

ASSESSING THE EFFECTS OF INVASIVE *LIGUSTRUM SINENSE* AND *LONICERA*
JAPONICA ON RARE AND FEDERALLY THREATENED
SCUTELLARIA MONTANA

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ABSTRACT

Few studies have directly evaluated the competitive interactions between invasive and co-occurring rare plants. Federally threatened *Scutellaria montana* Chapm. (large-flowered skullcap) is a rare herbaceous perennial endemic to southeastern Tennessee and northwestern Georgia. The forest understory habitat in which *S. montana* typically occurs often also contains invasive *Ligustrum sinense* (Chinese privet) and *Lonicera japonica* (Japanese honeysuckle), and these and other invasive plant species have been recognized as a potential threat to its conservation. To directly investigate the effects of invasive *L. sinense* and *L. japonica* on *S. montana*, a two-year field-based removal experiment was conducted in an *S. montana* occurrence in Chattanooga, TN. An interacting herbivory exclusion treatment was included to help isolate the effects of competition from non-insect herbivory, another possible pressure negatively influencing *S. montana*, and to isolate the effects of competition from apparent competition. I hypothesized that interspecific competition with *L. sinense* and *L. japonica* would negatively affect *S. montana* by reducing its organismal-level growth and fecundity. Additionally, I hypothesized that herbivory would negatively influence *S. montana* individuals due to the direct removal of aboveground biomass and that negative impacts would be exacerbated by concurrent competition with invasive species. My results suggest that invasive *L. sinense* and *L. japonica* do not exert any competitive affect on the organismal-level performance of *S. montana*. Instead, the presence of these invasive species favors the growth of *S. montana* individuals by protecting

them from herbivores. However, the demonstrated ability of both *L. sinense* and *L. japonica* to form monocultures in the forest understory remains a concern given the potential population-level impacts of such density on germination and recruitment of co-occurring species. Related research has suggested that other invasive species exhibiting no competitive effect on adults of rare species can suppress their germination and recruitment of juveniles. I suggest that future research include investigations of the influence of *L. sinense* and *L. japonica* on these processes in *S. montana*.

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CHAPTER 1
LITERATURE REVIEW: THE DIRECT EFFECTS OF INVASIVE SPECIES ON RARE
PLANT SPECIES

Introduction

Invasive species are species that have proliferated outside of their native range with associated detrimental ecological impacts (Lodge et al. 2006). For example, given their seeming ability to monopolize shared resources, invasive species have been associated with the replacement or displacement of native species in some systems (Vitousek 1986; Yurkonis and Meiners 2004). This is especially concerning for native species that are rare, threatened, and/or endangered. At present, invasive species are cited as threats to the continued survival of approximately half of all species afforded protection under the U.S. Endangered Species Act (Wilcove et al. 1998). For federally listed plant species in particular, this percentage is somewhat greater (~57%; Wilcove and Master 2005; Wilcove et al. 1998). Because the Endangered Species Act only covers those species that have gone through the political process of protection, it has been suggested that the actual number of plant species threatened by invasive species is even greater (Wilcove and Master 2005).

Lythrum salicaria (purple loosestrife) is a well cited example of the rapid proliferation of an invasive plant species into native systems. In wetlands that it invades, this species can replace up to 50% of native plant biomass (Thompson et al. 1987). Another invasive species that has

warranted much attention is *Ligustrum sinense* (Chinese privet). In many habitats, privet proliferation has been associated with decreased growth and germination of native species. The end result is a decrease not only in native species richness but also a decrease in overall species evenness (Greene and Blossey 2012). Invasions like these can affect native plant species at the individual, population, and community levels. At the individual level, invasive species have been associated with reductions in the amount of vegetative biomass and seeds produced by co-occurring native species (Gould and Gorchoy 2000; Greene and Blossey 2012; Miller and Gorchoy 2004). Associated reductions in individual fecundity can slow population growth of these native species (Greene and Blossey 2012; Miller and Gorchoy 2004). Such population-level impacts can manifest themselves at the community-level as a loss of diversity due to reductions in species richness and evenness (Brewer 2008; Flory and Clay 2009; Greene and Blossey 2012; Thomson 2005).

As invasive species and their effects have become more apparent, the scientific research community has focused increased attention on these topics. This research recently has included an increased number of investigations studying the potential mechanisms underlying species invasiveness, such as allelopathy, germination suppression, and competitive ability (Levine et al. 2003). Understanding such mechanisms could provide increased knowledge upon which to base eradication efforts and other land management decisions. In this review, I aim to focus on competition's role between invasive and rare plant species.

The Role of Competition in Plant Species' Invasiveness

There are many factors that could influence the proliferation of invasive plant species into natural areas and their potential associated impacts on native plant species (Huenneke and Thomson 1995). A commonly cited factor is the relative competitive ability of invasive species compared with that of native species (Gorchov and Trisel 2003; Hanula and Taylor 2009; Huenneke and Thomson 1995; Vila and Weiner 2004). Grime (1977) classically defined competition as 'the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space.' More recently, competition has been defined more generally as a reduction in fitness due to utilization of the same resource that is in limited supply (Gurevitch et al. 2006). Theoretically, a plant species capable of utilizing more resources from a shared pool than its neighbors would be competitively superior in a given environment. An inferior competitor would experience a greater reduction in fitness than a superior competitor, while a superior competitor would benefit both from the fitness reduction of its neighbors (reduction in fitness will lower the neighbors ability to utilize resources) and its own higher utilization of shared resources.

In a meta-analysis that examined 36 published pair-wise experiments, Vila and Weiner (2004), compared the effects of interspecific and intraspecific competition between and within invasive and native plant species. The authors found that native species saw a reduction in biomass when grown in competition with invasive species compared to when grown in monoculture. The opposite was true for invasive species, they grew better and accumulated more biomass when grown in competition with native species compared to when grown in monoculture (Vila and Weiner 2004). These findings led the authors to conclude that invasive

plant species are superior competitors compared to native plant species with which they co-occur.

The findings of individual research studies also have exemplified the competitive superiority of invasive plant species relative to co-occurring native plant species. Such studies have included investigations of invasive species of various life forms in various systems. For example, the invasive shrub *Ligustrum sinense* (Chinese privet) has been shown to outcompete co-occurring native herbs for light and soil resources, resulting in decreased stem height and numbers of leaves in these individuals (Greene and Blossey 2012; Hanula et al. 2009). Another invasive shrub, *Lonicera maackii* (bush honeysuckle), has been associated with reductions in survival and growth of co-occurring native tree saplings in forest understories (Gorchov and Trisel 2003). The invasive vine *Lonicera japonica* (Japanese honeysuckle) has been shown to reduce the growth of its tree hosts via below-ground competition for nutrients, specifically nitrogen (Dillenburg et al. 1993). The succulent *Carpobrotus edulis* (ice plant), which has invaded the coastal scrub habitat of California, is characterized by a root system that allows for better capture of water from fog relative to two co-occurring native shrubs experiencing population declines (D'Antonio and Mahall 1991). Similarly, *Bromus tectorum* (cheatgrass) also has been shown to outcompete native species for water, which has been associated with a reduction in their biomass in California grasslands (Melgoza et al. 1990).

However, not all studies investigating the competitive effects of invasive plant species on native plant species have drawn similar conclusions. Such studies have suggested other mechanisms to explain the proliferation and dominance of invasive species in native systems. The invasion of *Tamarisk ramosissima* (salt cedar) throughout riparian zones in the southwestern

U.S. and its associated replacement of native willow (*Salix* spp.) and cottonwood (*Populus* spp.) trees offers an example of one alternative mechanism. Because lowered water tables have been associated with salt cedar invasions, it was proposed that extremely high rates of transpiration (which effectively draw water from the soil, through the plant, and into the atmosphere) enable salt cedar to outcompete native species for water (Di Tomaso 1998). But recent research has shown that the transpiration rates of salt cedar do not differ significantly from those of native tree species, and that transpiration rates are typically site-specific rather than species-specific (Doody et al. 2011; Nagler et al. 2009). Instead, researchers suggested that salt cedar invasion is facilitated by its better tolerance of an altered water regime in the region that has lowered water table depths and increased soil salinity (Glenn and Nagler 2005).

The invasion of some grasslands in California provides another alternative mechanism for species' invasiveness. In these systems, invasive annual grasses have replaced native perennial grasses to the extent that many of the native grass species are now rare (Seabloom et al. 2003). However, research has shown that the native grasses in these systems utilize more water, nitrogen, and light than the invasive grasses, which suggests that the native species are stronger competitors (Seabloom et al. 2003). The invasive grasses, however, are able to establish more quickly in these systems following common disturbances, such as burning, grazing, and mowing. In contrast, recruitment of the native grass species following disturbance is limited by a combination of factors including their relatively low seed production, poor dispersal ability, and current rarity (Seabloom et al. 2003).

A meta-analysis conducted by Daehler (2003) further supports this concept. The analysis included 79 studies that directly compared the performance of invasive species with that of co-

occurring native species based on a variety of relevant traits. These ‘performance traits’ included individual-level growth rates, photosynthetic rates, tissue construction costs, and total leaf area; population-level survival rates, dispersal rates, germination rates, productivity, and fecundity; and competitive ability. The performance of native species relative to that of invasive species was ranked as either inferior, equal, or better (see Daehler 2003). Across all studies included in the meta-analysis, only ~13% suggested that invasive species performance was better than that of native species in all growing conditions. Of the 16 studies that investigated competition specifically as a performance trait, just ~31% concluded that invasive species were consistently competitively superior to native species regardless of resource availability. But in the remaining ~69% of studies, native species were either equally as competitive or more competitive than invasive species in at least some level of resource availability. Often, reduced resource availability favored native species, suggesting that they are better adapted to conditions in which competition for resources should be very strong. In contrast, native species were never more competitive than invasive species when resources were plentiful (Daehler 2003). Of the 31 studies that investigated fecundity or specific performance traits that influence reproductive success, ~45% concluded that invasive species performed better than native species, suggesting such traits may be more influential to species’ invasiveness than competitive ability.

These examples and other similar research findings have impacted the theoretical assumption that species’ invasiveness is facilitated by superior competitive abilities of invasive species relative to native species by demonstrating that other mechanisms often are influential. To better investigate this assumption, the competitive abilities of invasive plant species compared to co-occurring native plants is thus now being studied in more systems (see Figure

1.1). A search and review of published abstracts conducted in Web of Science included 111 total studies that examined competitive interactions between native and invasive plant species.

Almost 70 percent (76 of the 111) of these studies were published in the past five years. This recent search supported an earlier observation by Huenneke and Thomsom (1995) that not many studies directly compared the interactions between invasive species and species of concern for conservation. However, such studies would provide insight into efforts to manage such species in systems that often include invasive species.

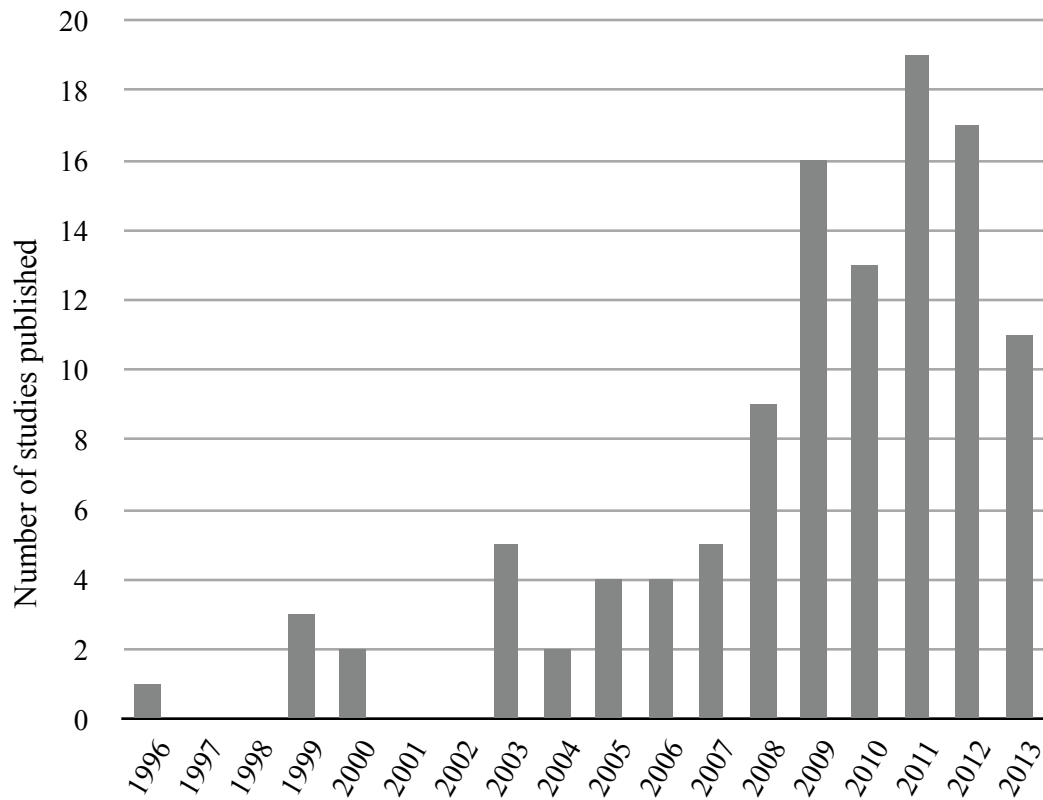


Figure 1.1. Results of a Web of Science search comparing the number of studies published each year that examine the direct effects of competition between invasive and native species.

