were collected during the first two weeks in August 2009 to reduce the effect of temporal variability.

A paired-sample t-test was used to test whether quadrats with bittersweet differed from quadrats without bittersweet in terms of richness, diversity, total abundance, and in terms of population size of four focal species (*Phlox stolonifera*, *Arisaema triphyllum*, *Viola sororia*, and *Thelypteris noveboracensis*). An adverse effect of bittersweet's presence on the community would be indicated by quadrats with bittersweet having lower plant abundance, lower richness, lower diversity, or smaller population sizes. The effect of bittersweet's abundance on these same dependent variables was examined with Pearson's correlation. A negative correlation might be interpreted as a negative effect of bittersweet's abundance on the community.

RESULTS

Community-based data in this study indicate that bittersweet negatively affects the herbaceous understory in the floodplain of Dingle Creek. Population-based data, however, suggest minimal harm from bittersweet.

Plots containing bittersweet had diminished diversity, richness, and total abundance compared to plots without the invasive plant (Figure 3). There was 13% less diversity (H') in plots containing bittersweet compared with plots not containing bittersweet ($t = -2.41$, $df = 24$, $p = 0.02$). Species richness was diminished by 11% in plots that contained bittersweet ($t = 2.21$, $df = 24$, $p < 0.04$). Total abundance (summed across all species) was measured two ways. When taken as the percent cover of all species present, total abundance was 25% less in plots containing bittersweet ($t = 3.03$, $df = 24$, $p < 0.006$). When represented as the number of shoots of all the species present, total abundance was 19% less in plots with bittersweet ($t = 2.07$, $df = 24$, $p < 0.05$). Despite these effects of the *presence* of bittersweet, the *abundance* of bittersweet had no detectable effects (Table 1; $p > 0.05$ for all relevant correlation analyses).

Although it seems reasonable to suspect that these community level effects of bittersweet would translate into population level effects, only one of the four populations I examined, *Thelypteris noveboracensis*, was less abundant in bittersweet plots relative to plots without bittersweet (Figure 4). I found no effect of bittersweet on the other three: *Phlox stolonifera*, *Viola sororia*, and *Arisaema triphyllum*. Moreover, of the 81 plant species in the study, only 24 occurred exclusively in quadrats that did not contain bittersweet (i.e., the 'without' treatment), perhaps reflecting competitive exclusion; but seven species occurred exclusively in quadrats that contained bittersweet (i.e., the 'with' treatment), and 50 of the 81 species occurred in both treatment groups (Appendix A).

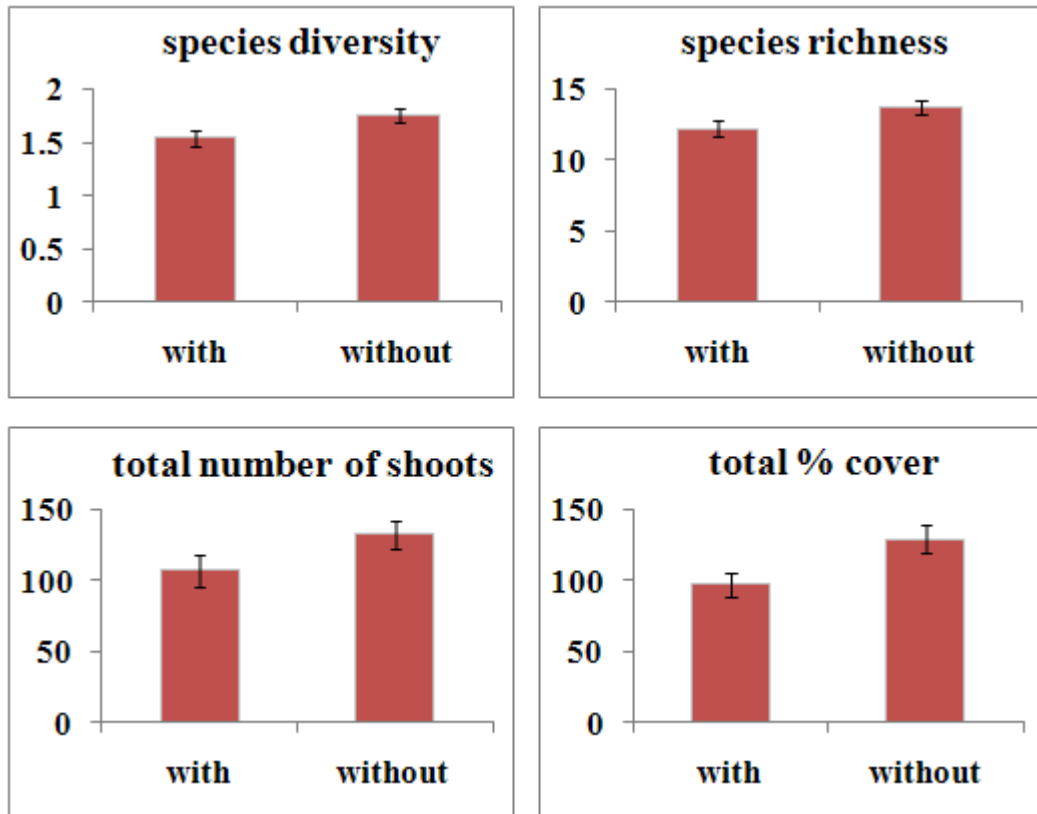


Figure 3. Mean (\pm se) species diversity (H'), species richness, and total plant abundance in quadrats with bittersweet versus quadrats without bittersweet.

Table 1. Abundance (cover & number of rooted shoots) and average size (basal area) of oriental bittersweet along with vegetation characteristics in each plot. The table is sorted by bittersweet's cover. The last column shows whether paired quadrats differed in species richness. For example, species richness was lower in the quadrat with bittersweet (w) than the quadrat without bittersweet (wo) in plot 16.

Plot	Oriental Bittersweet			Vegetation in Quadrats (Qt)				Species Richness Treatment Comparison
	Percent Cover	Number Rooted Shoots	Mean Basal Area (cm)	Species Richness	Species Diversity (H')	Number Rooted Shoots	Percent Cover	
15	1	1	0.13	18	2.23	179	105	w > wo
16	2	3	0.13	15	1.75	151	86.5	w < wo
19	3	5	0.23	13	1.36	190	96.5	w = wo
23	9	7	0.11	13	2.01	155	173	w < wo
5	10	1	1.27	14	1.59	85	57	w > wo
8	12	1	0.58	9	1.26	164	175	w < wo
9	20	3	3.89	11	1.13	34	52	w < wo
12	20	5	0.42	16	2.00	100	91.5	w > wo
18	20	3	0.36	15	1.44	50	73	w > wo
25	20	5	0.09	13	1.36	70	133.5	w < wo
3	25	8	0.58	15	1.63	84	59	w = wo
6	25	2	2.41	9	1.03	87	34.5	w < wo
2	30	5	0.23	9	1.55	74	67.5	w < wo
4	30	3	3.53	10	1.77	51	95	w < wo
17	30	6	0.22	10	1.58	60	40.5	w < wo
1	35	3	3.41	13	1.89	185	86.5	w = wo
7	35	2	0.52	13	2.03	50	162.5	w = wo
10	35	5	0.42	9	1.08	184	121.5	w < wo
11	40	2	0.69	18	2.17	92	130	w > wo
24	45	4	0.16	10	1.07	29	68	w < wo
21	50	7	0.23	9	1.01	40	102.5	w > wo
22	55	9	0.48	10	1.19	202	194	w < wo
14	65	9	0.29	11	1.72	131	53.5	w < wo
13	70	7	0.30	12	1.60	166	94	w < wo
20	70	8	0.30	11	1.19	67	77	w = wo

