AN EXERCISE IN COMPLEXITY:
INDIRECT INFLUENCES OF INVASION BY AN EXOTIC GRASS (*MICROSTEGIUM VIMINEUM*) ON FOREST FLOOR FOOD WEBS

by

JAYNA LYNN DeVORE

(Under the Direction of John C. Maerz)

ABSTRACT

Plants play a major role in the construction and maintenance of ecosystems, supporting green food webs through herbivory and brown food webs through detrital inputs, affecting abiotic habitat variables, and influencing energy flow through these systems by changing the structural context in which trophic transfers take place. Alterations in these communities, such as those following plant invasion, may therefore affect consumers within impacted habitats. However, the multifaceted roles of plants makes the nature and strength of these effects difficult to predict. This dissertation explores detritally and structurally-mediated effects through which invasion by the Asian grass *Microstegium vimineum* influences forest floor consumers through investigating belowground C dynamics, abiotic parameters, energy flow, and the growth and survival of 3200 American toads, 800 southern leopard frogs, and 200 eastern newts across eight independent invasion fronts. The mechanisms behind observed effects were further explored through manipulations of the presence of lycosid spider predators and short-term foraging and survival trials within paired invaded and uninvaded enclosures. Belowground, this plant was found to influence abiotic habitat parameters and carbon dynamics, potentially contributing to observed effects on the production of microarthropods. However, it also serves as an important basal resource, making it likely that bottom-up influences of this plant are a consequence of changes in detrital communites in invaded habitats rather than resource sequestration of nonindigenous plant tissues. Investigation of the mechanisms through which stilt grass influences the American toad demonstrated that structural changes initiated a contextually-mediated dampening of intraguild predation rates among lycosid spiders, increasing their survival, and thereby augmenting predation pressure on metamorphic toads. Interspecific comparisons of the effects of invasion on three amphibians utilizing disparate metamorphic strategies revealed that the nature of the influence of invasion may be predicted by the metamorphic strategy of the species in question, as small, actively foraging toads are susceptible to top-down pressures while larger, sit-and-wait leopard frogs are sensitive to bottom-up effects and cryptic, toxic eastern newts did not respond to trophic effects. This research demonstrates that invasion indirectly affects consumers through alterations in detrital inputs and habitat structure, although the nature and strength of these effects varies interspecifically.

INDEX WORDS: Invasive species, exotic plant, detrital food web, soil food web, root exudates, priming effect, belowground, aboveground, arthropod, structural complexity, contextually-mediated indirect effects, bottom-up, top-down, autogenic ecosystem engineer, trophic effects, metamorphic strategy, behavioral syndrome, intraguild predation, foraging strategy, Japanese stilt grass, *Microstegium vimineum,* lycosid spider, amphibian, American toad (*Anaxyrus [Bufo] americanus*)*,* Southern leopard frog (*Lithobates [Rana] sphenocephalus [sphenocephala]*)*,* eastern newt (*Notophthalmus viridescens*)

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Exotic invasion represents an increasingly ubiquitous component of anthropogenic environmental change (Mack et al. 2000). While essentially a natural process, recent increases in global connectivity, as a consequence of ever more prevalent trade and travel, have increased the rate of exotic introductions by orders of magnitude (Mack et al. 2000). Although the majority of introductions fail to take hold, some species prove to be wildly successful in their introduced range, often proving more productive and fecund than within their native habitat (Keane and Crawley 2002, Blumenthal 2005, 2006). Predicting which invaders will be successful has proven to be extremely difficult (Mack et al. 2000, Dietz and Edwards 2006), but the mechanisms that underlie successful invasions have been explored in a number of systems.

A driving factor in many successful invasions is enemy release, in which organisms benefit from the absence of their co-evolved predators, parasites, and pathogens within their introduced range (Keane and Crawley 2002, Blumenthal 2006). The effects of this release from the regulatory pressure of predation may be expected to be exceptionally strong among high-resource species (Blumenthal 2005, 2006). By definition, these species are those that devote the majority of their energy to rapid growth and reproduction rather than defense and, accordingly, are typically controlled by top-down pressures. When released from their predators, the rapid growth and high fecundity of these species can contribute to their spread. Since the exposure of native species to predation from local consumers continues, exotic invaders often experience reductions in competition, as well (Keane and Crawley 2002, Webster et al. 2008). Under these conditions, exotic invaders may also evolve increased competitive abilities, in which resources that would previously have been delegated to predator defense are allocated to further increases in growth, reproduction, or dispersal abilities (Blossey and Notzold 1995, Blumenthal 2005, Adams and Engelhardt 2009, Phillips et al. 2010, Flory et al. 2011). The mixing of genetic stocks from throughout native and introduced ranges (as well as hybridization with native species) can contribute to the evolutionary capabilities of these species (Blossey and Notzold 1995), and the fragmented nature of many invasive populations can further enable rapid evolution by these species by minimizing genetic momentum.

A large percentage of successful invaders are exotic plants, many of which are hyper-productive, high resource species (Baruch and Goldstein 1999, Allison and Vitousek 2004). While some of these species may benefit from novel weapons or an ability to exploit novel resources, with demonstrably catastrophic consequences in certain systems (Vitousek et al. 1987, Vitousek 1990, Mack et al. 2001), the majority lack such unique abilities and are superficially similar to native organisms. While the ecosystem consequences of novel abilities and traits have been established in a number of highly impacted systems (Vitousek et al. 1987, Vitousek 1990), the ways in which these more common, apparently innocuous invasions influence ecosystem properties and consumers living within invaded habitats can be difficult to recognize or predict. Effects are likely, however, as plants contribute the basal resources upon which trophic webs rely and often physically alter the structural complexity of their environments as they grow. They support green food webs through herbivory, brown food webs through detrital inputs of dead plant material and root exudates, and influence trophic dynamics by changing the structural context in which these interactions take place. Due to the importance of these processes to consumer communities it is likely that changes in plant communities will influence higher trophic levels; however, the majority of studies seeking to quantify the impact of changes in plant communities have focused on competitive changes in the distribution of other plant species, belowground influences on microflora, or effects on invertebrate herbivores (Kourtev et al. 2002, Levine et al. 2003, Carvalheiro et al. 2010). This is likely to underestimate the impact that plants have on trophic dynamics, as the consequences of changes in plant communities may be expected to influence consumers at all levels of the food web (Carvalheiro et al. 2010). Ultimately, investigators have proposed three major types of ecosystem-level effects that may follow plant invasion. They comprise the alteration of the flow, availability or quality of 1) nutrient resources within biogeochemical cycles, 2) trophic resources within food webs, and 3) physical resources such as living space, sediment, light, or water (Vitousek 1990, Crooks 2002).

Biogeochemical cycles

Belowground biogeochemical cycling can influence nutrient availability for below and aboveground food webs, and exotic plants exhibiting traits that differ from those of the historic plant community may also differ in their influences on soil biogeochemistry (Ehrenfeld et al. 2001, Liao et al. 2008). One trait that may cause these changes is the quality of detrital inputs. Addition of high-quality inputs to a detrital system has been shown to increase litter decomposition rates (Allison and Vitousek 2004, Ashton et al. 2005) and influence C cycling and via indirect effects on soil microorganisms (Ehrenfeld 2003). As the tissue quality of invaders is often higher than that of native plants, invasion may be expected to drive such effects. In fact, plant invasions have been associated with alterations in N cycling (Ehrenfeld 2003, Hawkes et al. 2005, Liao et al. 2008) and, in certain cases, may cause a ‘priming effect’, in which rates of C mineralization increase in response to the availability of labile resources (Fontaine et al. 2003, Liao et al. 2008, Strickland et al. 2010). Root exudates are another form of detritus that have the potential to drive such effects, as they are typically high-quality inputs that are known to stimulate microbial activity (Hamilton and Frank 2001) and can contribute substantially to both soil respiration and energy flow to detrital food webs (Hogberg et al. 2001, Pollierer et al. 2007, Wu et al. 2011), although the role of root exudates as a consequence of exotic invasion is not well understood (Ehrenfeld 2004). As carbon mineralization rates have been found to be indicative of the life history strategies of the microfloral decomposers, it is likely that this process is associated with the promotion of copiotrophic decomposers (Fierer et al. 2007). This rapid cycling may have repercussions on the detrital food web, resulting in increased nutrient losses from the system, as copiotrophic detritivores display a lower substrate affinity than their oligiotrophic competitors. Rapid C mineralization may also promote organisms that contribute little to the diet of aboveground predators (e.g. nematodes and protozoans) over edible organisms (e.g. collembolans and mites) (Moulder and Reichle 1972, Hendrix et al. 1986, Wardle et al. 2004).

Trophic resources

Alterations in plant communities can influence consumers through modifications in the availability of the basal resources upon which they rely; these changes have the potential to affect both belowground and aboveground food webs through modifications in above and belowground resource allocation by living plants, as well as changes in detrital input timing, quantity, and quality. As many successful invasive plants are relatively predator-free within their introduced range (Keane and Crawley 2002, Blumenthal 2006), especially when the invader is phylogenetically isolated from native plant species (Agrawal and Kotanen 2003), the majority of the resources produced by these plants are likely to enter the food web through belowground detrital channels. Recently, the influence of changes in belowground food webs on aboveground communities has received increasing attention, although the majority of food web studies seeking to connect belowground with aboveground processes have focused on plant-mediated effects on herbivore populations (Wardle 2002, Hines et al. 2006) or the influences of subsidies from detrital food webs on the suppression of herbivore populations via a “resource shunt”, in which detrital subsidies increase the abundance of generalist predators, leading to cascading implications for plant growth (Wise et al. 1999, Halaj and Wise 2002). However, focusing attention on the consequences of detrital pathways for herbivorous food webs generally impedes recognition of the fact that the detritus-based food web is the dominant pathway through which autotrophic production enters the food chain. Approximately 90% of plant material enters the food web as detritus, and most heterotrophs across a range of ecosystems derive some, if not most, of their energy through detrital pathways (Polis and Strong 1996, Moore et al. 2004, Sanders and Platner 2007). Accordingly, there is increasing evidence that detrital pathways may serve as more than an additional subsidy for generalist predators, but an important source of trophic resources that supports a diversity of invertebrate and vertebrate aboveground predators (Wyman 1998, Johnston 2000, Halaj and Wise 2002, Miyashita et al. 2003, Wolkovich 2010). Belowground components of this food web are composed of a diverse set of soil fauna that is responsive to alterations in detrital input quality (Paterson et al. 2008) and can even be influenced by the addition of a single plant species (Mitchell et al. 2010). Changes in plant communities may therefore influence soil community structure and function via a number of habitat alterations, such as the quantity, quality, and timing of litter inputs as well as microhabitat variables such as soil moisture and pH (Ehrenfeld et al. 2001), with potential implications for aboveground predators that rely on these resources. Accordingly, a number of studies have shown that invertebrate species composition and abundance can be altered by the invasion of a single exotic plant (Belnap and Phillips 2001, Belnap et al. 2005, Kappes et al. 2007, Topp et al. 2008). Despite this evidence, few have attempted to connect alterations in the belowground productivity of the detrital food web, through which nearly all of the material produced by exotic plants must pass, with the production of aboveground resources available to higher-level consumers.

Physical resources

The presence of an exotic plant can also alter the availability of physical resources such as soil moisture or sunlight (Ehrenfeld et al. 2001), or microhabitat variables like soil pH (Ehrenfeld et al. 2001) with potential implications for both plants and consumers within affected areas (Wyman and Hawksleylescault 1987, Feder and Burggren 1992, Civitello et al. 2008). Further influences on ecosystems can occur as plants directly affect the structure of their environment through endogenous growth processes (Jones et al. 1994, Blossey and Notzold 1995, Jones et al. 1997, Crooks 2002). Alterations in physical structure can have far-reaching repercussions throughout affected habitats, as even across diverse ecosystems environmental structure often plays a key role in fundamental processes such as species persistence (Janssen et al. 2007), reproduction (Sadeh et al. 2009), survival rates (McCormick 2009), resistance to disturbance (Petillon et al. 2010), physical trait development (Byers et al. 2010), behavior (Main 1987, Grabowski et al. 2008, Mattos and Orrock 2010), and trophic interactions (Crowder and Cooper 1982, Griffen and Byers 2006, Grabowski et al. 2008, Pearson 2009). Through their growth plants can therefore further influence food web dynamics, not as a direct participant by means of alterations in basal resource availability, but by modifying the spatially context in which organisms interact (Jones et al. 1997). The effects of engineering are thought to be especially influential in cases where the plant cover created is extensive (Jones et al. 1997); this is especially likely in cases of plant invasion, potentially rendering exotic plants exceptionally influential autogenic ecosystem engineers.

One potential result is that by increasing the structural complexity of their environment, these plants can positively affect the abundance of certain fauna (Crooks 2002, Janssen et al. 2007). Lycosid spiders, for example, are an important predatory group known to persist in higher densities in structurally complex habitats (Langellotto and Denno 2006). As these organisms are highly cannibalistic (Wagner and Wise 1996), this effect is likely attributable to reductions in intraguild predation associated with increased refuge availability (Wise and Chen 1999, Langellotto and Denno 2006, Rickers et al. 2006). As spiders are important in forest floor energy dynamics (Moulder and Reichle 1972), processes with the potential to alter their abundance could have repercussions throughout the forest floor ecosystem. For example, greater habitat complexity and resulting increases in spider densities can have implications for prey suppression, with complex environments associated with increased prey susceptibility to spider predation (Finke and Denno 2002) and reductions in prey abundance (Miyashita and Takada 2007).

Dissertation

This dissertation is an attempt to demonstrate the complex, indirect mechanisms through which forest floor consumers are influenced by the invasion of an exotic plant. I focus on the effects of invasion by the exotic annual grass *Microstegium vimineum* on belowground and aboveground processes and trophic interactions, as well as the implications of these effects for the performance of forest floor amphibians. Given the importance of plants as the source of trophic resources, controllers of biogeochemical cycles, and autogenic ecosystem engineers, changes in plant community are certain to influence consumers dwelling within invaded habitats.

However, while the direct effects of invasive plants and animals on competitors or prey are well studied, our understanding of how changes in plant communities impact consumer assemblages is limited and seldom mechanistic (Levine et al. 2003).

Focal invader: *Microstegium vimineum*

M. vimineum (Japanese stilt-grass, Nepalese browntop, Mary's grass, porcelain packing grass) is a highly invasive Asian annual grass (Poaceae) that was first reported naturalized in the United States in Tennessee in 1919 (Cole and Weltzin 2005) and has since become widespread throughout the eastern United States. This highly competitive plant prefers moist, partially shaded areas, and is common in a variety of habitats including forests and areas in or near wetlands (Zheng et al. 1997, Leicht et al. 2005, Schramm and Ehrenfeld 2010), where it frequently suppresses native plant production and diversity (Adams and Engelhardt 2009, Flory and Clay 2010a), and forms recalcitrant ground cover and a persistent seed bank (Royo and Carson 2006, Webster et al. 2008, Flory and Clay 2010b). Invasion by this plant is frequently facilitated by disturbance, such as flooding, earthworm activity, or road construction (Oswalt and Oswalt 2007, Mortensen et al. 2009, Nuzzo et al. 2009, Warren et al. 2011). Biomass production is greater within invasive populations of this plant, making it likely that it has evolved increased competitive abilities within its introduced range (Flory et al. 2011). Remarkably, while there have been many studies of woody and herbaceous plant invasions of grasslands, there have been very few studies of grass invasions of forests (Litton et al. 2008). Although the C:N ratio of culms of *M. vimineum* is similar to that of deciduous inputs (Strickland et al. 2010), the paucity of native forest floor plants in many of the systems invaded by this plant and the nitrogen-rich roots and leaves produced by this invader are likely to result in a net increase in labile resource inputs (Ehrenfeld et al. 2001). Additionally, the shallow roots of this invader, which occur predominantly in the litter layer and upper cm of soil (DeVore, pers. obs.), may contribute to the labile resources through the addition of root exudates (Bradford et al. in prep), although the influences of root dynamics on these processes is generally poorly understood (Ehrenfeld 2004). Invasion by this plant can influence N dynamics (Ehrenfeld 2003, Hawkes et al. 2005, Fraterrigo et al. 2011) and appears to result in a priming effect, as invaded areas have been associated with reductions in total soil C pools and microbial biomass C, as well as higher rates of glucose mineralization (Strickland et al. 2010). This plant has also been found to alter the structure and function of microbial communities (Kourtev et al. 2002, 2003) and influence arthropod abundance and richness (Marshall and Buckley 2009, McGrath and Binkley 2009, Simao et al. 2010), although the potential implications of these changes for forest floor vertebrates has not been determined. Stilt grass also affords a unique opportunity to examine how invasive plants influence forest floor food web dynamics. Unlike the native and exotic forest plants that utilize the C_3 photosynthetic pathway, stilt-grass utilizes C_4 photosynthesis. The carbon produced by this plant is therefore naturally enriched in the stable isotope ^{13}C, allowing for the use of stable isotopes to track the flow of stilt-grass carbon through belowground and aboveground food webs.

M. vimineum may also qualify as an ecosystem engineer (Baiser et al. 2008). Invasion by this plant significantly increases plant cover, often resulting in increased structural complexity; this effect is especially pronounced because the plant community of the forest floor habitat preferentially utilized by this invader is relatively depauperate (DeVore et al, unpub data), especially in areas experiencing high rates of herbivory (Webster et al. 2008, Flory and Clay 2010b). The implications of structural changes for native fauna have been demonstrated in cases of anthropogenic disturbance (Hawlena and Bouskila 2006), successional communities (Bultman et al. 1982), habitat degradation (McCormick 2009), and invasion by the exotic plant *Centaurea* *maculosa* (Pearson 2010), but the potential engineering effects of *M. vimineum* on forest floor consumers have not been previously considered.

Chapter summaries

Chapter two focuses on the belowground abiotic, biogeochemical, and bottom-up implications of plant invasion. This increasingly ubiquitous process has the potential to influence trophic resource availability within invaded habitats, either through sequestration of the energy resources produced by these plants or by influencing overall prey production in invaded habitats. By bringing together data on belowground C dynamics, microarthropod production, and the flow of carbon from *M. vimineum* litter and root exudates to small, forest floor predators dependent on detrital food webs, this chapter seeks to link together the implications of the addition of this novel plant for trophic resource availability within invaded areas and determine the degree to which exotic production contributes to native food webs.

In Chapter 3 I determine the mechanisms through which invasion influences the performance of metamorphic American toads and assess the relative importance of bottom-up and top-down effects. Although plant invasion is not expected to directly affect secondary consumers, the presence of an invader may lead to indirect effects on these species through alterations in basal resource availability or by changing the physical structure of their environment. Both of these effects can lead to trophic effects on the species in question, whether through influences on the availability of trophic resources or by changing the environmental context in which trophic transfers occur, thereby modifying pre-existing interactions between native species within these habitats.

Chapter 4 focuses on interspecific variation in the responses of three sympatric amphibian species to plant invasion and proposes that accounting for metamorphic strategies can improve our ability to predict the nature of these responses. Metamorphic strategies and compensatory behavioral syndromes are key components of the biology of a number of animal groups such as amphibians, fish, and many invertebrates (Werner 1986) that may influence their vulnerability to alterations in predation pressure (Denno et al. 2002) and prey availability (Werner and Anholt 1993, Resetarits and Chalcraft 2007). In this chapter I explore the relative sensitivity of three species of amphibian that utilize disparate metamorphic strategies to bottom-up and top-down processes initiated by plant invasion in order to determine if these trophic effects differentially influence species based on their biology.

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CHAPTER 2

ACROSS THE GAP: CONNECTING BELOWGROUND CONSEQUENCES OF INVASION BY THE EXOTIC GRASS *MICROSTEGIUM VIMINEUM* AND ENERGY FLOW TO ABOVEGROUND CONSUMERS[1]

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[1] DeVore, J.L., J.C. Maerz, and M.A. Bradford. To be divided into two manuscripts on soil-based effects and how invaders influence energy flow to aboveground consumers and submitted to Global Change Biology and Functional Ecology, respectively.

Abstract:

Exotic plant invasion is an increasingly ubiquitous process that has the potential to influence trophic resource availability within invaded habitats, either through sequestration of the energy resources produced by these plants or by influencing overall prey production in invaded habitats. As many exotic plants are relatively free of herbivory, detrital food webs may provide a mechanism through which nonindigenous resources support native consumers. In fact, subsidization of aboveground food webs by belowground resources is thought to improve ecosystem stability through the provision of resources that compliment potentially unstable, herbivorous food webs. However, detrital food webs are also sensitive to changes in the quality of detrital inputs and abiotic effects that frequently accompany plant invasion. If plant invasion is found to influence these food webs, as well, the implications of invasion for consumer communities are likely to extend beyond effects on herbivores in these habitats. We studied the belowground implications of invasion by the exotic grass *Microstegium vimineum* into forest floor habitats, including effects on C pools and biogeochemical cycling, which are likely to directly impact resource supply to belowground food webs. We also estimated the density of microarthropods in paired habitats where *M. vimineum* was present or absent to determine whether the production of potential trophic resources from detrital food webs was influenced by invasion. We then used isotopic techniques to trace the contribution of energy from this plant into forest floor consumers (American toads and lycosid spiders) that are reliant upon detrital food webs within these habitats. We also sought to determine whether living *M. vimineum* also contributed to detrital subsidies to lycosid spiders through root exudation. We found that invasion significantly influenced the abiotic soil environment and drove a priming effect within invaded soils, although mineralizable C pool size was not affected. Despite increased litter inputs

following invasion, microarthropod abundance was not positively affected by invasion and, in fact, the abundance of mites (the dominant microarthropod at our sites) was lower within invaded habitats. Resources produced by this exotic plant were incorporated into the tissues of American toads in proportion to their environmental presence, and living plant was also found to contribute to the diet of aboveground predators through root exudation. We infer that trophic resource produced by exotic plants are available to generalist predators through detrital food webs, but that overall resource availability may be affected by the presence of this plant due to alterations in belowground communities following invasion.

Introduction:

Autotrophic production provides the energy upon which food webs are based, making plants a vital component of ecosystems worldwide, but as a consequence of increasing anthropogenic connectivity a steadily increasing proportion of plants are nonindigenous (Mack et al. 2000). As many exotic plants are not targeted by herbivores (Keane and Crawley 2002) and invasive plants frequently outcompete native vegetation (Adams and Engelhardt 2009), reductions in the availability of indigenous energy sources have the potential to drive resource limitation within invaded habitats (Carvalheiro et al. 2010), especially when the invader is phylogenetically isolated from native plant species (Agrawal and Kotanen 2003). However, herbivorous pathways represent only one way in which plant carbon can enter food webs. Belowground, detrital food webs may also conduct energy produced by exotic species to organisms dwelling within invaded habitats via inputs of dead plant material or through root exudation from living plants (van der Putten et al. 2009). In systems where herbivory is minimal, the relative importance of this detrital food web network should increase.

Even within uninvaded systems approximately 90% of autotrophic production enters the food web as detritus, making it an important source of nutrients and organic material for belowground food webs, as well as a supply of energy for aboveground consumers (Polis and Strong 1996). Detrital systems are generally regarded to be donor controlled, as the rate of consumption does not immediately influence the rate of energy supply (although feedbacks between detrital input quality and aboveground plant production are common [Wardle 2002]). Alterations in donor identity may therefore be expected to influence consumers within these systems (Bezemer et al. 2010). The rate at which these resources become available to detrital food webs is controlled by the microfloral communities that drive belowground biogeochemical cycling (Wardle 2002). In this way these organisms influence the availability of nutrients for plants and trophic resources for heterotrophs that rely upon detrital food webs (Wardle 2002). This process is sensitive to alterations in the quality of nutrient inputs, and plant invasion has been demonstrated to have effects on both the structure and function of belowground microbial communities, including rates of biogeochemical cycling (Kourtev et al. 2002). Changes in the quality of litter inputs have been frequently proposed as the driver behind these changes (Ehrenfeld 2003), as invasive exotic plants are frequently highly productive, high nutrient plants that maintain larger leaves with higher nitrogen concentrations than native plants in order to support higher rates of photosynthesis (Ehrenfeld 2003, Blumenthal 2006, Leishman et al. 2007). Changes in plant identity can also influence microhabitat variables such as soil acidity, temperature, and moisture (Ehrenfeld et al. 2001), which can further affect decomposition (Kourtev et al. 2003, Fierer et al. 2005, Dijkstra and Cheng 2007) and habitat quality for belowground fauna.