The Role of Competition in Plant Species' Rarity

Since rarity has been associated widely with extinction vulnerability (Harnik et al. 2012), ecologists are especially concerned about how invasive plants will impact rare native plant species via competition and other potential mechanisms such as allelopathy or alteration of soil conditions preventing germination (Huenneke and Thomson 1995). In general, rare species are considered to be those that are very uncommon and scarce, and classic ecological theory suggested that rare species are rare because they are poor competitors (Griggs 1940). More recently, ecologists developed a more complex view of species' rarity and its potential causes. Specifically, modern ecologists typically consider seven distinct forms of rarity based on the combination of a species' population size, range size, and associated habitat type (see Rabinowitz 1981). In a classic flora designed to classify species of the British Isles, Rabinowitz et al. (1986) determined that ~61% of species were rare in some way. Of these species, 7% were characterized by small population sizes, 15% were found across a small geographic range, and 59% had narrow habitat specificity. Research suggests that the risk of extinction for a given species based on its rarity could be influenced by its distinct type of rarity. A meta-analysis of marine fossil records spanning 500 million years concluded that geographic range was primarily influential to determining extinction, habitat specificity was secondarily influential, and population size had little influence on species extinction (Harnik et al. 2012). This suggests that concerns about how invasive plants will impact rare native plant species might focus primarily on rare species that have small geographic ranges and/or narrow habitats.

The potential for invasive plant species to outcompete rare native plant species depends upon the role of competition in plant species' rarity. It has been suggested that plant species with

narrow endemism, in particular, are highly sensitive to competition (Walck et al. 1999b). In particular, their typical association with stressful (i.e. resource poor) habitats (Baskin and Baskin 1988; Casazza et al. 2005) suggests that narrow endemics may be unable to compete for resources in more productive habitats (Drury 1974). Lavergne et al. (2004) compared 20 endemic plant species from the Mediterranean area with 20 of their more widespread congeners, plants within the same genus and with similar traits. As predicted, the narrow endemics were found in habitats of steeper, rockier slopes with significantly lower vegetation canopy height, lower cover of herbaceous and woody species, and lower numbers of associate species. Overall, a combination of specific biological traits such as smaller overall stature and lower inflorescence heights combined to suggest that the local endemics in this study may be poor competitors for shared resources such as space, light, and pollinators relative to their more common congeners (Lavergne 2004).

Other research comparing endemic and widespread congeners has suggested similarly that narrow endemic plant species may be restricted from less stressful habitats by poor competitive ability. By comparing the narrow endemic *Solidago shortii* (Short's goldenrod) with its widespread congener *S. altissima* (tall goldenrod), for example, Walck et al. (1999b) found that *S. shortii* allocates more of its total biomass below ground and has a much greater root-to-shoot ratio, which allows it to better tolerate very dry habitats where competition for water is not strong due to the absence of other tolerant species. In contrast, its larger overall aboveground size affords *S. shortii* the ability to overtop its neighbors and acquire more light in less stressful habitat that numerous other species can tolerate.

Large-scale floristic research also has supported the hypothesis that narrow endemic plant species are poor competitors. Specifically, Médail and Verlaque (1997) examined ecological characteristics of ~3000 total and 215 endemic plant species found across southeastern France and Corsica, a region characterized by high species richness and endemism. These researchers attributed the high levels of endemism in the region that they studied to the high variability of the area and the many extremes of habitats that occur here. A trend observed in their study was that the proportion of endemic plant species that comprised the local floral of an area decreased with increasing taxa richness. The authors attributed this trend to increased competition from co-occurring species in areas with high species richness. Notably, the studied region also has experienced a relatively low degree of invasion by non-native plant species, which the authors suggest could allow less competitive endemic species to thrive (Médail and Verlaque 1997).

Grime (1977) classically described the life history of species that are able to survive well only in stressful habitats as 'stress-tolerance.' Stress tolerant species exhibit a range of features that represent adaptations for fitness in conditions that promote limited productivity, such as slow growth rates, long-lived organs, and slow acquisition and turnover of carbon, water, and mineral nutrients (Grime 1977). However, while these traits enable persistence in stressful habitats, they also are associated with a sacrifice in competitive ability in more productive habitats (Grime 1977). Thus, stress-tolerant plant species are not necessarily rare because they lack competitive ability but rather because they have evolved to survive in stressful habitats, which also tend to be rare (Lloyd et al. 2002).

Mechanisms other than poor competitive ability also have been implicated as causal to plant species rarity. Some studies have shown, for example, that rare species are often

characterized by traits that promote relatively low reproductive rates, suggesting that recruitment may be highly influential to plant species rarity. In a greenhouse-based comparison of *Cirsium fontinale* (fountain thistle), a species endemic to low-nutrient serpentine seeps and streams in northern and central California, with its more widespread congeners, researchers concluded that the endemic species competed well with its congeners even when grown with high nutrient availability (Powell and Knight 2009). Rarity in this species may not be due to competitive ability but rather another cause. Related investigations found that fountain thistle produced relatively low numbers of flower heads and seeds per flower head and experienced a low rate of pollinator visits relative to a number of its congeners in their respective natural habitats (Powell and Knight 2009; Powell et al. 2011). Similarly, Lavergne et al. (2005) demonstrated that pollinator visits were reduced in the narrow Mediterranean endemic *Aquilegia viscosa* (sticky columbine) relative to its more widespread congener *Aquilegia vulgaris* (common columbine). Herbivory also was shown to influence fertility negatively in *A. viscosa* via flower and seed predation (Lavergne et al. 2005).

While the previously described studies and others suggest that poor competitive ability is not always the cause of plant species' rarity, some studies indicate that rare plants actually may be strong competitors in their habitats, an attribute that could increase their chances of persistence as suggested by Rabinowitz et al. (1984). Their comparison of 'sparse' grasses with more common grasses revealed that the rare species were stronger competitors, at least at the seedling stage. Specifically, seedlings of the sparse grass species grew most when surrounded by seedlings of common species rather than when grown in higher proportions of its own species. In a related assessment of species' ranges and competitive abilities within families, the Poaceae

species of New Zealand exhibited a strong positive correlation between those factors (Lloyd et al. 2002). However, the same study revealed an opposite association in the Rosaceae family. Specifically, critically endangered and rare *Acaena rorida* (common name unknown) was a stronger competitor than all of its more common congeners. Similarly, Powell and Knight (2009) found that rare *C. fontinale* was affected less by competition than five of its more widespread congeners. Collectively, such findings suggest that the classic ecological assumption that rare plants are poor competitors is not always true.

Invasive Plant Species as Competitive Threats to Rare Plant Species

Invasive species and rare species often co-occur (Brigham and Schwartz 2003; Farnsworth 2004; Seabloom 2006). In the northeastern U.S., for example, Farnsworth (2004) reported that 47% of rare plant species co-occur with invasive plant species in at least one of their occurrences. Seabloom (2006) reported a positive correlation between the number of imperiled species and the number of non-native species in California; this correlation was strongest when only invasive non-native species were considered.

Primarily, invasive species tend to be associated with areas characterized by high human population densities and anthropogenic disturbance (Farnsworth 2004; Seabloom 2006). For example, the presence of invasive species has been shown to correlate positively with human population size in New England (Farnsworth 2004) and California (Seabloom 2006). Invasive species also correlate positively with development of land for anthropogenic uses in California (Seabloom 2006). In contrast, areas characterized by low accessibility and anthropogenic disturbance are thought typically to provide a refuge for rare or endemic plants. However, many

of these areas have become invaded through time (DeGruchy et al. 2005; Seabloom 2006). For example, invasive *Lonicera japonica* has been found in the understory of old-growth oak forests that have not been disturbed in more than 250 years. Many protected ecosystems in our national parks also are threatened by the presence of invasive species (Hiebert and Stubbendieck 1993). It also has been hypothesized generally that stressful habitats are more resistant to invasion than habitats rich in resources (Alpert et al. 2000). However, research findings have suggested that some invasive plant species do establish and proliferate in stressful habitats (DeGruchy et al. 2005). For example, a study conducted in Peninsula National Park in Ontario, Canada, determined that plots of low to high productivity were invaded to equal degrees (DeGruchy et al. 2005).

Research investigating the direct impacts of invasive plant species on specific co-occurring rare plant species has been limited (Brigham and Schwartz 2003; Denoth and Myers 2006), and research examining competitive interactions between invasive and rare species specifically has been even more scarce. During a comprehensive search of published scientific literature to date, I found just 16 studies that specifically reported the findings of research examining the direct effects of invasive plant species on rare plant species (see Table 1.1). Of these studies, 12 studied or determined competition by invasive plant species as a factor influential to rare plant species (see Table 1.1), with the remaining four studies suggesting that the outcome of interactions between invasive and rare plant species are determined by mechanisms other than competition. Of the 12 studies that do support that competition occurs between invasive and rare plant species, findings are mixed. Just five of these studies support the assumption that invasive plants species threaten rare plant species through superior

competition for shared resources across habits and life stages. Four of the the remaining eight studies suggest that the effects of competition with invasive plant species depends on environmental conditions and life stages of rare species. The other three studies suggest that competition with invasive plant species have neutral effects on rare plants species (refer to Table 1.1).

Table 1.1 Sixteen published papers studying the direct effects of invasive species on rare plants.

Study	Native Species	Invasive Species	Experimental Design	Mechanism of Effect
Invasive Species; Superior Competitors				
Meyer and Fourdrigniez 2011	<i>Ophiorrhiza subumbellata</i>	<i>Miconia calvescens</i> (velvet tree)	in field biocontrol experiment	competition for light
Rojas-Sandavol and Melendez-Ackerman 2012	<i>Harrisa protoricensis</i> (higo chumbo)	<i>Megathyrsus maximus</i> (Gunea grass)	in field removal and comparison of sites study	competition for water
Walck et al. 1999	<i>Solidago shortii</i> T & G (short's goldenrod)	<i>Coronilla varia</i> (crown vetch)	in field removal and glasshouse competition study	competition
Rhazi et al. 2009	<i>Isoetes setacea</i> (spring quillwort)	<i>Bolboschoenus maritimus</i> (saltmarsh bullrush)	greenhouse competition study	competition for water
Huenneke and Thomson 1995	<i>Cirsium vinaceum</i> (Mescalero thistle)	<i>Dipsacus sylvestris</i> (teasel)	in field removal and greenhouse competition study	competition
Effects of Competition Dependent Upon the Situation				
Combs et al. 2011	<i>Astragalus sinuatus</i> Piper (Whited's milkvetch)	<i>Bromus tectorum</i> L. (cheat grass)	in field removal experiment	competition with early life stages
Lesica and Shelly 1996	<i>Arabis fecunda</i> (mt. sapphire rockress)	<i>Centaurea maculosa</i> (spotted knapweed)	in field removal experiment	competition with early life stages
Miller and Duncan 2004	<i>Pachycladon cheesemanii</i>	<i>Hieracium</i> sp. (hawkweed)	in field removal experiment	competition with early life stages
Hamilton et al 1999	<i>Nassella pulchra</i> (Backworth purple needlegrass)	annual non-native grasses	in field and greenhouse experiment	water availability determines effects of competition
Rare Species as Good Competitors				
Leege et al. 2010	<i>Trillium reliquum</i> Freeman (relict trillium)	<i>Lonicera japonica</i> (Honeysuckle)	in field removal study	no effect seen
Denoth and Myers 2006	<i>Sidalcea hendersonii</i> S. Wats (Henderson's checkerbloom)	<i>Lythrum salicaria</i> (purple loosestrife)	in field removal and greenhouse competition study	no effect seen
Powell and Knight 2009	<i>Cirsium fontinale</i> (fountain thistle)	<i>Cirsium vulgare</i> (spear thistle)	greenhouse competition study	rare plant superior competitor
Negative Ecological Effects but Not Due to Competition				
Thomson 2005	<i>Oenothera deltoides</i> spp. <i>howelli</i> (antioch dunes native primrose)	<i>Bromus diandrus</i> (ripgut brome)	In field removal experiment	dead thatch preventing germination
McKinney and Goodell 2010	<i>Geranium maculatum</i> (spotted geranium)	<i>Lonicera maackii</i> (bush honeysuckle)	in field removal experiemnt	reduction of pollinator visits
Dangremond et al. 2010	<i>Ammophila arenaria</i> (European beachgrass)	<i>Lupinus tidestromii</i> (Tidestrom's lupine)	in field seed predation study	apparent competition
Kellner et al. 2012	<i>Rosa mollis</i> (soft downy rose)	<i>Rosa rugosa</i> (Japanese rose)	DNA and morphological traits comparison	hybridization decreasing fitness