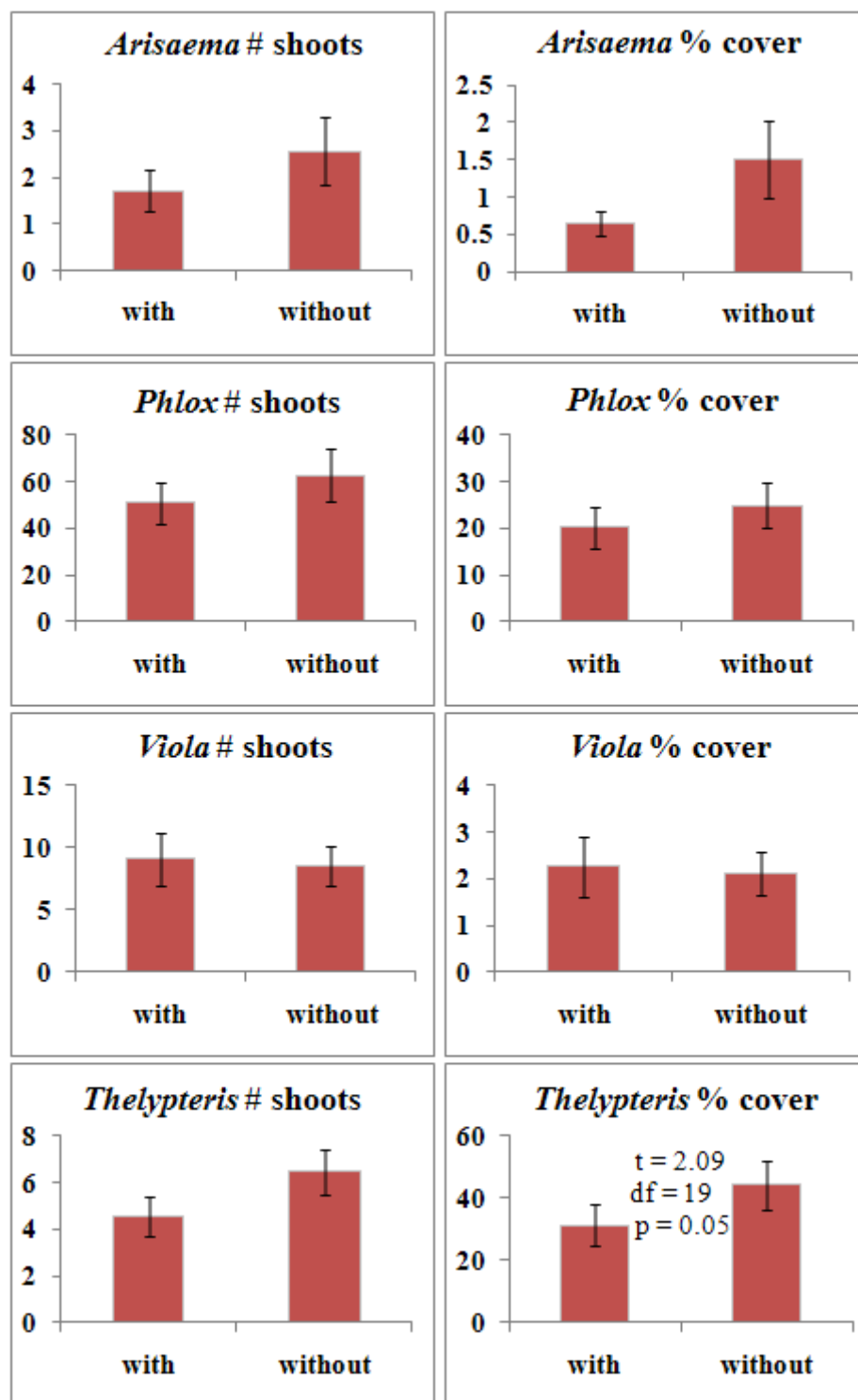


Figure 4. Mean (\pm se) abundance measured as number of rooted shoots and as percent cover for four native species in quadrats with bittersweet versus quadrats without bittersweet.

DISCUSSION

There is evidence from this study that bittersweet is having a negative effect on the herbaceous community of Dingle Creek in North Carolina. Although the encroachment of bittersweet in this area was previously known, my research documents its growing threat to this historic forest. This finding is important because bittersweet threatens the diversity, richness and total abundance of the understory. As noted in my introduction, the herb layer is a greater contributor to forest biodiversity than any other plant layer; therefore, this continuing influence could affect the ecosystem processes of this area.

Community Patterns

That declines in diversity, richness, and abundance are associated with bittersweet is not surprising given its prolific dispersal (Dreyer et al. 1987) and colonization, early emergence (McNab & Loftis 2002), and early height development. Plants with such characteristics have a considerable competitive advantage (Lavergne et al. 1999). Its morphological characteristics may be allowing bittersweet to arrive in my plots earlier than many other herb and tree species, taking their space, or if not, overtopping them (Ellsworth et al. 2004; McNab & Loftis 2002; Patterson 1974; Silveri et al. 2001; Lavergne et al. 1999). Once established, the plant is able to spread vegetatively in an array of environmental conditions, some of which have been altered by bittersweet and serve to benefit it. For example, in the fall, its long lasting leaves (Tibbetts & Ewers 2000) extend conditions of light inhibition until winter when its bright red fruits riddle the forest floor.

A logical question, of course, is why is bittersweet only exhibiting a modest effect on the understory of this area. Why doesn't this dreaded invader evidence greater dominance over the vegetation in the surveyed plots? I propose two explanations relating to temporal and spatial factors for the limited effects.

First is the temporal factor. I believe that bittersweet eventually will take over the forested floodplain where my study plots are located in a timely process of introduction, encroachment, and dominance. I cannot present experimental evidence of this claim, because my project is a single, snapshot observation. However, Fike and Niering (1999) depict a process of bittersweet's entry, spread, and eventual takeover of a community over four decades; and their depiction provides a model for understanding what may be happening at Dingle Creek. Fike and Niering find bittersweet joining the community and thriving with neighboring plants during its first two decades in the community; but in the beginning of the third decade there is a tipping point, with rapid bittersweet growth and sharp decline among neighboring species. In the last decade, there are few other species left, and bittersweet almost completely dominates. My project is analogous to Fike and Niering (1999) when bittersweet is first observed as an aggressive participant in the community.

Bittersweet and the other species can co-exist in the community at this stage of the vegetative game; but eventually the species will take over the floodplain and begin to engage more of its floodplain neighbors in competition. Over time, as species grow and spread, competitive forces will favor some species over others; and the outcome may be a greater decline in the diversity of the community.

Oriental bittersweet's highly developed morphology and physiology could be one of the major competitive advantages that will tip the scales in its favor. Bittersweet, like many lianas, possesses a shoot differentiation system whereby a division of labor among its shoots maximizes the amount of energy gained while minimizing the amount of energy lost. "Searcher shoots" search for support and are morphologically equipped with tendrils, adventitious roots, long internodes, and small leaves, where "ordinary shoots" account for the majority of the plant's light capture (LAR) and have short nodes and a large leaf area. The searcher shoots not only provide the majority of the plant's growth extension but are a minimal energy expenditure due to their

small leaves (Ichihashi et al. 2009). Though searcher shoots generally make up only a small percentage, approximately 1 to 6 % of the entire shoots, they can sprout both searcher and ordinary shoots in successive years (Ichihashi et al. 2009). This proportion of searcher shoots appeared to be consistent with the shoots I observed in my survey area.

As competition increases, shading and crowding will become more of a strain on the community and plants with certain morphologies and abilities will fare better than others. Oriental bittersweet is able to increase its height, biomass, and leaf mass when shaded (Leicht and Silander 2006). Collins and Wein (2000) found that certain plant species exhibit internode elongation, apical dominance, limitation of root growth and decreased branching in response to shading while others do not, and are therefore suppressed. Their study found that the vine-like annual, *Polygonum sagittatum*, was able to elongate more than the upright perennial, *Polygonum hydropiperoides*; this difference may be because vines are not limited by the same allometric restrictions placed on upright plants (Collins and Wein 2000). Harley & Bertness (1996) also compared the morphological responses of several plants to crowding and found that most vascular plants become taller and spindlier. Although this adaptive response increases fitness, it also causes them to have weaker stem structure and be more reliant on their neighbors for support. This tradeoff is not an issue for vines. So again, being a vine may put bittersweet at the top of the competitive hierarchy.

It is clear that bittersweet is very adept in its vertical growth, but its vegetative spread across a community is just as noteworthy. Regeneration in forest understories is dominated by vegetative propagation (Moora et al. 2009). Vegetative mobility may allow some species to colonize a more optimal space, increasing their survival along with community diversity (Moora et al. 2009). Given that bittersweet reproduces vegetatively and is very plastic, I would assume its rate of vegetative spread is quite rapid.

Adkison and Gleeson (2004) suggest, based on their study of forest understories, that

shade-tolerant plants have morphologies and physiologies that often permit them to avoid competitive exclusion resulting from shading. But this finding does not include shading by invasives like bittersweet that can completely cover other plants. Right now, bittersweet and numerous other plants co-exist in the studied plots. But, at some point in the future of this floodplain, the aggressive invader, with abilities to penetrate the overstory canopies and spread horizontally, may inhibit many taxa especially those that are not shade-tolerant, and possibly overtake this community.

My second explanation for the limited effect detected in this study is the fact that my site is located in the forest interior. It has been well established that invasive plants do well in areas directly contiguous to water flow, which facilitates abundant water, light, propagule dispersal, and soil disturbance (Tickner et al. 2001; Brown & Peet 2003; Jansson et al. 2005; McNab & Loftis 2002), and that such plants thrive in areas such as roads, where disturbance has opened corridors of light (Leicht-Young et al. 2007; Ellsworth et al. 2004; Manee 2008). Also, it seems logical that invasives face greater growth challenges in the forest interior, where such resources are less plentiful. Consequently, I found that bittersweet was rampant and large at the creek side and near the road running alongside Dingle Creek, but was much less established on the floodplain between those areas of dominance. Bittersweet is expanding its presence in the forested area where my plots are located; but this area will take longer to access and dominate than was the case with the creek side and roadside.

Although the magnitude of bittersweet's effect is not great in the floodplain at this time, bittersweet is extending its presence in this part of the landscape; and it is creating a continued, negative influence on the overall community of Dingle Creek. I propose that once bittersweet has conquered more ground, it likely will take over all of the interior forest just as it has on the creek bank and dirt road. When this stage is reached other plants in this community are likely to disappear. The long term prognosis may be negative for particular low growing life forms; and

those that grow more vertically, especially vines, may be the ones left in existence with bittersweet in this community.

Population Patterns

Given the reduced diversity, richness, and total abundance, I was surprised to find little evidence of bittersweet's effect on particular populations. Of the four frequently occurring native species, only one, *Thelypteris noveboracensis*, was found to be less abundant in the presence of bittersweet.

There are credible reasons for bittersweet's negative impact on *Thelypteris noveboracensis*. *Thelypteris noveboracensis* is very particular in its habitat requirements, and is negatively affected by a too shady environment (Hill 2006). Perhaps bittersweet has created too much cover and shade for *T. noveboracensis* along Dingle Creek.