Root exudation of mucilage, sugars, amino acids, and organic acids provides another mechanism through which plants may affect resource inputs to belowground food webs (Hutsch et al. 2002). Recent photosynthate from root exudates contributes substantially to soil respiration (Hogberg et al. 2001, Wu et al. 2011) and is rapidly incorporated into belowground microbial biomass (Hogberg et al. 2008). Accordingly, there is increasing evidence that they provide a key resource for detrital consumers (Pollierer et al. 2007). Although potential effects of this resource have not been investigated in exotic plant systems, this process provides a pathway through which photosynthetic production may enter food webs despite a lack of herbivory upon aboveground plant material, and may therefore provide a trophic link between living invasive plants and forest floor consumers via the detrital food web.

The pathway that conveys detrital energy from microbial decomposers to the aboveground food web is comprised of a diverse set of soil fauna that is also responsive to alterations in detrital input quality (Paterson et al. 2008). Although detritivores have traditionally been considered to be generalist consumers, there is evidence that individual plants can differ greatly in their effect of belowground food webs, with different species supporting their own detrital food webs (Bezemer et al. 2010). This further increases the likelihood that detrital communities will respond to invasion-driven changes in plant communities. In fact, because exotic plants frequently differ in quality from native plants (Ehrenfeld and Scott 2001, Allison and Vitousek 2004, Leishman et al. 2007) and produce more biomass (Liao et al. 2008), exotic plant invasions should have strong effects on recipient communities. Accordingly, a number of studies have shown that invertebrate species composition and abundance can be altered by the addition of a single exotic plant (Belnap and Phillips 2001, Belnap et al. 2005, Kappes et al. 2007, Topp et al. 2008, Wolkovich et al. 2009). In cases where plant invasion influences the production of invertebrates, invasions are likely to lead to extended effects on higher level consumers.

Microstegium vimineum

Microstegium vimineum (Japanese stilt grass) is an Asian annual grass (family: Poaceae) that has invaded throughout the Eastern and Midwestern United States since it was initially reported in Tennessee in 1919. This shade-tolerant plant commonly invades mesic forest understory habitats such as forested floodplains, where it is known to impede succession through the formation of a recalcitrant understory (Royo and Carson 2006, Webster et al. 2008, Flory and Clay 2010b). Invasion by *M. vimineum* is frequently accompanied by declines in native plant productivity and diversity (Flory and Clay 2010a), attributable to its high competitive abilities as well as selective herbivory on native competitors (Leicht et al. 2005, Webster et al. 2008, Adams and Engelhardt 2009, Flory and Clay 2010b). Higher biomass production has been demonstrated within invasive populations, making it likely that this plant has evolved increased competitive abilities within its introduced range (Flory et al. 2011). Invasion generally results in a net increase in forest floor plant cover (Flory and Clay 2010b, Strickland et al. 2010) where it has been recorded at densities of over 1,300 stems/m^2 (Brewer 2011) and can lead to average increases in vegetation cover of 200% (Marshall and Buckley 2009). The presence of this plant has been associated with a number of ecosystem changes including biogeochemical effects such as increased rates of nitrification (Ehrenfeld et al. 2001, Ehrenfeld 2003, Hawkes et al. 2005) and litter decomposition (Ashton et al. 2005), as well as influences on the structure and function of microbial communities (Kourtev et al. 2002, 2003). The shallow roots of this invader, which occur predominantly in the litter layer and upper cms of soil (DeVore, pers. obs.), may contribute to labile resources through the addition of root exudates, although the influences of root dynamics on these processes is generally poorly understood (Ehrenfeld 2004). Although the changes in soil properties and belowground nutrient dynamics that follow invasion by this plant may be expected to influence native food webs, and invertebrate communities have been found to respond significantly to the presence of this plant (Marshall and Buckley 2009, McGrath and Binkley 2009, Simao et al. 2010), the potential for bottom-up influences of *M. vimineum* invasion on native consumers remains unstudied.

Here we explore the multifaceted mechanisms through which invasion by this exotic plant can influence resource availability within invaded habitats through effects on carbon availability stemming from altered belowground carbon storage, microbial function, biogeochemical effects, and microarthropod production. Given previously observed influences of invasion on microbial structure and function (Kourtev et al. 2002, 2003), we hypothesized that increases in labile carbon inputs accompanying invasion by this plant would increase belowground active microbial biomass and drive a priming effect, in which C turnover rates increase due to the stimulation of microbial communities (especially those that specialize in the decomposition of recalcitrant soil C). We expected that this would lead to decreases in the size of belowground C pools by increasing microbial activity or promoting copiotrophic decomposer communities. We theorized that this would negatively affect the density of detrital invertebrates in the litter of impacted habitats, as rapid decomposition can be associated with "leakier" biogeochemical cycling leading to nutrient losses, or promote detrital communities with limited connection to aboveground food webs (Hendrix et al. 1986, Wardle et al. 2004). The presence of this C4 invader within a plant community that utilizes the C3 photosynthetic pathway provided us with a unique opportunity to use its isotopic signature to track the contributions of this plant through recipient food webs. As the degree to which trophic resources produced by this exotic plant contributes to aboveground food webs is unknown, we used this signature to test whether resources produced by an exotic plant and routed through belowground pathways are an important source of energy for aboveground predators, such as American toads (*Anaxyrus [Bufo] americanus*) and lycosid spiders, which may serve as a link between belowground and aboveground food webs (Scheu 2001). We expected to find that these food webs trophically connect this plant with forest floor predators, although we presumed that root exudates would not contribute significantly to these resources, given the relatively low biomass allocation that *M. vimineum* makes to its shallow roots.

Methods:

Study sites

We located eight actively progressing invasion fronts within the Georgia Piedmont physiographic region in the southeastern U.S., and isolated 7.6 m^2 plots with 1m high silt fencing on either side of each front. These invasion fronts actively progressed during the course of this work, implying that preexisting underlying edaphic characteristics were not responsible for the absence of the grass at the uninvaded sites. The silt fencing enclosures largely impeded progression into uninvaded study plots, but we weeded all uninvaded sites to some degree to prevent invasion. Four sites were located in Whitehall Forest (N33.89° W83.37°), two in Hard Labor Creek State Park (N33.67°, W83.60°), and two in the Oconee National Forest (N33.20°, W83.49°); all sites represented independent invasions. In order to determine whether the biomass of litter inputs varied between invaded and uninvaded sites we removed three ¼ m^2 quadrats of litter from random positions within each pen in 2006 and 2008. This litter was removed down to the mineral soil post leaf-fall, all twigs were removed, and the litter was air dried and weighed. One Hard Labor site was not identified as a potential study location until the spring of 2007, so litter from this pen was not included in mass analysis due to the possibility that prior decomposition would affect the results. We utilized a repeated measures ANOVA analysis using both treatment and locational block to compare litter input masses. To determine whether potential differences were attributable to greater deciduous litter fall at invaded sites, large (32.3" L x 20.4" W x 16.7" H) plastic bins were placed in the center of each pen in the summer of 2008 prior to leaf drop; we dried and weighed the collected leaves as an estimate of relative litter fall in each pen. Disturbance at the two Oconee sites tipped a litter bin at each location, so we excluded those sites from litter fall analysis. The production of *M. vimineum* varied between sites, so we used isotopic techniques to determine the contribution of *M. vimineum* to the litter inputs of each of these invaded pens. We accomplished this by pooling the three quadrats of litter that had been collected from each pen in 2006 and removing subsamples of native (principally deciduous leaf litter) and *M. vimineum* inputs from each one. Full and subsamples were then air-dried, ground with a Wiley mill, and oven dried. A subsample of the ground material from each sample was then ball milled to a fine powder and submitted for C:N and stable isotope ratio analysis by the University of Georgia Analytical Chemistry Laboratory using a NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy) coupled to a continuous-flow isotope-ratio mass spectrometer (Thermo, San Jose, CA, USA). We used a standard mixing model technique to determine the relative contribution of native and *M. vimineum* inputs, given the values that this technique established for each at each site (Post 2002).

Objective 1: Does the presence of M. vimineum *influence belowground properties such as abiotic soil properties, belowground C pools, and active microbial biomass?*

We conducted soil sampling monthly from May through November of 2008. We took field measurements of soil moisture and temperature (10cm depth) in triplicate at each sampling occasion as well as during additional site visits; when multiple measurements were taken within a given month, we averaged those readings and used the mean value for each site such that each site's monthly value represents between one and five separate sampling dates. Soil sampling locations were haphazardly chosen by blinding tossing three markers into each pen and consisted of pulling 8cm diameter, 0-10cm depth soil cores from selected positions. We sieved together replicate cores (4mm) and either air-dried them for carbon analysis or stored them fresh at 5°C until analysis. Gravimetric soil moisture, pH, substrate-induced respiration (SIR), and mineralizable C were all measured using fresh soils at each sampling occasion; we performed two analytical replicates of each analysis. We dried soil subsamples for 105°C for 24 hours in order to determine the gravimetric soil moisture, and measured pH using a 1:1 soil:H_2O volumetric ratio. We determined substrate induced respiration, which provides a measure of active microbial biomass, in accordance with Fierer and Schimel (2003) wherein soil slurries were preincubated with excess substrate for one hour, followed by a 4 hour incubation period at 20°C. We then estimated respiration by measuring the concentration of CO_2 within the headspace via infra-red gas analysis (IRGA; Li-Cor Biosciences, Model LI-7000). We determined mineralizable C, which estimates the size of the belowground labile C pool, through 60-day C mineralization assays, in which we maintained soils at 20°C and 65% water holding capacity for 60 days while periodically taking measurements of respiration rates using static incubation techniques and IRGA analysis of headspace CO_2 concentrations (Fierer et al. 2005). When we plotted CO_2 production against time, the area under the curve provided an estimate of mineralizable C. We estimated the contribution of *M. vimineum* to belowground carbon pools at these sites through fractionation methods in combination with isotopic techniques as described in Strickland et al (2010).

Objective 2: Does microarthropod density differ in uninvaded and invaded habitats?

We estimated microarthopod densities in May 2008 through the use of litter extractions. Unlike pitfall trapping, which provides a measure of both abundance and activity, this measure returns density estimates. Given that structural habitat changes that follow invasion by *M. vimineum* may influence movement within these habitats, we took this method to be more likely to provide accurate estimates of microarthropod densities. We removed three ¼ m^2 quadrats of litter from random positions within each pen; litter was removed down to the mineral soil, any living plant material within the quadrat was clipped at soil level and included, and samples from each pen were pooled into Ziploc™ bags and chilled until extraction (<48 hrs). We extracted arthropods on Berlese funnels under 60 watt bulbs into vials of 75% ethanol and enumerated invertebrates under a dissecting scope; all macro- and mesoarthropods (>2mm in length) were removed, after which the sample was split into 5 graduated petri dishes (r=5cm). We quantified and identified to order all microarthropods that were found within five randomly selected $1cm^2$ subsamples within each dish. We then determined the average density of each order within these 20 $1cm^2$ subsamples and extrapolated those values out to the total dish area ($78cm^2$). We then used this abundance estimate to determine the average density of each invertebrate order. We conducted these estimates at six sites; three within Whitehall Forest, two within Hard Labor Creek State Park, and one within the Oconee National Forest.

Objective 3: Do resources produced by M. vimineum *contribute to those consumed by forest floor predators?*

Between mid-May and mid-June of 2007 we raised metamorphic *A. americanus* from egg strings and, following metamorphosis, stocked them into enclosures at the previously described paired sites at each of the eight invasion fronts at a density of 100 individuals per $58m^2$ pen (methodology described in DeVore 2011). As terrestrial mortality rates are relatively high for this species (Werner 1986), stocking high number of toadlets ensured that some would survive to the following spring. However, this stocking density of 1.7 metamorphic toads per m^2 is still low for dispersing toadlets, as this species is known to transform and invade terrestrial habitats en masse (Werner 1986) where they form aggregations (Arnold and Wassersug 1978, Hayes 1989). These toads remained confined within these habitats until the following spring when all 53 of the survivors were harvested in May of 2008. The small size at metamorphosis common to this species (~0.08g in this study) in combination with the rapid growth rates they displayed ensured that, at the time of recapture, the majority of tissue formation occurred within these habitats (7163% increase in mass; mean mass at recapture= 5.81g: range=1.49 to 19.64g). Only locational blocks in which toads from both treatments survived to recapture were included in further analysis; due to complete mortality at one Whitehall pen and extreme flooding at an Oconee site, only six locations were included. We euthanized toads with neutral pH-buffered MS 222 immediately following collection, removed their digestive tracts, and dried, ground and submitted whole bodies for C:N and stable isotope ratio analysis by the University of Georgia Analytical Chemistry Laboratory. We performed lipid content corrections by regressing the $\delta^{13}C$ values of individual toads from uninvaded cages against their C:N ratio and generating predicted $\delta^{13}C$ values *sensu* Post (2007). We then utilized deciduous and *M. vimineum* values from each pen to determine the apparent contribution of *M. vimineum* to the tissues of toads within both invaded and uninvaded pens through the use of a standard mixing model (Post 2002). Since the passage of plant material through belowground, detrital systems can result in ^{13}C enrichment, likely due to microbial activity (Hyodo et al. 2010), we attributed "apparent" contributions of *M. vimineum* to toads confined within uninvaded habitats to this enrichment process, and subtracted this contribution from the values calculated for toads within invaded habitats in order to determine the actual contribution of this C4 plant to these consumers. We then regressed the contribution of *M. vimineum* to these toad tissues against the contribution to litter inputs in order to determine whether the proportion of carbon resources within litter inputs produced by this plant invader was a significant predictor of its contribution to the tissues of an aboveground consumer.

Objective 4: Does living M. vimineum *provide resources to aboveground consumers?*

In November 2008 we set up five blocks of cages (consisting of 175 gallon Reptariums® with footprint dimensions of 74cm x 122cm) within an invaded floodplain in Whitehall Experimental Forest. We dug 10cm deep depressions to the dimensions of these enclosures, set all cages within the impressions, and froze the soil from each location for >1 week before replacing it within the cage. We then stocked all cages with an equal amount of deciduous leaf litter, which we collected from just outside the invaded habitat, mixed thoroughly, froze, air dried, and weighed. Freezing ensured that no spiders existed within these cages prior to their introduction and that no known herbivores (i.e. orthopterans and hemipterans; Bradford et al. 2010) were present within the study enclosures. We then randomly assigned cages within each block to treatments such that each contained an "invaded" and an "uninvaded" enclosure and seeded invaded cages with ~50 seed heads that we collected from adjacent plants. Neither treatment received any detrital subsidies from *M. vimineum.* The enclosures were allowed to mature over the winter and spring months, after which we subsidized any "invaded" cages that had not experienced extensive *M. vimineum* growth in early May through hand-planting of adjacent sprouts. Detritivorous invertebrates successfully colonized these cages during this time, but the fine mesh excluded potential herbivores and, accordingly, we did not observe any leaf or stem damage during the course of the study. In mid-May all cages were stocked with equal quantities of lycosid spiders that we collected from the adjacent habitats and paired by size. We also stocked each cage with 20 metamorphic toads in June 2009 as a part of a larger experiment (see DeVore 2011); these toads served as an additional prey base, and no toads survived until all spiders were recaptured in August. In this way all spiders were confined upon soils from invaded habitats that lacked *M. vimineum* detritus; those from the treatment group were in cages that contained living *M. vimineum,* while the control group cages lacked living plant. We euthanized collected spiders via freezing, oven dried their whole carcasses at 105ºC, ground them to a fine powder, and submitted them to the University of Georgia Analytical Chemistry Laboratory for C:N and stable isotope ratio analysis. We corrected isotopic readings for lipid content using the methodology described above for toads (Post et al. 2007). Using a randomized complete block design we compared δ^{13}C readings from invaded and uninvaded cages via MANOVA in Statistica 9 (StatSoft Inc 2011). As herbivores had been excluded from these enclosures and spiders do not directly consume plant tissues, we assumed that additional enrichment beyond that exhibited by spiders in the control cages was indicative of carbon flow from living *M. vimineum* to this aboveground predator.

Results:

Study site litter inputs

The mass of litter inputs was greater in invaded habitats, for an overall 14% increase in litter inputs ($F_{1,6}$=8.104, p=0.029); locational block was also a significant predictor of litter input mass ($F_{6,6}$=6.799, p=0.017). Mean increases in litter inputs were 22% in 2006 and 5% in 2008. Increased litter inputs were not attributable to differential deciduous litter fall within invaded pens, as neither treatment nor location were significant predictors of litter fall ($F_{1,4}$=1.719, p=0.26 and $F_{4,4}$=2.340, p=0.22, respectively), and litter fall mass, on average, was 19% greater within uninvaded sites. C:N ratios of post-leaf fall culms were significantly (46%) higher in *M.*

vimineum plants than in native litter inputs ($p=0.032$); there was no significant effect of locational block on these ratios ($p=0.774$).

Objective 1: Does the presence of M. vimineum *influence belowground properties such as abiotic soil properties, belowground C pools, and active microbial biomass?*

Belowground, the presence of *M. vimineum* was associated with a significant increase in soil water content ($F_{1,7}=11.37$, $p=0.012$; 19.0% increase; Figure 2-1) and a marginally significant effect on soil pH ($F_{1,7}=4.459$, $p=0.073$; 38.8% increase; Figure 2-2). The relationship between *M. vimineum* presence and soil temperature varied temporally ($F_{8,56}=3.012$, $p=0.007$); temperatures tended to be higher in invaded habitats during the growing season but lower in the winter months (see Figure 2-1), an effect that a post-hoc Newman-Keuls test demonstrated to be statistically significant in May and August ($p<0.05$). Locational block also had a significant, month-dependent influence on soil water content ($F_{42,42}=1.852$, $p=0.024$) and soil temperature ($F_{56,56}=11.32$, $p<0.0001$) while soil pH varied by sampling date ($F_{6,42}=3.695$, $p=0.005$), being highest in July (pH 5.83) and lowest in October (pH 5.56). Neither active microbial biomass (as measured by substrate induced respiration; SIR) or total mineralizable carbon storage were influenced by invasion ($p=0.243$ and 0.863, respectively; Figure 2-3). However, SIR values were influenced by month ($F_{6,42}=49.51$, $p<0.001$) and there was a significant interactive effect between locational block and month on mineralizable carbon pool size ($F_{42,42}=2.446$, $p=0.002$). Analysis of the carbon contributions of *M. vimineum* to litter inputs and belowground carbon pools revealed a significant linear relationship between the two ($p=0.008$, $n=8$; $r^2=0.668$, slope 0.317).

Objective 2: Does microarthropod density differ in uninvaded and invaded habitats?

Total microarthropod density was not significantly affected by invasion status ($F_{1,5}$=2.742, p=0.159; Figure 2-4). Over 90% of individuals belonged to one of three orders; Acari (65.2%; range 25.5-62.8%), Collembola (21.6%; range 6.3-62.8%), and Thysanoptera (8.4%; range 0.7-21.9%). There were, however, differential influences of *M. vimineum* presence on microathropod densities; there was a marginally significant decrease in Acari densities of 35.5% ($F_{1,5}$=4.515, p=0.087), Collembola abundances were not affected (10.8% decrease; $F_{1,5}$=0.1900, p=0.681), and Thysanoptera densities increased by 118.4%, although this result was not statistically significant ($F_{1,5}$=3.900, p=0.105). Microarthropods <2mm belonging to additional invertebrate orders (Aranae, Chilopoda, Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera, Orthoptera, Pauropoda, Protura, Pseudoscorpionida, and Symphyla) were also present at some sites, but constituted a small proportion of the aboveground microarthropod fauna. The density of these remaining microarthropods was not affected by invasion status ($F_{1,5}$=0.1973, p=0.675).

Objective 3: Do resources produced by M. vimineum *contribute to those consumed by forest floor predators?*

Toads within uninvaded habitats displayed significant ^{13}C enrichment as compared to available basal resources (4.609±0.378; mean±95% CI), but those in invaded habitats exhibited additional enrichment. Isotopic tracing of carbon resources produced by *M. vimineum* in the tissues of this consumer revealed that this additional enrichment was significantly correlated with the contribution of *M. vimineum* to litter inputs (p=0.0004; r^2=0.47), such that *M. vimineum* carbon was incorporated into toad tissues proportionally to its input into the detrital resource pool (see Figure 2-5). The contribution of *M. vimineum* to litter inputs was a better predictor of its presence within toad tissues than its presence in belowground carbon pool values.

Objective 4: Does living M. vimineum *provide resources to aboveground consumers?*

The ^{13}C enrichment of lycosid spiders in enclosures containing living plant was 7% greater as compared to those from habitats where living plant was absent (p=0.030; Table 2-1), indicating that energy resources produced by living *M. vimineum* contributed significantly to the tissues produced by these predators. Resources derived from living plants comprised 1.97% ± 1.49% (mean ± 95% CI; min 0, max 7.30%) of the tissues of these organisms.

Discussion:

It is clear that plant invasion can affect soil properties (Ehrenfeld et al. 2001, Kourtev et al. 2002, 2003, Allison and Vitousek 2004), arthropod communities (Belnap and Phillips 2001, Belnap et al. 2005, Kappes et al. 2007, Topp et al. 2008), and the foraging success of higher level consumers (Maerz et al. 2005), implying that bottom-up effects initiated by exotic plant invasion play an important role in structuring both belowground and aboveground communities. Historically, plant effects on communities have focused largely on herbivory pathways (e.g. Denno et al. 2002) whereas plant effects on detrital pathways are relatively poorly studied (Wardle 2002); however, most heterotrophs across a range of ecosystems derive some if not most of their energy from detritus (Polis and Strong 1996, Moore et al. 2004). Here we investigated potential influences of plant invasion on nutrient resources through biogeochemical cycling as well as trophic resources within food webs and have found that *M. vimineum* influences both belowground nutrient cycling and microarthropod production from detrital channels. Despite these effects, resources produced by this exotic invasive plant provide a significant amount of energy to native forest floor consumers, apparently through belowground, detrital food webs that are subsidized by both dead plant material and root exudates from this plant.

Objective 1: Does the presence of M. vimineum *influence belowground properties such as abiotic soil properties, belowground C pools, and active microbial biomass?*

We did not see evidence that *M. vimineum* influenced physiologically active microbial biomass (as estimated through SIR responses) or microbially active C (as measured by mineralizable C). This is in contrast to Kourtev et al. (2002, 2003), who found that invasion increased SIR responses, but complies with previous work done at these sites which found no effect on SIR responses to invasion despite increases in C mineralization rates (Strickland et al. 2010, 2011). Although our result implies that overall belowground carbon availability remained unchanged following invasion, additional contemporaneous work at these sites has demonstrated that faster cycling, particulate organic matter pools are significantly depleted at invaded sites, leading to a 29% decrease in native POM carbon within invaded habitats that is partially mitigated by the addition of *M. vimineum*-derived carbon resources for an overall 25% decrease in belowground POM (Strickland et al. 2011). This effect has been attributed at one of our sites to a priming influence of *M. vimineum* invasion (Strickland et al. 2010), wherein inputs of labile carbon into decomposer pathways have increased C mineralization rates by stimulating microbial activity (Kuzyakov 2010). As priming effects are driven by increased carbon inputs into detrital food webs, our finding that overall carbon storage remained unaffected despite an increase in mineralization rates is not unusual (Kuzyakov 2010). Losses of native POM following invasion demonstrate that mineralization rates of native carbon sources also increased, likely through these priming effects. This demonstrates that the effects of invasion can extend beyond the decomposition of the invader, influencing turnover of native detritus as well, and indicates that microbial changes accompanying plant invasion can also alter the availability of indigenous energy resources. A similar result was also observed by Ashton et al. (2005), who found while working in forests with similar abiotic characteristics where *M. vimineum* was present or absent that site status (native vs. invaded) was a better predictor of decomposition rates than litter identity (native vs. exotic), such that both litter types decomposed more rapidly within invaded sites, a finding shared by Ehrenfeld et al. (2001).