Collectively, the five published studies that evidence the potential for invasive plant species to outcompete rare plant species across all habitats and life stages suggest that competition can involve various resources and species of various habits and influence a variety of traits influential to fitness. For example, Meyer and Fourdrigniez (2011) found that interspecific competition for light by the invasive tree *Miconia calvescens* (velvet tree) negatively affected the rare shrub *Ophiorrhiza subumbellata* (common name unknown) in the understory of montane cloud forests of Tahiti, French Polynesia. Specifically, the successful introduction of a fungal pathogen for biological control of *M. calvescens* increased light availability in the forest understory, which was associated with increased flower and fruit production, seed recruitment, and juvenile recruitment of *O. subumbellata* (Meyer and Fourdrigniez 2011). Via an experiment involving partial and complete removal treatments, Rojas-Sandavol and Melendez-Ackerman (2012) elucidated that competition by the invasive grass *Megathyrus maximus* (Guinea grass) for water reduced survival, growth, and reproduction of the rare cactus *Harrisia portoricensis* (higo chumbo) on Mona Island, Puerto Rico, USA. In another field removal study, Walck et al. (1999a) determined that competition from the invasive forb *Coronilla varia* (crown vetch) and *Festuca arundinacea* (tall fescue) reduced the number of flowering ramets produced by the extremely rare herb *Solidago shortii* in an early successional site in northeastern Kentucky, USA. The same study also reported the findings of a related greenhouse experiment in which *S. shortii* was grown without and with various densities of the commonly co-occurring invasive grass *F. arundinacea*. These findings suggested that both relative yield and flowering of *S. shortii* were suppressed by competition with *C. varia* and *F. arundinacea* (Walck et al. 1999a). A greenhouse experiment also examined competition between

the rare quillwort *Isoetes setacea* (spring quillwort) and invasive *Bolboschoenus maritimus* (saltmarsh bullrush), two plants that co-occur in temporary pools in southern France (Rhazi et al 2009). Groups of *I. setacea* were planted in monoculture or in competition with *B. maritimus*. The accumulation of biomass in underground tubers was measured for both species across different hydrological conditions, and types of substrate. The invasive *B. maritimus* accumulated much greater tuber biomass than *I. setacea* across all treatments along with decreasing performance of the rare species when grown in competition (Rhazi et al. 2009). Although the driest conditions greatly reduced the competitive advantage of *B. maritimus*, competition never effected the invasive species performance while always negatively effecting the rare *I. setacea* (Rhazi et al. 2009). In another greenhouse study, Huenneke and Thomson (1994) concluded that competition with the invasive species *Dipsacus sylvestris* (teasel) negatively affected rare *Cirsium vinaceum* (Mescalero thistle) with which it co-occurs in the Lincoln National Forest in California. Specifically, a greenhouse-based competition experiment was used to demonstrate that interspecific competition greatly reduced rosette diameter of *C. vinaceum* as a measure of its growth (Huenneke and Thomson 1994).

Four additional studies suggest that competition with invasive species can affect rare species in certain circumstances, with competition limited to early life stages or only under specific resource availability. For example, Combs et al. (2011) demonstrated that recruitment of *Astragalus sinuatus* (Whited's milkvetch) in sagebrush steppe communities of Washington greatly increased when the co-occurring invasive grass *Bromus tectorum* (cheatgrass) was removed. The authors hypothesized that *B. tectorum* depletes moisture at the soil surface and suppressed *A. sinuatus* recruitment; however, the long tap root of fully developed *A. sinuatus*

would allow adults of this species to avoid competition for water by the invasive grass (Combs et al. 2011). Another field-based removal experiment also found that competition with an invasive species affected recruits of a rare plant species but not later life stages (Lesica and Shelly 1996). Specifically, researchers found that the presence of invasive *Centaurea maculosa* (spotted knapweed) in open rocky sites of the foothills in southwestern Montana did not influence survivorship, fecundity, or growth of rare *Arabis fecunda* (Mt. Sapphire rockcress) adults, but increased the mean age of its populations through time via suppression of germination and early establishment (Lesica and Shelly 1996). Miller and Duncan (2004) utilized a field-based removal experiment in rocky outcrops of alpine grasslands in New Zealand to test the competitive effects of invasive *Hieracium* sp. (hawkweed) on the rare herb *Pachycladon cheesemanii* (common name unknown). In their experiment, seeds of the rare species were added to plots established in suitable habitat for *P. cheesemanii*. Removal of *Hieracium* from plots resulted in increased recruitment and survival of *P. cheesemanii* seedlings but the influence of the invasive species on plants of later life stages was not assessed (Miller and Duncan 2004).

In other studies investigating the effect of invasive plant species on rare species, resource availability rather than plant life stages was an influential factor in determining competitive effects. For example, Hamilton et al. (1999) determined that water availability influenced competition between invasive annual grasses and the rare bunchgrass *Nassella pulchra* (Barkworth purple needlegrass) in grasslands of California. Specifically, with a field-based removal experiment, these researchers showed that both aboveground biomass and seed production of *N. pulchra* were suppressed by the presence of invasive grasses when water was a limiting resource in the system (Hamilton et al. 1999). An associated greenhouse experiment

examined the effects of drought which also favored the rare species. Above ground biomass was diminished greatly in the invasive annual grasses but no difference was seen in density of seedlings or accumulation of biomass for *N. pulchra* (Hamilton et al. 1999). The invasive annual grasses are better competitors for water when water is a limiting resource and but are not as drought resistant as the rare *N. pulchra*, a specific range of water availability favored the invasive species.

In contrast to previously described research reports, three studies suggest that invasive plant species have neutral effects on rare plant species. Leege et al. (2010) studied the invasive *L. japonica* effects on the rare trillium *Trillium reliquum* (relict trillium) in understory hardwood forest ecosystems in Georgia. The removal of *L. japonica* from experimental plots had no effect on leaf area as a growth metric of *T. reliquum* (Leege et al. 2010). Research conducted by Denoth and Myers (2007) in wetlands of the Pacific Northwest similarly determined that invasions of *Lythrum salicaria* had no effect historically on the frequency of rare *Sidalcea hendersonii* (Henderson's checkerbloom) in their shared habitat. In a related manipulative experiment, removal of *L. salicaria* had the same effect on both stem height and biomass accumulation of *S. hendersonii* as removal of co-occurring native competitors (Denoth and Myers 2007). Consequently, any replacement of native plant species by *L. salicaria* in these habitats did not increase competitive pressure on *S. hendersonii*. In an associated greenhouse-based experiment, the rare species was more negatively influenced by competition with native species than with the invasive species (Denoth and Myers 2007). Greenhouse experimentation was used by other researchers to show that rare *Cirsium fontinale* (fountain thistle) accumulates the same amount of biomass when grown with intraspecific competition as when grown with

interspecific competition from invasive *Cirsium vulgare* (spear thistle; Powell and Knight 2009). Collectively, these results refute typical assumptions that invasive species are superior competitors compared to the native species they may replace or the rare species they are co-occurring with.

The four final research studies of the 16 examining interactions between invasive and rare plant species have supported the assumption that invasive species negatively impact rare species, however these studies show that factors other than competition are responsible. For example, Thomson (2005) found that recruitment rates of rare *Oenothera deltoides* ssp. *howellii* (Antioch Dunes native primrose) increased in grasslands following removal of the invasive grass *Bromus diandrus* (ripgut brome). However, this response only occurred when the removal treatments included the removal of dead *B. diandrus* thatch. Thus, active competition for resources from *B. diandrus* did not influence the rare species in these systems (Thomson 2005). In another study, McKinney and Goodell (2010) determined that presence of the invasive shrub *Lonicera maackii* (bush honeysuckle) decreased pollinator visits to flowers of *Geranium maculatum* (spotted geranium) in forests of Ohio, which suggested that invasive species was outcompeting the rare species for shared pollinators. However, pollinator visits to *G. maculatum* decreased similarly even when flowers of *L. maackii* were removed. Consequently, the researchers suggested that reduced light availability when *L. maackii* was present caused the associated decrease in pollinators by reducing flower access and/or visibility (McKinney and Goodell 2010). Invasive plant species have been shown to negatively impact rare plant species through apparent competition, the presence of the invasive plant species increases pressure from herbivores or predators on the rare plant species. Specifically, the invasion of *Ammophila arenaria* (European

beachgrass) in California foredune grasslands reduces establishment and long-term population growth of rare *Lupinus tidestromii* (Tidestrom's lupine) by attracting granivorous *Peromyscus maniculatus* (deer mice) to their shared habitat (Dangremond et al. 2010). Additionally, *A. arenaria* also is thought to stabilize the dune landscape, reducing wind disturbance upon which *L. tidestromii* recruitment depends (Dangremond et al. 2010). Hybridization also can reduce recruitment of populations of rare plant species, in particular when these species are closely related. For example, a study comparing co-occurring populations of invasive *Rosa rugosa* (Japanese rose) and rare *Rosa mollis* (soft downy rose) in Germany determined that 45% of the supposed *R. mollis* population was actually comprised of hybrid individuals. Low genetic diversity and seed set of this population was a result of hybridization rather than competition for shared resources with the invasive species (Kellner et al. 2012).

Although there is no singular trait shared universally by all invasive plant species or all rare plant species that determines the outcomes of their interactions, the previously described research collectively suggests that competitive ability can play a role in interactions between invasive and native species, but that other mechanisms also can influence interactions between their interactions. Research conducted by Witkowski (1991) suggests that in some situations, both competition and other mechanisms can simultaneously influence such interactions. Specifically, Witkowski (1991) describes that replacement of native *Protea repens* (common sugarbrush) by the invasive shrub *Acacia saligna* (orange wattle) in the South African fynbos involves superior competitive ability of the invasive species, but also comparatively high seed production by *A. saligna* and its alteration of the local fire regime in a way that promotes its survival relative to that of *P. repens*. I suggest that similar interactions and combinations of

mechanisms can determine the outcome of interactions between invasive and rare species.

Understanding the role that competition plays in interactions between invasive and co-occurring rare plant species can provide guidance for the development of management and conservation plans. Although removal of invasive species due to their assumed ability to outcompete rare species is a common plan of action, in some situations (see Denoth and Myers 2006), disturbance caused by such removal could inadvertently favor the invasive species and exacerbate its proliferation. Thomson (2005) concluded that the most successful regime for removing invasive *B. diandrus* from habitats in which it co-occurs with rare *O. deltoides* involved removal in a manner well timed with germination of the rare species. Such conclusions exemplify the idea that situations in which removal of invasive species is warranted also could benefit from increased information about the specific ways in which invasive species influence co-occurring rare plants. Certainly, competition is an important interaction to consider when evaluating the effects of invasive plant species on rare plant species. In my review, more than 80% of relevant studies (=13 of 16) demonstrate that competition occurs between co-occurring invasive and rare plants. However, the making the assumption that invasive plant species outcompete rare plant species due to superior competitive ability because of the many cited studies demonstrating detrimental effects is short-sighted, and this assumption could negatively impact the management and conservation of rare plant species.

CHAPTER 2

ACCESSING THE EFFECTS OF INVASIVE *LIGUSTRUM SINENSE* AND *LONICERA JAPONICA* ON RARE AND FEDERALLY THREATENED *SCUTELLARIA MONTANA*

Introduction

Invasive plant species are considered a threat to the conservation of many rare plant species (Wilcove and Master 2005). Yet, few studies address the direct effects of invasive species on rare plants (refer to Chapter 1; Denoth and Myers 2006; Huenneke and Thomson 1995; Thomson 2005). Instead, the negative effects of invasive species on rare species has been historically inferred from studies that compare invaded sites to non-invaded sites or from observations of the abundance of invasive species in a rare species' habitat (Gorchov and Tiesel 2003; Thomson 2005). Similarly, in ecology it has been assumed that invasive species generally outcompete rare plants; an assumption due to the importance of competition in invasions (Crawley 1990) and the detrimental effects of these invasions. However, the competitive ability of invasive species relative to that of rare species often also has been assumed without direct testing (Baker 1974, Crawley 1990; Drury 1974; Griggs 1940, Vila and Weiner 2004).

A recent meta-analysis by Vila and Weiner (2004) does suggest that invasive plant species are generally superior competitors relative to native species. However, a related meta-analysis by Daehler (2003) suggests that the impacts of invasive plant species on native plant species do not always involve differences in their competitive abilities. My review of peer-

reviewed research of the direct impacts of invasive species on rare species suggested that competitive ability can play a role in interspecific interactions between invasive and rare plants, but that other mechanisms also can be influential (see Chapter 1). However, given the limited number of studies examining the direct effects of native plant species on rare plant species, there remains a need for more research investigating such effects (Walck et al. 1999a).

Scutellaria montana Chapm. (large-flowered skullcap) is a rare plant species that has been afforded federal protection under the U.S. Endangered Species Act since 1986 (USFWS 1986). This species was first described in 1878 from occurrences on mountains near Rome, Georgia (Floyd County; Chapman 1878). Between its discovery and federal listing, only four more collections of *S. montana* were documented over a range of two counties in northwestern Georgia (Gordon and Walker counties) and two in Tennessee (Hamilton and Marion counties; USFWS 1985). When first listed as endangered, only about 7000 total plants across 10 occurrences were known (USFWS 1985). Recovery objectives for downlisting *S. montana* called for documentation of 15 protected or managed self-sustaining populations or 25 total protected or managed populations with 10 of those being self-sustaining (USFWS 1996). In 2002, *S. montana* was reclassified as threatened because approximately 48,000 individuals across 32 sites had been documented by that time in nine counties in Georgia and four in Tennessee (USFWS 2002).