Another explanation for *T. noveboracensis*'s decreased abundance in plots with bittersweet could be water availability. While *T. noveboracensis* can tolerate a range of soil moisture conditions, soil moisture is positively correlated with its distribution and abundance (Hill & Silander 2001). Other environmental factors that diminish the abundance of *T. noveboracensis* are changes in soil pH (preference is between 3.8 and 4.1 (Greller et al. 1990), and alterations in soil nutrient contents and conditions (Hill 2006). Perhaps bittersweet has altered water resources, soil pH and/or soil nutrients at Dingle Creek, thereby inhibiting the fern population.

Why are the other species able to coexist with bittersweet? It is unclear why *Arisaema triphyllum* and *Phlox stolonifera* both appear to be unaffected by bittersweet. There is nothing in their life histories that would offer explanations for their resistance. The lack of effect may simply reflect the fact that bittersweet is still young, small, and not yet capable of competitively excluding certain plants. This follows in line with my proposed ideas about temporal and spatial dynamics, which may also offer part of the explanation.

Light availability, as mentioned in the introduction, is a crucial environmental factor in the growth of most plants. Though I chose to only monitor plots containing young shoots of bittersweet, it was impossible to ignore the larger vines because they have become integrated into the overstory canopies. I did not survey Dingle Creek before the bittersweet invasion, but it seems logical that its infiltration into the canopy has created a more shaded environment than experienced by the understory before the invasion. I assumed that this development would inhibit other species. However, finding a general consensus from research on how variations of light affect the herbaceous understory is difficult, perhaps because different species respond differently (Tinya 2009). As already noted, Adkison and Gleeson (2004) found no loss of understory species as productivity increased. Even separate populations of the same species respond differently to light and other environmental variables. A study examining nine populations of *Phlox drummondii* hypothesized that genetic differences between the populations were the reason for their varied responses to changing moisture, light, nutrients, temperature, and competition (Schwaegerle & Bazzaz 1987). It would stand to reason that plant responses to independent variables are also somewhat based on past selective pressures and would be best studied on a site-by-site basis and may even vary within the same location.

Viola sororia is a semi-shade tolerant (Antlfinger et al. 1985; Curtis 1984) perennial that produces a small leaf rosette from an underground rhizome (Solbrig 1981). It has the potential to produce chasmogamous flowers in the spring and cleistogamous flowers in the middle and late summer (Solbrig 1981). Though it may not flower twice a year, or even once every year, its fruits produce a generous amount of seeds (Solbrig 1981; Niering & Olmsted 1979) that are able to remain dormant in the soil. Seedlings that emerge early are able to obtain a larger size and produce more seeds (Solbrig 1981), thus have a higher chance of reproduction (Kelly & Levin 1997). *Viola sororia* is one of the first understory herbs to appear in early spring, blooming as early as February, (Wofford 1989). This phenology gives the species an increased chance for

high fecundity. This trait may be the basis for *V. sororia*'s ability to coexist with bittersweet whose primary growth begins in April (McNab & Loftis 2002). It grows well into summer, so it is also adaptable to changing conditions in the canopy (Antlfinger et al. 1985), though too much shading, which will most likely occur in the future at this site, reduces its growth and reproduction (Antlfinger et al. 1985).

Management Implications

The findings of my study and those of others (Fike & Niering 1999; McNab & Loftis 2002) suggest important guidance for protecting biological diversity in the Dingle Creek area and elsewhere. My research should encourage monitoring of properties and pro-active protection against bittersweet and other invasives. If we ignore the warnings of numerous studies, then Dingle Creek and other areas with bittersweet may be in for quite a change in the future.

The literature is far from settled on what to do about invasive species in such communities. Even with the current options on invasive control and management, most, when enacted or not enacted, have undesirable consequences (Dukes et al. 2009; Chornesky & Randall 2003; Zavaleta et al. 2001). Where fire is recommended as a method of control for many invasives, including bittersweet (Chornesky & Randall 2003; McNab & Loftis 2002), it was shown to increase the abundance of invasive, *Ligustrum camara*, as it did nothing to suppress its allelopathic chemicals in the soil, perhaps giving the plant an advantage in post fire succession (Gentle & Duggin 1997). Removal of an invasive plant infestation often opens space for another invader to establish (Truscott et al. 2008; Lyon and Gross 2005; Alvarez & Cushman 2002) and greatly disrupts the habitat through soil upheaval and disturbance of the plant community (Truscott et al. 2008; D'Antonio et al. 1998; Zavaleta et al. 2001). Treatment with herbicides infiltrates chemicals into the surrounding community (McNab & Loftis 2002) and watershed. In addition to the uncertainties and downsides that accompany methods of removal, elimination of invasive species is time-consuming, labor intensive, and expensive (Urgenson et al. 2009).

With large-scale invasions, a comprehensive survey assessing the extent of the situation should first be performed. Other current threats to the community in question need to be examined and prioritized before beginning treatment, as the eradication of an invasive involves a concert of procedures and large amounts of money, resources, and time (Urgenson et al. 2009; Miller 2003). Long term planning strategies based on input from scientists, managers, and policy makers (Dukes et al. 2009; D'Antonio et al. 2004; Lyon & Gross 2004; Chornesky & Randall 2003) should be formulated.

Chornesky and Randall (2003) propose the alternative approach of allocating physical and financial resources towards the restoration of native communities instead of towards eradication. They suggest creating regulating processes such as fire and flooding and planting native species. Research investigating the idea of “suppressive species” (van Ruijven et al. 2003) to see if certain species do indeed have the ability to decrease invasion would be worth exploring.

According to the North Carolina Department of Agriculture and Consumer Services website, oriental bittersweet is classified as a “Class C” State Noxious Weed prohibiting its sale and distribution in North Carolina. But education is greatly needed to encourage compliance and prevent further spread (Pimentel et al. 2005; Lavergne et al. 1999), especially for those in horticultural fields and in the craft trade (Dreyer 1994). Nationwide, Pimentel et al. (2005) urge that focus be placed on preventing the entrance of invasives through airports and seaports.

There are some practical strategies for managing invasions of bittersweet. It is possible to slow the spread of small patches by hand removal of the plant (including the entire root and runners); this can be done successfully when the invasion is detected early (Chornesky & Randall 2003). For larger plants, clipping works (McNab & Loftis 2002), but the roots of clipped plants still produce ample shoots, so these suckers need to be killed as well; triclopyr is a popular herbicide used for treating these sprouts (Dreyer 1988; Dreyer 1994; Kaufman & Kaufman 2007). Physically removing large vines from trees can harm the tree, instead cutting and treating the

vines with triclopyr is recommended (Dreyer 1994). Again, precautions need to be taken to prevent root suckers from growing up the cut vine, so cutting needs to occur at ground level as well as at a height of 5 ft. (Kaufman & Kaufman 2007). In conjunction with these methods, any neighboring sources of seed must be eradicated (Ellsworth et al. 2004; Dreyer 1994). Persistence is mandatory when using these methods of control because the soil seed bank can allow regeneration to occur for several years (Dreyer 1994). Though not a possibility at Dingle Creek, weekly mowing greatly reduces the invasive (Dreyer 1994; Kaufman & Kaufman 2007), whereas irregular mowing (2-3 times per year) encourages root sprouting (Dreyer 1994). Detailed methods for eradication are given in Dreyer (1988), and the value of various eradication methods are discussed in Williams and Timmins (2003) book on bittersweet.

Future Research

Examining whether or not bittersweet is affecting diversity, richness, and total abundance, as I have done, is just one step in a series of many that are necessary to help understand the alterations it may make upon its environment. We should explore further the relationship between bittersweet and other species sharing the same territory (Stinson et al. 2007; Alvarez & Cushman 2002). If only the net patterns are examined, pertinent knowledge of the individual species in the community will be lost (Levine 2000). Conducting controlled experiments where species that were found exclusively in 'without' plots are planted in plots with and without bittersweet would determine whether these missing plants are being competitively excluded by the invasive or whether they were exclusively in 'without' plots due to chance or for other reasons. These experiments should control for variables such as shade and water availability, and measure soil chemistry to gain valuable insight into the nature of this exotic plant's existence and dominance. Also, comparison among numerous plots at different sites would provide greater confidence in the patterns observed here; and long-term research of the same site would provide greater insight into the stages of a bittersweet invasion.

Conclusions

This project documents the presence and negative effect of bittersweet on the understory community of Dingle Creek's riparian area in western North Carolina's Biltmore Estate. The research also suggests that bittersweet may be inhibiting some species in varying ways that are important for the future biological diversity of this historic forest community. Those populations currently not inhibited by bittersweet seem to have traits that permit their co-existence with the current stage of the invasion.

My study adds to the understanding of bittersweet mainly by documenting the negative effect of bittersweet on the diversity, richness and total abundance of this riparian community. This initial investigation should help scientists and managers further understand the continuing threat of this invasive plant. It is important that future projects investigate complex interactions among bittersweet, individual species, and the total community as we attempt to deal with such invasions.

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APPENDIX A

List of plant taxa from samples at Dingle Creek study site. Each taxon is identified as living in plots with bittersweet, in plots without bittersweet, or in both treatment groups.