However, we found little evidence for our previous interpretation in Strickland et al. (2010, 2011) that it was a lack of replication that prevented the detection of significant losses in total mineralizable C following invasion. In fact, visual inspection of our data seems to imply that mineralizable C accumulates in invaded soils during the growing season but become depleted when *M. vimineum* has senesced, potentially lending credence to our hypothesis in Strickland et al. (2010) that root exudates are an important contributor to belowground C resources within invaded habitats. Although we lack statistical support for this observation, likely at least partially due to the difficulties of detecting changes in C pools due to spatial variation and site specific resolvability (Saby et al. 2008, Throop and Archer 2008), these mean changes in overall pool size at least confirm that temporal data is necessary before generalizations about the overall effects of invaders on belowground C storage can be made. It appears that June, the month for which we presented data on relative C pool sizes across our eight forested sites in Strickland et al. (2011), was also the month in which the most marked difference in C pool size existed. Based on this data, we may have overestimated the potential effects of *M. vimineum* on overall belowground C storage within invaded habitats in our discussion of such effects in Strickland et al. (2010), as the temporal data presented here reveals that the effects on this invader on carbon dynamics may be more complex than was previously thought. However, the influences of invasion on losses of faster cycling carbon pools were significant, and although we did not resolve C turnover rates at all of the sites included in this study, we have found that invasion increased rates of C mineralization at one of our sites (Strickland et al. 2010). It is therefore still likely that C turnover rates are higher in invaded habitats. This would not necessarily lead to losses in total belowground C storage, if input rates were also higher in invaded habitats (Kuzyakov 2010), potentially due to inputs of labile C from root exudation.

Invaded areas were also associated with a number of altered abiotic characteristics that can influence C dynamics, so it is possible that abiotic effects associated with invasion contribute to POM loss in invaded environments. Increases in pH, for example, can drive increased C cycling by changing the forms of organic acids, making them available for uptake (Kourtev et al. 2003). While the majority of plant invasions have been associated with increased soil acidity (Weidenhamer and Callaway 2010), invasion by *M. vimineum* has been repeatedly associated with decreased acidity in both field and experimental invasions (Ehrenfeld et al. 2001, McGrath and Binkley 2009). As *M. vimineum* preferentially utilizes nitrate as a nitrogen source (Fraterrigo et al. 2011), the utilization of which results in the secretion of OH^- or HCO_3^- following uptake, pH changes may result from the altered nitrogen dynamics (Ehrenfeld et al. 2001). The presence of *M. vimineum* was also periodically associated with a warming effect during the growing season, which can also increase decomposition rates (Fierer et al. 2005), and increased soil moisture, which has been demonstrated to intensify priming effects (Dijkstra and Cheng 2007).

Although working in the field across existing invasion fronts provides more realistic data about system responses to invasion than greenhouse experiments, it also raises questions of causality. In this case care was taken to locate adjacent habitats upon level forest floors experiencing active invasion, however, as *M. vimineum* invasion frequently follows disturbance such as flooding (a relatively common occurrence in the forested floodplain habitats where this research took place), it is possible that invasion was progressing from moist soils into adjacent, drier soils (Oswalt and Oswalt 2007). However, mats of vegetation left by plant invaders can positively influence soil moisture (Standish 2004) and, as invasion by *M. vimineum* commonly results in the deposition of a thatch layer that has been hypothesized to increase water retention (Ehrenfeld et al. 2001, Adams and Engelhardt 2009, Flory and Clay 2010b), these differences in soil moisture may also be attributable to this effect.

Objective 2: Does microarthropod density differ in uninvaded and invaded habitats?

Although we found that inputs of detrital resources were significantly greater in invaded plots, as is likely the case following many plant invasions (Liao et al. 2008), we did not observe a corresponding increase in microarthropod densities. Conversely, invasion was associated with decreased densities of the most abundant microarthropod order associated with the detrital food web; the Acari. This effect was slightly ameliorated by a marked but non-significant 108% increase in Thysanoptera larvae, generalist phytophagous invertebrates that suck cellular juices (Ananthakrishnan 1993) and could potentially represent recruitment to this novel food source (Andow and Imura 1994). Although changes in aboveground arthropod communities following *M. vimineum* invasion have been demonstrated previously (Marshall and Buckley 2009, Simao et al. 2010), here we focused on microarthropods that are typically associated with forest floor, detrital food webs.

Interestingly, Marshall and Buckley (2009) compared microarthropod densities across three invasion fronts in the Cumberland Plateau of Tennessee and found that mite abundances in plots under *M. vimineum* were greater, driving overall increases in microarthropod abundances within invaded habitats. They hypothesized that these increases in Acari abundance are attributable to the stable environment that slowly decomposing *M. vimineum* litter provides, increases in the bioavailability of nutrients such as P and Ca in invaded habitats as a consequence of increased soil pH within invaded environments, or thatch-driven stabilization of moisture and temperature. Interestingly, given similar abiotic effects of invasion on the litter matrix, soil pH, soil moisture, and soil temperature, we observed the opposite influence on mite abundance. As the effects of invasion on microbial communities were not investigated in their system, we cannot say whether invasion influenced carbon dynamics. However, the soils in their study were initially extremely acidic (pH 4.5-5.3 in uninvaded habitats), so increases in pH (to pH 5.3-6.0 at their sites) and corresponding increases in nutrient bioavailability that follow plant invasion may be a more important driver in those habitats. The pH of our sites originally approximated those of invaded sites in their study and further approached neutral following invasion. It is likely that, in extreme environments such as the highly acidic soils of the Cumberland Plateau, abiotic influences of invasion will influence detrital communities more significantly than food web effects. In fact this effect has been observed in desert systems, where the abiotic effects of invasion repressed potentially positive bottom-up effects due to substantial changes in habitat type (Wolkovich et al. 2009). Given this, we would argue that abiotic effects observed in our system alone are less likely to be sufficiently drastic to drive the observed influences, raising the possibility that another process is responsible. However, these conflicting results do reinforce that the relative importance of the multifaceted influences of plant invasion may differ depending on pre-existing environmental conditions, making it important to account for initial environmental characteristics when predicting the effects of invaders.

Detrital invertebrates have also been found to respond positively to plant invasion in a number of other systems (Gratton and Denno 2005, 2006, Kappes et al. 2007, Topp et al. 2008) leading, in combination with decreases in herbivory, to an increase in the relative importance of detrital food webs within invaded habitats (Gratton and Denno 2006, Carvalheiro et al. 2010). In this way detrital food webs provide a critical mechanism through which trophic resources produced by exotic plants may support native consumer communities within impacted systems. However, the complexity of belowground food webs makes the implications of alterations in detrital inputs for aboveground invertebrate production difficult to predict. For example, bacterial decomposition channels have limited linkage with aboveground food webs, so shifts from a fungal to a bacterial based decomposition channel (a demonstrated consequence of stilt grass invasion in some systems [Ehrenfeld et al. 2001]) may negatively influence aboveground invertebrate production (Wardle et al. 2004). Additionally, copiotrophic decomposers frequently display lower substrate affinities, potentially leading to resource loss within rapidly cycling systems (Hendrix et al. 1986). Through these processes, the addition of labile resources to detrital food webs may have negative ramifications for invertebrate production, especially in the case of mite production, as this group is largely reliant on fungal resources (Schroter et al. 2004, Coleman 2008). The priming effect that we have observed within these sites therefore raises the possibility that the observed effect on mite production is a bottom-up consequence of microfloral stimulation within invaded habitats.

Another possibility is that top-down processes are responsible for the observed effects. Invasion by *M. vimineum* increases structural complexity in our study system, with positive influences on lycosid spider survival within invaded habitats (DeVore 2011). However, in cases where increased top-down pressure from wolf spiders has been observed they have typically been associated with lower densities of Collembola (Wise 2004), a group that was not significantly influenced by invasion status. Nevertheless, spiders are extremely important in forest floor energy dynamics (Wise et al. 1999), and increases in structural complexity have been found to lead to cascading top-down influences on ecosystem properties such as nutrient cycling and litter decomposition rates in some systems (Wise et al. 1999, Lawrence and Wise 2000, 2004, Wise 2004, Miyashita and Niwa 2006), so this possibility deserves further exploration.

Although investigations into possible top-down effects and the influence of priming effects on the production of aboveground microarthropods could further illuminate the nature of this effect, our finding that the presence of *M. vimineum* can alter the availability of invertebrates associated with detrital food webs demonstrates that the effects of invasion by this plant may reach beyond influences on plant communities and herbivorous food webs. This can be expected to result in even more far-reaching effects on overall resource availability and community composition within invaded habitats.

Objective 3: Do resources produced by M. vimineum *contribute to those consumed by forest floor predators?*

Although the importance of detrital resources has long been recognized by ecologists, there has been relatively little recognition of the role of detritus within food web research (Moore et al. 2004). However, belowground resources may improve ecosystem stability through the provisioning of resources that compliment those provided through herbivorous channels (Polis and Strong 1996, Moore et al. 2004), a process that may be especially important following plant invasion due to an increased reliance on detrital food webs (Gratton and Denno 2006). Isotopic enrichment of American toads within uninvaded habitats demonstrates that this species is dependent upon these detrital food webs, as ^{13}C enrichment beyond that of basal resources is indicative of belowground microbial processing (Hyodo et al. 2010). This makes toads, like many generalist forest floor predators, a link between below and aboveground food webs (Scheu 2001). We found no indication that resources produced by *M. vimineum* were less accessible to this consumer than those of native producers, as the contribution of this plant to toad tissues were proportionate to its presence in detrital inputs. This is a novel finding that connects a vertebrate predator to resources produced by an invasive plant and highlights the fact that a lack of herbivory does not mean that invasive plants are trophically disconnected from forest floor consumer populations (as has been previously assumed, e.g. Watling et al. 2011). Although this finding that trophic resources produced by *M. vimineum* support a forest floor consumer may be interpreted as evidence that nonnative resources are a potential energy source, it is important to recognize that species relying on detrital food webs may still be sensitive to overall changes in trophic resource availability following invasion, even where nonindigenous resources are not sequestered.

Objective 4: Does living M. vimineum *provide resources to aboveground consumers?*

Root exudation may provide a pathway through which recent photosynthate from invasive plants reaches detrital food webs (Hogberg et al. 2008). Although the importance of carbon inputs from root exudation to soil respiration in native plant communities has been repeatedly demonstrated (reviewed by Hogberg and Read 2006), the possibility that labile carbon exudates from invasive plants may drive belowground effects or contribute to trophic resources has not been explored (Weidenhamer and Callaway 2010). In the case of invasion by *M. vimineum* we did not predict that this process would be a significant source of resources because of very low biomass allocation to roots by this plant (~1.5%; Bradford et al., unpublished data). However, living *M. vimineum* was found to be a significant source of energy for lycosid spiders following confinement in enclosures that excluded known herbivores, indicating the presence of a trophic link between a living invasive plant and a forest floor predator that occurs independent of herbivory. As we found that Thysanoptera were relatively abundant in invaded habitats, we cannot rule out the possibility that this group may represent a potential herbivorous link between living *M. vimineum* and aboveground predators that deserves further attention. We feel confident that root exudates are a significant contributor to belowground food webs, however, we have since confirmed their role at this site through the use of pulse-chase experiment, in which ^{13}C label was found to be rapidly incorporated into belowground microbial pools and later recovered in lycosid spiders (Bradford et al. in prep). Although *M. vimineum* allocates little biomass to roots, it is still possible that root exudation is an important driver of nutrient acquisition in this plant. Plants have been shown to use root exudation to influence decomposition rates and thereby increase nutrient availability in nearby soils, leading to positive effects on photosynthetic rates (Hamilton and Frank 2001). As annual plants typically exhibit suites of traits that allow them to maximize resource uptake (Roumet et al. 2006), it is possible that root exudation is similarly important in this annual grass. Another possibility is that *M. vimineum*'s status as an invasive plant increases the likelihood that it will produce substantial amounts of root exudates. Given that many invasive plants are high resource, fast-growing plants that maintain high levels of nitrogen within their leaves in order to support photosynthetic machinery (Leishman et al. 2007), the possibility that high levels of root exudation contributes to nutrient acquisition among invasive plants deserves further exploration.

Root exudates also provide a possible explanation for the observed increases in carbon mineralization rates (Strickland et al. 2010), especially given that *M. vimineum* litter is relatively recalcitrant and therefore unlikely to drive such influences (although the roots and leaves of this plant have a relatively low C:N ratio; Strickland et al. 2010). Increased availability of root exudates is known to stimulate microbial activity (Hamilton and Frank 2001), root exudates from understory plants can contribute substantially to soil respiration (Wu et al. 2011), and the marked increase in understory plant cover that follows plant invasion in our system (Marshall and Buckley 2009, Brewer 2011) is likely to increase the availability of recent photosynthate to detrital food webs. Increased root exudation of labile carbon within invaded habitats coupled with abiotic changes (e.g. increased soil moisture, temperature and pH) that either favor rapid decomposition or increase the magnitude of priming influences have the potential to stimulate microbial activity, increasing carbon mineralization rates within invaded habitats. The influence of root exudates by invasive plants on belowground biogeochemical cycling merits further study; if priming effects driven by root exudates are important drivers of microbial activity in invaded systems (Blagodatskaya and Kuzyakov 2008), this process could contribute to our understanding of why decomposition rates have been found to be higher in invaded sites, regardless of litter type (Ashton et al. 2005). Observations by Kourtev et al. (2002) that effects of invasion on microbial communities are especially marked in the soil surrounding the roots may support these findings. Possible bottom-up effects of this process on detrital food webs also merit further investigation.

We also advocate for further investigations into the importance of exotic root exudates as a source of energy for native aboveground consumers, as our methods did not allow us to estimate the percentage of their dietary carbon that lycosid spiders derived from this resource. Although the rapid growth and long-term confinement of toads within invaded plots enabled us to determine what contribution *M. vimineum* had made to their tissues, the spiders in this study were already large when they were stocked and only experienced short-term confinement. However, a significant portion of their tissues (~2%) was comprised of carbon from root exudates, so it is likely that these exudates are a key source of energy within invaded habitats. This result supports the findings of Pollierer et al. (2007), who demonstrated that carbon from root exudates is a key component in detrital food webs, contributing far more to dietary carbon than resources from litter inputs, although root exudates from an invasive plant have not previously been proposed as an energy resource for consumers within impacted habitats.

Conclusions

Plant invasion and subsequent losses in native plant abundance have generated concern that resource availability may decrease in invaded habitats. However, invasive plants are likely to contribute substantially to detrital food webs through inputs of both dead plant material and root exudates from living plants. Here we demonstrate that detrital food webs effectively convey resources produced by *M. vimineum* to aboveground consumers, and we see no evidence that detrital resources produced by this exotic invasive plant are less available to consumers than those generated by native producers. This is in contrast to observed effects of plant invasion on the availability of resources through herbivorous channels in other systems, where decreases in resource availability are frequently a consequence of underutilization of exotic production (Gratton and Denno 2006, Carvalheiro et al. 2010). However, the presence of this plant was associated with altered abiotic soil properties, stimulation of microbial activity, and reductions in the abundance of mites within invaded habitats. We therefore argue that the availability of detrital resources to aboveground consumers is less likely to be influenced by sequestration of nonindigenous trophic resources than by overall effects on belowground food webs that could translate into broad changes in the availability of resources produced by both native and exotic detritus in invaded habitats.

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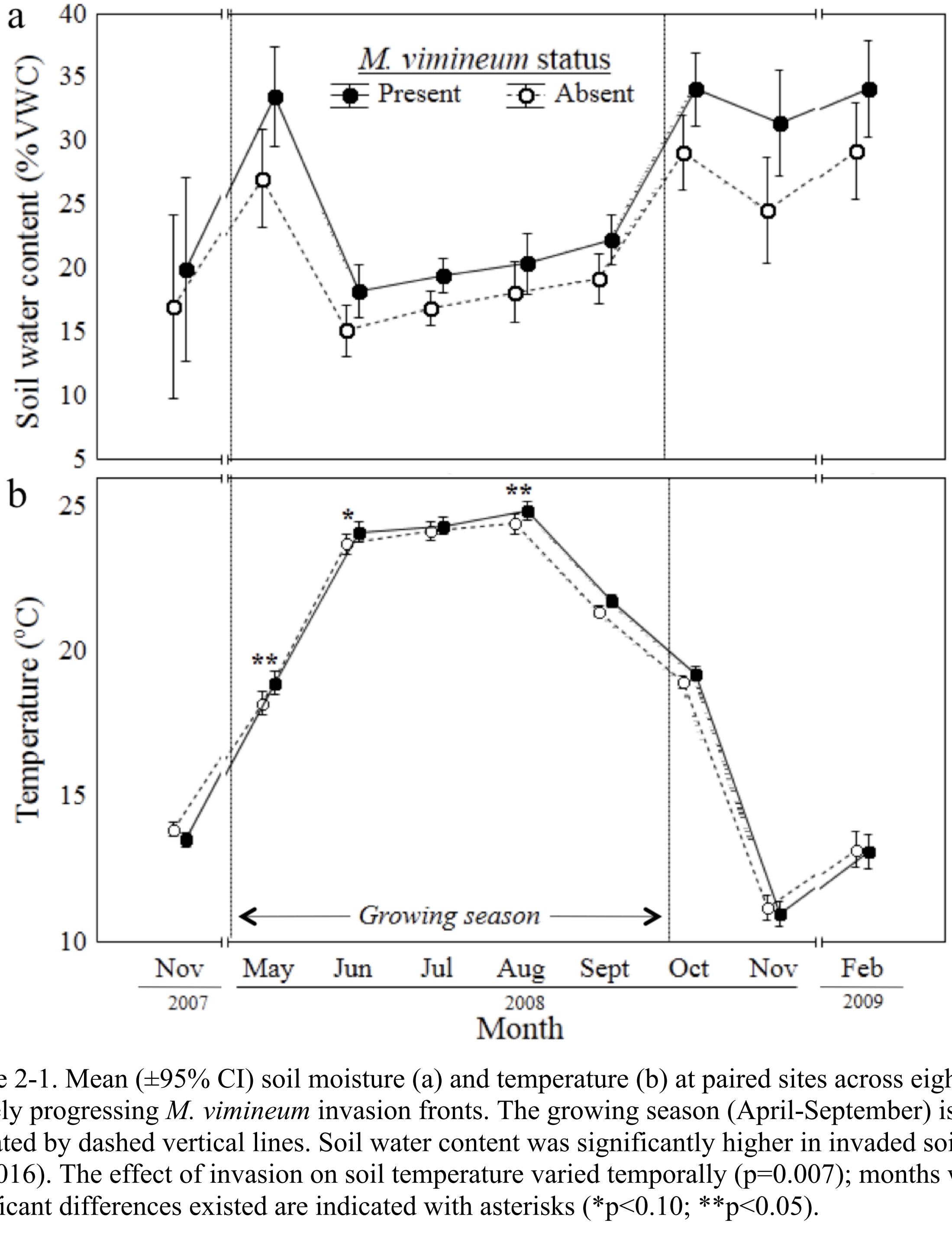

Figure 2-1. Mean (±95% CI) soil moisture (a) and temperature (b) at paired sites across eight actively progressing *M. vimineum* invasion fronts. The growing season (April-September) is indicated by dashed vertical lines. Soil water content was significantly higher in invaded soils ($p=0.016$). The effect of invasion on soil temperature varied temporally ($p=0.007$); months where significant differences existed are indicated with asterisks (*$p<0.10$; **$p<0.05$).

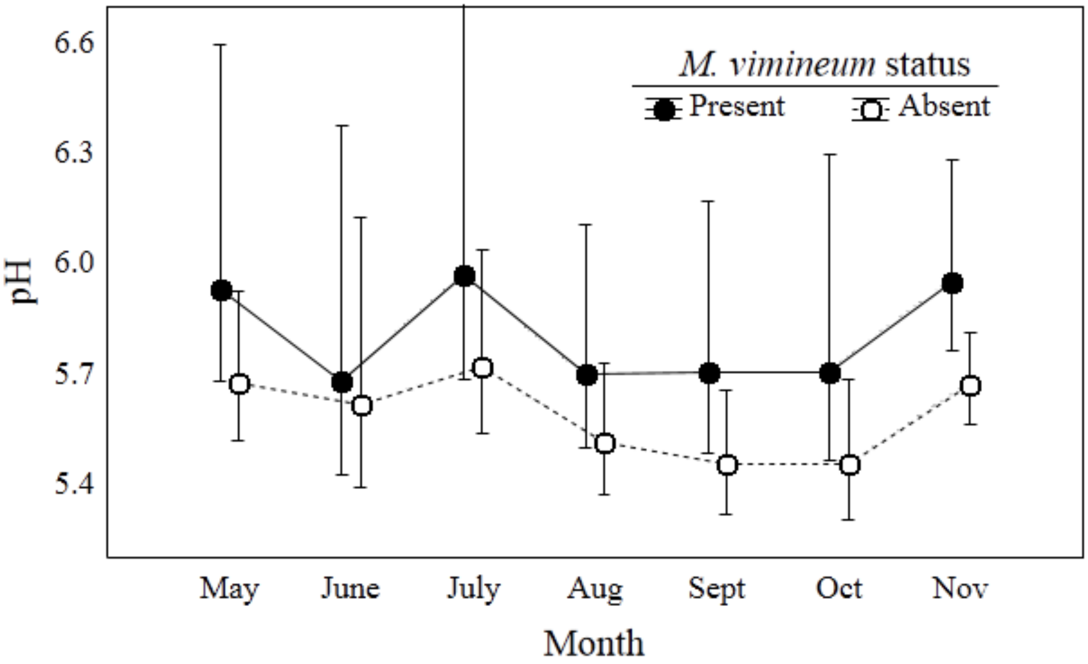

Figure 2-2. Mean (±95% CI) soil pH at paired plots where *M. vimineum* is present or absent (n=8). Repeated measures MANOVA of inverse log transformed data revealed that pH was higher in invaded habitats (p=0.073). pH also varied significantly by month (p=0.005), but there was no significant interaction between the two (p=0.772).