Even though it has been downlisted from endangered to threatened, *S. montana* remains relatively rare and endemic to a small geographical range from northwestern Georgia to southeastern Tennessee (USFWS 2002). Rabinowitz (1981) classically described seven types of species rarity with geographical range, habitat specificity, and population numbers as

determining characteristics. In a recent meta-analysis of 500 million years of marine fossil records, Harnik (2012) concluded that geographical range is the most influential form of rarity in determining extinction. This is especially concerning for *S. montana* considering that about 80 percent of the known individuals of this species are found within an area of only 27,000 acres in the Tennessee River Gorge (USFWS 2002). Harnik (2012) also determined that rare species characterized by habitat specificity are second-most at risk for extinction. This is concerning for *S. montana* since its associated habitat is becoming increasingly scarce due to land-use changes (USFWS 1986). Specifically, mature oak-hickory hardwood forests with well drained acidic soils are typically distinct from the typical forest of the region and have been described as highly important where *S. montana* occurs (Bridges, as cited by USFWS 2000; Fail and Sommers 1993; Sutter 1993; USFWS 1985).

The scarcity of the preferred habitat of *S. montana*, in particular, was cited by the U.S. Fish and Wildlife Service as the primary threat to the continued survival of *S. montana* when it was listed originally as endangered in 1986 (USFWS 1986). However, upon reclassifying *S. montana* as threatened in 2002, the possible negative effects of invasive species like *Ligustrum sinense* (Chinese privet) and *Lonicera japonica* (Japanese honeysuckle) on the species also were recognized (USFWS 2002). Both *L. sinense* and *L. japonica* are members of the ‘dirty dozen,’ a list that describes the invasive species of highest concern in the southern Appalachians given there demonstrated proliferation in habitats of that region (Kuppinger 2000).

Research of *L. sinense* has shown the presence of this species is associated with reductions in native species richness and abundance of native plant species in habitats where it invades (Wilcox and Beck 2007). The magnitude of reductions in native species diversity,

richness, and evenness attributed to *L. sinense* invasions have been directly linked to the percent coverage of *L. sinense* in invaded habitats (Hart and Holmes 2013; Merriam and Feil 2003).

Related manipulative experiments have demonstrated increases in both native stems and overall species diversity of communities following *L. sinense* removal (Merriam and Feil 2003).

Research of *L. japonica* also has shown the presence of this species to be associated with decreased diversity in the habitats where it invades (Oosting 1942). Invasion by *L. japonica* has resulted in its dominance in the understory and herbaceous layer as well as altering native species coverage and composition (Barden and Matthews 1980; Oostings and Livingston 1964). In a study examining local extinctions and colonization the presence of *L. japonica* was shown to decrease diversity in the local plant community by preventing local colonizations by native species (Yurkonis and Meiners 2004).

Although the competitive ability of neither *L. japonica* nor *L. sinense* relative to co-occurring native species has rarely been assessed directly, their demonstrated proliferation and dominance in forest understories that they invade suggests potential competitive superiority. Research has evidenced that *L. sinense*, in particular, negatively affected the individual-level performance of 20 native species (Greene and Blossey 2012). Although the scope of the study could not determine the exact mechanism by which the performance of native plants was suppressed, competition for light was the proposed cause (Greene and Blossey 2012). This hypothesis is supported by a comparative study of *L. sinense* to *Forestiera ligustrina* (upland swampprivet), a confamilial native shrub that occurs in the forests *L. sinense* is invading. In this study, invasive *L. sinense* had a higher ratio of leaf area to total plant biomass and a more

evergreen habit than native *F. ligustrina*, giving *L. sinense* a spatial and temporal advantage in competition for light (Morris et al. 2002).

In contrast, research has suggested that the invasiveness of *L. japonica* may not be explained by superior competitive ability relative to co-occurring native species. Specifically, Davison and Forman (1992) suggested that native *Podophyllum peltatum* (mayapple) competed more strongly for light than *L. japonica* when light became more available in the forest understory following disturbance. Although both species expanded their coverage following canopy opening, the increased coverage by *L. sinense* did not result in a reduction in diversity in the herbaceous layer whereas the increased coverage of *P. peltatum* was associated with reduced diversity. Surrrette and Stephens (2008) came to similar conclusions in their examination of a forest in Mississippi invaded by *L. japonica*. Although low overall species diversity was correlated with high percent coverage of *L. japonica*, abiotic factors such as disturbance, decreased fire frequency, and compacted soils were implicated as more influential to the decline in overall species diversity than the presence of *L. japonica* (Surrrette and Stephens 2008). In addition, research by Leege et al. (2010) that used growth parameters to evaluate interspecific competition between *L. japonica* and rare native *Trillium reliquum* (relict trillium) found no effect of *L. japonica* on the rare species

Given the hypothesis of the poor competitive ability of *S. montana* (Patrick et al. 1995) and its often cited preference of relatively open understory habitat (Mulhouse et al 2008; Nix 1993; Patrick et al. 1995; Sutter 1993), it may be assumed that both *L. sinense* and *L. japonica* could threaten the continued survival of *S. montana*. However, Hopkins (1999) reported that there was no correlation between canopy luminance and *S. montana* biomass at the organismal

level in the Tennessee River Gorge in Marion County, Tennessee, which refutes this hypothesis. Specifically, Hopkins (1999) found that *S. montana* plant size was associated positively with herbaceous coverage of the forest understory. More direct experimentation is required to improve understanding of the potential competitive effects of *L. sinense* and *L. japonica* on *S. montana* at both organismal and population levels.

To directly investigate the impacts of invasive *L. sinense* and *L. japonica* on rare *S. montana*, I conducted a manipulative experiment with fully-crossed invasive species and herbivory treatments. This research was designed primarily to investigate the response of *S. montana* to interspecific competition with invasive species through removal treatments. Herbivore exclosures were included in the research design to help isolate the effects of competition from the effects of herbivory, which also could negatively influence the success of *S. montana* (Kile 2011), and to isolate the effects of competition from apparent competition via the potential attraction of herbivores to nearby *S. montana* by invasive species presence. To address these goals, I aimed specifically to: 1) quantify the main effects of interspecific competition with invasive species on *S. montana* individuals and 2) determine the effects of interactions between the presence of invasive species and herbivory on *S. montana* individuals. I hypothesized that interspecific competition with *L. sinense* and *L. japonica* would negatively affect *S. montana* by reducing individual-level growth and fecundity that negative impacts would be exacerbated by concurrent herbivory.

Methods

Study Species

The perennial herb *S. montana* is described as having solitary, square hairy stems that can range from 30 to 60 cm tall (Patrick et al. 1995; USFWS 2002). Phyllotaxis is opposite with lanceolate to ovate leaves that are 2- to 10-cm long and 3- to 5-cm wide (Coder 1994; Patrick et al 1995). Leaves have a 1- to 2-cm-long petiole with crenate to serrate margins (USFWS 2002). An important distinguishing characteristic of *S. montana* compared to its commonly co-occurring congeners *S. ovata*, *S. pseudoserrata*, and *S. elliptica* is the pubescence of its leaves. The leaf surface of *S. montana* has glandular and non-glandular pubescence that covers the entire upper and lower leaf surface giving the leaves a velvety feel, while the pubescence or glands of congeners does not cover the entire surface (Patrick et al. 1995; USFWS 2002). The florescence also distinguishes *S. montana* since it has the largest corolla of species in its genus (Patrick et al. 1995) at 2.6- to 3.5-cm in length (USFWS 2002). The flowers of *S. montana* are irregular with two joined petals that form an erect white-fading-to-blue tube with a double lip at the top. The upper petal forms a three-lobed hood that caps the flower (Patrick et al. 1995; USFWS 2002). The inflorescence is a terminal, leafy-bracted raceme (USFWS 2002).

The overall low number of *S. montana* individual is thought to be in part due to its low reproductive success. During a multi-year survey, Hopkins (1999) determined that *S. montana* is pollen limited; many plants were not pollinated and those that were often had very few pollen grains deposited. Although different types of pollinators, such as several species of bees (Johnson 1991), butterflies, wasps, and hummingbirds (Kemp and Knaus 1990), have been observed visiting *S. montana* flowers, studies suggest that overall visits from pollinators are

infrequent (Cruzan 2001, Hopkins 1999). A specialist pollinator adapted to *S. montana* has not been identified and the lack of a specialist pollinator and low pollinator services are thought to limit its seed set (Cruzan 2001; USFWS 2002). The proportion of *S. montana* flowers that form fruits has been shown to be fairly low, (i.e., 30-44 percent as reported by Kemp and Knauss 1990; 10 percent as reported by Kemp 1987) relative to that of its congeners (i.e., 75-93 percent as reported by Collins according to USFWS 2000).

Study Location

Our study site was located on property owned by the Volkswagen Group of America (Herndon, VA) near their manufacturing facility in Chattanooga, Tennessee, in the Enterprise South Industrial Park. Adjacent to the Volkswagen property is the ~1100- ha (2,800-acre) Enterprise South Nature Park. Two distinct occurrences of *S. montana* are found on Volkswagen's property in hardwood forest adjacent to the western edge of the Nature Park. Each occurrence is surrounded by a 6-ft chain-link fence and both are managed to provide protection for the species (Personal communication with Enterprise South Nature Center park rangers). I used one of these occurrences in this study. The chosen occurrence is comprised of about 250 total individuals across two distinct groups of plants with approximately 100 m between the groups. The more northern group occurs in a relatively sparse understory, while the more southern group occurs in a denser understory. Both invasive species are fairly ubiquitous throughout the site. However, *L. japonica* is the more dense invasive species in the southern group and *L. sinense* is the more dense invasive species in the northern group of *S. montana*. Neither invasive species dominate cover in the understory but both have the highest stem count

in their respected group and are observably very prominent species with the entire study site. During the summer of 2011, evidence of deer presence and herbivory were observed personally within the fenced area. Access to the site by deer was possible through gaps in the fence caused by treefalls resulting from severe weather events earlier in the year.

Experimental Design

Twelve 1-m² plots were identified and temporarily flagged in the summer of 2011 within the southern group of *S. montana* in the study site. Plots were established such that each plot included at least three individuals of *S. montana*; more individuals were included in plots when possible. There were four possible treatment combination of interacting invasive species and herbivory treatments: 1) plots accessible to non-insect herbivores with invasive plant species present (control), 2) plots accessible to non-insect herbivores with invasive plant species removed. 3) plots exclosed from non-insect herbivores with invasive plant species present, and 4) plots exclosed from non-insect herbivores with invasive plant species removed. Treatments were assigned randomly to the 12 plots. This resulted in three plots for each treatment.

Herbivore exclosures were installed in early April 2002. Exclosures consisted of 1-m³ frames constructed of 0.5-in-diameter PVC (polyvinyl chloride) pipe connected at the corners with PVC corner joints. Frames were then wrapped with 1-in-aperture hex-wire mesh (i.e., chicken wire) secured to the frames with cable ties as described by Benson (2012) and modified from Frankland and Nelson (2003). Additional 1-m² flat PVC squares were constructed to permanently mark non-exclosures and help control for the presence of PVC. This facilitated the identification of invasive plants for removal from treatment plots throughout the study

duration. Exclosures and PVC squares were staked to the ground with 8-in tent stakes attached with cable ties.

Invasive species removal treatments involved cutting individuals at the soil surface to remove biomass while minimizing soil disturbance (Lesica and Shelly 1996). The first removal treatment for the 2012 growing season occurred in early May; *S. montana* plants had emerged but had not yet flowered. Due to the exhibited persistence and lack of effectiveness of a single removal treatment (Hanula et al. 2009), plots were checked throughout the growing season every two to three weeks and any additional sprouting or growth of invasive species were also removed. In 2013, the first removal treatment occurred in early April before *S. montana* individuals emerged and was continued through the growing season.

The northern group of *S. montana* within the study site was discovered in spring 2012 and added to my study at that time. Because these *S. montana* plants had emerged before their inclusion in this study, some individuals had already been browsed. Most notably, three individual plants that had been browsed were included in plots with assigned herbivory exclosure treatments. When these browsed plants were removed from our analyses there were no qualitative differences compared to when they were included in the analysis. For this reason I included them in my analysis and presented the results in which they were included. Given the size and spatial distribution of plants in the northern group, I was able to established 14 total plots in that location, three plots for each the exclosure treatments and four plots for each of the non-excluded treatments.

All individual *S. montana* included in my study were labeled with metal tags to enable identification for monitoring in May 2012. In total, 106 *S. montana* individuals were included in

the study in 2012, and 108 individuals were included in the study in 2013. In total, individual across both southern and northern groups comprised seven non-exclosed control plots with invasive species present, seven non-exclosed plots with invasive species removed, six exclosed plots with invasive species present, and six exclosed plots with invasive species removed.