Taxon	Type of Plot in which Taxon Occurred
<i>Acer</i> sp.	both
<i>Arisaema triphyllum</i>	both
<i>Aster</i> sp.	both
<i>Athyrium asplenioides</i>	both
<i>Berberis vulgaris</i>	both
<i>Botrychium biternatum</i>	both
<i>Buxus</i> sp.	both
<i>Carex</i> sp. 1	with
<i>Carex intumescens</i>	without
<i>Carex</i> sp. 2	both
<i>Carpinus</i> sp.	both
<i>Celastrus orbiculatus</i>	with
<i>Chasmanthium</i> sp.	both
<i>Chimaphila maculata</i>	without
<i>Dicanthelium</i> sp.	without
<i>Elaeagnus umbellata</i>	both
<i>Elephantopus carolinianus</i>	both
<i>Fagus</i> sp.	without
<i>Galium</i> sp.	both
<i>Geranium maculatum</i>	without
<i>Glechoma hederacea</i>	both
<i>Heracleum</i> sp.	without
<i>Houstonia caerulea</i>	without
<i>Ilex opaca</i>	both
<i>Ipomoea</i> sp.	without
<i>Lactuca</i> sp.	with
<i>Leersia virginica</i>	both
<i>Ligustrum</i> sp.	both
<i>Lindera benzoin</i>	both
<i>Lonicera japonica</i>	both
<i>Lycopus virginicus</i>	both
<i>Maianthemum racemosum</i>	both
<i>Medeola virginiana</i>	without
<i>Microstegium vimineum</i>	both
<i>Mitchella repens</i>	both
<i>Osmorhiza longistylis</i>	both
<i>Oxalis stricta</i>	both
<i>Parthenocissus quinquefolia</i>	both
<i>Phlox stolonifera</i>	both
<i>Phryma leptostachya</i>	without
<i>Pinus strobus</i>	both
Poaceae 1 (bamboo)	both
Poaceae 2	both

Taxon	Type of Plot in which Taxon Occurred
Poaceae 3	without
Poaceae 4	both
Poaceae 5	both
Poaceae 6	without
Poaceae 7	without
Poaceae 8	with
Polygonum sagittatum	without
Polygonum sp.	both
Polystichum acrostichoides	both
Potentilla simplex	both
Prenanthes sp.	both
Ranunculus hispidus	without
Ranunculus recurvatus	without
Ranunculus sp. 1	both
Ranunculus sp. 2	both
Rosa multiflora	both
Rubus sp.	without
Salvia sp.	with
Sassafras albidum	without
Senecio vulgaris	both
Smilax glauca	without
Smilax rotundifolia	both
Solidago nemoralis	without
Solidago sp.	both
Thalictrum sp.	both
Thaspium trifoliatum	both
Thelypteris noveboracensis	both
Toxicodendron radicans	with
Tradescantia sp.	both
Trifolium sp.	without
unknown 1	without
unknown 2	both
unknown 3	with
unknown 4	without
unknown 5	with
unknown 6	without
Verbesina alternifolia	both
Viola sororia	both
Vitis labrusca	both