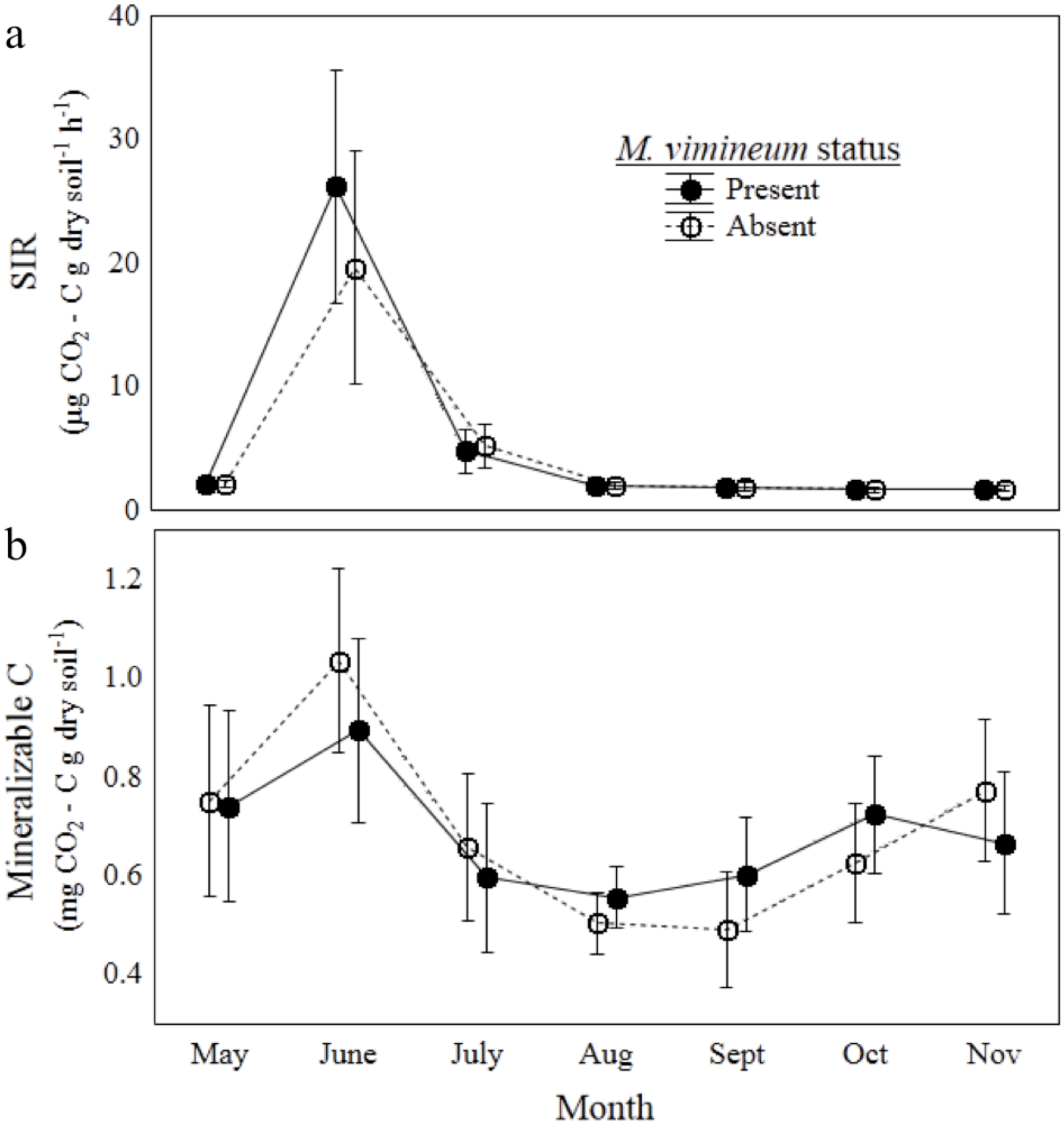

Figure 2-3. Mean (±95% CI) substrate induced respiration (a measure of active microbial biomass) and mineralizable carbon content in soils (0 to 10 cm) at paired plots where *M. vimineum* is present or absent (n=8). Neither measure was significantly influenced by invasion status.

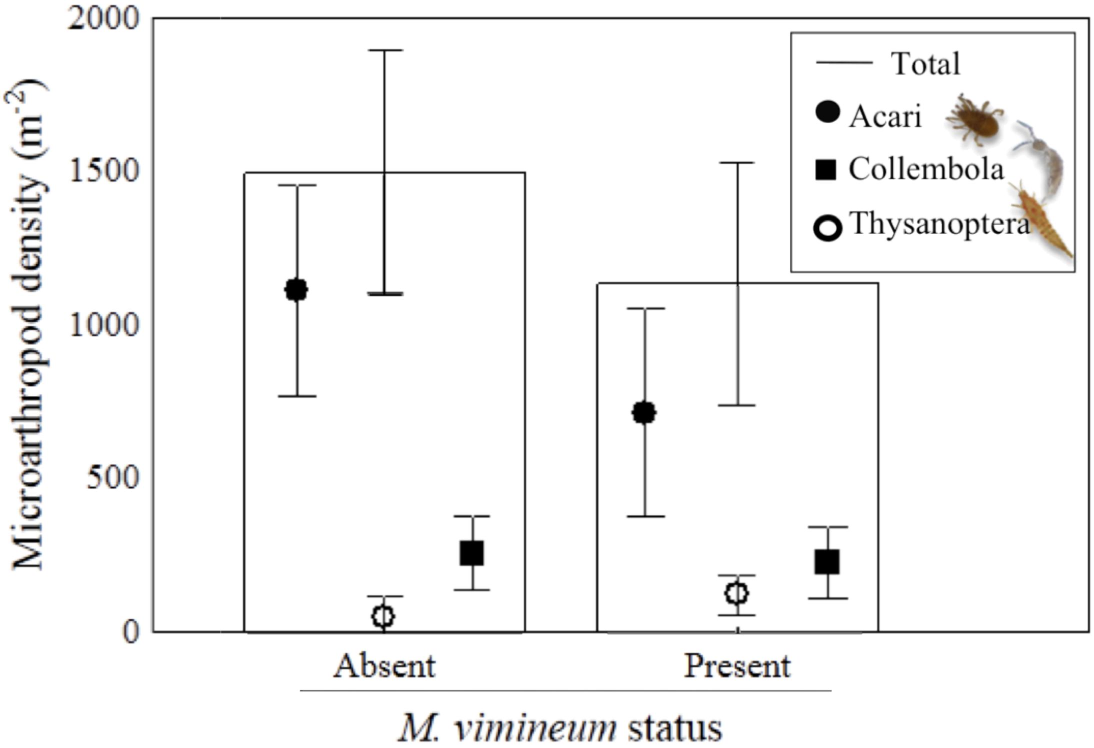

Figure 2-4. Mean (±95% CI) May microarthropod (<2mm) density across six actively progressing *M. vimineum* invasion fronts; overall densities were not significantly influenced by invasion status ($p=0.159$). Three invertebrate orders comprised >90% of microarthropods at all sites; their mean densities (±95% CI) are depicted as points within each treatment bar. Although Acari densities were lower in invaded habitats ($p=0.087$), neither Collembola nor Thysanoptera were significantly affected ($p=0.681$ and 0.105, respectively).

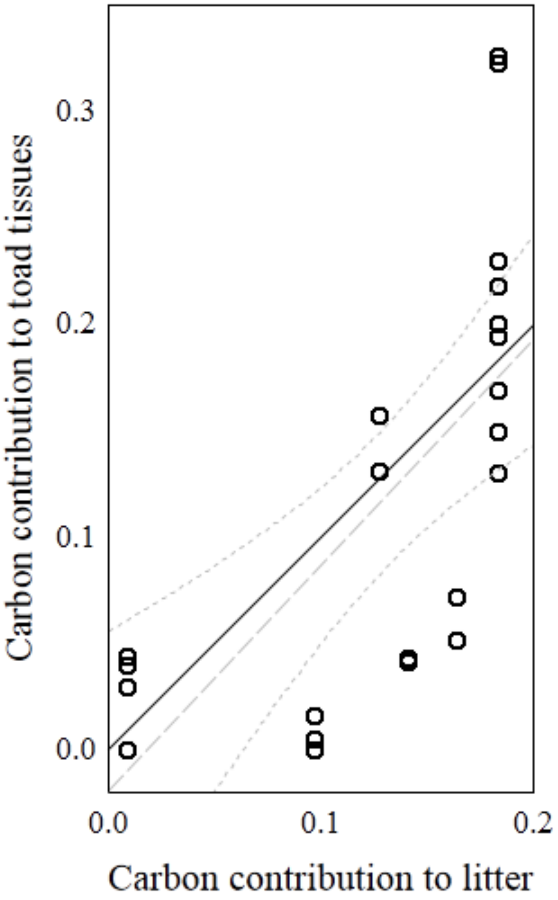

Figure 2-5. The proportion of carbon in the tissues of *A. americanus* that was fixed by *M. vimineum* as a function of this plant's carbon contribution to forest floor litter inputs. Individual toads used in this analysis had been confined within invaded habitats experiencing varying degrees of *M. vimineum* cover for ten months. Dotted lines indicate a linear relationship between these factors ± 95% confidence intervals. The solid line represents a hypothetical scenario in which the carbon from this exotic plant is incorporated into toad tissues in proportion to its environmental presence. The proportion of *M. vimineum* carbon in the litter was a significant predictor of its contribution to toad tissues ($p=0.0004$; $r^2=0.47$) and this relationship appears to be linear such that carbon from this plant is utilized by this predator in proportion to its environmental presence.

Table 2-1. Results of a multivariate ANOVA analysis on the effects of the presence of living *M. vimineum* on the isotopic signature of the tissues of lycosid spiders that had been confined within paired enclosures during the growing season. The tissues of spiders confined within cages containing living plants were significantly more enriched in ^{13}C, indicating that a greater proportion of their carbon was derived from *M. vimineum*.

Source	DoF	MS	F	p
Intercept	*1*	*3.527490*	*4958.061*	*<0.0001*
Treatment	1	0.003912	5.498	**0.030**
Block	4	0.001338	1.881	0.155
Error	*19*	*0.000711*		

CHAPTER 3

REFUGE PROVISIONING FOR GENERALIST INTRAGUILD PREDATORS INCREASES TOP-DOWN PRESSURE ON AMERICAN TOADS FOLLOWING JAPANESE STILT-GRASS INVASION[1]

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[1] DeVore, J.L. and J.C. Maerz. To be submitted to Ecology.

Abstract:

Despite the knowledge that communities are structured by an interplay of direct and indirect effects, the difficulties involved in predicting the nature of indirect effects often results in their omission from predictions of the impacts of environmental change. Predicting these influences can be especially difficult when the presence of a single species drives multiple types of effects. For example, plants are important as autotrophic basal resources, so plant community changes are expected to have bottom-up effects on consumers; however, plants also affect the architecture of environments, thereby potentially altering abiotic conditions and interactions between predators and their prey by changing the environmental context in which these interactions take place. Although this structural engineering may play a role in mediating trophic interactions between consumer species, plant modifications of predator-prey dynamics are seldom considered in the context of plant community change. In order to understand the importance of indirect effects on forest floor consumers we apply this concept to understanding the impact of Japanese stilt-grass (*Microstegium vimineum*) invasions on the terrestrial performance of recently metamorphosed American toads (*Anaxyrus [Bufo] americanus*).

We used 3,200 metamorphic American toads (*A. americanus*) stocked into 16, 58m^2 enclosures on either side of eight independent invasion fronts to measure the impact of *M. vimineum* on six-week survival and growth rates of this forest floor carnivore. We found that metamorphic toad survivorship was significantly lower in invaded habitats, but that the growth of surviving toads was not related to invasion status. To investigate habitat alterations initiated by plant invasion with the potential to influence this species through indirect effects, we investigated potential top-down and bottom-up mechanisms behind these reductions in survivorship by assessing prey abundances and performing factorial manipulations of *M.*

vimineum/lycosid spider presence/absence. Edible microarthropod (toad prey) abundance was lower in *M. vimineum* invaded habitats, but this did not appear to affect toad growth. However, we frequently observed predation events on toads by lycosid spiders. In field cages, spiders persisted at a higher density in cages with stilt-grass, and toad survival rates were lowest in cages with the combined presence of stilt-grass and spiders. We found no significant difference in toad survival between cages with and without stilt-grass in the absence of spiders. Our results demonstrate that despite bottom-up effects of stilt-grass invasion on prey availability, it is the contextually-mediated effect of stilt-grass invasion on cannibalism and intraguild predation rates among lycosid spider abundance that causes an increased, density-mediated top-down effect on toad performance. This work provides an example of the complex mechanisms through which indirect effects can influence species interactions and highlights how the dominant influences of exotic invaders may be driven by the modification of pre-existing interactions between native species.

Introduction:

Ecosystems are comprised of spatially explicit associations of biotic and abiotic elements within which there is a flow of nutrients, biomass, or energy (Odum 1969). These highly complex systems are regulated by both direct and indirect effects (Schmitz 2010), but while the nature of direct effects such as competition and predation can often be predicted, the mechanisms through which indirect effects influence consumer communities remain some of the least understood processes in ecological interactions (Jones et al. 1997). As indirect effects often operate through complex mechanisms that can involve interactions between habitat structure, trophic dynamics, behavioral modifications, and other core biological concepts, understanding the mechanisms behind these types of effects can be particularly challenging (Schmitz 2010).

However, these effects are often integral to structuring ecosystems, contributing to the structuring of trophic relationships and influencing basic services such as nutrient cycling (Lawrence and Wise 2000, 2004, Schmitz 2010).

Indirect effects arise when one organism influences another, not directly, but due to an effect on an intermediate species that then leads to an effect on a third through linked influences. These influences can be trophic and density-mediated (in which the first species directly alters the density of the intermediate species, thereby influencing a third- e.g. trophic cascades, exploitative competition, apparent competition, indirect mutualism- aka DMIIs), trophic and behaviorally mediated (in which the presence of the first species alters the behavior of the intermediate species, thereby altering its influence on a third- i.e. trait-mediated indirect influences- aka TMIIs), or contextually-mediated (in which one organism alters the strength or nature of a pre-existing interaction between a second and third species by changing the environmental context in which this interaction takes place- CMIIs [Wootton 1994, Werner and Peacor 2003]). While density-mediated indirect effects are a well-accepted fixture in trophic ecology, forming the basis of our understanding of energy transfer through ecological systems (Wootton 1994), the nature of trait and contextually- mediated interactions makes predicting the strength and direction of these effects more difficult (Werner and Peacor 2003). For this reason, these effects are often excluded from the predictive modeling exercises with which ecologists attempt to understand the consequences of environmental change, despite evidence that they frequently drive stronger responses than density-mediated effects (Werner and Peacor 2003, Schmitz et al. 2004, Griffen and Byers 2006).

Plant invasion is a process that has the potential to drive indirect effects on consumers living within invaded habitats. As many exotic plants are predator-free within their introduced range (Keane and Crawley 2002), these species have limited potential to drive direct, bottom-up effects on consumer communities through increased resource availability. However, they may indirectly influence these communities through competitively driven alterations in the native plant community, changes in the quality or quantity of inputs to detrital food webs, or by changing the environmental context of the habitat by altering the abiotic properties or structural complexity of the environment. In fact, all of these effects have been observed as a consequence of exotic invasion; for example, arthropod communities have been found to respond to losses in plant diversity following plant invasion (Carvalheiro et al. 2010, Simao et al. 2010), invasion-driven alterations in belowground nutrient inputs have been found to influence the structure and function of belowground communities (Kourtev et al. 2002, 2003), abiotic consequences of plant invasion have been found to influence biogeochemical and abiotic ecosystem properties (effects may be especially pronounced when the invader demonstrates a novel trait; e.g. nitrogen fixation or a unique rooting system [Vitousek et al. 1987, Mack et al. 2000])), and structural alterations have been found to drive trait and density-mediated indirect effects (e.g. on arthropod prey via the provisioning of attachment points for web-building spiders [Pearson 2010]).

An important trophic linkage that may be altered by CMIIs following plant invasion is the intraguild or cannibalistic linkage between species or individuals filling similar trophic positions. Intraguild predation and cannibalism, in which predators prey upon each other as well as a shared prey base, often play a key role in the maintenance of species diversity (Amarasekare 2007, Borer et al. 2007, Rudolf 2007), and the strength of this interaction has been found to decrease with increased structural complexity in a number of ecosystems (reviewed by Janssen et al. 2007, McCormick 2009). Through autotrophic ecosystem engineering— by which an organism may alter the structure and complexity of the habitat through its own growth (Jones et al. 1994, 1997)— the spatial context of invaded ecosystems is often significantly altered (Crooks 2002), with potential implications for the trophic connections within these landscapes (Jones et al. 1997). When this process leads to increases in structural complexity, positive effects are expected for the persistence of intraguild prey (Langellotto and Denno 2004, Janssen et al. 2007), potentially leading to increased pressure on shared prey (Finke and Denno 2002, Vance-Chalcraft et al. 2007). Therefore, through the modification of ecosystem properties, engineers can promote one group via positive, CMIIs on intraguild prey via refuge provisioning, to the detriment of another, via negative, DMIIs on the shared prey of these predators (Jones et al. 1997, Crooks 2002).

However, in cases where alterations in plant communities are the driver behind these indirect effects, potential bottom-up influences must also be taken into account. As plants provide the basal resources that support consumer populations, changes in these communities have the potential to drive ramifications throughout the food web. In habitats where these exotic species support few native herbivores, as is relatively common in cases where exotic invasion is promoted by enemy release (Keane and Crawley 2002), these bottom-up effects are likely to be propagated entirely through detrital food-webs. In fact, even in native plant communities, approximately 90% of autotrophic production enters the food web as detritus, and most heterotrophs across a range of ecosystems derive energy through detrital pathways (Polis and Strong 1996, Johnston 2000, Moore et al. 2004, Sanders and Platner 2007). Belowground components of this food web are composed of a diverse set of soil fauna that is responsive to alterations in detrital input quality (Paterson et al. 2008), so alterations in the quantity, quality, and timing of litter inputs and abiotic factors such as soil moisture and pH resulting from plant invasion may influence soil community structure and function (Ehrenfeld et al. 2001). This has potential implications for aboveground predators that rely on belowground food-webs as a key source of trophic resources, the importance of which may only be expected to increase following the declines in herbivore populations that frequently follow plant invasion (Simao et al. 2010).

In order to explore the potential detritally and structurally-mediated indirect influences of plant invasion on a forest floor consumer, we first tested the survivorship and growth of metamorphic American toads across eight actively progressing invasion fronts to determine whether the presence of this plant influences its performance. We then tested potential mechanisms that may be expected to affect this consumer by measuring abiotic factors and prey abundance within these habitats and performing factorial manipulations of plant invader/intraguild predator presence/absence. In this way we sought to detect any effects that may arise as a result of bottom-up trophic cascades within the detrital food-web (thereby influencing the density of the microarthropod prey of this species), contextually mediated indirect effects of plant presence on lycosid spiders (cannibalistic, intraguild predators of metamorphic toads), and resulting, density mediated influences mediated by these spiders on metamorphic toad survival (see Figure 3-1).

Methods:

Plant invader: Microstegium vimineum *(Japanese stilt grass)*

Microstegium vimineum (Japanese stilt grass, Mary's grass, porcelain packing grass) is a highly invasive Asian annual grass that was first reported naturalized to the United States in Tennessee in 1919 (Cole and Weltzin 2005) and has since become widespread in moist, shaded forest floor habitats throughout the eastern United States (Zheng et al. 1997). This plant exhibits certain traits thought to predict an invader's potential to have ecosystem-level effects (Ehrenfeld 2004); its horizontal coverage is greater than that of forest floor natives, it forms dominating ground cover, it produces nitrogen rich leaves and roots, it has a high growth rate, and its shallow rooting system differs from the rooting systems of native plants. Invasion by this plant has been shown to influence belowground carbon cycling (Strickland et al. 2010), shrinking faster-cycling belowground carbon pools (Strickland et al. 2010, 2011), and has been associated with declines in arthropod diversity and abundance (Adams and Engelhardt 2009, Simao et al. 2010, DeVore 2011a), giving it the potential to drive bottom-up effects on forest floor consumers. It has also been deemed an ecosystem engineer (Baiser et al. 2008), as invasion by this plant significantly increases forest floor plant cover, often resulting in increased structural complexity (see Figure 3-2). This effect is especially pronounced because the plant community of the habitat preferentially utilized by this invader within the southeastern United States is often naturally depauperate (Marshall and Buckley 2009, DeVore pers. obs.), whereas *M. vimineum* has been documented grow at densities of over 1,300 stems/m^2 (Brewer 2011) and lead to average increases in vegetation cover of 200% (Marshall and Buckley 2009). Herbivory on this plant is minimal (but see Bradford et al. 2010) and unlikely to contribute to trophic resources utilized by the forest floor predators involved in this research (Sanders and Platner 2007), so the carbon fixed by this plant is likely to pass to these consumers solely through detrital food webs.

Response species: Anaxyrus (Bufo) americanus *(American toad)*

A. americanus was chosen as a response species due to its role as a forest floor predator, where it is likely that they are highly dependent upon the detrital food web (Scheu 2001). Their small size at metamorphosis (averaging 0.09 g in this study) renders them vulnerable to predation by invertebrate predators, while their high rate of terrestrial growth minimizes the influence of the aquatic environment on their terrestrial success (Werner 1986, Goater 1994, Beck and Congdon 1999). The terrestrial phase of this species utilizes toxic secretions from its parotid glands to defend itself, especially against mammals and birds (Arnold and Wassersug 1978, Wells 2007), which is thought to reduce predation risk during this life stage (Werner 1986)- however, this defense is unlikely to prove effective against invertebrate predators with piercing mouthparts. This species is also methodologically appealing because it is a widespread, readily available organism that can be easily raised from egg masses in large numbers and occurs commonly in areas susceptible to *M. vimineum* invasion; once they metamorphose they are easily marked, recaptured, and contained, allowing for direct observation of survivorship and growth rates.

Intermediate species

Intraguild predator

Lycosid spiders are an important predatory group known to persist in higher densities in structurally complex habitats (Denno et al. 2002, Langellotto and Denno 2006, Bultman and DeWitt 2008). As these organisms are highly cannibalistic (Wagner and Wise 1996), and intraguild predation is important in the regulation of their densities (Wagner and Wise 1996), this effect is likely attributable to reductions in rates of intraguild predation and cannibalism associated with increased refuge availability (Wise and Chen 1999, Langellotto and Denno 2006, Rickers et al. 2006). In fact, predicted patterns of intraguild predation have been found to be exceptionally strong in this group (Vance-Chalcraft et al. 2007). Greater habitat complexity and resulting increases in spider densities can have implications for the suppression of the shared prey of this group, with complex environments associated with increased prey susceptibility to spider predation (Finke and Denno 2002) and reductions in prey abundance (Miyashita and Takada 2007).

Prey base

Metamorphic toads feed principally on forest-floor invertebrates that are produced through detrital food-webs (i.e. Acari, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, and Hymenoptera [Flowers and Graves 1995]). As detritial food-webs are responsive to changes in nutrient inputs, cascading bottom-up effects on the abundance of toad prey are possible, and, in fact, reduced arthropod production has been experimentally demonstrated following *M. vimineum* invasion (Simao et al. 2010).

Site description

In the fall of 2006 a number of *M. vimineum* invasion fronts were identified; four in Whitehall Forest, Athens, GA; two in Hard Labor Creek State Park, Rutledge, GA; and two in the Oconee National Forest, Eatonton, GA. Invasion fronts that were selected for inclusion in this study had to have a $58m^2$ invaded area and a nearby uninvaded area of equal size with similar elevation and habitat characteristics. Care was taken to ensure that these invasion fronts were actively progressing, which commonly occurred from the direction of roadsides or soil disturbances. In fact, by the end of the study period all of the paired uninvaded sites had experienced some level of invasion, necessitating hand weeding. For some it was only the presence of the silt fencing that was used to construct amphibian enclosures, acting as a barrier to seed dispersal, that prevented complete invasion of the study area. This implies that underlying edaphic characteristics were not responsible for the variation in invasion status. During the two years for which these sites were monitored, free-ranging *A. americanus* were encountered at every site, indicating that they commonly utilize these habitats.