Data Collection

Data were collected both early and late in the growing season for the 2012 and 2013 growing seasons. The first data collection coincided with the first observed flowering of *S. montana*, which occurred in mid-May 2012 and early June 2013. In 2012 data was also collected in June. Flowering of *S. montana* in 2012 was earlier than expected so data was also collected in June as was previously anticipated. The second data collection coincided with the first observed senescence, which occurred in mid-September during both years. Data collected included measurements of stem height and counts of the numbers of leaves, branches, stems, and flowers of each *S. montana* individual in the study plots. Each plant also was classified according to its life stage as either juvenile (<10-cm tall without evidence of reproduction) or adult (<10-cm tall with evidence of reproduction or \geq 10-cm tall) in accordance with definitions used by Benson (2012). The presence of damage to aboveground biomass such as stems or leaves also was recorded and attributed to either browsing or insects. Plants were considered browsed if biomass such as portions of stems and whole leaves were missing. Insects were blamed if partial leaf area was missing.

Data Analysis

To examine the influence of invasive species and herbivory on growth of *S. montana* individuals, the percent changes in stem height and numbers of leaves during the 2012 growing season were calculated as the difference between the September and May measures of these variables for each plant divided by its May value and multiplied by 100. Percent change in stem height during the 2013 growing season was calculated similarly from early June to September. Because no significant difference was seen in percent change in leaf numbers in year 2012, no significant differences were seen between treatments in a similar herbivory study by Benson (2012), and the numbers of leaves on *S. montana* are highly variable (personal observation; Benson 2012; Boyd et al. 2010), I did not count leaves over the 2013 growing season. To examine the influence of invasive species and herbivory on individual plant growth between years, the percent change in stem height from 2012 to 2013 was calculated for both the early and late growing season as the difference between the 2013 and 2012 measures of this variable for each individual plant divided by its 2012 value and multiplied by 100. To examine the influence of invasive species and herbivory on fecundity, the percent change in the number of flowers produced per individual plant between years was similarly calculated from early-season data. Mean percent changes of all variables of individual plants were averaged within plots.

Because branching due to herbivory seems to be a typical response in *S. montana* (herbivory removes apical dominance which results in branching), I examined the influence of invasive species and herbivory on plant architecture. The percentage of *S. montana* individuals that experienced branching or had more than one stem in each plot also was calculated for both the 2012 and 2013 growing seasons. Similarly, the percentage of total plants browsed in each

plot, as well as the percentage of plants of various life stages – adult, flowering, and vegetative (i.e., non-flowering) – that were browsed also were calculated for the 2012 growing seasons. No herbivore damaged was observed for any *S. montana* individual included in this study in 2013, which was expected because gaps in the chain link fence surrounding the studied *S. montana* occurrence resulting from storm damage were repaired. These repairs were not planned at the initiation of our study. As a result, I analyzed the percentage of total plants and plants of different life stages browsed in 2012 only. In addition, plants that were present during both the 2012 and 2013 growing seasons were classified as either experiencing an increase, decrease, or no change in their numbers of flowers. To examine the influence of invasive species and herbivory on influencing reproductive effort, the mean percentage of plants that experienced an increase in flowering and the mean percentage of plants that experienced a decrease in flowering from 2012 to 2013 were calculated for each treatment combination.

A two-way step-wise analysis of variance (ANOVA) was conducted to evaluate the main effects and interactions of invasive species and herbivory treatments on *S. montana*, specifically plant architecture, flowering, and growth. Because there was a significant difference between plants occurring in the northern and southern groups of our study site for some calculated variables, group was treated as a random factor in the model. In the analysis, factors were removed in a stepwise manner with the least significant factor beginning with interactions and then addressing main effects removed from each step. If an effect had a $P \leq 0.15$ it was kept in the model because it was considered influential. The last step in which a factor was included in the model was the model from which the F- and P- values were determined. Effects were still

only reported as significant if they had a $P \leq 0.05$. All statistical analyses were performed using IBM SPSS Statistics Version 20 software (IBM Corp., Armonk, NY).

Results

Individual-level Growth

The mean percent change in stem height during the 2012 growing season differed significantly between the northern and southern groups of *S. montana* in our study site ($F_{1,20} = 6.738$, $P = 0.017$) and was influenced significantly by the presence of invasive species ($F_{1,20} = 7.028$, $P = 0.015$). In contrast, mean percent change in stem height during the 2012 growing season was not influenced by non-insect herbivory or interactions ($P > 0.28$ in all cases). Across invasive species and herbivory treatments, the southern group of plants experienced a small decrease in stem height while the northern group of plants experienced an increase in stem height during the 2012 season (-1.23% versus 6.46%; Figure 2.1). Across specific locations and herbivory treatments, *S. montana* individuals exhibited a greater percent increase in stem height when invasive species were present than when invasive species were removed (7.19% versus -0.62% respectively; Figure 2.2).

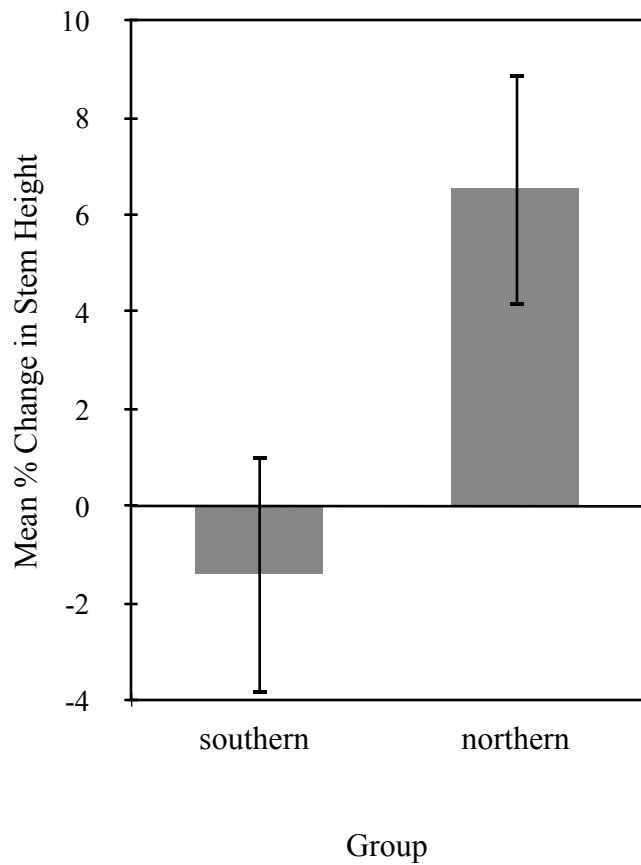
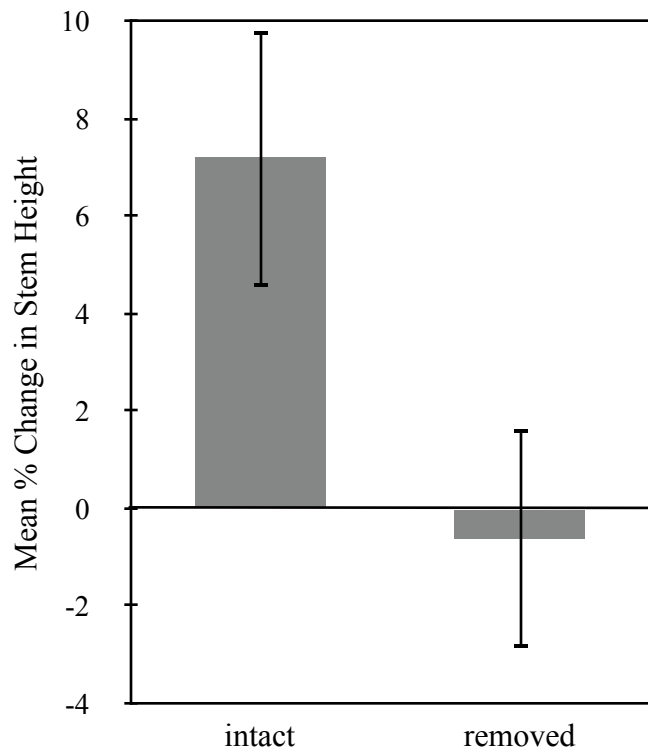


Figure 2.1 Mean percent change of stem height (+SE) of *S. montana* during the 2012 growing season comparing effects of group



Invasive species

Figure 2.2 Mean percent change of stem height (+SE) of *S. montana* during the 2012 growing season comparing effects of removal

In 2013, mean percent change in stem height during the growing season did not differ significantly between groups, herbivory treatments, or invasive species treatment levels ($P > 0.20$ in all cases). Similarly, the mean percent change in leaf number during the 2012 growing season did not differ significantly between groups, herbivory, removal treatments, or interactions ($P > 0.15$ in all cases).

The mean percent change in stem height of *S. montana* individuals from the beginning of the growing seasons between 2012 to 2013 was significantly influenced by the interaction of plant location and herbivory treatments ($F_{3,22}=9.328$, $P<0.001$; Figure 2.3). Specifically, individuals exposed to herbivores (i.e., in non-exclosure plots) in the southern group experienced a decrease in mean stem height between years, compared to an increase in all other treatment combinations. However, the mean percent change in stem height late in the growing seasons was not influenced significantly by the main or interactive effects of treatments ($P>0.40$ for all cases).

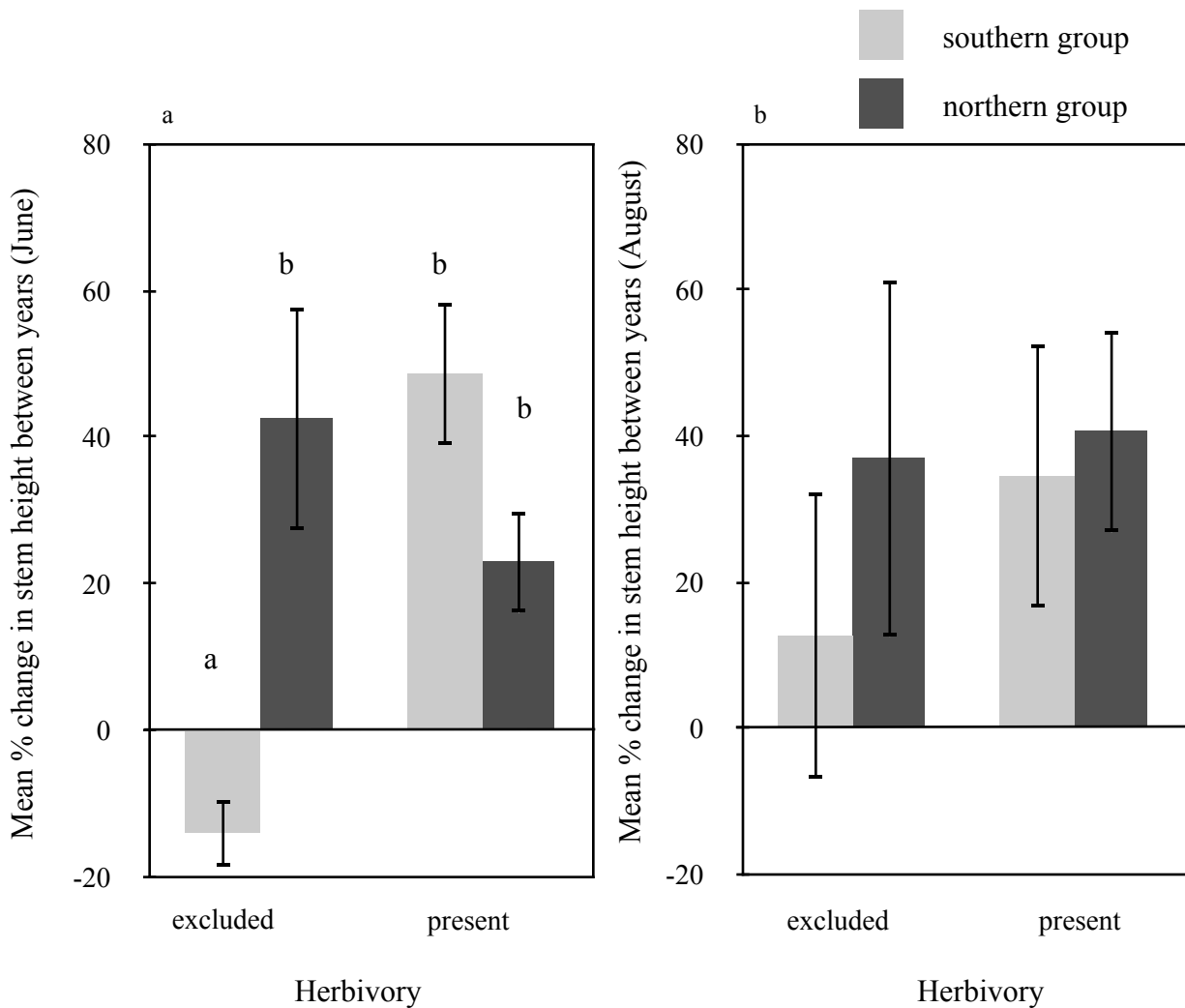


Figure 2.3 Percent change in stem height (+SE) between years for June (a) and August (b) showing the difference due to the interactive effect of herbivory and site

Flowering and Reproductive Effort

The mean percent change in the number of flowers produced by *S. montana* individuals from 2012 to 2013 did not differ significantly between groups, herbivory, or invasive species treatment levels ($P > 0.175$ in all cases). The mean percentage of total *S. montana* plants per plot that experienced decreased flowering from 2012 to 2013 differed significantly between the northern and southern groups in my study site ($F_{1,22} = 12.069$, $P = 0.002$) and was influenced significantly by herbivory ($F_{1,22} = 8.767$, $P = 0.007$). Specifically, a greater percentage of total plants experienced decreased flowering between years in the southern group, the group with the much denser understory, than in the northern group (13.7% versus 42.4% respectively; Figure 2.4).