APPENDIX B

Complete set of data taken at Dingle Creek. Quadrats (Qt) that contained more than one individual of *Celastrus orbiculatus* include multiple values of basal area.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
1	with	<i>Celastrus orbiculatus</i>	3	35	3.81, 3.76, 2.67
1	with	<i>Berberis vulgaris</i>	1	1	.
1	with	<i>Vitis labrusca</i>	1	0.5	.
1	with	<i>Polystichum acrostichoides</i>	1	9	.
1	with	<i>Lindera benzoin</i>	1	4	.
1	with	<i>Parthenocissus quinquefolia</i>	2	1	.
1	with	<i>Viola sororia</i>	4	1	.
1	with	<i>Leersia virginica</i>	5	1	.
1	with	<i>Carex sp. 2</i>	5	10	.
1	with	<i>Tradescantia sp.</i>	5	7	.
1	with	<i>Lonicera japonica</i>	6	1	.
1	with	<i>Arisaema triphyllum</i>	7	1	.
1	with	<i>Mitchella repens</i>	42	25	.
1	with	<i>Phlox stolonifera</i>	105	25	.
1	without	<i>Rubus sp.</i>	1	5	.
1	without	<i>Trifolium sp.</i>	1	0.5	.
1	without	<i>Polystichum acrostichoides</i>	1	4	.
1	without	<i>Parthenocissus quinquefolia</i>	1	1	.
1	without	<i>Elephantopus carolinianus</i>	1	1	.
1	without	<i>Polygonum sp.</i>	2	1	.
1	without	<i>Lycopus virginicus</i>	2	1	.
1	without	<i>Lindera benzoin</i>	2	5	.
1	without	<i>Lonicera japonica</i>	3	5	.
1	without	<i>Tradescantia sp.</i>	3	10	.
1	without	<i>Arisaema triphyllum</i>	6	1	.
1	without	<i>Viola sororia</i>	13	1	.
1	without	<i>Phlox stolonifera</i>	135	40	.
1	without	<i>Carex sp. 2</i>	.	20	.
2	with	<i>Celastrus orbiculatus</i>	5	30	0.03, 0.23, 0.30, 0.36, 0.25
2	with	<i>Botrychium biternatum</i>	1	1	.
2	with	<i>Pinus strobus</i>	1	1	.
2	with	<i>Arisaema triphyllum</i>	1	0.5	.
2	with	<i>Lycopus virginicus</i>	3	1	.
2	with	<i>Solidago sp.</i>	3	9	.
2	with	<i>Poaceae 2</i>	9	25	.
2	with	<i>Ranunculus sp. 1</i>	10	1	.
2	with	<i>Lonicera japonica</i>	16	9	.
2	with	<i>Chasmanthium sp.</i>	30	20	.
2	without	<i>Carpinus caroliniana</i>	1	4	.
2	without	<i>Pinus strobus</i>	1	3	.
2	without	<i>Polystichum acrostichoides</i>	1	1	.
2	without	<i>Poaceae 3</i>	1	1	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
2	without	<i>Carex sp. 2</i>	1	5	.
2	without	<i>Acer sp.</i>	1	0.5	.
2	without	<i>Lindera benzoin</i>	2	9	.
2	without	<i>Ligustrum sp.</i>	3	9	.
2	without	<i>Arisaema triphyllum</i>	3	1	.
2	without	<i>Fagus sp.</i>	3	1	.
2	without	<i>Ranunculus sp. 1</i>	5	1	.
2	without	<i>Parthenocissus quinquefolia</i>	5	1	.
2	without	<i>Poaceae 4</i>	8	1	.
2	without	<i>Lonicera japonica</i>	11	8	.
2	without	<i>Chasmanthium sp.</i>	12	4	.
2	without	<i>Lycopus virginicus</i>	13	4	.
2	without	<i>Phlox stolonifera</i>	41	7	.
3	with	<i>Celastrus orbiculatus</i>	8	25	0.71, 0.58, 0.64, 0.53, 0.43, 0.51, 0.69, 0.58
3	with	<i>Elephantopus carolinianus</i>	1	1	.
3	with	<i>Oxalis stricta</i>	1	0.5	.
3	with	<i>Smilax rotundifolia</i>	1	0.5	.
3	with	<i>Arisaema triphyllum</i>	1	0.5	.
3	with	<i>Maianthemum racemosum</i>	1	1	.
3	with	<i>Salvia sp.</i>	1	1	.
3	with	<i>Smilax rotundifolia</i>	2	1	.
3	with	<i>Polygonum sp.</i>	3	1	.
3	with	<i>Lycopus virginicus</i>	4	0.5	.
3	with	<i>Athyrium asplenioides</i>	6	20	.
3	with	<i>Phlox stolonifera</i>	8	1	.
3	with	<i>Lonicera japonica</i>	9	1	.
3	with	<i>Poaceae 4</i>	11	4	.
3	with	<i>Mitchella repens</i>	12	1	.
3	with	<i>Ranunculus sp. 2</i>	23	25	.
3	without	<i>Maianthemum racemosum</i>	1	1	.
3	without	<i>Pinus strobus</i>	1	1	.
3	without	<i>Acer sp.</i>	1	0.5	.
3	without	<i>Lindera benzoin</i>	2	1	.
3	without	<i>Carpinus caroliniana</i>	2	0.5	.
3	without	<i>Smilax rotundifolia</i>	2	0.5	.
3	without	<i>Athyrium asplenioides</i>	3	25	.
3	without	<i>Phlox stolonifera</i>	3	1	.
3	without	<i>Poaceae 4</i>	3	1	.
3	without	<i>Thelypteris noveboracensis</i>	6	20	.
3	without	<i>Carex sp. 2</i>	7	9	.
3	without	<i>Poaceae 5</i>	7	9	.
3	without	<i>Viola sororia</i>	9	0.5	.
3	without	<i>Ranunculus sp. 1</i>	26	1	.
3	without	<i>Mitchella repens</i>	63	20	.
4	with	<i>Celastrus orbiculatus</i>	3	30	1.83, 2.29, 6.48
4	with	<i>Polystichum acrostichoides</i>	1	25	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
4	with	<i>Pinus strobus</i>	1	1	.
4	with	<i>Lonicera japonica</i>	1	1	.
4	with	<i>Carex sp. 2</i>	1	4	.
4	with	<i>Tradescantia sp.</i>	1	5	.
4	with	<i>Vitis labrusca</i>	1	20	.
4	with	<i>Poaceae 4</i>	2	1	.
4	with	<i>Arisaema triphyllum</i>	2	1	.
4	with	<i>Lindera benzoin</i>	8	25	.
4	with	<i>Phlox stolonifera</i>	33	12	.
4	without	<i>Elephantopus carolinianus</i>	1	5	.
4	without	<i>Carpinus caroliniana</i>	1	1	.
4	without	<i>Prenanthes sp.</i>	1	1	.
4	without	<i>Polystichum acrostichoides</i>	1	4	.
4	without	<i>Medeola virginiana</i>	2	3	.
4	without	<i>Poaceae 4</i>	2	1	.
4	without	<i>Heracleum sp.</i>	2	2	.
4	without	<i>Poaceae 4</i>	2	1	.
4	without	<i>Viola sororia</i>	3	1	.
4	without	<i>Phlox stolonifera</i>	3	1	.
4	without	<i>Lonicera japonica</i>	4	4	.
4	without	<i>Lycopus virginicus</i>	5	1	.
4	without	<i>Lindera benzoin</i>	5	1	.
4	without	<i>Arisaema triphyllum</i>	13	3	.
4	without	<i>Poaceae 6</i>	15	5	.
4	without	<i>Ranunculus sp. 2</i>	25	1	.
4	without	<i>Mitchella repens</i>	72	25	.
5	with	<i>Celastrus orbiculatus</i>	1	10	1.27
5	with	<i>Osmorhiza longistylis</i>	1	0.5	.
5	with	<i>Verbesina alternifolia</i>	1	0.5	.
5	with	<i>Polystichum acrostichoides</i>	1	20	.
5	with	<i>Arisaema triphyllum</i>	1	1	.
5	with	<i>Oxalis stricta</i>	2	0.5	.
5	with	<i>Lonicera japonica</i>	2	0.5	.
5	with	<i>Polygonum sp.</i>	3	0.5	.
5	with	<i>Microstegium vimineum</i>	3	0.5	.
5	with	<i>Ranunculus sp. 1</i>	4	0.5	.
5	with	<i>Thelypteris noveboracensis</i>	6	20	.
5	with	<i>Carex sp. 1</i>	6	1	.
5	with	<i>Chasmanthium sp.</i>	9	0.5	.
5	with	<i>Viola sororia</i>	12	1	.
5	with	<i>Phlox stolonifera</i>	34	10	.
5	without	<i>Osmorhiza longistylis</i>	1	1	.
5	without	<i>Houstonia caerulea</i>	1	0.5	.
5	without	<i>Thelypteris noveboracensis</i>	2	10	.
5	without	<i>Polystichum acrostichoides</i>	2	7	.
5	without	<i>Ranunculus hispidus</i>	2	0.5	.
5	without	<i>Oxalis stricta</i>	3	0.5	.
5	without	<i>Polygonum sp.</i>	3	1	.
5	without	<i>Arisaema triphyllum</i>	6	3	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
5	without	<i>Viola sororia</i>	11	1	.
5	without	<i>Microstegium vimineum</i>	27	25	.
5	without	<i>Phlox stolonifera</i>	130	40	.
6	with	<i>Celastrus orbiculatus</i>	2	25	4.29, 0.53
6	with	<i>Arisaema triphyllum</i>	1	0.5	.
6	with	<i>Senecio vulgaris</i>	1	1	.
6	with	<i>Pinus strobus</i>	1	0.5	.
6	with	<i>Viola sororia</i>	2	0.5	.
6	with	<i>Carex sp. 2</i>	2	1	.
6	with	<i>Thaspium trifoliatum</i>	2	0.5	.
6	with	<i>Microstegium vimineum</i>	3	0.5	.
6	with	<i>Carpinus caroliniana</i>	5	5	.
6	with	<i>Phlox stolonifera</i>	70	25	.
6	without	<i>Botrychium biternatum</i>	1	0.5	.
6	without	<i>Polystichum acrostichoides</i>	1	16	.
6	without	<i>Parthenocissus quinquefolia</i>	1	5	.
6	without	<i>Arisaema triphyllum</i>	1	0.5	.
6	without	<i>Chimaphila maculata</i>	1	0.5	.
6	without	<i>Pinus strobus</i>	1	1	.
6	without	<i>Rubus sp.</i>	2	12	.
6	without	<i>Thelypteris noveboracensis</i>	3	35	.
6	without	<i>Smilax rotundifolia</i>	3	12	.
6	without	<i>Carex sp. 2</i>	6	15	.
6	without	<i>Lonicera japonica</i>	6	4	.
6	without	<i>Carpinus caroliniana</i>	6	5	.
6	without	<i>Microstegium vimineum</i>	9	1	.
7	with	<i>Celastrus orbiculatus</i>	2	35	0.48, 0.56
7	with	<i>Ilex opaca</i>	1	40	.
7	with	<i>Parthenocissus quinquefolia</i>	1	5	.
7	with	<i>Smilax rotundifolia</i>	1	0.5	.
7	with	<i>Polystichum acrostichoides</i>	1	10	.
7	with	<i>Lonicera japonica</i>	1	1	.
7	with	unknown 5	1	1	.
7	with	<i>Lindera benzoin</i>	2	25	.
7	with	<i>Thaspium trifoliatum</i>	2	5	.
7	with	<i>Carpinus caroliniana</i>	3	9	.
7	with	<i>Thelypteris noveboracensis</i>	3	40	.
7	with	<i>Carex sp. 2</i>	6	15	.
7	with	<i>Mitchella repens</i>	8	1	.
7	with	<i>Phlox stolonifera</i>	20	10	.
7	without	<i>Lonicera japonica</i>	1	0.5	.
7	without	<i>Galium sp.</i>	1	0.5	.
7	without	<i>Oxalis stricta</i>	1	0.5	.
7	without	<i>Ilex opaca</i>	1	30	.
7	without	<i>Acer sp.</i>	1	0.5	.
7	without	unknown 4	1	0.5	.
7	without	<i>Parthenocissus quinquefolia</i>	2	1	.
7	without	<i>Carpinus caroliniana</i>	2	5	.
7	without	<i>Polystichum acrostichoides</i>	4	50	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
7	without	<i>Lindera benzoin</i>	5	10	.
7	without	<i>Thelypteris noveboracensis</i>	5	25	.
7	without	<i>Mitchella repens</i>	15	1	.
7	without	<i>Phlox stolonifera</i>	100	40	.
8	with	<i>Celastrus orbiculatus</i>	1	12	0.58
8	with	<i>Polystichum acrostichoides</i>	1	7	.
8	with	<i>Verbesina alternifolia</i>	1	9	.
8	with	<i>Lindera benzoin</i>	2	1	.
8	with	<i>Carex sp. 2</i>	3	9	.
8	with	<i>Mitchella repens</i>	4	0.5	.
8	with	<i>Viola sororia</i>	5	0.5	.
8	with	<i>Arisaema triphyllum</i>	5	3	.
8	with	<i>Thelypteris noveboracensis</i>	13	95	.
8	with	<i>Phlox stolonifera</i>	130	50	.
8	without	<i>Lindera benzoin</i>	1	1	.
8	without	<i>Ilex opaca</i>	1	7	.
8	without	<i>Carpinus caroliniana</i>	1	0.5	.
8	without	<i>Ranunculus sp. 1</i>	1	0.5	.
8	without	<i>unknown 1</i>	1	1	.
8	without	<i>Oxalis stricta</i>	2	0.5	.
8	without	<i>Solidago nemoralis</i>	2	1	.
8	without	<i>Carex sp. 2</i>	3	1	.
8	without	<i>Poaceae 7</i>	6	0.5	.
8	without	<i>Thelypteris noveboracensis</i>	7	60	.
8	without	<i>Mitchella repens</i>	8	1	.
8	without	<i>Lonicera japonica</i>	9	3	.
8	without	<i>Phlox stolonifera</i>	130	65	.
9	with	<i>Celastrus orbiculatus</i>	3	20	4.06, 2.54, 5.08
9	with	<i>Viola sororia</i>	1	0.5	.
9	with	<i>Arisaema triphyllum</i>	1	0.5	.
9	with	<i>Galium sp.</i>	1	2	.
9	with	<i>Carpinus caroliniana</i>	1	0.5	.
9	with	<i>Lindera benzoin</i>	1	0.5	.
9	with	<i>Ranunculus sp. 1</i>	1	0.5	.
9	with	<i>Botrychium biternatum</i>	1	1	.