Production of metamorphs

A. americanus egg strings were collected at both Whitehall Forest and the Oconee National Forest in early March and hatched indoors in aerated 10-gallon tanks. Seven days after hatching, tadpoles were hand-counted into 550L Tahiti lawn pond liners (MacCourt®), each of which had been stocked with 400g of leaf litter and equipped with overflow pipes and screen covers to maintain water depths and exclude predators, respectively. As larval densities have been shown to influence later terrestrial performance (Goater 1994), each pool was stocked with 1,200 tadpoles to ensure that tadpole densities were consistent. Pools were fed equal quantities of Tetra ReptoMin® every other day to subsidize food provided by natural algal growth; the average amount of food that could be consumed by a pool in 15 minutes was provided (~15mL). When the tadpoles began to approach metamorphosis we dropped the water levels slightly so that half of the upper level of the garden pond was exposed, allowing metamorphs to escape the water. Metamorphs who had completed tail absorbtion were transferred to indoor bins, where they were maintained on beds of moist sphagnum moss and air-dried leaves and fed fruit flies ad libitum until they could be released (10>5 days).

Pen survival and growth measurements

Open-topped, 7.6m x 7.6m pens were installed on either side of the eight previously described invasion fronts using 1m tall silt fencing; fencing was buried to a depth of ~16cm with an inward curvature to prevent escapes, and lidded 1qt buckets were installed at each corner for use as pitfall traps during capture periods. Because the presence of course woody debris may influence amphibian performance, all such debris was removed, and each pen was instead equipped with six 0.5m^2 oak coverboards, positioned in two rows at equal intervals. As toadlets reached metamorphosis (between mid-May and mid-June) they were randomly assigned to treatments and released into pens in two cohorts of 50 toadlets each (2007) or four cohorts of 25 toadlets each (2008), after which 100 toadlets had been stocked into each of the 16 pens. This stocking density of 1.7 metamorphic toads per m^2 is well within those that may be expected of dispersing toadlets, as this species is known to transform and invade terrestrial habitats en masse (Werner 1986) where they frequently form aggregations (Arnold and Wassersug 1978, Hayes 1989), and the high rate of initial mortality (which is typical at this life stage [Werner 1986]) quickly reduced densities to ~0.34 (max 0.41, min 0.03) toads per m^2 within six weeks. Individuals from egg masses that had been collected in Whitehall Forest ponds were released in Whitehall Forest and Hard Labor Creek State Park pens, while those from the Oconee National Forest were released in pens at that location. Each toadlet was given a single toe clip to indicate its cohort (i.e. release date) for a total of 1,600 batch clipped toadlets per year. In 2008, five toadlets per cohort per pen were individually marked for the determination of growth rates, for a total of 320 individually tracked metamorphs (the extremely small size of metamorphic toadlets— ours averaged 0.10g at metamorphosis—prevented us from individually marking all 3,200). Recapture occurred in August and consisted of a three day (2007) or a three day, one night closed capture period (2008) that utilized both pitfall trapping and hand searches. Pitfall traps were opened during the first day of searching and checked daily, while hand searches were conducted at every capture occasion; these consisted of walking slowly in parallel lines through the pen while stirring the litter until the entire area had been covered twice, as well as searching under coverboards, along fencing, and under vegetation. Search durations were 30-60min for day searches and 60-120min for night searches. All captured toads were weighed, measured, and (in the case of toads that had initially received batch clips), individually marked via toe-clipping after capture, and the extremely high capture probability observed for this species ensured that

~98% toads had been processed by the end of the capture period (closed capture periods continued at 6-week intervals until the following May, allowing for an accurate determination of capture probabilities). For a given individual no more than one toe on each foot was taken and a maximum of three toes were used. Inner toes on the front feet were not clipped. Abundances for each pen were determined using the Robust Design estimator in Program MARK (subsequent capture periods were included in the model to improve abundance estimates, although only the results from the first capture period were analyzed further in this study), and arcsine transformed survival estimates were analyzed via repeated measures ANOVA analysis (treating each block as a unit of replication) in Statistica 10 (StatSoft Inc 2011) to determine the effect of invasion status, locational block, year, and potential interactions on survival. Growth rates were determined for surviving toadlets that had been individually marked at metamorphosis in 2008 by dividing the difference in mass between release and recapture by the number of days that had passed; individuals were used as replicates in this analysis to avoid over-weighting individuals in pens experiencing low survivorship; these results were analyzed via ANOVA in Statistica 10 (StatSoft Inc 2011), assuming a complete randomized block design that accounted for both treatment and locational block. Since size at metamorphosis may influence the survival probabilities of amphibians (Werner 1986, Beck and Congdon 1999), we also performed an ANCOVA analysis on the success or failure of these 320 individually-marked toads to survive to the capture period, utilizing a binomial distribution with a logit link function in Statistica 10.

Prey availability

Prey availability was estimated through the use of litter extractions. These were conducted in May 2008, immediately prior to metamorph release. Three ¼ m^2 quadrats of litter were removed from random positions within each pen; litter was removed down to the mineral soil, and the samples from each pen were pooled into Ziploc™ bags and chilled until extraction (<48 hrs). Extraction of arthropods occurred on Berlese funnels under 60 watt bulbs into vials of 75% ethanol. Invertebrate enumeration was conducted under a dissecting scope; all macro- and mesoarthropods (>2mm in length) were removed, as they were considered too large to serve as prey items for metamorphic toads, after which the sample was split into 5 graduated Petri dishes (r=5cm). Microarthropods were identified to order and quantified in five randomly selected 1cm^2 subsamples within each dish. The average density of each order within these 20 subsamples was determined and values were extrapolated out to the total dish area (78cm^2). This abundance estimate was then used to determine the average density of each invertebrate order. We confined our density analysis to observed invertebrate orders that have been documented as prey items for young *Anaxyrus;* Acari, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, and Hymenoptera (Flowers and Graves 1995).

Factorial spider x Microstegium vimineum *cage experiment*

In November of 2008 five locational blocks of four cages each were established in a randomized 2x2 factorial design within an invaded floodplain habitat in Whitehall Forest. 175 gallon Reptariums ® were used for this purpose; these provided fully enclosed cages of equal volume, each with a footprint of 0.9m^2. Ten cm deep depressions were dug to match the footprints of each cage, which was set in the resulting impression. To kill any spiders, and thus prevent their accidental introduction into the cages, the soil that was produced from each trench was frozen solid in a walk-in freezer for a minimum of 10 days before being returned to the corresponding cage. Leaf litter was also introduced to each enclosure soon after leaf-fall in order to mimic the forest floor environment. This litter was taken from just beyond the invasion front to ensure similar leaf composition (while prohibiting the introduction of unwanted *M. vimineum* seeds) and was collected over an area matching that of the total footprint of the cages (18 m^2). This litter was mixed, weighed, frozen solid for a minimum of one month, and subdivided by mass such that each cage would receive an equal quantity of spider-free litter subsidies. Two cages within each block were then randomly assigned to *M. vimineum* treatments and each was seeded with ~50 seed heads that had been collected from adjacent plants. These enclosures were then left to mature over the winter and spring months, during which time they quickly became colonized with small soil invertebrates. Cages that experienced low *M. vimineum* recruitment the following May were subsidized through the hand planting of sprouts collected adjacent to the enclosures (all plants were drowned for a minimum of 1 hour to ensure that no spiders were introduced during this process). Any native plants that sprouted were not disturbed, but *M. vimineum* sprouts germinating within cages that had been designated as uninvaded were removed.

Cages that had been randomly selected to receive spider treatments were then stocked with pulses of lycosid spiders. All spiders were hand collected by headlamp within the adjacent floodplain by searching for eye shines. Spiders tended to fall within natural size groupings and were visually sorted by size class (in general; <0.01g: tiny, 0.01-0.05g: small, 0.10-0.20g: medium, >0.3g: large). They were then housed individually (with wet paper towel to prevent desiccation) for <36 hours prior to being stocked into cages. Each cage received an equal number of spiders from each size class. The first pulse of spider introductions occurred in mid May and second pulse was introduced in early June. As intraguild predation and cannibalism are thought to be major regulators of spider densities, driving larger influences on their survival than predation by natural enemies (Wagner and Wise 1996, Langellotto and Denno 2006), these populations were then allowed to self-regulate through density-dependent mortality. As spiders have been demonstrated to prey on organisms up to or less than their own size (Moulder and Reichle 1972) only the densities of spiders ≥0.10g (the approximate mass of the metamorphic toads that were stocked) were monitored after stocking. Smaller spiders were not taken to be a predation risk, although they may have served as an additional prey source to both larger spiders and toads.

In June of 2009, two weeks after the second pulse of spider introductions, each cage was stocked with 20 individually marked metamorphic toads. Five days after release, these toads were recaptured through hand searches, identified, and rereleased over a three-day capture period. The number of spiders large enough to pose a predation risk (≥0.1g) persisting within each cage was also estimated during this period by capturing and individually marking each spider that was encountered using nontoxic Elmer's® neon paint writers. As lycosid spiders are more evident at night, each cage was also searched after sunset for ten nights. As no new captures were made after the fourth night, we were reasonably certain that all spiders over 0.1g had been marked by this time. Spiders were photographed at each capture occasion so that individuals who molted (thereby shedding their markings) could still be identified via photo comparison. Despite repeated searches, no spiders were ever observed in the spider-free treatment cages. Spider abundances in invaded and native cages were square root transformed and compared via ANOVA analysis, using a complete randomized block design. Toad capture probabilities were high (>95%), so analyses were conducted on the number known alive within each cage. Toad abundance was also square root transformed, then analyzed via a factorial ANOVA to account for potential effects of spider presence, *M. vimineum* presence, and any interaction between the two. Treatments were blocked by location in order to account for any variability caused by this factor. All analyses were conducted in STATISTICA 10 (StatSoft Inc 2011).

Results:

Pen survival and growth

Metamorphic toad survivorship was found to be significantly lower in invaded habitats (66% decrease; p=0.0046; see Figure 3-3). There were also significant effects of cohort (p=0.0003) and locational block (p=0.0002), although the influence of locational block interacted significantly with the year of the study as well as the cohort (p=0.049 and 0.047, respectively; Table 3-1). The growth rate of survivors was not affected by invasion status (1.6% reduction, p=0.935; see Figure 3-5). Significant effects of locational block on growth were observed, however, with mean weighted growth rates (± 95% CI) for a given location ranging from 8.08±5.06 to 34.88±17.64 mg/day (p<0.001: n=6; 6), indicating that the resolution of our analysis was sufficient to detect differences in growth rates where they existed. According to linear regression analysis, growth rates within a pen were not significantly correlated with corresponding toad abundance estimates (adj R^2=0.09). We did find, however, that size at metamorphosis was a significant covariate in predicting the short-term terrestrial survival of metamorphic toads (p<0.001), although invasion status continued to be a significant factor for this individually marked subset of the stocked population (n=320; p=0.04). Logistic regression of survival probabilities by treatment was conducted in Statistica 10 (StatSoft Inc 2011) in order to illuminate these effects (see Figure 3-4).

Prey availability

There was a marginally significant effect of invasion on the abundance of edible microarthropods (30.1% reduction; p=0.091; Figure 3-5).

Factorial spider x Microstegium vimineum *cage experiment*

Lycosid spiders (≥0.10g) persisted at significantly higher densities in invaded cages; the presence of *M. vimineum* increased their survival by 28% (see Figure 3-6; p=0.035). Spider presence negatively affected toad survival regardless of invasion status (their presence caused a 1,000% increase in mortality; p<0.001), but this effect was enhanced in the presence of *M. vimineum*, such that, even when survival reductions that could be attributable to abiotic effects were removed, the influence of spider presence on survival was 64% greater in cages containing invasive grass (p=0.047). Toad survival in the absence of spiders was high (0.955±0.027) and was not significantly affected by the presence of *M. vimineum* (p=0.065), although survival was marginally lower in invaded cages (see Table 3-2).

Discussion:

These results demonstrate that the presence of the invasive plant *M. vimineum* degrades habitat suitability for metamorphic *A. americanus* through indirect influences on their survival. By using a multi-trophic level approach to explore the mechanisms behind this effect we have found that, although invasion by *M. vimineum* appears to decrease the overall abundance of edible aboveground microarthropods, there is no apparent effect of reduced prey availability on this small, actively foraging forest floor consumer. Instead, the dominant influence of *M. vimineum* on *A. americanus* is a result of increased top-down pressures associated with invertebrate predator accumulation in areas of greater structural complexity (see Figure 3-7). The high rate of mortality observed in invaded predation enclosures is likely common within this species, whose initial post-metamorphosis penetration into the terrestrial environment appears to be marked by a window of rapid predation-induced mortality similar to those documented in many diminutive post-settlement consumers exhibiting Type III survivorship (a phenomenon that is exceptionally well-documented in marine systems [Almany and Webster 2006])). Further investigations have revealed that susceptibility to this pressure may be confined to a short period immediately following metamorphosis (DeVore 2011b). The absence of this phenomenon within predator exclosures implies that predators such as lycosid spiders are likely to be a major source of post-emergence mortality for this species.

The potential of spiders to suppress prey populations has been well documented (Finke and Denno 2002, 2006); spiders are abundant predators on the forest floor, thought to be the dominant predatory force in these communities, where they annually consume approximately 44% of mean annual standing prey (Moulder and Reichle 1972). Ground-dwelling lycosid spiders, in particular, rely principally upon the detrital food web for resource acquisition (Sanders and Platner 2007). Population dynamics in this group has been found to be exceptionally responsive to the effects of habitat structure (Schuldt et al. 2008); influences on their density appear to be driven principally by the availability of refuge from intraguild predation and cannibalism, which is a major density-dependent mortality factor in this group (Wagner and Wise 1996). The influences of vertebrate predators (Wise and Chen 1999), natural enemies (Wagner and Wise 1996), prey abundance (Bultman and Uetz 1984), and litter quality (Bultman and Uetz 1984), however, appear to play secondary or negligible roles in the regulation of lycosid spider densities. While many in-situ experiments on the effects of structural complexity on spider abundances have been unable to establish whether immigration, predation by other species, or direct cannibalism were responsible for the higher densities within structurally complex habitats, and there has been a question as to whether or not increased complexity was automatically correlated with greater prey abundances (Langellotto and Denno 2004), we have found that, in a system where aboveground prey abundance is actually lower within invaded, structurally complex habitats, and other potential predators were excluded, the effects of cannibalism and intraguild predation alone are sufficient to recreate these patterns in within closed populations. In fact, cannibalistic encounters were frequently observed in uninvaded cages, where refuge use was largely limited to burrows constructed by the spiders or vertical displacement along the mesh walls (which occurred principally at night). Within invaded cages, however, spiders were able to establish territories more effectively by also using *M. vimineum* stalks as both vertical refuges and barriers to visual exposure.

Given that the increased structural complexity associated with invasion by this plant appears to be the dominant mechanism through which *M. vimineum* mediates energy flow between these two native consumers, this effect may be relatively generalizable to other systems in which structural alterations have taken place. In fact, lycosid spider densities have been shown to increase following *Vinca minor* invasion (Bultman and DeWitt 2008), thatch addition (Bultman and DeWitt 2008), and the provisioning of faux leaves (Bultman and Uetz 1984) or plastic plant mimics (Schmidt and Rypstra 2010), but, while spiders may enjoy refuge from intraguild predation within these habitats, attack success on prey appears to be largely independent of structural complexity (Bultman and DeWitt 2008, Schmidt and Rypstra 2010), resulting in density-mediated predatory effects. Since these predators utilize a sit-and-pursue strategy (Schmitz and Suttle 2001) and preferentially attack mobile prey (Moulder and Reichle 1972), species that utilize active foraging techniques (such as juvenile toads) are likely to be especially vulnerable to predation. Although our experimental design did not allow us to distinguish the direct, predatory influence of increased spider densities from potential indirect, behavior or stress-based responses among metamorphic toads, we did find that a 28% increase in spider densities in invaded cages led to a 64% decrease in toad survivorship. The nonlinearity of this response could be attributable to increases in structural hindrances to predator escape (Rieder et al. 2010), non-consumptive effects resulting from a stress-based response to increased predator presence within these treatments (Schmitz et al. 1997, Preisser et al. 2007), or increased foraging activity within invaded environments that led to increased exposure to predation (Heinen 1994).

Although the influences of top-down pressures can sometimes be ameliorated by bottom-up processes (Denno et al. 2002), this is unlikely to happen within this system, as the availability of edible prey items decreased following invasion. Despite observed reductions in prey availability, growth rates in between treatments were similar. While this could be a consequence of reduced competition in invaded habitats, regression analysis did not reveal significant evidence of density dependent effects on growth rates (likely because the densities utilized here are much lower than those in which density-dependent effects have been observed in this species [Harper and Semlitsch 2007]). This lack of a significant bottom-up effect may be a benefit of the active foraging strategy utilized by juvenile toads, allowing them to compensate for reduced prey density through increased activity (Werner and Anholt 1993). Lowered prey abundance has the potential to further increase the exposure of metamorphic toads to predation through trait-mediated indirect effects (Werner and Peacor 2003), in which their augmented activity in these habitats increases their susceptibility to sit-and-pursue predators (Huey and Pianka 1981, Krivan and Schmitz 2004); in fact, increased activity has been experimentally demonstrated among hungry metamorphic toads, leading to increased snake predation (Heinen 1994). Technically, toads and spiders are also intraguild predators (although the size of monitored spiders in this experiment precludes them from ingestion by small toads), but due to the shared prey base between these organisms we are also unable to establish whether the reductions in microarthropod abundance are a consequence of bottom-up processes resulting from post-invasion alterations in detrital inputs, or driven by increased spider densities within these habitats (DeVore 2011a), although changes in microbial communities (Kourtev et al. 2003) and reductions in arthropod abundance have both been experimentally demonstrated following invasion by this grass (Simao et al. 2010). These studies support the common generalization that detrital food webs are donor-controlled (Wardle 2002, Gruner 2004), but the potential for spiders to suppress the abundance of invertebrate detritivores has been established in a number of systems (Wise et al. 1999, Miyashita and Takada 2007), including forest floor food webs (Lawrence and Wise 2000, Wise 2004, Miyashita and Niwa 2006).

In certain cases, structurally-mediated modifications in food web interactions and survival rates can be secondary to effects initiated by abiotic changes resulting from autotrophic invasion (e.g. Byers et al. 2010, Wolkovich 2010). In fact, changes in temperature and moisture following *M. vimineum* invasion have been hypothesized to be the cause of increased mortality in hard ticks within these habitats (Civitello et al. 2008). As amphibians are ectotherms with permeable skin, and water uptake in this group can be further affected by changes in pH, significant changes in environmental parameters such as moisture, temperature, or soil acidity would be likely to drive a response in the survival or growth in our model species (Feder and Burggren 1992). Although we did observe a slightly lower survival probability in invaded predator exclosures than in exclosures that did not contain the grass, which could be indicative of an abiotic effect, this effect was negligible in comparison to predatory effects (as compared to uninvaded, spider-free control cages, the effect of spider/*M. vimineum* presence was 12 times that of abiotic *M. vimineum* influences alone). Additionally, observed abiotic influences of this grass within the large enclosures where toad survivorship and growth were monitored included increased soil moisture and decreased soil acidity (DeVore 2011a), both of which are expected to positively influence the performance of amphibians (Feder and Burggren 1992).

Invasive species are frequently implicated as the second leading cause of species endangerment (Wilcove et al. 1998, Wilcove and Master 2005), but it is often not direct effects of the invaders driving these losses. Rather, indirect effects caused by their presence in the environment may render the habitat less suitable for natives. Accordingly, studies of the impacts of plant invasions have frequently noted differences in community composition across invasion boundaries (Gratton and Denno 2005, 2006, Kappes et al. 2007, Bultman and DeWitt 2008, Wolkovich et al. 2009), but while this may speak to alterations in habitat suitability, the mechanisms that are driving these effects are only rarely explored, especially when indirect interactions are driving these changes. While the impacts of plant invasion on trophic structure have traditionally been considered to be relatively minor compared to those driven by animal invasion (Vitousek 1990)— given that the addition of a novel predator can have cascading trophic effects disproportionate to the resources involved (Mack et al. 2000)— plant invasion can alter a number of ecosystem characteristics, and influences on native consumers should be expected (van der Wal et al. 2008). Although a priori expectations may be that the influence of plant invasion will be manifested principally through bottom-up effects, in this case we found that a contextually-mediated dampening of cannibalistic and intraguild predation among wolf spiders made increased top-down pressure the dominant consequence of invasion for consumer performance within this system, despite the absence of an exotic predator. While direct impacts of animal invasion on prey, hosts, and competitors are demonstrably catastrophic in many systems (Mack et al. 2000), we would argue that indirect influences are likely to be far more common, influence far more species, and have the potential to operate with similar strength as direct effects.

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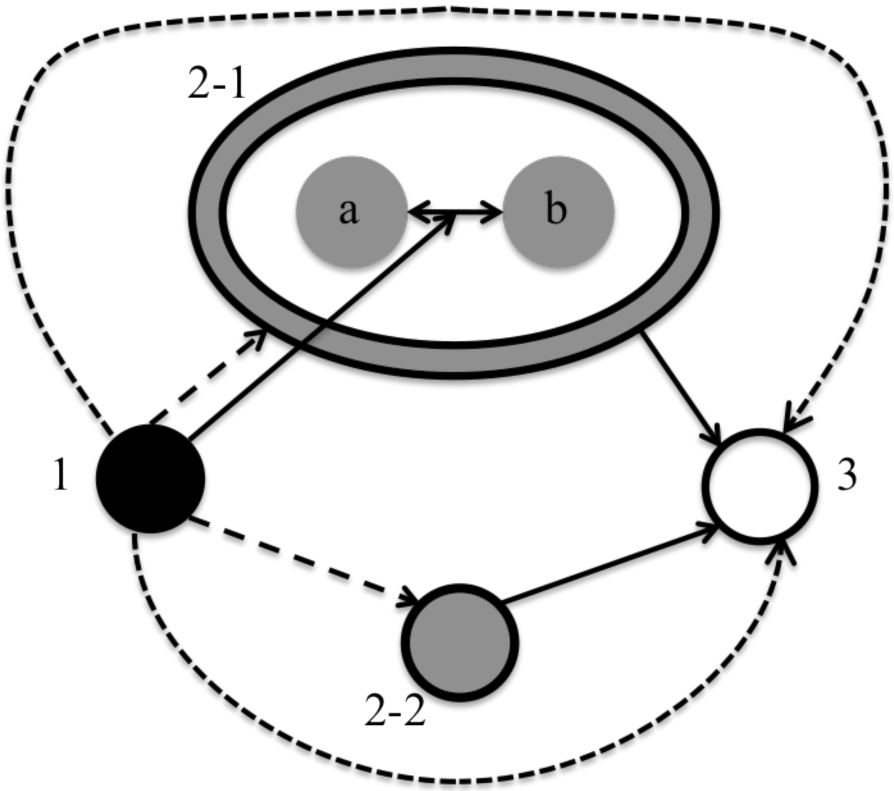

Figure 3-1. Potential indirect effects of a novel plant (1) on a consumer (3) via intermediate species: predators (2-1) and prey (2-2).

The upper, top-down interaction between 1 and 3 arises through contextually mediated indirect effects, in which the presence of 1 influences the strength of cannibalistic or intraguild interactions between 2-1-a and 2-1-b, leading to an indirect effect of the plant on the density of 2-1. Altered densities of 2-1 influence the strength of top-down pressure on 3; leading to a density mediated indirect effect between 1 and 3.

The lower, bottom-up interaction between 1 and 3 occurs through changes in detrital inputs produced by 1, changing the availability of microarthropod prey (potential mechanisms driving this change are discussed by DeVore [2011a]), which then leads to an indirect effect of the plant on a consumer species via a bottom-up density-mediated effect.

Figure 3-2. Metamorphic toads on an invaded (left panel; note the coverboard in the foreground) and uninvaded (right panel) forest floor, exemplifying the extreme structural habitat alterations that follow *M. vimineum* invasion.