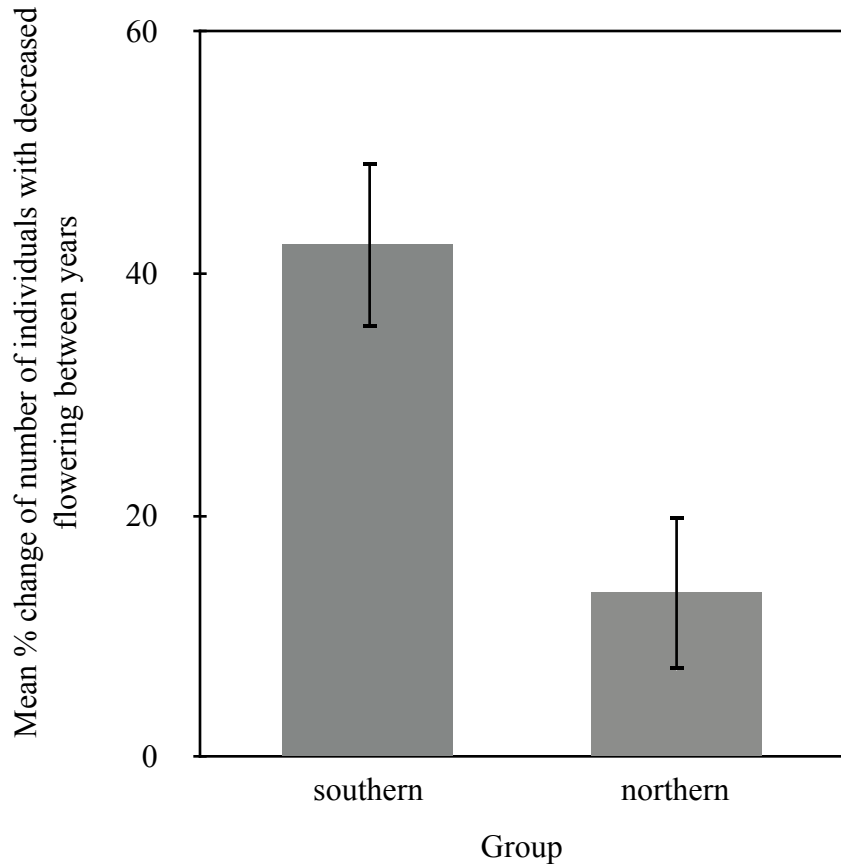


Figure 2.4 Mean percent of flowers per plot decreasing flowering (+SE) in *S. montana* between the 2012 and 2013 growing season comparing groups

Across groups and invasive species treatments, a greater percentage of plants protected from herbivores (i.e., in exclosed plots) experienced decreased flowering from 2012 to 2013 than plants accessible to herbivores (14.7% versus 39.2% respectively; Figure 2.5). Although not significant ($F_{1,24}=2.724$, $P=0.112$), plots accessible to non-insect herbivores (i.e., non-exclosed) housed a higher percentage of plants that experienced increased flowering from 2012 to 2013 in comparison with plots protected by herbivores (57.7% versus 32.8%, respectively).

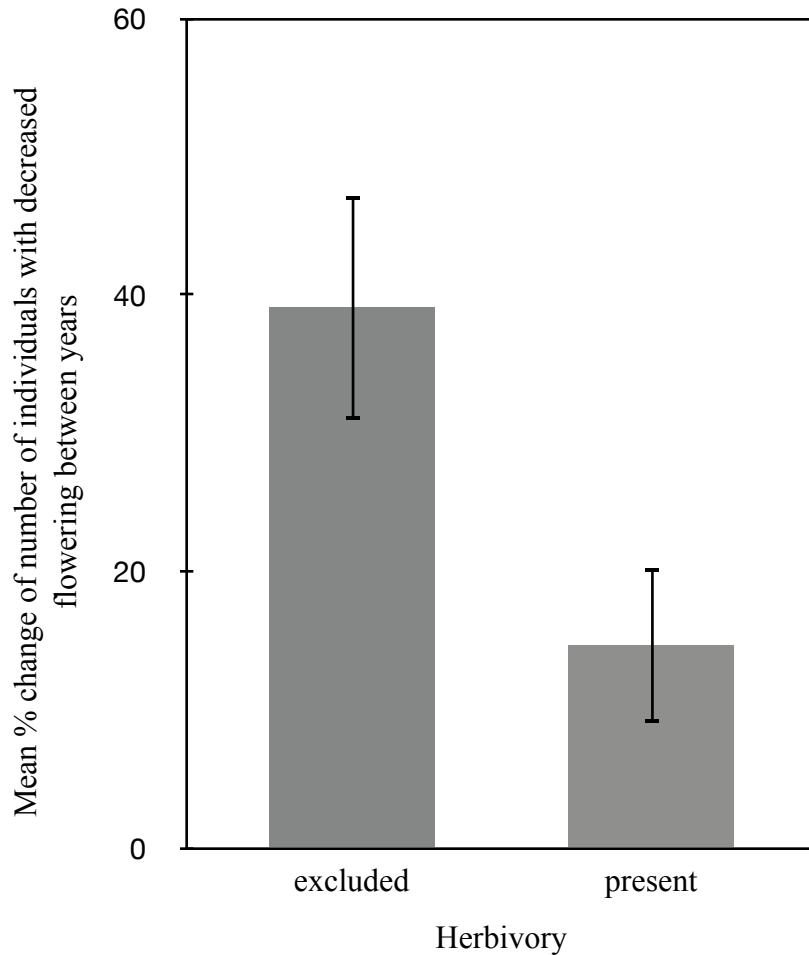


Figure 2.5 Mean percent of flowers per plot decreasing flowering (+SE) in *S. montana* between the 2012 and 2013 growing season comparing herbivory treatments

Plant Architecture and Herbivory

During the 2012 growing season, herbivory had a significant influence on the mean percentage of *S. montana* individuals that had more than one stem. Specifically, plots accessible to non-insect herbivores (i.e., non-excluded plots) housed a greater mean percentage of multi-stemmed individuals than plots protected from herbivores (64.9% versus 49.1% respectively; $F_{1, 24}=4.339$, $P=0.048$; Figure 2.6). There also was a higher percentage of plants that exhibited branching in plots accessible to herbivores in 2012 in comparison with plots protected from

herbivores, although this trend was not significant (60.7% versus 43.4% respectively; $F_{1,24}=2.548$, $P=0.12$ Figure 2.6).

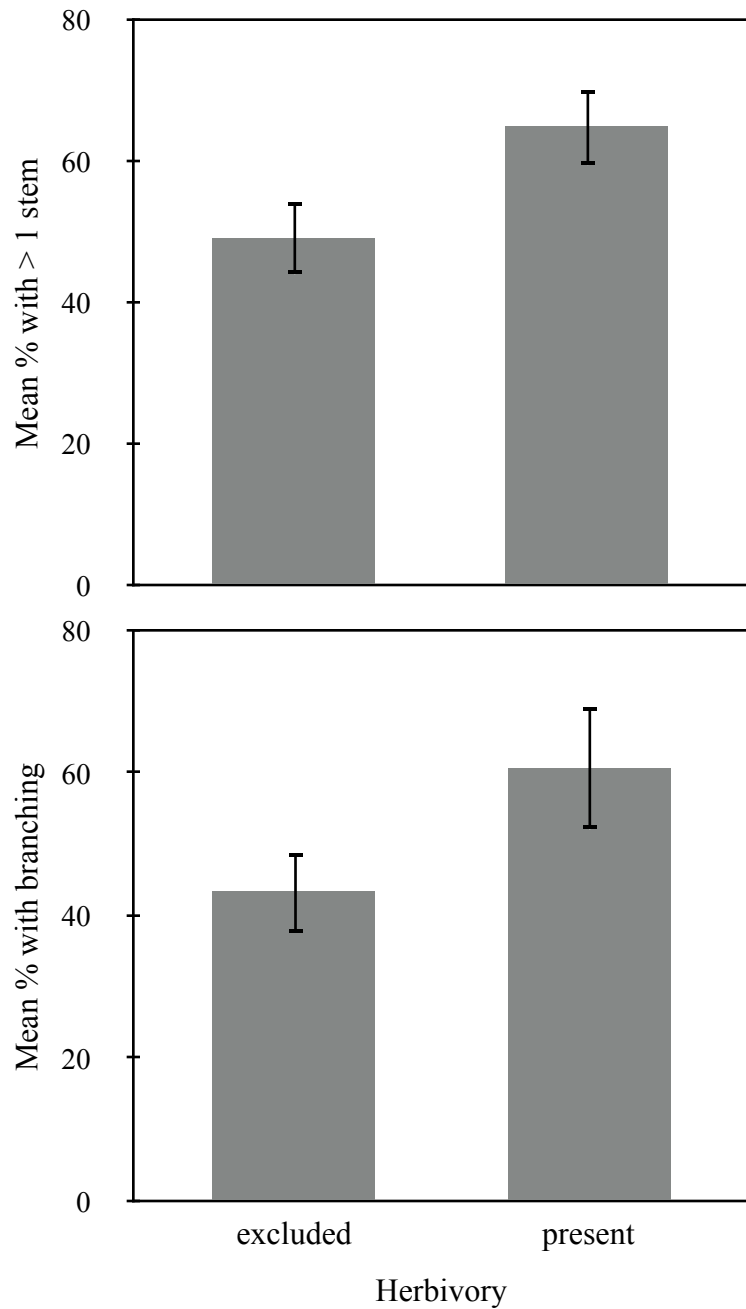


Figure 2.6 Mean percent of individuals with more than one stem (+SE) and mean percent of individuals with branching (+SE) in the 2012 growing season in *S. montana*

In contrast to 2012, no significant differences were seen during the 2013 growing season between groups, herbivory, or invasive species treatment levels in either the mean percentage of *S. montana* individuals that exhibited or had more than one stem ($P > 0.07$ in all cases).

I analyzed the percentage of total plants and plants of different life stages browsed in 2012, the only year herbivory was present in this study. There were no significant differences in the mean percentages of total plants, adult plants, or flowering plants browsed due to the main or interactive effects of groups, herbivory, and invasive species treatment levels ($P > .20$ in all cases). In contrast, the mean percentage of vegetative (i.e., non-flowering) plants evidencing damage by herbivores was influenced significantly by invasive species when considered across groups and herbivory treatment levels. Specifically, this variable was greater for plots in which invasive species were removed than plots with intact invasive species (53.8% versus 22.2% respectively; $F_{1,1} = 07.447$, $P = 0.016$; Figure 2.7). Because the northern group of *S. montana* was included in this study post-emergence in 2012 and plants had already experienced some herbivory, I also analyzed this variable in the southern group only to exclude the influence of pre-study herbivory in these results. Within the southern group, a greater mean percentage of vegetative plants also was browsed in plots in which invasive species were removed versus plots in which invasive species were intact (66.7% versus 16.7% respectively; $F_{1,5} = 6.154$, $P = 0.056$; Figure 2.7).