9	with	<i>Smilax rotundifolia</i>	2	0.5	.
9	with	<i>Lonicera japonica</i>	3	1	.
9	with	<i>Thelypteris noveboracensis</i>	6	35	.
9	with	<i>Phlox stolonifera</i>	16	10	.
9	without	<i>Lindera benzoin</i>	1	1	.
9	without	<i>Polystichum acrostichoides</i>	1	9	.
9	without	<i>Poaceae 7</i>	1	0.5	.
9	without	<i>Carex intumescens</i>	1	0.5	.
9	without	<i>Rosa multiflora</i>	1	1	.
9	without	<i>Botrychium biternatum</i>	1	1	.
9	without	<i>unknown 1</i>	1	4	.
9	without	<i>Ranunculus sp. 1</i>	1	0.5	.
9	without	<i>Verbesina alternifolia</i>	1	1	.
9	without	<i>Carex sp. 2</i>	3	1	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
9	without	<i>Ranunculus recurvatus</i>	3	1	.
9	without	<i>Thelypteris noveboracensis</i>	4	25	.
9	without	<i>Smilax rotundifolia</i>	4	1	.
9	without	<i>Viola sororia</i>	4	1	.
9	without	<i>Chasmanthium sp.</i>	4	9	.
9	without	<i>Lonicera japonica</i>	5	1	.
9	without	<i>Microstegium vimineum</i>	11	7	.
9	without	<i>Phlox stolonifera</i>	35	9	.
10	with	<i>Celastrus orbiculatus</i>	5	35	0.43, 0.51, 0.25, 0.53, 0.36
10	with	<i>Parthenocissus quinquefolia</i>	1	0.5	.
10	with	<i>Glechoma hederacea</i>	2	1	.
10	with	<i>Tradescantia sp.</i>	2	5	.
10	with	<i>Rosa multiflora</i>	4	15	.
10	with	<i>Viola sororia</i>	4	3	.
10	with	<i>Carex sp. 2</i>	4	1	.
10	with	<i>Phlox stolonifera</i>	12	1	.
10	with	<i>Lonicera japonica</i>	15	10	.
10	with	<i>Microstegium vimineum</i>	140	85	.
10	without	<i>Tradescantia sp.</i>	1	0.5	.
10	without	<i>Ranunculus sp. 1</i>	1	0.5	.
10	without	<i>Polystichum acrostichoides</i>	2	20	.
10	without	<i>Senecio vulgaris</i>	3	1	.
10	without	<i>Thelypteris noveboracensis</i>	3	10	.
10	without	<i>Galium sp.</i>	3	1	.
10	without	<i>Arisaema triphyllum</i>	5	3	.
10	without	<i>Viola sororia</i>	10	5	.
10	without	<i>Lonicera japonica</i>	11	7	.
10	without	<i>Microstegium vimineum</i>	14	9	.
11	with	<i>Celastrus orbiculatus</i>	2	40	0.79, 0.58
11	with	<i>Solidago sp.</i>	1	1	.
11	with	<i>Pinus strobus</i>	1	0.5	.
11	with	<i>Microstegium vimineum</i>	1	0.5	.
11	with	<i>Smilax rotundifolia</i>	1	0.5	.
11	with	<i>Galium sp.</i>	1	0.5	.
11	with	<i>Poaceae 2</i>	2	5	.
11	with	<i>Lindera benzoin</i>	2	6	.
11	with	<i>Oxalis stricta</i>	2	1	.
11	with	<i>Toxicodendron rydbergii</i>	3	3	.
11	with	<i>unknown 2</i>	3	9	.
11	with	<i>Thelypteris noveboracensis</i>	3	9	.
11	with	<i>Carex sp. 2</i>	3	4	.
11	with	<i>Poaceae 5</i>	3	5	.
11	with	<i>Polystichum acrostichoides</i>	4	50	.
11	with	<i>Leersia virginica</i>	6	16	.
11	with	<i>Viola sororia</i>	11	4	.
11	with	<i>Lonicera japonica</i>	12	5	.
11	with	<i>Phlox stolonifera</i>	33	10	.
11	without	<i>Smilax rotundifolia</i>	1	4	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
11	without	<i>Galium sp.</i>	1	0.5	.
11	without	<i>Ilex opaca</i>	1	0.5	.
11	without	<i>Ranunculus sp. 1</i>	1	0.5	.
11	without	<i>Polygonum sagittatum</i>	1	0.5	.
11	without	<i>Phlox stolonifera</i>	1	1	.
11	without	<i>Ranunculus recurvatus</i>	1	0.5	.
11	without	<i>Thalictrum sp.</i>	2	7	.
11	without	<i>Berberis vulgaris</i>	2	1	.
11	without	<i>Polystichum acrostichoides</i>	4	90	.
11	without	<i>Polygonum sp.</i>	5	4	.
11	without	<i>Viola sororia</i>	7	4	.
11	without	<i>Oxalis stricta</i>	8	7	.
11	without	<i>Lonicera japonica</i>	9	4	.
11	without	<i>Microstegium vimineum</i>	70	50	.
12	with	<i>Celastrus orbiculatus</i>	6	20	0.46, 0.38, 0.41, 0.41, 0.43
12	with	<i>Polystichum acrostichoides</i>	1	25	.
12	with	<i>Senecio vulgaris</i>	1	0.5	.
12	with	<i>Senecio vulgaris</i>	1	0.5	.
12	with	<i>unknown 2</i>	1	1	.
12	with	<i>Parthenocissus quinquefolia</i>	1	0.5	.
12	with	<i>Tradescantia sp.</i>	1	3	.
12	with	<i>Thelypteris noveboracensis</i>	1	1	.
12	with	<i>unknown 5</i>	1	1	.
12	with	<i>Poaceae 4</i>	1	1	.
12	with	<i>Oxalis stricta</i>	2	1	.
12	with	<i>Rosa multiflora</i>	2	1	.
12	with	<i>Arisaema triphyllum</i>	3	1	.
12	with	<i>Lindera benzoin</i>	5	20	.
12	with	<i>Carex sp. 2</i>	17	16	.
12	with	<i>Phlox stolonifera</i>	28	9	.
12	with	<i>Viola sororia</i>	34	10	.
12	without	<i>Polystichum acrostichoides</i>	1	35	.
12	without	<i>Botrychium biternatum</i>	1	0.5	.
12	without	<i>unknown 2</i>	1	1	.
12	without	<i>Ranunculus sp. 1</i>	1	1	.
12	without	<i>Ipomoea sp.</i>	1	1	.
12	without	<i>Lindera benzoin</i>	3	9	.
12	without	<i>Leersia virginica</i>	3	3	.
12	without	<i>Oxalis stricta</i>	4	0.5	.
12	without	<i>Carex sp. 2</i>	8	4	.
12	without	<i>Lonicera japonica</i>	15	3	.
12	without	<i>Phlox stolonifera</i>	22	7	.
12	without	<i>Viola sororia</i>	30	5	.
12	without	<i>Microstegium vimineum</i>	.	.	.
13	with	<i>Celastrus orbiculatus</i>	7	70	0.43, 0.43, 0.08, 0.08, 0.30, 0.48, 0.28
13	with	<i>Berberis vulgaris</i>	1	0.5	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
13	with	<i>Thaspium trifoliatum</i>	1	0.5	.
13	with	<i>Carpinus caroliniana</i>	1	0.5	.
13	with	<i>Smilax rotundifolia</i>	1	0.5	.
13	with	<i>Tradescantia sp.</i>	2	1	.
13	with	<i>Senecio vulgaris</i>	3	1	.
13	with	<i>Parthenocissus quinquefolia</i>	3	1	.
13	with	<i>Carex sp. 2</i>	4	7	.
13	with	<i>Thelypteris noveboracensis</i>	6	25	.
13	with	<i>Viola sororia</i>	19	7	.
13	with	<i>Microstegium vimineum</i>	50	10	.
13	with	<i>Phlox stolonifera</i>	75	40	.
13	without	<i>Oxalis stricta</i>	1	0.5	.
13	without	<i>Carpinus caroliniana</i>	1	0.5	.
13	without	<i>Phryma leptostachya</i>	1	4	.
13	without	<i>Polystichum acrostichoides</i>	2	6	.
13	without	<i>Smilax rotundifolia</i>	2	5	.
13	without	<i>Pinus strobus</i>	2	1	.
13	without	<i>Senecio vulgaris</i>	4	2	.
13	without	<i>Parthenocissus quinquefolia</i>	4	1	.
13	without	<i>Phlox stolonifera</i>	4	1	.
13	without	<i>Lonicera japonica</i>	6	3	.
13	without	<i>Thelypteris noveboracensis</i>	6	30	.
13	without	<i>Arisaema triphyllum</i>	6	7	.
13	without	<i>Carex sp. 2</i>	13	25	.
13	without	<i>Viola sororia</i>	24	7	.
13	without	<i>Microstegium vimineum</i>	105	50	.
14	with	<i>Celastrus orbiculatus</i>	9	65	0.15, 0.43, 0.43, 0.15, 0.15, 0.25, 0.38, 0.20, 0.46
14	with	<i>Lindera benzoin</i>	1	1	.
14	with	<i>Botrychium biternatum</i>	1	0.5	.
14	with	<i>Parthenocissus quinquefolia</i>	1	1	.
14	with	<i>Toxicodendron rydbergii</i>	1	4	.
14	with	<i>Lactuca sp.</i>	1	1	.
14	with	<i>Rosa multiflora</i>	2	1	.
14	with	<i>Oxalis stricta</i>	3	1	.
14	with	<i>Microstegium vimineum</i>	10	2	.
14	with	<i>Carex sp. 2</i>	19	15	.
14	with	<i>Viola sororia</i>	32	7	.
14	with	<i>Phlox stolonifera</i>	60	20	.
14	without	<i>Parthenocissus quinquefolia</i>	1	1	.
14	without	<i>Pinus strobus</i>	1	0.5	.
14	without	<i>Vitis labrusca</i>	1	7	.
14	without	<i>Elaeagnus umbellata</i>	2	9	.
14	without	<i>Ranunculus recurvatus</i>	2	0.5	.
14	without	<i>Athyrium asplenoides</i>	3	20	.
14	without	<i>Galium sp.</i>	3	4	.
14	without	<i>Oxalis stricta</i>	4	1	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
14	without	<i>Lonicera japonica</i>	4	1	.
14	without	<i>Thelypteris noveboracensis</i>	5	25	.
14	without	<i>Carex sp. 2</i>	5	5	.
14	without	<i>Thaspium trifoliatum</i>	7	25	.
14	without	<i>Lycopus virginicus</i>	16	12	.
14	without	<i>Viola sororia</i>	20	7	.
14	without	<i>Phlox stolonifera</i>	40	9	.
14	without	<i>Microstegium vimineum</i>	42	16	.
15	with	<i>Celastrus orbiculatus</i>	1	1	0.13
15	with	<i>Verbesina alternifolia</i>	1	9	.
15	with	<i>Thaspium trifoliatum</i>	1	1	.
15	with	<i>Thalictrum sp.</i>	1	1	.
15	with	<i>Botrychium biternatum</i>	1	0.5	.
15	with	<i>Ranunculus sp. 1</i>	1	0.5	.
15	with	<i>Tradescantia sp.</i>	2	4	.
15	with	<i>Carpinus caroliniana</i>	2	0.5	.
15	with	<i>Smilax rotundifolia</i>	2	1	.
15	with	<i>Senecio vulgaris</i>	2	0.5	.
15	with	<i>Parthenocissus quinquefolia</i>	2	1	.
15	with	<i>Lindera benzoin</i>	3	4	.
15	with	<i>Poaceae 8</i>	4	5	.
15	with	<i>Lonicera japonica</i>	6	2	.
15	with	<i>Carex sp. 2</i>	9	12	.
15	with	<i>Viola sororia</i>	18	2	.
15	with	<i>Mitchella repens</i>	19	16	.
15	with	<i>Microstegium vimineum</i>	40	20	.
15	with	<i>Phlox stolonifera</i>	65	25	.
15	without	<i>Arisaema triphyllum</i>	1	1	.
15	without	<i>Polystichum acrostichoides</i>	1	12	.
15	without	<i>Oxalis stricta</i>	1	1	.
15	without	<i>Microstegium vimineum</i>	1	0.5	.
15	without	<i>Carpinus caroliniana</i>	1	0.5	.
15	without	<i>Elaeagnus umbellata</i>	2	12	.
15	without	<i>Pinus strobus</i>	2	4	.
15	without	<i>Lindera benzoin</i>	3	25	.
15	without	<i>Carex sp. 2</i>	5	25	.
15	without	<i>Ranunculus sp. 1</i>	6	1	.
15	without	<i>Lonicera japonica</i>	8	7	.
15	without	<i>Viola sororia</i>	10	5	.
15	without	<i>Thelypteris noveboracensis</i>	11	88	.
15	without	<i>Phlox stolonifera</i>	85	35	.
16	with	<i>Celastrus orbiculatus</i>	3	2	0.23, 0.15, 0.01
16	with	<i>Botrychium biternatum</i>	1	0.5	.
16	with	<i>Elephantopus carolinianus</i>	1	4	.
16	with	<i>Carpinus caroliniana</i>	1	1	.
16	with	<i>Chasmanthium sp.</i>	1	0.5	.
16	with	<i>Toxicodendron rydbergii</i>	2	2	.
16	with	<i>Polygonum sp.</i>	2	0.5	.
16	with	<i>Microstegium vimineum</i>	2	0.5	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
16	with	<i>Lycopus virginicus</i>	2	1	.
16	with	<i>Oxalis stricta</i>	2	0.5	.
16	with	<i>Parthenocissus quinquefolia</i>	3	2	.
16	with	<i>Lonicera japonica</i>	3	2	.
16	with	<i>Lindera benzoin</i>	4	16	.
16	with	<i>Viola sororia</i>	8	1	.
16	with	<i>Carex sp. 2</i>	9	25	.
16	with	<i>Phlox stolonifera</i>	110	30	.
16	without	<i>Lindera benzoin</i>	1	4	.
16	without	<i>Rubus sp.</i>	1	1	.
16	without	<i>Polystichum acrostichoides</i>	1	1	.
16	without	<i>Elephantopus carolinianus</i>	1	35	.
16	without	<i>Thaspium trifoliatum</i>	1	4	.
16	without	<i>Polygonum sp.</i>	1	0.5	.