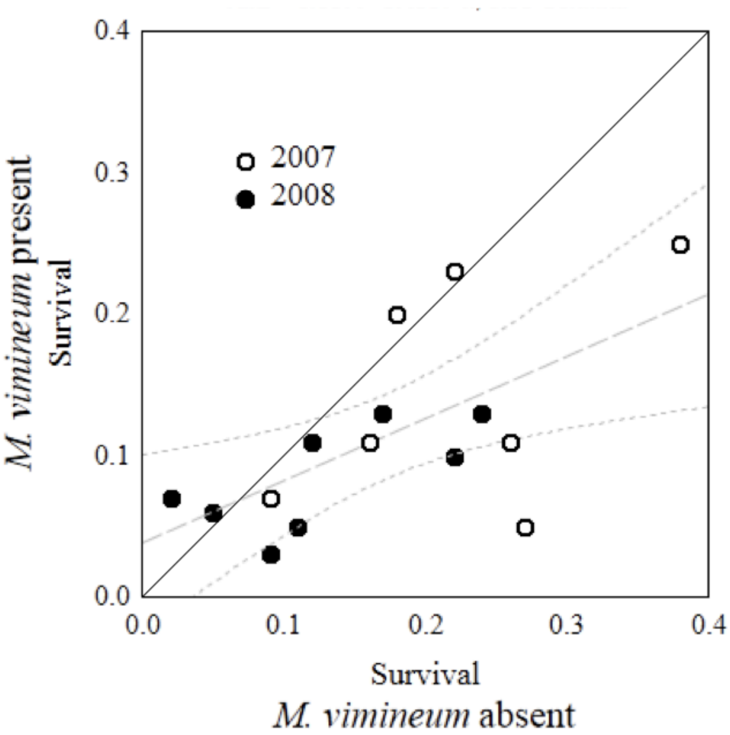

Figure 3-3. Proportion of stocked *A. americanus* surviving within invaded pens to first census as a function of survival within paired native terrestrial habitats (n=8, repeated over two years). Dashed lines represent the relationship between survival in native and invaded habitats ±95% confidence intervals ($p=0.012$, $r^2=0.398$), whereas the solid line represents a theoretical 1:1 relationship in which there is no effect of invasion on toadlet survival. Survival was significantly lower in invaded enclosures ($p=0.004$).

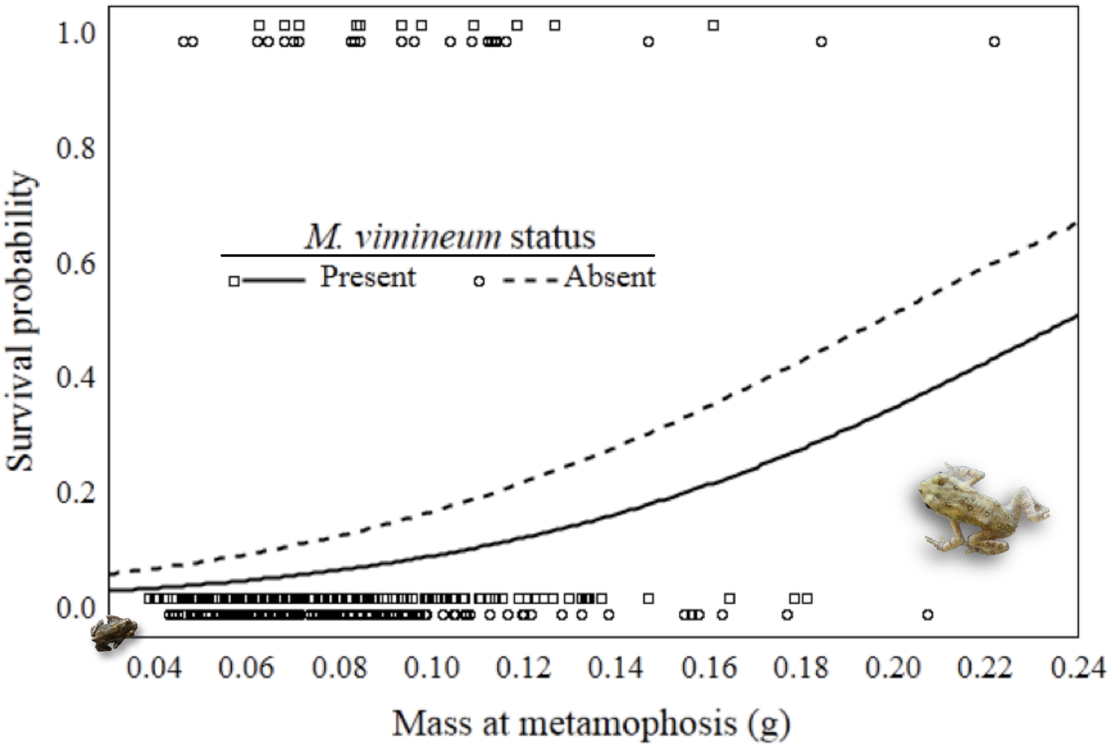

Figure 3-4. Logistic regression analysis depicting the probability of surviving to capture as a function of mass at metamorphosis for American toads in habitats where *M. vimineum* is absent (dashed line) or present (solid line). Squares designate individuals in invaded habitats that either survived (1) or did not (0), while circles represent individuals in uninvaded habitats. ANCOVA analysis revealed that both mass at metamorphosis and *M. vimineum* status were significant predictors of survival probability ($p<0.001$ and $p=0.047$, respectively). Metamorphic toad images represent the smallest and largest individuals for which pre-release measurements were taken and are depicted at actual size.

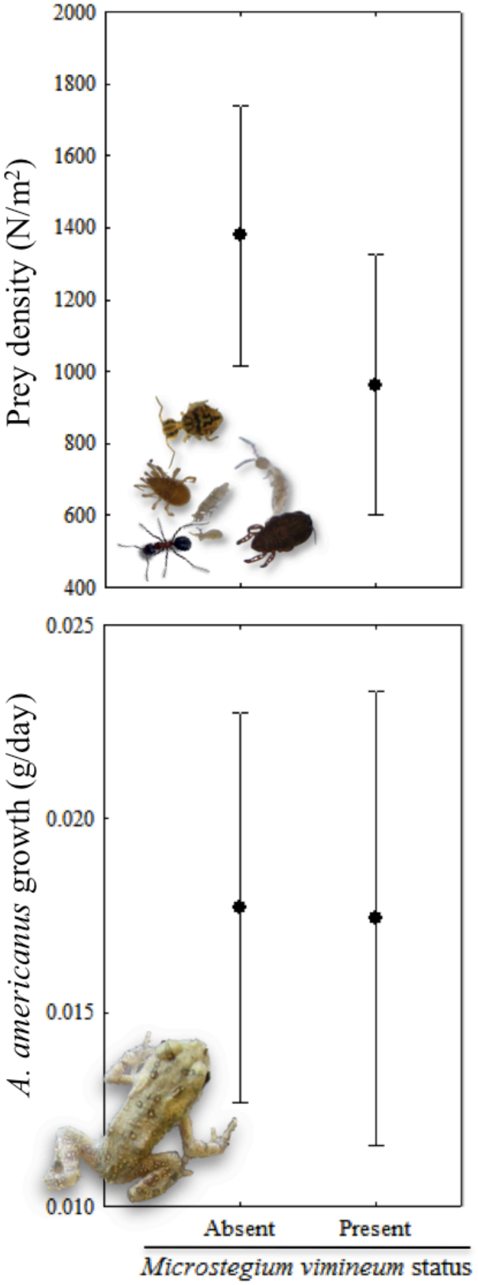

Figure 3-5. The density of microarthropods (<2mm) belonging to orders that are known prey of metamorphic *A. americanus* (upper panel; n=6) and the terrestrial growth rates of *A. americanus* to six-weeks post metamorphosis (lower panel; n=23, 12) across eight *M. vimineum* invasion fronts.

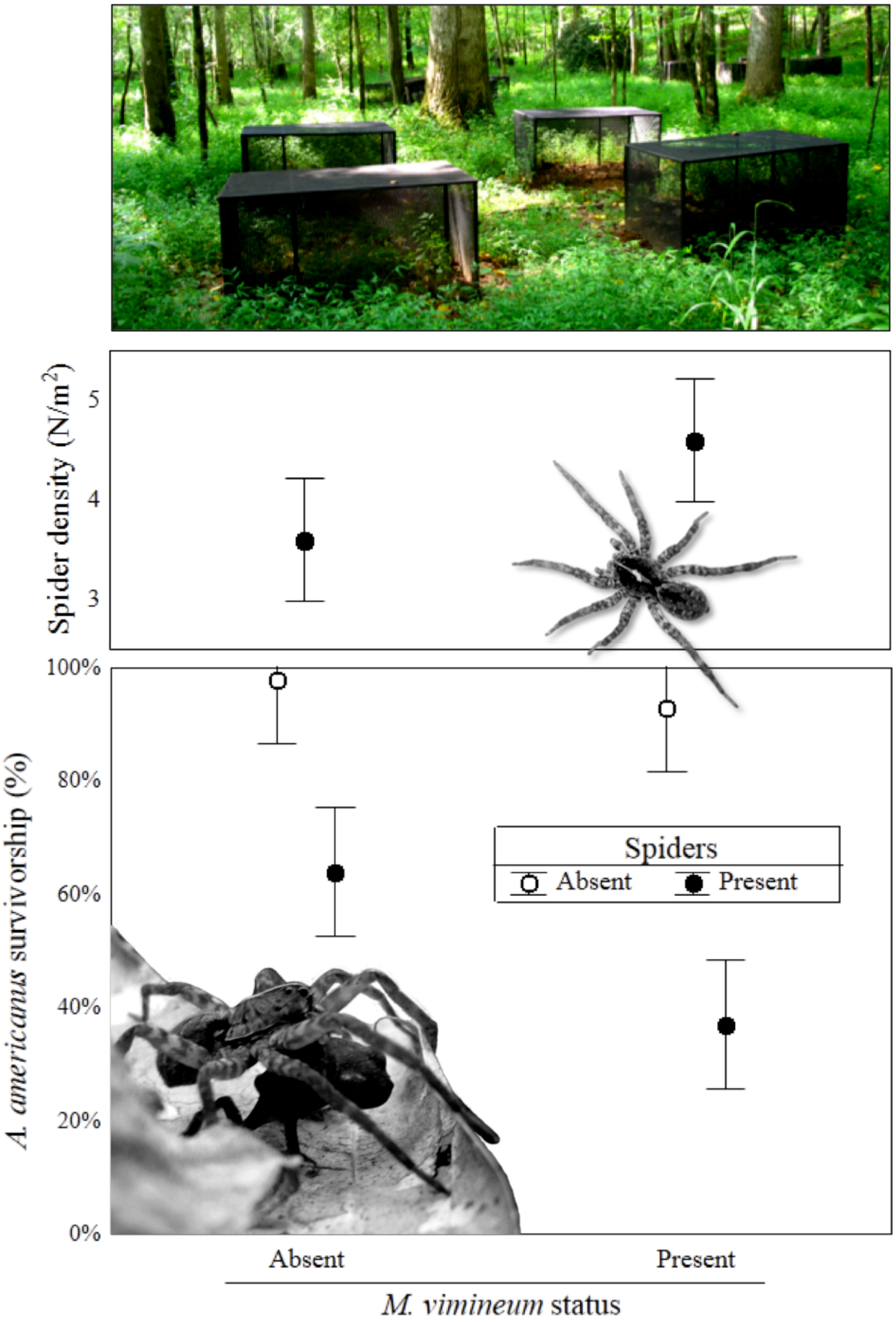

Figure 3-6. *Top panel:* One block of factorial spider x *M. vimineum* treatment cages in an invaded floodplain. *Middle panel:* Density of lycosid spiders ≥0.1g persisting in 1m^2 spider treatment cages (p=0.035, n=5). *Bottom panel:* Metamorphic toad survival to 5 days post-release within factorial treatment cages (*M. vimineum* x spider interaction p=0.0477, n=5). The image in the bottom corner documents a predation event.

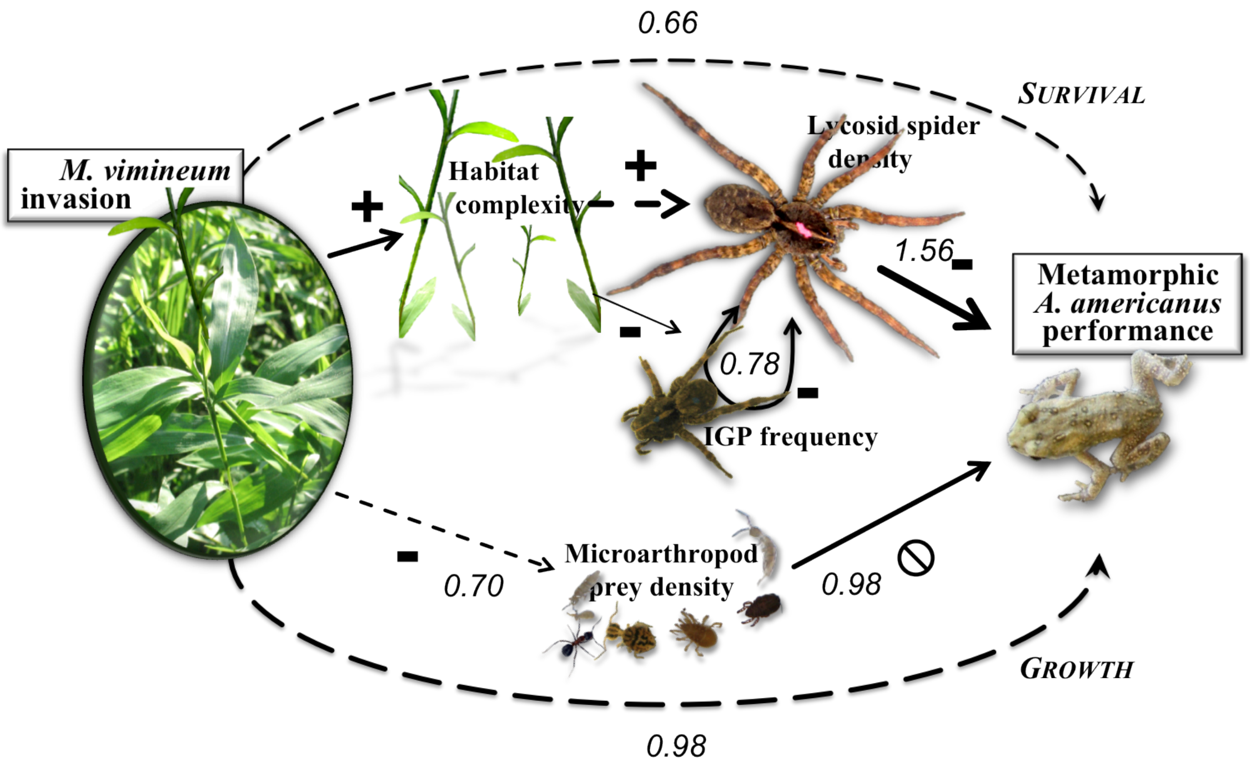

Figure 3-7. Explored mechanisms through which invasion by *M. vimineum* can indirectly affect the growth and survival of metamorphic American toads. Direct (solid line) and indirect (dashed line) influences are portrayed; ambient conditions are taken to be those observed in native habitats. These effects are mediated by changes in structural complexity and belowground nutrient inputs that follow invasion by this exotic plant. The potential for bottom-up effects via reduced prey abundances in these areas (0.70x ambient densities) was observed, but these did not significantly affect the growth of this species (0.98x ambient growth). Top-down effects occurred via a contextually-mediated dampening influence on a cannibalistic trophic link among spiders (0.78x ambient strength), which then led to an increased, density-mediated influence of *M. vimineum* on metamorphic toad survival via spider predation (1.56x ambient strength). No significant abiotic effects of invasion on toad survival were observed (0.95x ambient- this linkage is not pictured). Overall, the environmental influence of habitats containing *M. vimineum* on the survival and growth rate of *A. americanus* (as measured in large outdoor field enclosures and compared to uninvaded habitats) were 0.66 and 0.98, respectively.

Table 3-1. Results of a repeated-measures ANOVA analysis on the influences of treatment (presence/absence of *M. vimineum*), locational block, cohort (metamorphosis/release date), and year on the number of metamorphic A. americanus surviving to capture (sqrt transformed) in paired invaded and uninvaded pens.

Source	DoF	MS	F	p
Intercept	*1*	*3.403*	*1762.735*	*<0.001*
Location	7	0.050	25.763	**<0.001**
Treatment	1	0.035	17.894	**0.004**
Cohort	1	0.096	49.591	**<0.001**
Location*Treatment	7	0.007	3.722	0.052
Location*Cohort	7	0.008	3.892	**0.047**
Treatment*Cohort	1	0.000	0.065	0.807
Error	*7*	*0.002*		
Year	1	0.010	1.960	0.204
Year*Location	7	0.020	3.809	**0.049**
Year*Treatment	1	0.001	0.248	0.634
Year*Cohort	1	0.002	0.385	0.555
Year*Location*Treatment	7	0.002	0.356	0.902
Year*Location*Cohort	7	0.008	1.541	0.291
Year*Treatment*Cohort	1	0.006	1.142	0.321
Error	*7*	*0.005*		

Table 3-2. Results of a factorial ANOVA analysis on the effects of the presence of spiders and/or the invasive grass *M. vimineum* on square root transformed metamorphic toad survival.

Source	DoF	MS	F	p
Intercept	*1*	*1390.963*	*3253.159*	*<0.001*
Block	4	1.946	4.552	0.086
M. vimineum	1	5.859	13.703	**0.021**
Spiders	1	40.929	95.723	**0.001**
Block**M. vimineum*	4	0.402	0.940	0.523
Block*Spiders	4	1.935	4.526	0.086
*M. vimineum**Spiders	1	3.405	7.964	**0.048**
Error	*4*	*0.428*		

CHAPTER 4

METAMORPHIC STRATEGY PREDICTS SUSCEPTIBILITY TO ALTERATIONS IN TOP-DOWN AND BOTTOM-UP INFLUENCES INITIATED BY PLANT INVASION[1]

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[1] DeVore, J.L. and J.C. Maerz. To be submitted to Ecology.

Abstract:

Metamorphosis is a common biological process during which an irreversible ontogenetic transition leads to a sudden shift in challenges. Certain trade-offs are inherent in the timing of and size at metamorphosis; for example, individuals that metamorphose early and small have frequently minimized mortality within the first environment, but may face increased risk upon recruitment to the second. Species have developed a number of strategies to optimize this transition and, in order to ensure that they reach reproductive size, their post-metamorphic behavior is often optimized to maximize the effectiveness of this strategy. The reciprocal nature of this transition raises the possibility that a species' vulnerability to alterations in the quality of their secondary habitat may vary as a function of metamorphic strategy. In order to explore the interplay between disparate metamorphic strategies and environmental change we monitored the post-metamorphic performance of three forest floor amphibian species to alterations in top-down, bottom-up, and abiotic factors driven by Japanese stilt-grass (*Microstegium vimineum*) invasion. We stocked metamorphic American toads (*Anaxyrus [Bufo] americanus*), southern leopard frogs (*Lithobates [Rana] sphenocephalus*), and eastern newts (*Notophthalmus viridescens*) into 58m^2 enclosures on both sides of eight independent invasion fronts. Using robust capture periods we tracked the survival and growth of these 2,600 marked amphibians for ten months. We found that the initial 6-week survival of metamorphic *A. americanus* was significantly lower in invaded habitats, but that this effect diminished ontogenetically as *A. americanus* grew larger. These reductions in metamorphic toad survival were driven by increased abundances of predatory lycosid spiders in invaded habitats. *L. sphenocephalus* survival was not affected by invasion status; however, *L. sphenocephalus* growth was reduced in invaded habitats. This is consistent with reduced prey availability in invaded areas. Neither the high survival rates or slow growth rate of *N. viridescens* were significantly influenced by invasion status. These results show species-specific responses to habitat changes resulting from plant invasion. We hypothesize that species that metamorphose early and forage actively to support rapid post-metamorphic growth are more susceptible to increased predation pressure, whereas species that metamorphosed at a larger size and are more cryptic, ambush foragers may be less vulnerable to predation but more affected by alterations in resource availability. In contrast, species with flexible time horizons to reproduction may prioritize survival over growth by aestivating when faced with adverse environmental conditions, thereby minimizing the chances of trophic effects. These results demonstrate that metamorphic strategies can influence the nature and strength of the responses of related species to environmental change, and support theoretical models that predict the prioritization of either growth or survival as a function of size at and timing of metamorphosis.

Introduction:

Metamorphosis is a key transition in the ontogeny of many species, as it represents the point at which one environment, and the resources and risks therein, are traded for an entirely different habitat, in which the challenges typically differ substantially. Metamorphosis is thought to be maintained because it allows for the strategic optimization of the balance between predation risk and growth potential within an organism's life span, ultimately leading to positive influences on fecundity due to an earlier age or larger size at reproduction (Werner 1986, Rowe and Ludwig 1991). The majority of species undergo metamorphosis, including many insects, fishes, marine invertebrates, and amphibians, and variability in the timing of this transition has repeatedly been found to significantly influence post-metamorphic performance (Altwegg and Reyer 2003, Chelgren et al. 2006, Allen and Marshall 2010, Holmes and McCormick 2010).

Even within closely related species interspecific variation in the size at and timing of this transition can be dramatic, and reflects a range of alternative strategies that have proven successful through both the larval and adult stages, thereby allowing for the continued reproduction of the species. Importantly, post-metamorphic behaviors such as foraging and predator avoidance are often compensatory to the timing of metamorphosis. For example, rapid growth may be prioritized in species that metamorphose small, incentivizing active foraging strategies (Werner 1986).

Amphibians are widely recognized as model organisms for studying the factors affecting, and consequences of, variation in metamorphosis (Wilbur and Collins 1973, Werner 1986). Although the majority of research on this group has focused on the influence of alterations in larval habitat quality, modeling exercises presented by Werner (1986) as well as Rowe and Ludwig (1991) have sought to highlight the terrestrial stage as a period of major importance for amphibian populations. For the majority of species, this time represents a key period for growth, with >80% of mass gain occurring within terrestrial habitats (Werner 1986). Werner proposes that we should visualize the timing of this transition as it relates to future fecundity which, because size variation at reproduction is frequently correlated with reproductive output (Werner and Anholt 1993, Wells 2007), is influenced by both growth potential and the probability of mortality. Therefore, where mortality and growth potential are both size-dependent functions, amphibians should metamorphose when the ratio of mortality (μ) to growth (g) is lower in the secondary habitat than in the larval environment. He argues that species utilizing toxic defenses (e.g. *Notophthalmus* or *Bufo*) could reach this point at a relatively small size, due to decreases in terrestrial μ (i.e. predation risk) associated with these toxins. However, despite a similarity in the use of toxins to lower terrestrial mortality rates, he points out that these two groups represent vastly different strategies. For *Bufo,* high potential for terrestrial growth incentivizes metamorphosis, despite relatively high mortality within this environment (i.e. μ/g). *Notophthalmus*, conversely, experiences much higher growth rates within aquatic habitats than terrestrial environments. However, the extreme toxicity of the terrestrial eft phase of this species lowers their terrestrial predation risk to such a degree that metamorphosis is incentivized by the high probability of survival within this environment (μ/g). For species that do not utilize toxic defenses (e.g. *Rana*) terrestrial habitats pose a significant mortality risk (high values of μ). The elevated risk of predation in these environments limits the foraging activity of these species and, consequently, growth potential. For these species selection favors metamorphosis at a larger size, effectively extending the time until metamorphosis.