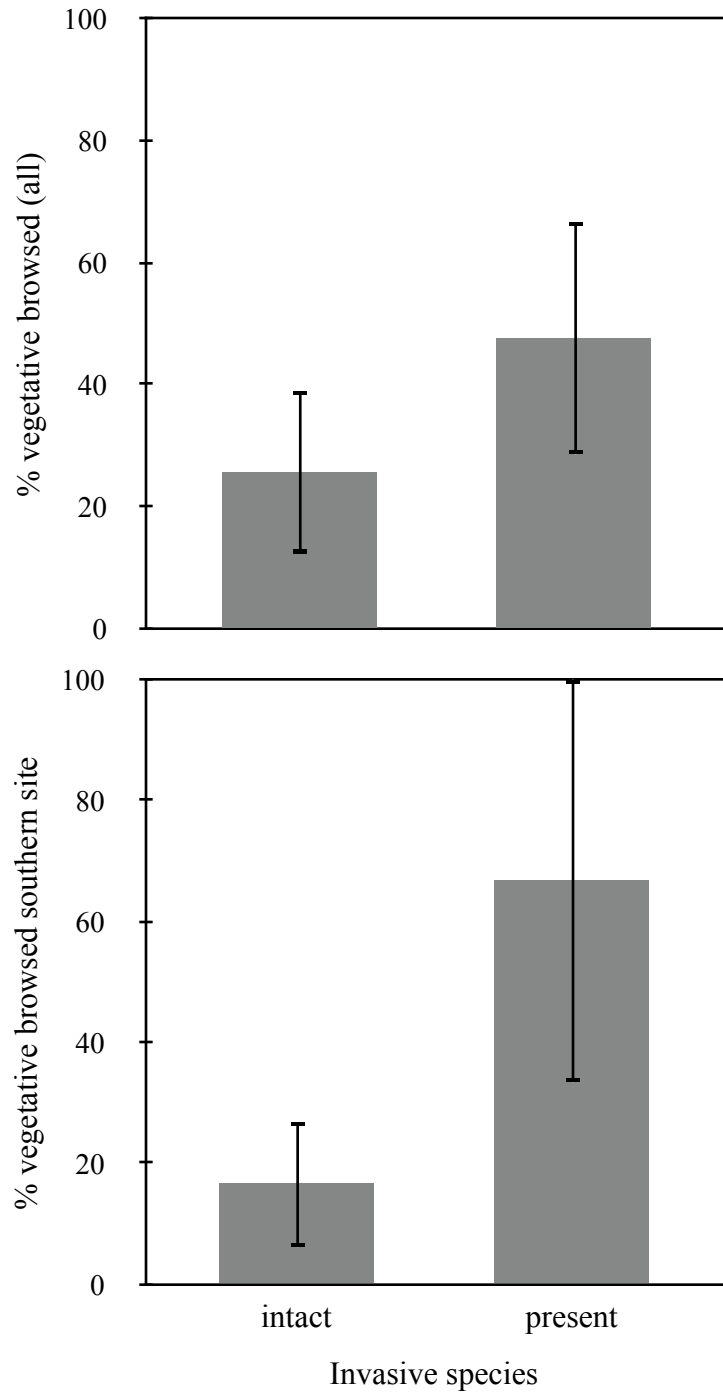


Figure 2.7 Mean percent change of vegetative individuals browsed (+SE) in *S. montana* during the 2012 growing season for the entire site and the southern grouping

Discussion

Although I hypothesized that co-occurring invasive plant species would negatively influence growth and fecundity of rare *S. montana*, the results of this study suggest that interspecific competition from invasive *L. sinense* and *L. japonica* does not negatively impact the individual-level performance of *S. montana*. In contrast, variables that were significantly influenced by invasive species treatment levels in this study (mean percent change during the 2012 growing season and the mean percent of vegetative *S. montana* individuals browsed) suggest that invasive species may facilitate the success of *S. montana* by providing it with protection from non-insect herbivores. Specifically, the mean stem height of *S. montana* individuals from the beginning to the end of the 2012 growing season decreased when invasive species were removed from the immediate vicinity (refer to Figure 2.2) which could be attributed to greater visibility and accessibility of *S. montana* to non-insect herbivores. This conclusion is supported by the lack of any difference in the mean percent change in stem height of *S. montana* between invasive species treatment levels during the 2013 growing season following fence repairs that excluded deer from the studied occurrence. Although the numbers of leaves produced per *S. montana* individual were not similarly influenced positively by invasive species presence during the 2012 growing season, the lack of significant effects of invasive species on these variables supports the idea that competition from invasive species is not negatively affecting *S. montana*'s performance.

Removal of invasive species in this study was associated with a greater percentage of vegetative *S. montana* individuals browsed during 2012 (refer to Figure 2.7), which further supports the idea that invasive species could protect *S. montana* individuals from non-insect

herbivores. However, invasive species presence did not similarly influence browsing of flowering plants or plants of various ages (i.e., adults versus juveniles). Because white-tailed deer are relatively sensitive to short wavelengths of the visible spectrum, including blue light (Jacobs et al. 1994; VerCauteran and Pipas 2003), I suggest that *S. montana* plants with the characteristic bluish-purple flowers of this species may have been highly visible to deer, even if protected under a cover of co-occurring invasive plant species. In contrast, non-flowering *S. montana* plants could be afforded comparatively effective protection from herbivores by invasive species presence in their immediate vicinity.

In multiple studies plants have shown increased growth and survivorship facilitated by protection from herbivory by a neighbor (Callaway et al. 2005; Gorchov and Trisel 2003; Rebollo et al. 2002; Rousset and Lepart 2000). Inedible plants such as *Cirsium obalatum* (wavyleaf thistle) and *Veratrum lobelianum* (white hellebore) or plants with natural defenses such as the spines of *Opuntia polyacantha* (plains pricklypear) protect neighboring plants from herbivory and resultantly increase diversity and individual plant growth in their given communities (Callaway et al. 2005; Rebollo et al. 2002). Shrubs have also been shown to simply hide saplings from herbivores and increase survival and plant growth (Rousset and Lepart 2000). Even an invasive shrub, *Lonicera maackii* (bush honeysuckle) has been shown to provide protection and increase survival and growth for native tree saplings in a recovering field woodlot in Ohio (Gorchov and Trisel 2003). Removal of *L. maackii* resulted in decrease growth of *Quercus rubra* (red oak) and *Acer saccharum* (sugar maple) saplings due to herbivory. The decrease in stem height over the 2012 growing season in plots where invasive species were removed (refer to Figure 2.2) and the increase in vegetative plants browsed in plots where the

invasive species were removed (refer to Figure 2.7) supports that the presence of *L. sinenense* and *L. japonica* seem to shelter *S. montana* from herbivory. The invasive species *L. japonica* and *L. sinense* are not preferential food for deer during spring and summer (Crawford 1982) and help protect *S. montana* from herbivory.

The importance of a sparse understory, as cited by Nix (1993), was also reiterated in the results of my study. There was a significant difference between change in stem height for the 2012 growing season between the northern and the southern group. The southern group saw a decrease in stem height compared to an increase in stem height observed in the northern group. I attribute this difference in change in stem height to the difference in understory cover for each group, the southern group which is located under the observably denser understory between the two groups saw less growth over the season (refer to figure 2.2). The importance of a sparse understory is also demonstrated by the significant difference seen in flowering between the southern and northern group. The much denser understory of the southern group shows a higher percentage of plants decreasing flowering between years (refer to figure 2.4).

Also, my examination of the percentage of *S. montana* individuals experiencing increased or decreased flowering from 2012 to 2013 suggests that non-insect herbivory also plays an important role in determining fecundity and reproductive effort in this species. Specifically, a greater percentage of plants protected from non-insect herbivores (i.e., in enclosed plots), experienced reduced numbers of flowers between years of this study than plants accessible to herbivores (refer to Figure 2.5). Conversely, the percentage of plants experiencing increased numbers of flowers showed a trend of increasing (although not significantly so) in plots exposed to herbivores than those protected by enclosures. Considered collectively, these results suggest

that herbivory stimulates flower production. As suggested by Benson (2012), thinning of the understory by herbivores could decrease competition for shared resources by co-occurring plants, which could benefit *S. montana*. In an earlier study, Nix (1993) reported that *S. montana* does not perform well within relatively dense understories and prefers some openness in its habitat. Here, I suggest that the overall thinning of vegetation by non-insect herbivores increased resources available to *S. montana* to allocate toward reproduction. This possibility is supported by the significant differences in how flowering changed from 2012 to 2013 among the two *S. montana* groups in my study site. Specifically, the northern group, which occurs in an observable less dense understory than the southern group, experienced a comparatively lower percentage of plants with decreased flowering from 2012 to 2013.

In contrast to my findings, Kettering et al. (2009) found a reduction in growth and flowering in the endangered *Liatris ohlingerase* (scrub blazing star) due to pressure from herbivory, which suggests that other rare plant species respond to herbivory differently than *S. montana*. However, Kettering et al. (2009) also reported that plants experiencing herbivory were more likely to produce multiple stems than individuals protected from herbivores, a result confounded by my findings. In addition, the increased branching I observed for *S. montana* accessible to herbivores (i.e., in non-exclosed plots; refer to figure 2.6) supports findings by King (1992) and Benson (2012) in their studies of this species. Increased numbers of stems and branches could theoretically support more leaves and therefore increase the total photosynthetic capacity of a plant. As such, herbivory could promote increased energy acquisition via photosynthetic activity and positively influence reproductive efforts as a result. These are exactly the results the perennial herb *Sedum maximum* (giant stonecrop) demonstrates resulting

in more flowers and higher underground biomass accumulation when browsed (Olejniczak 2011). Additionally, the thinning of surrounding vegetation by herbivores also could promote photosynthetic activity by providing *S. montana* individuals with increased light availability, which also could ultimately increase the energy availability for reproduction in this species.

The significant percent decrease in stem height that occurred from early in the growing seasons in 2012 to 2013 across *S. montana* individuals in the southern group accessible to non-insect herbivores (see figure 2.3) suggests that herbivory pressure may have increased throughout the two-season duration of this study. However, this suggests the change reflects differences in plant phenology between years given the complete lack of browsing damaged observed for any plants in 2013. During 2012, *S. montana* emerged earlier in the season (mid-April) than its late May emergence in 2013, which could have resulting in taller plants by June 2012 than June 2013. In contrast, there were no significant differences in the mean percent change in stem height among herbivory treatment levels within or across groups when this variable was compared in the late growing season (i.e., Sept) between years.

Conclusion

The importance of a sparse understory was reiterated by my study. However, interspecific competition with *L. sinense* and *L. japonica* did not have detrimental effects on *S. montana* as suggested by the lack of a positive response by *S. montana* to invasive species removal in this study. Instead, the presence of the invasive species appeared to facilitate growth of *S. montana* by protecting it from non-insect herbivores. However, my results also suggest that herbivory may increase reproductive output by *S. montana*. As such, the protection from

herbivores afforded to *S. montana* by invasive species presence could have negative implications for this species at the population-level due to potentially suppressed recruitment as a consequence of decreased seed production. Future research utilizing multiple levels of an artificial thinning treatments could help to elucidate the mechanisms underlying the growth and reproductive responses observed in this study. An interacting herbivory exclusion treatment could be included to help isolate the effects of increase light availability from compensatory growth resulting from thinning by herbivores. A simulated herbivory treatment of *S. montana* grown from seed and under controlled conditions could also be useful in separating the effects of herbivory on compensatory growth. Although competition with the invasive species *L. sinense* and *L. japonica* did not negatively influence *S. montana* in this study, the demonstrated ability of these invasive species to suppress the recruitment and germination of native plant species (see Greene and Blossey 2012; Yurkonis and Meiners 2004) remains a concern, especially given their potential indirect link to reproduction via herbivory protection as suggested by my results. Invasive species that do not negatively impact existing rare plants have been shown through competition to prevent germination (Combs et al. 2001; Lesica and Shelly 1996; Miller and Duncan 2004) and these interactions should be examined between the invasive species *L. sinense* and *L. japonica* and the rare plant *S. montana*.

CHAPTER 3

MANAGEMENT, CONSERVATION, AND RESEARCH IMPLICATIONS

Invasive plant species are considered a threat to the continued persistence of rare plant species (Wilcove and Master 2005); however, research examining interactions between these types of species is limited (Brigham and Schwartz 2003; Denoth and Myers 2006). This thesis comprehensively reviewed this limited literature and added to the body of research investigating the direct effects of invasive plant species on rare plant species. Specifically, the study described in this thesis investigated potential competition between invasive *Ligustrum sinense* (Chinese privet) and *Lonicera japonica* (Japanese honeysuckle) and rare and federally endangered *Scutellaria montana* (large-flowered skullcap). Although this particular species is known to occur in only nine counties in northwestern Georgia and four counties in southeastern Tennessee (USFWS 2002), *S. montana* exemplifies a rare plant species potentially threatened by invasions of non-native species into its habitat.

It often has been assumed by ecologists that invasive plant species negatively impact rare plant species and that the mechanism of this impact is a stark difference in their competitive abilities. However, the negative impact of invasive plant species on rare plant species has been inferred from studies that observed the abundance of invasive species in rare species' habitat or compared rare plant occurrences in invaded sites with those in non-invaded sites without direct testing (Gorchov and Tiesel 2003; Thomson 2005). In my study, the lack of any competitive effect of *Ligustrum sinense* (Chinese privet) or *Lonicera japonica* (Japanese honeysuckle) on *S. montana* supports the nearsightedness of the assumption that invasive species are superior

competitors relative to rare plant species. Collectively, my research and that described in the 16 published studies that directly examined interactions between invasive and rare plant species suggest that it is just as likely that invasive plant species will have no competitive effect on co-occurring rare plant species. Consequently, I suggest that plans developed for the management and conservation of rare plant species consider the possibility that invasive plant species may post a threat, but not assume that this will be the case.

Although competition with invasive species did not negatively affect the growth of *S. montana* at the organismal level in my study, the influence of invasive species on its germination and recruitment were not assessed. These variables and their population-level implications are a concern, however, since I observed very few *S. montana* juveniles in my study sites. While it is possible this could be due to the inherently low reproductive rates of *S. montana* (Cruzan 2001; Hopkins 1999), it has been demonstrated that both *L. sinense* and *L. japonica* can suppress germination and recruitment of co-occurring native plant species (see Greene and Blossey 2012; Yurkonis and Meiners 2004). Other invasive plant species have been shown to directly reduce population of rare plant species, in particular, by suppressing their germination (see Combs et al. 2011; Lesica and Shelly 1996; Miller and Duncan 2004). A future removal study examining the effects of both *L. sinense* and *L. japonica* on germination and recruitment of *S. montana* would help to further understanding of their impacts on this rare species.