16	without	<i>Acer sp.</i>	1	0.5	.
16	without	<i>Botrychium biternatum</i>	1	0.5	.
16	without	<i>Arisaema triphyllum</i>	1	0.5	.
16	without	<i>Parthenocissus quinquefolia</i>	2	2	.
16	without	<i>Lonicera japonica</i>	2	1	.
16	without	<i>Carpinus caroliniana</i>	2	0.5	.
16	without	<i>Oxalis stricta</i>	4	0.5	.
16	without	<i>Carex sp. 2</i>	9	30	.
16	without	<i>Viola sororia</i>	10	2	.
16	without	<i>Microstegium vimineum</i>	10	1	.
16	without	<i>Phlox stolonifera</i>	180	50	.
17	with	<i>Celastrus orbiculatus</i>	6	30	0.23, 0.13, 0.05, 0.28, 0.43, 0.20
17	with	<i>Lonicera japonica</i>	1	0.5	.
17	with	<i>Smilax rotundifolia</i>	1	1	.
17	with	<i>Chasmanthium sp.</i>	1	2	.
17	with	<i>Lindera benzoin</i>	1	20	.
17	with	<i>Oxalis stricta</i>	2	0.5	.
17	with	<i>Viola sororia</i>	3	0.5	.
17	with	<i>Parthenocissus quinquefolia</i>	4	3	.
17	with	<i>Carex sp. 2</i>	4	9	.
17	with	<i>Microstegium vimineum</i>	8	2	.
17	with	<i>Phlox stolonifera</i>	35	2	.
17	without	<i>Rosa multiflora</i>	1	1	.
17	without	<i>Rubus sp.</i>	1	1	.
17	without	<i>Solidago sp.</i>	1	1	.
17	without	<i>Oxalis stricta</i>	1	0.5	.
17	without	<i>Lindera benzoin</i>	1	20	.
17	without	<i>Geranium maculatum</i>	5	20	.
17	without	<i>Carex sp. 2</i>	5	6	.
17	without	<i>Arisaema triphyllum</i>	6	9	.
17	without	<i>Lonicera japonica</i>	6	3	.
17	without	<i>Microstegium vimineum</i>	9	7	.
17	without	<i>Parthenocissus quinquefolia</i>	9	6	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
17	without	<i>Senecio vulgaris</i>	10	5	.
17	without	<i>Viola sororia</i>	12	3	.
17	without	<i>Phlox stolonifera</i>	65	20	.
18	with	<i>Celastrus orbiculatus</i>	3	20	0.36, 0.38, 0.33
18	with	<i>Parthenocissus quinquefolia</i>	1	0.5	.
18	with	<i>Lindera benzoin</i>	1	0.5	.
18	with	<i>Elephantopus carolinianus</i>	1	1	.
18	with	<i>Parthenocissus quinquefolia</i>	1	0.5	.
18	with	<i>Acer sp.</i>	1	0.5	.
18	with	<i>Polystichum acrostichoides</i>	1	10	.
18	with	<i>Potentilla simplex</i>	1	0.5	.
18	with	<i>Botrychium biternatum</i>	1	0.5	.
18	with	<i>Arisaema triphyllum</i>	1	0.5	.
18	with	<i>Viola sororia</i>	2	0.5	.
18	with	<i>Phlox stolonifera</i>	2	1	.
18	with	<i>Oxalis stricta</i>	2	1	.
18	with	<i>Ligustrum sp.</i>	2	1	.
18	with	<i>Thelypteris noveboracensis</i>	10	40	.
18	with	<i>Mitchella repens</i>	23	15	.
18	without	<i>Arisaema triphyllum</i>	1	1	.
18	without	<i>Pinus strobus</i>	1	0.5	.
18	without	<i>Elephantopus carolinianus</i>	1	1	.
18	without	<i>Mitchella repens</i>	1	1	.
18	without	<i>Parthenocissus quinquefolia</i>	1	1	.
18	without	<i>Carex sp. 2</i>	1	1	.
18	without	<i>Smilax glauca</i>	2	10	.
18	without	<i>Athyrium asplenoides</i>	2	25	.
18	without	<i>Carpinus caroliniana</i>	3	1	.
18	without	<i>Berberis vulgaris</i>	3	1	.
18	without	<i>Lonicera japonica</i>	6	2	.
18	without	<i>Thelypteris noveboracensis</i>	10	50	.
18	without	<i>Phlox stolonifera</i>	13	4	.
19	with	<i>Celastrus orbiculatus</i>	5	3	0.41, 0.25, 0.30, 0.15, 0.01
19	with	<i>Lindera benzoin</i>	1	1	.
19	with	<i>Carpinus caroliniana</i>	1	0.5	.
19	with	<i>Parthenocissus quinquefolia</i>	1	0.5	.
19	with	<i>Chasmanthium sp.</i>	1	1	.
19	with	<i>Galium sp.</i>	2	0.5	.
19	with	<i>Oxalis stricta</i>	3	1	.
19	with	<i>Potentilla simplex</i>	4	2	.
19	with	<i>Thelypteris noveboracensis</i>	4	16	.
19	with	<i>Carex sp. 2</i>	5	5	.
19	with	<i>Viola sororia</i>	10	1	.
19	with	<i>Microstegium vimineum</i>	14	4	.
19	with	<i>Polygonum sp.</i>	19	4	.
19	with	<i>Phlox stolonifera</i>	125	60	.
19	without	<i>Polystichum acrostichoides</i>	1	20	.
19	without	<i>Lycopus virginicus</i>	1	1	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
19	without	<i>unknown 2</i>	1	1	.
19	without	<i>Elephantopus carolinianus</i>	1	0.5	.
19	without	<i>Dicanthelium sp.</i>	2	4	.
19	without	<i>Potentilla simplex</i>	3	4	.
19	without	<i>Carex sp. 2</i>	4	2	.
19	without	<i>Poaceae 5</i>	4	2	.
19	without	<i>Viola sororia</i>	5	1	.
19	without	<i>Thelypteris noveboracensis</i>	6	50	.
19	without	<i>Mitchella repens</i>	6	1	.
19	without	<i>Phlox stolonifera</i>	130	65	.
20	with	<i>Celastrus orbiculatus</i>	8	70	0.48, 0.30, 0.18, 0.33, 0.23, 0.41, 0.33, 0.18
20	with	<i>Arisaema triphyllum</i>	1	0.5	.
20	with	<i>Lindera benzoin</i>	1	1	.
20	with	<i>Elephantopus carolinianus</i>	1	1	.
20	with	<i>Pinus strobus</i>	1	0.5	.
20	with	<i>Carpinus caroliniana</i>	2	0.5	.
20	with	<i>Viola sororia</i>	2	0.5	.
20	with	<i>Carex sp. 2</i>	4	5	.
20	with	<i>Leersia virginica</i>	4	1	.
20	with	<i>Lonicera japonica</i>	7	3	.
20	with	<i>Thelypteris noveboracensis</i>	10	50	.
20	with	<i>Phlox stolonifera</i>	34	14	.
20	without	<i>Rubus sp.</i>	1	1	.
20	without	<i>Maianthemum racemosum</i>	1	1	.
20	without	<i>Lindera benzoin</i>	1	2	.
20	without	<i>Leersia virginica</i>	1	0.5	.
20	without	<i>Lonicera japonica</i>	3	4	.
20	without	<i>Carex sp. 2</i>	3	20	.
20	without	<i>Poaceae 5</i>	3	20	.
20	without	<i>Microstegium vimineum</i>	4	1	.
20	without	<i>Viola sororia</i>	6	1	.
20	without	<i>Thelypteris noveboracensis</i>	9	95	.
20	without	<i>Phlox stolonifera</i>	80	35	.
21	with	<i>Celastrus orbiculatus</i>	7	50	0.08, 0.28, 0.51, 0.10, 0.28, 0.36, 0.01
21	with	<i>Lindera benzoin</i>	1	12	.
21	with	<i>Ranunculus sp. 1</i>	1	0.5	.
21	with	<i>Carpinus caroliniana</i>	2	1	.
21	with	<i>Arisaema triphyllum</i>	3	0.5	.
21	with	<i>Lonicera japonica</i>	4	1	.
21	with	<i>Thelypteris noveboracensis</i>	5	70	.
21	with	<i>Viola sororia</i>	6	0.5	.
21	with	<i>Carex sp. 2</i>	8	16	.
21	with	<i>Phlox stolonifera</i>	10	1	.
21	without	<i>Smilax rotundifolia</i>	1	15	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
21	without	<i>Oxalis stricta</i>	1	0.5	.
21	without	<i>Lindera benzoin</i>	1	0.5	.
21	without	<i>Lonicera japonica</i>	4	1	.
21	without	<i>Carex sp. 2</i>	5	1	.
21	without	<i>Viola sororia</i>	5	0.5	.
21	without	<i>Thelypteris noveboracensis</i>	16	95	.
21	without	<i>Phlox stolonifera</i>	160	70	.
22	with	<i>Celastrus orbiculatus</i>	9	55	0.15, 0.18, 0.18, 0.28, 0.28, 0.36, 0.36, 2.29, 0.25
22	with	<i>Elephantopus carolinianus</i>	1	1	.
22	with	<i>Prenanthes sp.</i>	1	1	.
22	with	<i>Poaceae 5</i>	1	1	.
22	with	<i>Leersia virginica</i>	2	1	.
22	with	<i>Lonicera japonica</i>	5	2	.
22	with	<i>Thelypteris noveboracensis</i>	7	75	.
22	with	<i>Carex sp. 2</i>	10	20	.
22	with	<i>Viola sororia</i>	10	1	.
22	with	<i>Mitchella repens</i>	15	2	.
22	with	<i>Phlox stolonifera</i>	150	90	.
22	without	<i>Maianthemum racemosum</i>	1	0.5	.
22	without	<i>Arisaema triphyllum</i>	1	0.5	.
22	without	<i>Polygonum sp.</i>	1	0.5	.
22	without	<i>Smilax rotundifolia</i>	1	1	.
22	without	<i>Elephantopus carolinianus</i>	1	1	.
22	without	<i>Dicanthelium sp.</i>	2	6	.
22	without	<i>Parthenocissus quinquefolia</i>	2	1	.
22	without	<i>Carex sp. 2</i>	5	7	.
22	without	<i>Viola sororia</i>	6	1	.
22	without	<i>Thelypteris noveboracensis</i>	14	80	.
22	without	<i>Glechoma hederacea</i>	65	60	.
22	without	<i>Phlox stolonifera</i>	65	25	.
23	with	<i>Celastrus orbiculatus</i>	7	9	0.38, 0.36, 0.01, 0.01, 0.01, 0.01, 0.01
23	with	<i>unknown 2</i>	1	1	.
23	with	<i>Lycopus virginicus</i>	1	1	.
23	with	<i>Pinus strobus</i>	1	1	.
23	with	<i>Thelypteris noveboracensis</i>	3	16	.
23	with	<i>Thaspium trifoliatum</i>	3	5	.
23	with	<i>Poaceae 2</i>	3	25	.
23	with	<i>Arisaema triphyllum</i>	3	1	.
23	with	<i>Microstegium vimineum</i>	4	1	.
23	with	<i>Elaeagnus umbellata</i>	4	20	.
23	with	<i>Lonicera japonica</i>	8	12	.
23	with	<i>Carex sp. 2</i>	9	30	.
23	with	<i>Viola sororia</i>	25	10	.
23	with	<i>Phlox stolonifera</i>	90	50	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
23	without	<i>Elaeagnus umbellata</i>	1	25	.
23	without	<i>Polygonum sp.</i>	1	1	.
23	without	<i>Polystichum acrostichoides</i>	1	7	.
23	without	<i>Acer sp.</i>	1	0.5	.
23	without	<i>Parthenocissus quinquefolia</i>	1	1	.
23	without	<i>Poaceae 2</i>	1	5	.
23	without	<i>Carpinus caroliniana</i>	1	0.5	.
23	without	<i>Rosa multiflora</i>	1	1	.
23	without	<i>Galium sp.</i>	2	1	.
23	without	<i>Carex sp. 2</i>	2	3	.
23	without	<i>Thelypteris noveboracensis</i>	3	5	.
23	without	<i>Viola sororia</i>	5	1	.
23	without	<i>Smilax rotundifolia</i>	8	25	.
23	without	<i>Ranunculus recurvatus</i>	12	2	.
23	without	<i>Phlox stolonifera</i>	50	25	.
23	without	<i>Microstegium vimineum</i>	60	30	.
24	with	<i>Celastrus orbiculatus</i>	4	45	0.41, 0.05, 0.05, 0.13
24	with	<i>Viola sororia</i>	1	0.5	.
24	with	<i>Ranunculus sp. 1</i>	1	0.5	.
24	with	<i>Berberis vulgaris</i>	1	0.5	.
24	with	<i>Phlox stolonifera</i>	1	0.5	.
24	with	<i>Tradescantia sp.</i>	1	1	.
24	with	<i>Poaceae 1 (bamboo)</i>	2	4	.
24	with	<i>Carex sp. 2</i>	2	3	.
24	with	<i>Poaceae 2</i>	2	4	.
24	with	<i>Thelypteris noveboracensis</i>	6	50	.
24	with	<i>Mitchella repens</i>	12	4	.
24	without	<i>Rubus sp.</i>	1	12	.
24	without	<i>Sassafras albidum</i>	1	4	.
24	without	<i>Tradescantia sp.</i>	1	1	.
24	without	<i>Poaceae 2</i>	1	1	.
24	without	<i>Smilax rotundifolia</i>	2	1	.
24	without	<i>Viola sororia</i>	3	1	.
24	without	<i>Chasmanthium sp.</i>	3	16	.
24	without	<i>Arisaema triphyllum</i>	4	1	.
24	without	<i>Carex sp. 2</i>	4	16	.
24	without	<i>Galium sp.</i>	7	16	.
24	without	<i>Thelypteris noveboracensis</i>	8	90	.
24	without	<i>Phlox stolonifera</i>	80	65	.
25	with	<i>Celastrus orbiculatus</i>	5	20	0.23, 0.18, 0.01, 0.01, 0.01
25	with	<i>Pinus strobus</i>	1	0.5	.
25	with	<i>Smilax rotundifolia</i>	1	2	.
25	with	<i>Poaceae 1 (bamboo)</i>	2	9	.
25	with	<i>Carpinus caroliniana</i>	2	0.5	.
25	with	<i>Aster sp.</i>	2	0.5	.
25	with	<i>Oxalis stricta</i>	3	0.5	.
25	with	<i>Poaceae 2</i>	3	15	.