Rowe and Ludwig (1991) further improved this model by incorporating a time horizon for reproduction. They demonstrate that individuals that metamorphose at a small size must devote themselves to rapid terrestrial growth, despite the increased risk that is often associated with active foraging techniques, in order to reach reproductive size by the following spring (Werner and Anholt 1993), whereas those that enter this environment at a large size should develop strategies to maximize survival, even where these lead to decreased growth. However, in cases where this time horizon is flexible (e.g. in the case of *Notophthalmus*, where reproduction is frequently delayed for five to seven years) we would expect that this incentive to prioritize rapid growth at the expense of survival would not be as strong.

A subsequent attempt to validate these predictions in two species of *Rana* through the manipulation of larval conditions and subsequent monitoring of post-metamorphic growth and survival could not detect an intraspecific compensatory relationship between size at metamorphosis and post-metamorphic growth rates, thereby failing to find support for these predictions (Altwegg and Reyer 2003). Here we adopt a different strategy to explore these predictions by tracking the performance of three species that, due to longstanding interspecific variation in μ and g values, are expected to have developed alternate, stable post-metamorphic strategies that maximize future fecundity. Rather than manipulating larval conditions, we raised each species at consistent densities in predator-free enclosures without variation in food availability, but we then tracked the growth and survival of post-metamorphic individuals in paired enclosures across an invasion-driven environmental gradient that alters both predator persistence and prey density (potentially influencing the terrestrial values of μ and g, respectively). We seek to determine whether interspecific variation in the nature or strength of responses to these novel habitat alterations can be predicted by accounting for the differential metamorphic strategies utilized by these species. In accordance with the predictions of Werner (1986), Rowe and Ludwig (1991) we predict that species that metamorphose at a small size will prioritize growth at the expense of increased vulnerability to alterations in predation pressure, whereas those that are relatively large at metamorphosis will not risk predation for additional growth, rendering them susceptible to changes in prey abundance. We also expect that species with flexible time horizons to reproduction will be less incentivized to risk predation in order to increase growth, regardless of initial size.

Methods:

Study organisms- General biology

Anaxyrus [Bufo] americanus- American toad

Tadpoles of this species metamorphose early, small, and en masse over a short time span (Arnold and Wassersug 1978); the influence of size at metamorphosis on terrestrial success in this family is disputed, as their small size at metamorphosis and high rate of terrestrial growth appears to minimize the long-term influence of the aquatic environment on their terrestrial success (Werner 1986, Goater 1994, Beck and Congdon 1999). Although their small size at metamorphosis renders them extremely vulnerable, this species utilizes toxic secretions from its parotid glands to defend itself from predation, especially by mammals and birds (Wells 2007). The acquisition of these toxins is thought to be an advantage of ant specialization (Clarke 1974, Wells 2007) and is likely to reduce predation risk during this life stage (Werner 1986), although piercing invertebrate predators are unlikely to be affected by these defenses (DeVore 2011b), and initial post-metamorphic mortality rates are extremely high. Although adults typically utilize a sit-and-wait foraging strategy, juveniles of this species are active, diurnal foragers, which is likely a strategy intended to increase growth rates during this vulnerable stage and, in fact, post-metamorphic growth rates are high in this species (Werner 1986). This species is highly terrestrial, loyal to home territories, and relatively desiccation resistant (Dole 1972).

Lithobates [Rana] sphenocephalus- Southern leopard frog

Metamorphosis is not synchronized in this species, and typically occurs over a number of weeks, after which juveniles disperse independently into terrestrial habitats. In this family, size at metamorphosis is positively related to survivorship and adult body size (Altwegg and Reyer 2003) and the relatively large size at metamorphosis is hypothesized to be a consequence of increased susceptibility to terrestrial predation that occurs at smaller body sizes (Werner 1986). Unlike American toads, this species is not defended from predation by toxic secretions, is relatively susceptible to desiccation, and likely relies on their larger body size and behavioral adaptations to reduce terrestrial predation pressure. These nocturnal sit-and-pursue predators exhibit limited movement (except during rain events, when they may range widely), typically remaining obscured under the litter layer within a small home range (Dole 1965). When discovery is imminent they are highly elusive, avoiding predators through rapid jumps with frequent directional changes before settling back into the litter (Dole 1965).

Notophthalmus viridescens- Eastern newt

This species utilizes a complex life history strategy; aquatic larvae emerge at an intermediate size as terrestrial efts over an extended metamorphic period (although they may also remain in the breeding pond as neotenic individuals). Aquatic growth rates are high, but survival in this environment is low. In contrast, terrestrial efts experience extremely slow growth rates, but high survival (Werner 1986). Previous work has found that terrestrial efts only reach reproductive size after two to seven years (Lannoo 2005), at which point they return (often permanently) to the aquatic environment (Werner 1986). During the terrestrial phase efts are highly toxic, desiccation resistant, and extremely cryptic, often emerging from cover only during rain events (Wells 2007). Although the source of their toxicity is unresolved, it is probable that they produce the potent neurotoxin tetrodotoxin endogenously, likely at a high metabolic cost (Hanifin 2010), which may be a factor in their slow growth. While the low risk of predation associated with this life history strategy is thought to be responsible for its high survivorship, the low growth rates displayed by this species are a theoretically supported, documented consequence (Werner and Anholt 1993). Although they both utilize toxic defenses, this species can be thought of as the counterpart of the American toad, whose high growth rates, low survivorship, and high fecundity reflect the trade-offs associated with variability in amphibian life-history strategies.

Invasion-driven terrestrial environmental gradient

One increasingly ubiquitous driver of terrestrial habitat change is plant invasion; this widespread consequence of anthropogenic connectivity affects many habitats that are utilized by amphibians. Plant invasion is likely to change a number of habitat characteristics; since plants provide the basal resources that support food webs, influence the structure of habitats as they grow through ecosystem engineering, and alter abiotic components of the forest floor, the effects of plant invasion are often manifested in a number of ways. The component of invasion-driven habitat change that influences consumers living within these habitats is likely to vary as a function of the life history strategy of the consumer in question.

An increasingly prevalent invader that can drive ecosystem-level effects is *Microstegium vimineum* (Japanese stilt grass, Mary's grass, porcelain packing grass, Nepalese brown-top). This highly invasive Asian annual grass has become widespread in moist, shaded forest floor habitats throughout the eastern United States (Zheng et al. 1997, Cole and Weltzin 2005). Herbivory on this plant is minimal (but see Bradford et al. 2010), as with many exotic invasive plants (Keane and Crawley 2002), so resources produced by this plant reach consumers nearly exclusively through detrital food-webs. These food webs are a key source of trophic resources for many forest floor consumers (Polis and Strong 1996, Johnston 2000, Moore et al. 2004), including amphibians (Wyman 1998, DeVore 2011a). The presence of this plant is known to have a number of effects on invaded habitats, resulting in reductions in the diversity and cover of native plants (Adams and Engelhardt 2009), increased soil pH and moisture (DeVore 2011a), altered microbial community structure and function (Kourtev et al. 2002, 2003), reduced aboveground microarthropod abundances (Simao et al. 2010, DeVore 2011b, a), increases in structural habitat complexity (Baiser et al. 2008), and the accumulation of lycosid spiders due to structurally-mediated decreases in cannibalism and intraguild predation within these habitats (DeVore 2011b). Invasion by this plant can also have implications for vertebrate consumers, as previous investigations by DeVore et al (2011a) have illustrated that the survival of metamorphic toadlets is negatively influenced by the presence of *M. vimineum* due to increased predatory pressure from lycosid spiders dwelling within invaded habitats (DeVore 2011a). Whether these results can be generalized to other, related species has not been established, as interspecific and ontogenetic factors may be expected to mediate these effects.

Site description

In the fall of 2006 a number of *M. vimineum* invasion fronts were identified; four in Whitehall Forest, Athens, GA; two in Hard Labor Creek State Park, Rutledge, GA; and two in the Oconee National Forest, Eatonton, GA. Invasion fronts that were selected for inclusion in this study had to have a $58m^2$ invaded area and a nearby uninvaded area of equal size with similar elevation and habitat characteristics. Care was taken to ensure that these invasion fronts were actively progressing, which commonly occurred from the direction of roadsides or soil disturbances. By the end of the study period all of the paired uninvaded sites had experienced some level of invasion, necessitating hand weeding. For some it was only the presence of the silt fencing that was used to construct amphibian enclosures, acting as a barrier to seed dispersal, that prevented complete invasion of the study area, which implies that underlying edaphic characteristics were not responsible for the variation in invasion status. During the two years for which these sites were monitored, free-ranging *A. americanus, L. sphenocephalus,* and *N. viridescens* were encountered at seven, four, and two of these eight sites, respectively, indicating that these species commonly utilize these habitats.

Production and marking of metamorphs

Anaxyrus americanus

A. americanus egg strings were collected at both Whitehall Forest and the Oconee National Forest in early March, 2008 and hatched indoors in aerated 10-gallon tanks. Seven days after hatching, tadpoles were hand-counted into 550L Tahiti lawn pond liners (MacCourt®), each of which had been stocked with 400g of leaf litter and equipped with overflow pipes and screen covers to maintain water depths and exclude predators. Since *Anaxyrus* tadpoles access shallow waters for basking, the variation in depth provided by this two-tiered pond was desirable. As larval densities have been shown to influence later terrestrial performance (Goater 1994), each pool was stocked with 1,200 tadpoles to ensure that tadpole densities were consistent. Pools were fed equal quantities of Tetra ReptoMin® every other day to subsidize food provided by natural algal growth; the amount of food that could be consumed by a pool in 15 minutes was provided (~15mL). When the tadpoles began to approach metamorphosis we dropped the water levels slightly so that half of the upper level of the garden pond was exposed, allowing metamorphs to escape the water. Metamorphs who had completed tail absorbtion were transferred to indoor bins, where they were maintained on beds of moist sphagnum moss and air-dried leaves with a diet of wingless fruit flies until they could be released (10>5 days). As the period of metamorphosis (May 18th- June 11th) continued these toadlets were randomly assigned to treatments and released into pens in four cohorts of 25 toadlets each between 5/27 and 6/19, after which 100 toadlets had been stocked into each of the 16 pens. Individuals from egg masses who had been collected in Whitehall Forest ponds were released in Whithall Forest and Hard Labor Creek State Park pens, while those from the Oconee National Forest were released in pens at that location. Each toadlet was given a single toe clip to indicate its cohort (ie release date), and at each release a subset of five metamorphs per pen were given additional individual clips for a total of 320 individually marked and 1,280 batch clipped toadlets. The extremely small size of toad metamorphs and their toes prevented us from individually marking all 1,600 that were released. Mass, digital images, and snout-vent length (SVL; in order to reduce stress on toadlets this was determined through measurement of calibrated digital images using ImageJ®) were recorded for all individually marked toadlets. In the case of batch-clipped toadlets the average mass of individuals within each cohort of was recorded for every pen. Toads who had initially received a batch clip were individually marked at the first capture period such that, although the exact size at metamorphosis for these individuals was unknown, the release date was evident, and these toadlets could be individually identified during subsequent recapture events. The extremely high capture probability observed for this species resulted in the capture and marking of 98% of surviving toads by the end of the first capture period. For a given individual no more than one toe on each foot was taken and a maximum of three toes were used. Inner toes on the front feet were not clipped, as they can be important for breeding. This stocking density of 1.7 metamorphic toads per m^2 is low for dispersing toadlets, as this species is known to transform and invade terrestrial habitats en masse (Werner 1986) where they form aggregations (Arnold and Wassersug 1978, Hayes 1989), and the high rate of initial mortality quickly reduced densities to ~0.34 (max 0.41, min 0.03) toads per m^2 within six weeks.

Lithobates sphenocephalus

L. sphenochephalus eggs were collected at both Whitehall Forest and the Oconee National Forest in early March, 2008 and maintained in aerated indoor 10-gallon tanks. As with *A. americanus* tadpoles, hatchlings were removed to outdoor bins seven days post-hatch but, as this species utilizes deeper, more permanent water bodies than *A. americanus,* the bins used for this species consisted of screened 1000L stock tanks filled to a depth of 40-45 cm and stocked with 550g of air-dried leaf litter. A low-floating 0.5 x 0.3 m rectangular mat with plastic edges and fiberglass screened interior was added to each bin to allow metamorphosing individuals to bask while maintaining water contact. Feeding methodologies were identical to those described for *A. americanus* above, although the amount of food consumed by this species was slightly greater (~20mL/tank). Metamorphs were hand-captured or dip-netted from bins within two days of completing tail absorption and transferred to indoor bins containing water pools, moist sphagnum moss, and air-dried leaves where they were fed pin-head crickets until their release into pens at the appropriate site (7>3 days). During this time all froglets were individually marked and their mass, SVL, and digital images were recorded. Attempts to use visual implant elastomer the previous year had led to high mortality rates in the lab and indiscernable marks following a year in the field, so the toe clipping methodology described above was used, which allowed individuals to be held with 100% survivorship rates until their release date was reached. Fifty individually marked leopard frogs per pen were released in five cohorts of ten each, for a total of 800 tracked frogs. Separation in release dates reflected variability in the date of metamorphosis; releases occurred between June 19 and July 18, 2008. Studies of terrestrial density dependence in a related species (*Rana lessonae*) revealed only minor effects at densities of 8.3m^{-2} (Altwegg 2003), so this stocking density of 0.86m^{-2} was not expected to drive density-dependent effects.

<u>*Notophthalmus viridescens*</u>

Egg masses were unavailable for this species, since *N. viridescens* females wrap eggs individually in vegetation, so adults in breeding condition were captured from ponds in Whitehall Forest in November and December of 2007, and 1 female and 4 males were added to each of six half-full 1000L stock tanks. Pond matter (including substrate, leaves, and vegetation) was also added to promote breeding behaviors, and adult newts were removed in January to prevent them from canabilizing their offspring. Seven additional 550L Tahiti lawn pond liner (MacCourt®) bins were set up on June 26th and stocked with leaves, vegetation, and water from a Whitehall pond before being stocked with wild caught larvae that were dipnetted directly from ponds in Whitehall forest. Larvae were collected from these bins as they metamorphosed; individuals included in this study were restricted to those that emerged between June 27th and September 4th, although efts continued to transform after this date. Upon metamorphosis, efts were transferred to cups containing damp sphagnum moss and air dried leaves, where they were fed wingless fruit flies ad libitum until their release. Each eft was individually marked with toe clips and their mass, SVL, and digital images were recorded (SVL was measured through the use of ImageJ®). Since efts metamorphose over an extended time period (if at all; some maintain a paedomorphic aquatic lifestyle through to adulthood), these releases occurred between July 3 and September 4, 2008 as efts became available. The last release occurred on the first day of the first capture interval so determination of eft abundances began at the second capture period. Only pens in Whitehall Forest and Hard Labor Creek State Park were stocked with this species; Whitehall Forest pens were stocked with 17 individuals each, while every Hard Labor pen received 16 efts, for densities of $0.29m^{-2}$ and $0.28m^{-2}$, respectively, and a total of 200 tracked individuals.

Monitoring terrestrial survival and growth

Capture periods followed a robust design with a four primary capture periods. These began six weeks after the final anuran release and continued at six week intervals through October 2008. As encounter frequencies were very low during the winter months, searches were then discontinued until the final capture period in April of the following spring. Long-term survival analysis was precluded at one site in the Oconee National Forest due to severe flooding in February 2009, so subsequent searches were conducted at the remaining seven sites and results from this site were not included in survival analyses. Each of the four primary search periods contained four secondary occasions, comprised of three day searches and one night search conducted over four consecutive days. Pitfall traps were opened during the first day of searching, checked daily, and closed between primary capture periods. Hand searches were also conducted at every occasion, these consisted of walking slowly in parallel lines through the pen while stirring the litter until the entire area had been covered twice, as well as searching under coverboards, along fencing, and under vegetation; search durations were >30min for day searches and >60min for night searches. Both day and night searches were conducted because we found that, while *A. americanus* is most easily encountered during the day, *L. sphenocephalus* is more active after sunset. *N. viridescens* was most frequently encountered during rainfall, so efforts were made to structure capture periods so that each pen would be searched at least once during a rain event (when possible for that primary period). Every time an amphibian was caught its mark was identified, measurements of mass and SVL were recorded, and its photo was taken against a grid of known dimensions. As the toes of *N. viridescens* regenerated quickly, individuals of this species were identified through visual comparisions of spot pattern photographs; although *L. sphenocephalus* typically maintained their toe clips through the duration of the experiment, all frog identifications were confirmed through spot pattern comparisons, as well. This method allowed us to estimate and account for interspecific varation in capture probabilites. Growth rates between release and the first subsequent capture period were determined by substracting the initial mass from the mass at recapture and dividing the difference by the number of days that passed between release and initial recapture; for *A. americanus,* in which only a subset of each cohort had been individually marked and weighed, only these individuals were used in growth rate calculations.

Population estimation

As initial abundances were known and penned populations were closed to immigration, survival rates were inferred through the estimation of abundances for each species at every primary capture occaision. These estimates were calculated through the use of the Robust Design Closed Captures estimator in Program MARK (White and Burnham 1999). Optimal models varied interspecifically, as did the estimate accuracy; for *A. americanus* the high capture probability allowed for the estimation of variable recapture probabilities within and between primary capture periods and well as variable temporary emigration (e.g. movement belowground) probabilities for each pen, yet 94% of the 48 abundance estimates presented were identified with 95% accuracy. In *L. sphenocephalus* the optimal model was that capture probabilities are equal within a treatment at a geographic region (where the regions were taken to be either Whitehall Forest or Hard Labor Creek State Park/Oconee National Forest) but varied temporally and between treatments. Estimates of eft abundance however, were more difficult to accurately estimate due to extremely low recapture probabilities (averaging 0.05 per capture occasion). In order to increase the number of recaptures (and, thereby, the accuracy of the model) estimates were made by holding the capture and recapture probabilities within all pens equal within each primary capture occaision, but allowing them to vary temporaly. Temporary emigration was taken to be random and, as such, was not estimated by the model. Although this model provided the best fit, there was still significant uncertainty associated with the estimates it produced.

Statistical analysis

Our main objectives were to identify interspecific differences in size at metamorphosis, growth, and survival, as well as the influences of invasion-driven habitat change on these three species. Size at metamorphosis was analyzed via ANOVA for all individually measured amphibians (n= 320, 400, and 200 for *A. americanus, L. sphenocephalus,* and *N. viridescens,* respectively), as were the short-term growth rates of the survivors that were captured and processed at the subsequent capture period (n=35, 203, 30, respectively). Intraspecific effects of invasion on growth rates were also calculated for individuals surviving within each treatment type via main effects ANOVA in Statistica 10 (StatSoft Inc 2011). For each species the proportion of the population surviving to the capture periods was calculated based on abundance estimates generated by Program MARK, which were arcsine square root transformed and analyzed via a repeated measures ANOVA analysis that accounted for both between (locational block and treatment) and within factors (time, time*block, time*treatment).

A. americanus- Ontogenetic measurements of short-term survival and prey capture success

To investigate potential ontogenetic shifts in the effects of invasion on short-term survivorship or an individual's ability to capture prey (as indicated by the presence of stomach contents, sensu Huey et al. 2001) we conducted seven-day trials across two independent invasion fronts. This was accomplished by removing the bottoms from twenty 5-gallon buckets, five of which were pounded 15 cm deep on either side each invasion fronts in Whitehall Forest in May of 2008 (sensu Maerz et al. 2005). Each bucket enclosure was immediately stocked with five metamorphic toads and covered with window screening. Seven days later—after a night of rain, which should promote foraging by this species—all surviving toads were removed and gastric lavage was used to determine whether feeding had occurred. This trial was repeated in August with 6-week post-metamorphosis individuals, stocked at a density of one per enclosure. Enclosures were considered to be the unit of replication and the proportion of toads that had survived or fed in each habitat type were compared using ANOVA analysis (StatSoft Inc 2011).

Results:

Interspecific variability

Mass at metamorphosis varied interspecifically (see Figure 4-1) such that there were significant size differences between species at release into the terrestrial environment; *A. americanus* was extremely small at metamophosis (mean 0.0816g; range 0.0387 to 0.2215g; n=320), *N. viridescens* averaged 1.24 times this size (mean 0.1826g; range 0.0981 to 0.3546g; n=200), and *L. sphenocephalus* was the largest species included, averaging 6.58 times the mass of *A. americanus* at metamorphosis (mean 0.6186g; range 0.2990 to 1.0406g; n=800). Significant interspecific variation in post-metamorphic growth rates was also present ($F_{2,255}$=16.32, p<0.001; Figure 4-2), ranging from 0.8±4.0 mg/day in *N. viridescens* to 9.9±1.7 mg/day for *L. sphenocephalus* and 16.6±3.8 mg/day in *A. americanus* (means ± 95% CI); a post-hoc Tukey HSD test revealed that all species differed significantly in growth rate (p<0.001 in all cases). Observations of these species confirmed reports of interspecific differences in behavior, and capture probabilities reflected this variability. *A. americanus* was easily detected during active, diurnal foraging and escape responses in this species consisted of actively hopping, further facilitating capture (mean capture probability= 0.7). *L. sphenocephalus* was more difficult to detect as they remained hidden under litter and did not attempt active escape until capture was imminent, at which point they would leap rapidly with frequent directional changes before returning, immobile, to a position under the litter layer. Pitfall trapping and dusk or nocturnal pen searches—when this species was more likely to respond actively to disturbance—contributed significantly to capture rates for this species (mean capture probability= 0.4). *N. viridescens* was highly cryptic and seldom observed above the litter layer, emerging exclusively during precipitation, and was most frequently discovered under cover items (often individuals would return to the same location for the duration of a primary capture period) or captured in pitfall traps during rain events (mean capture probability= 0.05). There were also time-dependent significant difference in species survival; the survival of *N. viridescens* was significantly higher than that of the other two species during the first two capture periods in which their abundance was estimated, and the survival of *R. sphenocephalus* was significantly higher than that of *A. americanus* during the first capture period (Tukey HSD; $p<0.05$).

Treatment effects: Terrestrial survival and growth

The influence of *M. vimineum* invasion on amphibian survival varied interspecifically. The presence of stilt grass was not a significant predictor of the survival of leopard frogs and efts (Table 4-1). Analysis of toad survival, however, revealed a significant time*treatment interaction, such that post-metamorphic survival to six weeks was reduced by 39% in the presence of stilt grass, but this reduction did not lead to a significant effect on long-term survival (Table 4-1; Figure 4-3). A post-hoc Newman-Keuls test revealed that this initial reduction in post-metamorphic survival was statistically significant ($p=0.018$). Influences on growth also varied; the growth rate of leopard frogs surviving to first capture was reduced by 28% in invaded habitats ($F_{1,194}=3.68$, $p=0.056$; n=107, 96), and there were non-significant reductions in the growth of efts and toads of 118% ($F_{1,23}=0.322$, $p=0.58$; n=15, 15) and 1.6% ($F_{1,26}=0.00672$, $p=0.94$; n=23, 12), respectively. Locational block was also a significant predictor of growth rates for all species (p= <0.0001, 0.0166, and 0.0006 for leopard frogs, efts, and toads, respectively).

A. americanus- Ontogenetic measurements of short-term survival and prey capture success

No effect of invasion on the presence of stomach contents in metamorphic toads was observed (87% captured prey, with a 1% increase in invaded habitats; $F_{1,17}=0.341$, $p=0.948$), but a significant 49% reduction in short-term (7-day) survival was observed in invaded enclosures ($F_{1,17}=24.94$, $p<0.001$; Figure 4-4). When the trial was repeated with 6-week-old toads foraging success remained consistent (on average 85% captured prey, with an 11% reduction in invaded habitats; Wald $\chi^2=0.386$, $p=0.534$), but all toads survived in both habitat types.