In contrast to assumption about the negative impacts of invasive species on rare plant species, my study demonstrated that the presence of invasive *L. sinense* and *L. japonica* protected *S. montana* from herbivory to some extent. Although this protection was associated with increased growth of *S. montana* individuals, I also found that a lack of herbivory was

associated with decreased reproduction of *S. montana*, which suggests that such protection may limit population-level growth of *S. montana*. In the perennial herb *Sedum maximum* (giant stonecrop) herbivory has been shown to increase fecundity immediately and during future growing seasons through a release of apical dominance, which stimulates branching, new leaf production, and greater energy acquisition via photosynthetic activity (Olejniczak 2011). If herbivory benefits *S. montana* similarly, invasive species could negatively influence its fecundity through the protection they provide from herbivory.

In previous research investigating the impacts of non-insect herbivores on *S. montana*, herbivory was also shown to be beneficial to *S. montana* (see Benson 2012). While it was assumed that associated thinning of competing understory vegetation increase light availability to *S. montana* (see Benson 2012, also Mulhouse 2008), this was not explicitly tested. Future research imposing different levels of artificial thinning in *S. montana* occurrences could help to elucidate better how light availability affects this rare species. A interacting herbivory enclosure treatment could be included to help isolate the effects of increase light availability from potential compensatory growth resulting from thinning by herbivores.

The results of my research and subsequent related studies could be used by the Volkswagen Group of America (Herndon, VA) to best support occurrences of *S. montana* on the property of their manufacturing facility in Chattanooga, TN, as well as by land managers of protected occurrences in the adjacent Enterprise South Nature Park. My study site as well as another occurrence of *S. montana* on Volkswagen property currently are surrounded by a 6-ft-tall chain link fence, which successfully excluded deer from my study site during the 2013 growing season. Because no non-insect herbivore damage was observed on *S. montana* individuals

included in my study during the 2013 growing season, I assume that deer are the primary browser of this species. Although I would not recommend removal of the fence at this point, based on my results, I also would not recommend repairing any damage to the fence if it were to occur. Ironically, the use of a fencing to protect *S. montana* from herbivory to increase its survival may be detrimental to its protection from extinction. However, if future research is able to elucidate the mechanisms by which herbivory influences *S. montana*, removal of the fence or at least providing openings in the fence through which deer can enter may be the best course of action.

Continued monitoring of *S. montana* on the Volkswagen property in Chattanooga, TN, is encouraged along with efforts to minimize the invasion of *L. sinense* and *L. japonica*. Although my study does not show effects due to competition due to the densities the invasive species exist at my study site at this point, it did show the importance of a sparse understory. Although both *L. sinense* and *L. japonica* are ubiquitous throughout the site, they are fairly small or young plants. The invasion of the site at Volkswagen is probably fairly new and compared to many other invasions is not that far advanced, neither of the two invasive species dominate the understory as they are capable of doing (refer to Greene and Blossey 2012; Barden and Matthews 1980). Although *S. montana* is not being negatively impacted through competition, as *L. sinense* and *L. japonica* continue to persist and proliferate throughout the site there is a strong possibility they will change the composition and structure of the understory and negatively effect *S. montana* by altering the important sparse understory. For this reason, I would suggest continued monitoring along with removal treatments in order to keep the invasion of *L. sinense* and *L. japonica* from altering the understory and negatively effecting *S. montana*.

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APPENDIX A

TABLE A.1 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN STEM HEIGHT FOR 2012 OF *SCUTELLARIA MONTANA*
INDIVIDUALS

Table A.1 Summary of step wise two-way ANOVA results for mean percent change in stem height for 2012 of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated for the period from June to September in 2012, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × group	1	16	0.000	0.991
herbivory × group	1	17	0.298	0.592
removal × herbivory	1	18	1.234	0.281
herbivory	1	19	0.402	0.533
removal	1	20	7.028	0.015
group	1	20	6.738	0.017

APPENDIX B

TABLE A.2 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN STEM HEIGHT FOR 2013 OF *SCUTELLARIA MONTANA*
INDIVIDUALS

Table A.2 Summary of step wise two-way ANOVA results for mean percent change in stem height for 2013 of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated for the period from June to September in 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	16	0.0002	0.990
removal × group	1	17	0.045	0.834
herbivory × group	1	18	0.173	0.682
removal	1	19	0.083	0.776
group	1	20	0.578	0.455
herbivory	1	21	1.729	0.201

APPENDIX C

TABLE A.3 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN STEM HEIGHT FOR 2013 OF *SCUTELLARIA MONTANA*
INDIVIDUALS

Table A.3 Summary of step wise two-way ANOVA results for mean percent change in leaves for 2012 of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated for the period from June to September in 2012, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.002	0.961
removal × group	1	20	0.051	0.824
removal	1	21	0.010	0.923
herbivory	1	1	0.155	0.761
group	1	2	0.589	0.523
herbivory × group	1	22	1.937	0.153

APPENDIX D

TABLE A.4 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN STEM HEIGHT BETWEEN YEARS FOR JUNE OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.4 Summary of step wise two-way ANOVA results for mean percent change in stem height between years for June of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated between June 2012 and June 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.750	0.397
group	1	1	0.027	0.893
removal	1	1	0.211	0.726
herbivory	1	1	0.298	0.682
removal × group	2	20	1.569	0.233
herbivory × group	3	22	9.328	0.0004

APPENDIX E

TABLE A.5 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN STEM HEIGHT BETWEEN YEARS FOR SEPTEMBER OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.5 Summary of step wise two-way ANOVA results for mean percent change in stem height between years for September of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated between September 2012 and September 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.032	0.861
herbivory × group	1	20	0.233	0.635
removal × group	1	21	0.637	0.434
removal	1	22	0.264	0.612
herbivory	1	23	0.414	0.526
group	1	24	0.662	0.424

APPENDIX F

TABLE A.6 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT CHANGE IN FLOWERS BETWEEN YEARS OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.6 Summary of step wise two-way ANOVA results for mean percent change in flowers between years of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated between May 2012 and June 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	11	0.292	0.600
herbivory × group	1	12	0.957	0.347
removal × group	1	13	2.049	0.176
removal	1	14	1.349	0.265
group	1	15	1.927	0.247
herbivory	1	16	1.442	0.186

APPENDIX G

TABLE A 7 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH DECREASED FLOWERING
BETWEEN YEARS OF *SCUTELLARIA MONTANA* INDIVIDUALS

Table A.7 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with decreased flowering between years of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent was calculated between May 2012 and June 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	18	0.022	0.884
herbivory × group	1	19	0.508	0.484
removal × group	1	20	1.475	0.238
removal	1	21	0.812	0.377
herbivory	1	22	8.767	0.007
group	1	22	12.069	0.002

APPENDIX H

TABLE A.8 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH INCREASED FLOWERING
BETWEEN YEARS OF *SCUTELLARIA MONTANA* INDIVIDUALS

Table A.8 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with increased flowering between years of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Mean percent change was calculated between May 2012 and June 2013, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.003	0.958
removal × group	1	20	0.553	0.466
herbivory × group	1	21	1.847	0.185
group	1	22	0.0002	0.997
removal	1	23	1.104	0.304
herbivory	1	24	2.724	0.112

APPENDIX I

TABLE A.9 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH MORE THAN ONE STEM OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.9 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with more than one stem of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Stems were counted in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.167	0.688
removal × group	1	20	1.425	0.247
herbivory × group	1	21	2.213	0.152
group	1	22	0.014	0.925
removal	1	23	0.023	0.884
herbivory	1	24	4.339	0.048

APPENDIX J

TABLE A.10 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH BRANCHING FOR 2012 OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.10 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with branching of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Branching was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × group	1	19	0.163	0.691
removal × herbivory	1	20	0.165	0.689
herbivory × group	1	21	0.230	0.637
group	1	22	0.08	0.768
removal	1	23	0.0863	0.363
herbivory	1	24	2.584	0.121

APPENDIX K

TABLE A.11 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH BRANCHING FOR 2013 OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.11 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with branching of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Branching was observed in the 2013 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
herbivory × group	1	15	0.103	0.751
removal × herbivory	1	16	0.225	0.641
removal × group	1	17	0.233	0.634
herbivory	1	18	1.490	0.235
removal	1	19	2.154	0.156
group	1	20	3.492	0.074

APPENDIX L

TABLE A.12 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS WITH MORE THAN ONE STEM FOR 2013 OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.12 Summary of step wise two-way ANOVA results for mean percent per plot of individuals with more than one stem of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Stems were counted in the 2013 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
herbivory × group	1	15	0.0002	0.990
removal × group	1	16	0.045	0.834
removal × herbivory	1	17	0.173	0.682
herbivory	1	18	0.083	0.776
removal	1	19	0.578	0.455
group	1	20	1.729	0.201

APPENDIX M

TABLE A.13 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUALS BROWSED FOR OF *SCUTELLARIA MONTANA*
INDIVIDUALS

Table A.13 Summary of step wise two-way ANOVA results for mean percent per plot of individuals browsed of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Browsing was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.018	0.095
herbivory × group	1	20	0.40	0.529
removal × group	1	21	1.425	0.246
removal	1	22	0.011	0.916
group	1	23	0.124	0.728
herbivory	1	24	12.363	0.002

APPENDIX N

TABLE A.14 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF INDIVIDUAL ADULTS BROWSED OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.14 Summary of step wise two-way ANOVA results for mean percent per plot of individual adults browsed of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Browsing was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	19	0.079	0.781
herbivory × group	1	20	0.291	0.596
removal × group	1	21	1.335	0.261
removal	1	22	0.051	0.824
group	1	23	0.796	0.382
herbivory	1	24	15.649	0.001

APPENDIX 0

TABLE A.15 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF FLOWERING INDIVIDUALS BROWSED OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.15 Summary of step wise two-way ANOVA results for mean percent per plot of flowering individuals browsed of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Browsing was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	15	0.081	0.780
herbivory × group	1	16	0.406	0.533
removal	1	17	0.012	0.913
group	1	1	0.124	0.784
removal × group	1	18	0.303	0.228
herbivory	1	20	1.113	0.304

APPENDIX P

TABLE A.16 SUMMARY OF STEP WISE TWO-WAY ANOVA RESULTS FOR MEAN
PERCENT PER PLOT OF VEGETATIVE INDIVIDUALS BROWSED OF
SCUTELLARIA MONTANA INDIVIDUALS

Table A.16 Summary of step wise two-way ANOVA results for mean percent per plot of vegetative individuals browsed of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at both groups in the study site. Browsing was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	error df	F Ratio	P
removal × herbivory	1	12	0.022	0.883
herbivory × group	1	13	0.139	0.715
group	1	14	0.615	0.446
removal × group	1	15	4.086	0.066
removal	1	1	7.447	0.016
herbivory	1	1	33.187	0.0000

APPENDIX Q

TABLE A.17 SUMMARY OF TWO-WAY ANOVA RESULTS FOR MEAN PERCENT PER
PLOT OF VEGETATIVE INDIVIDUALS BROWSED OF *SCUTELLARIA MONTANA*
INDIVIDUALS

Table A.17 Summary of two-way ANOVA results for mean percent per plot of vegetative individuals browsed of *Scutellaria montana* individuals within each of the four treatment combinations (non-exclosed plots with invasive species present, *Control*; non-exclosed plots with invasive species removed; exclosed plots with invasive species present; exclosed plots with invasive species removed) at the southern group in the study site. Browsing was observed in the 2012 growing season, where herbivory and removal were considered the fixed independent variables and group was considered a random factor.

Source of variation	degrees of freedom	F Ratio	P
removal	1	6.154	0.056
herbivory	1	24.615	0.004
removal × herbivory	1	6.154	0.056
error	5		

VITA

Jordan J. Sikkema born in Fulton, Illinois to Douglas and Alice Sikkema. His family moved to Chattanooga, Tennessee where he attended and graduated from Chattanooga Christian School in 2000. Jordan attended Trinity Christian College near Chicago, Illinois after high school and graduated with a Bachelors of Science with majors in Biology and Chemistry in 2004. After college, Jordan worked for JFNew and Associates in the Chicagoland area as a field technician working in the hands on labor of environmental restoration and conservation. In 2006, Jordan moved to Bay Saint Louis, Mississippi to volunteer after hurricane Katrina. This resulted in a job as the volunteer and construction coordinator at Lagniappe Presbyterian Church, an church that rebuilt homes with volunteers after the storm. After working on the coast of Mississippi for five years, Jordan decided to pursue his Master of Science in Environmental Science and moved back to Chattanooga to do so in 2011. He completed his Masters of Science in Environmental Science in December of 2013 and is looking forward to applying his knowledge in the field of environmental management and conservation.