Qt	Treatment	Taxon	# Shoots	% Cover	Basal Area (cm)
25	with	<i>Ranunculus sp. 1</i>	3	0.5	.
25	with	<i>Lonicera japonica</i>	4	5	.
25	with	<i>Galium sp.</i>	5	4	.
25	with	<i>Arisaema triphyllum</i>	6	2	.
25	with	<i>Thelypteris noveboracensis</i>	8	85	.
25	with	<i>Phlox stolonifera</i>	30	9	.
25	without	<i>Lindera benzoin</i>	1	2	.
25	without	<i>Berberis vulgaris</i>	1	5	.
25	without	<i>Potentilla simplex</i>	1	0.5	.
25	without	<i>Elaeagnus umbellata</i>	2	3	.
25	without	<i>Viola sororia</i>	2	0.5	.
25	without	<i>Carpinus caroliniana</i>	3	1	.
25	without	<i>Poaceae 1 (bamboo)</i>	3	15	.
25	without	<i>Aster sp.</i>	3	2	.
25	without	<i>Ligustrum sp.</i>	4	5	.
25	without	<i>Botrychium biternatum</i>	6	1	.
25	without	<i>Thelypteris noveboracensis</i>	11	90	.
25	without	<i>Mitchella repens</i>	11	2	.
25	without	<i>Lonicera japonica</i>	13	16	.
25	without	<i>Phlox stolonifera</i>	17	9	.