Discussion:

There are a number of factors that contribute to species vulnerability to environmental pressures. For example, susceptibility to predation may vary with body size (Holmes and McCormick 2010), activity level (Werner and Anholt 1993, Brodin and Johansson 2004), or crypsis (Main 1987). Likewise, the potential for bottom-up effects may vary based on diet breadth (Jiang and Morin 2005) and foraging mode (Werner and Anholt 1993, Brodin and Johansson 2004). Species may therefore adopt multiple strategies to optimize the same parameter; for example, early metamorphosis, active terrestrial foraging and ant specialization in *A. americanus* all serve to maximize growth (g), albeit at the cost of a reciprocal increase in post-metamorphic predation risk (μ). The utilization of these suites of complementary post-metamorphic behaviors within a species represents the development of evolutionarily stable behavioral syndromes (Sih et al. 2004) that, in order to maximize future fecundity, favor interrelated behaviors that maximize either growth or survival in the post-metamorphic environment as an appropriate function of metamorphic strategy. Since these species typically optimize one parameter at the expense of another, interspecific disparities in post-metamorphic priorities are expected to lead to conflicting responses to environmental change, even within related species. By investigating the responses of three amphibian species to environmental change, this study shows that the metamorphic strategy and associated post-metamorphic behaviors (hereafter, metamorphic syndromes) utilized by these species influence both the nature and strength of their responses to alterations in trophic pressures, thereby causing both interspecific and ontogenetic variablity in sensitivity to environmental change.

When exposed to an invasion-driven gradient that has been found to simultaneously increase the persistence of predatory lycosid spiders and decrease the abundance of edible arthropods (DeVore 2011b), we found that species utilizing disparate metamorphic syndromes responded to different aspects of the environmental change (see Table 4-2). The dominant detectable influence of these habitat alterations on the small, actively foraging species *A. americanus* was increased top-down pressure driven by the accumulation of invertebrate predators in invaded habitats (DeVore 2011b), but by six weeks after metamorphosis invasion status no longer significantly influenced their survival, and the rapid growth rate exhibited by survivors of this species was not affected by invasion. In contrast, a species that metamorphosed at a larger size and utilized a cryptic, sit-and-pursue foraging strategy, *L. sphenocephalus,* displayed no increased risk of predation within invaded habitats, but the growth rate of this species was lower in invaded environments. In the case of the highly cryptic, aposomatic, toxic *N. viridescens* no significant effects of invasion on their relatively high survival or extremely low growth rates were observed. These results support our hypotheses that species that metamorphose at a small size and prioritize rapid growth are suceptible to increased predatory pressure. In contrast, those that metamorphose at a larger size and exhibit strategies that minimize the risk of predation have compromised their ability to compensate for decreases in prey abundance. Finally, a well-protected species that routinely delays maturation (*N.*

viridescens) is likely to aestivate during adverse environmental conditions, and therefore show no significant response in survival or growth. In the case of our study system, plant invasion also drives abiotic effects that would be expected to improve amphibian performance (such as increased soil moisture and decreased soil acidity [DeVore 2011a]), so the magnitude of the effects estimated here are likely to be conservative (Wells 2007). This is especially true because severe drought during our study period resulted in visible mortality of *L. sphenocephalus* between the second and third capture periods, and likely contributed to the observed aggregation and aestivation of *N. viridescens* under cover items during this time (a known response to desiccation risk [Wells 2007]), so any positive abiotic effects on performance would be expected to be exacerbated during this extreme weather event.

These results support theoretical models that predict the optimization of either growth or survival as a function of size at metamorphosis. While previous studies have failed to find evidence of intraspecific compensation in response to size at metamorphosis (Altwegg and Reyer 2003), here we present novel evidence in support of these models by comparing the performance of three species that have evolved alternate, stable metamorphic syndromes in order to maximize reproductive success. Due to the interrelated nature of predation risk and growth optimization, an interesting mechanistic question that deserves further exploration is whether increased predation risk further suppressed foraging in *L. sphenocephalus* via behaviorally-mediated nonconsumptive effects (Preisser et al. 2007)*,* thereby contributing to reductions in growth in invaded habitats or, conversely, if decreased prey availability further exposed toadlets to predation by driving increases in foraging effort or speed (Werner and Anholt 1993). It is possible that reductions in survival or growth may be observed even when direct drivers are absent, and we propose that the metamorphic syndrome of a species may better predict the nature of their response to trophic alterations than direct measurement of the trophic factors involved, with the expectation that certain species will exhibit altered growth rates, while others will respond via altered mortality rates, regardless of whether environmental alterations have initiated top-down or bottom-up effects.

These results also have significant applied implications. Recently, amphibians have received increasing attention due to their status as the most threatened vertebrate group in the world with over 1/3 of species threatened with extinction (Kiesecker et al. 2001, Blaustein and Kiesecker 2002, Collins and Storfer 2003), but they also represent one of the oldest terrestrial vertebrate groups, inhabiting every continental landmass except Antarctica and utilizing a diverse array of life history strategies. Accordingly, this group has developed a number of strategies to optimize their size at and timing of metamorphic transitions, and each represents a trade-off, in which abiotic susceptibilities, predation risk, and growth are balanced in both aquatic and terrestrial habitats (Werner 1986). Although research and modeling exercises seeking to understand the impacts of environmental variation on this group have traditionally focused on the influences of environmental change on the larval stage, with the goal of maximizing size at metamorphosis or improving the timing of departure from this environment (Wilbur and Collins 1973, Johansson et al. 2001, Day and Rowe 2002), the influences of environmental change in the secondary habitat of these species have received less attention. However, mortality during the terrestrial life phase of these species is more likely to contribute to population declines (Biek et al. 2002, Vonesh and De la Cruz 2002) and body size has been related to reproductive output in all investigated amphibian species (Wells 2007). By accounting for the metamorphic syndrome of a species, we may improve our ability to predict how environmental change will influence its performance (i.e. mortality and growth rates), and better understand why some species are in rapid decline while sympatric species are unaffected. In this case, we found that an increasingly prevalent component of anthropogenic habitat change, exotic plant invasion, drove differential effects on amphibians, but that we were able to predict the nature of these effects by accounting for both the trophic implications of plant invasion and the metamorphic syndrome of the species studied. We therefore believe that accounting for metamorphic strategy and compensatory post-metamorphic behaviors may improve our ability to predict the responses of species of concern to environmental change.

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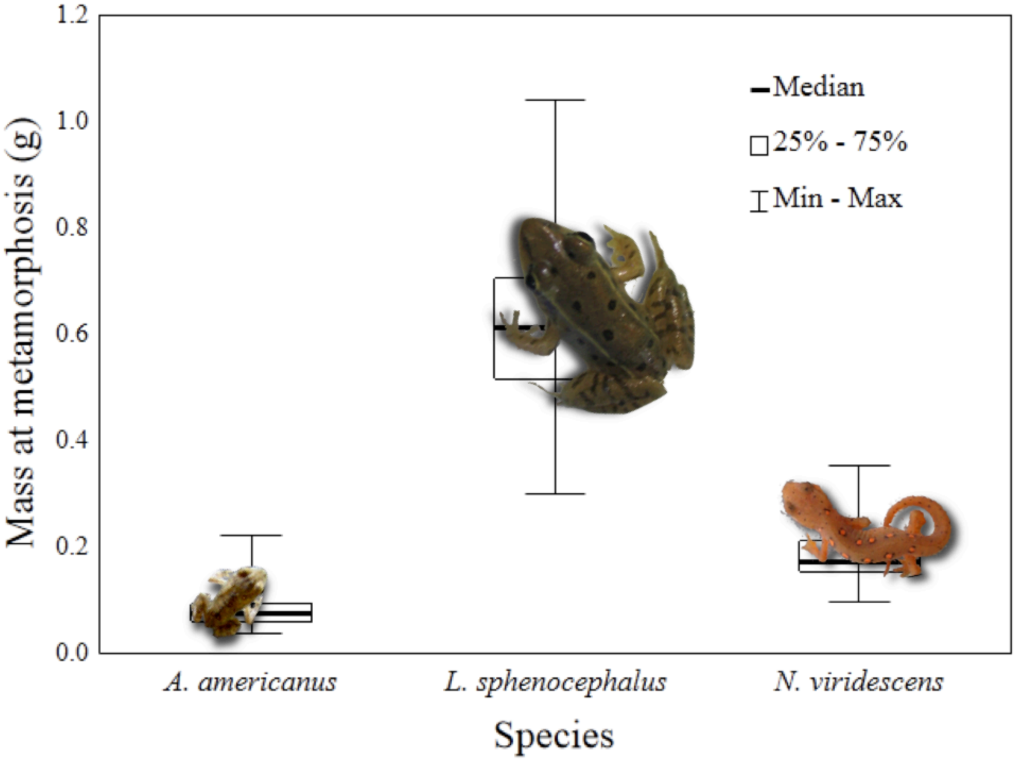

Figure 4-1. Mass at metamorphosis of stocked amphibian populations, based on pre-release measurements of individuals. The number of individual measurements made varied interspecifically; n= 320, 800, and 200 for American toads, southern leopard frogs, and eastern newts, respectively.

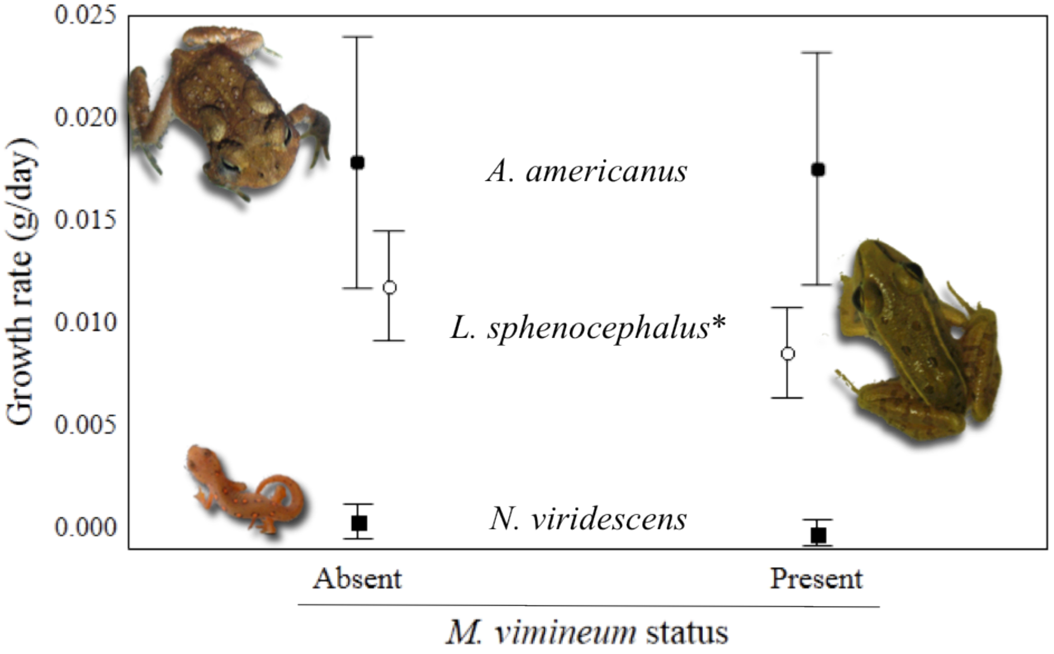

Figure 4-2. Mean (±95%CI) growth rates between release and first recapture of amphibians within native and invaded habitats. Only *L. sphenocephalus* experienced marginally significant reductions in growth within invaded habitats (p=0.056; n=107 native, 97 invaded). The growth of *A. americanus* (p=0.94; n=23 native, 12 invaded) and *N. viridescens* (p=0.58; n=15 native, 15 invaded) were not significantly affected by invasion status. There were significant differences in the growth rates of all species (p<0.001).

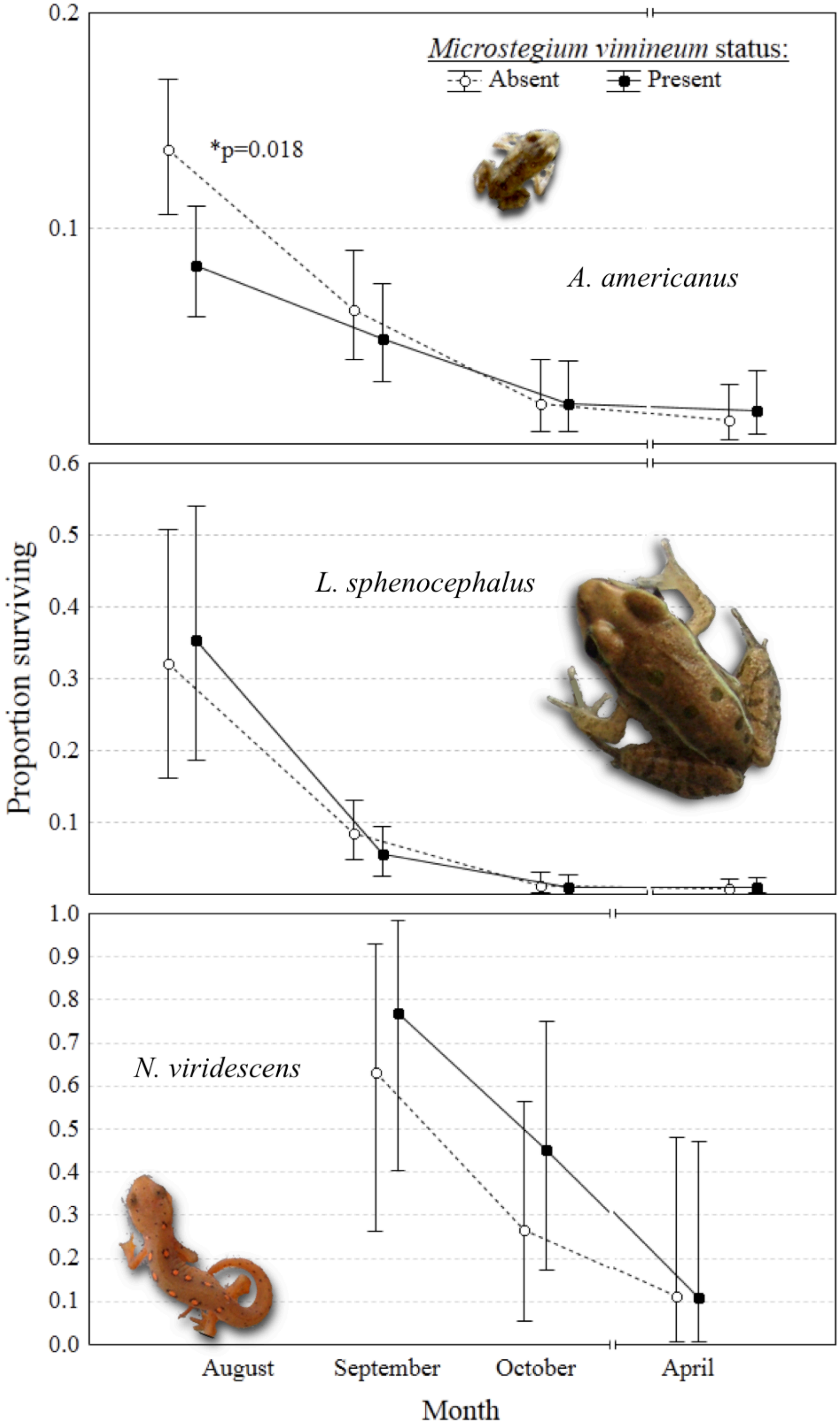

Figure 4-3. Proportion of the stocked amphibian population surviving through time within paired *M. vimineum* invaded and uninvaded plots (mean ± 95% CI). Initial abundances were 100, 50, and 16 to 17 for *A. americanus, L. sphenocephalus,* and *N. viridescens*, respectively. An interaction between time and treatment existed for *A. americanus* (p=0.019; n=7). No significant effect of invasion was observed for *L. sphenocephalus* or *N. viridescens* (n=7, 6).

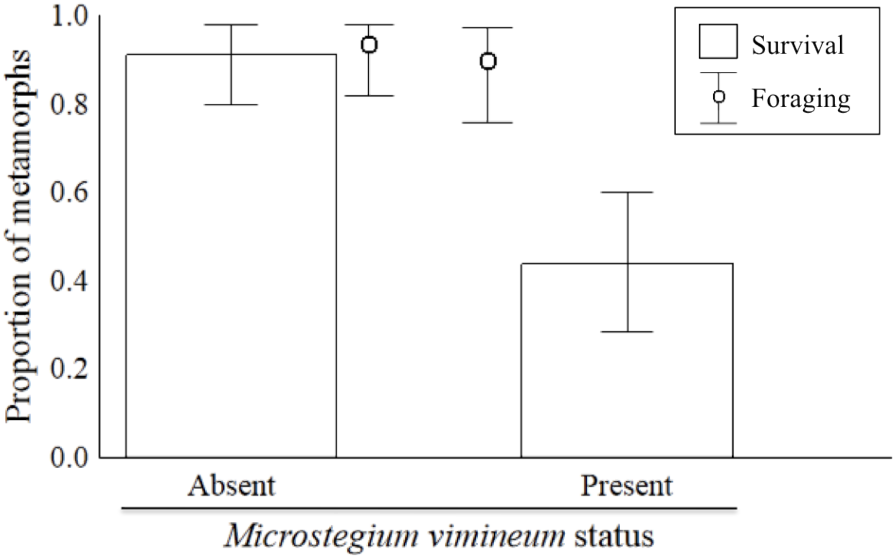

Figure 4-4. Bars represent the proportion of the stocked metamorphic toad population surviving for seven days in small enclosures that were paired across two independent, progressing invasion fronts. Each enclosure was initially stocked with five individuals; the proportion of the surviving amphibian population that detected prey during this time is depicted as points. Means ± 95% CI are depicted; survival was significantly lower within invaded habitats ($p<0.001$, $n=10$, but the presence of stomach contents, as determined from gastric lavage, was not affected ($p=0.948$, $n=10$). When repeated with 6-week-old toads, survival was 100% in both treatments.

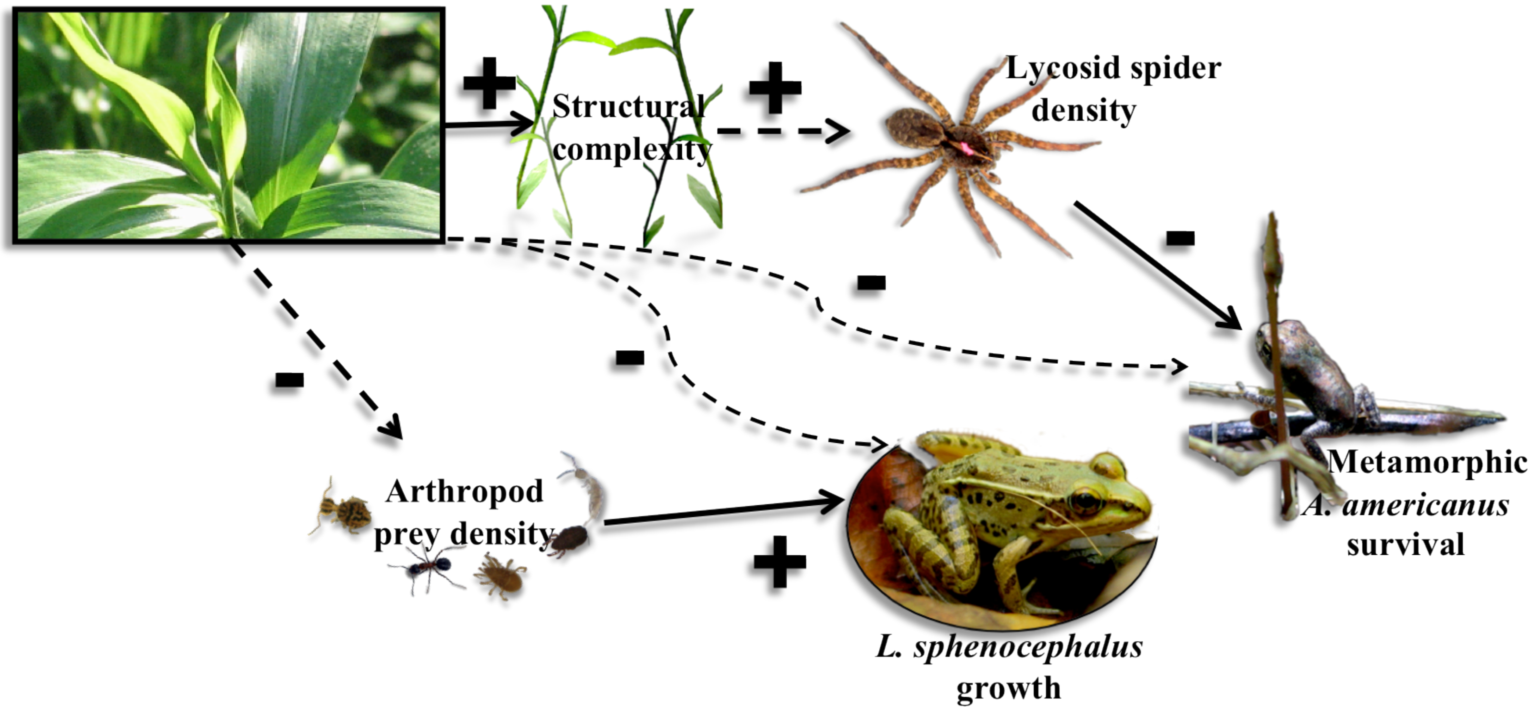

Figure 4-5. Indirect influences of invasion by the exotic grass *Microstegium vimineum* on forest floor consumers. Increased top-down pressure on metamorphic toads within these environments has been demonstrated following invasion as a result of reduced rates of cannibalism and intraguild predation among lycosid spiders, resulting in spider accumulation (DeVore 2011b). Leopard frog survival is not significantly affected by predation, but the growth of this species is significantly lower in invaded habitats, likely as a result lower prey availability or capture success in invaded habitats. Potential for behaviorally-mediated indirect effects also exists, as increased predator abundances can suppress foraging behavior via nonconsumptive effects, and decreased prey availability can lead to increased foraging effort or speed, thereby increasing exposure to predation.

Figure 4-6. Behavioral characteristics may be partially responsible for the differential responses to invasion by *M. vimineum* by these amphibians.

Top panel: Juvenile *A. americanus* are diurnal, active foragers of the forest floor.

Middle panel: *L. sphenocephalus* is a nocturnal sit-and-pursue predator that generally remains concealed under the litter layer.

Bottom panel: *N. viridescens* is a highly cryptic, toxic, slow growing species, emerging to forage and migrate nearly exclusively during rain events.

Anaxyrus americanus survival

Source	*SS*	*DoF*	*MS*	*F*	*p*
Intercept	2.385035	1	2.385035	258.6526	0.000004
Block	0.311213	6	0.051869	5.6251	**0.027073**
Treatment	0.008120	1	0.008120	0.8806	0.384252
Error	0.055326	6	0.009221		
Time	0.427706	3	0.142569	82.2241	**<0.000001**
Time*Block	0.059868	18	0.003326	1.9182	0.088320
Time*Treatment	0.021974	3	0.007325	4.2243	**0.019950**
Error	0.031210	18	0.001734		

Lithobates sphenocephalus survival

Source	*SS*	*DoF*	*MS*	*F*	*p*
Intercept	4.039866	1	4.039866	303.6621	0.000002
Block	0.646100	6	0.107683	8.0942	**0.011199**
Treatment	0.000549	1	0.000549	0.0412	0.845773
Error	0.079823	6	0.013304		
Time	2.580774	3	0.860258	57.3858	**<0.000001**
Time*Block	0.603158	18	0.033509	2.2353	**0.048334**
Time*Treatment	0.015869	3	0.005290	0.3529	0.787600
Error	0.269834	18	0.014991		

Notophthalmus viridescens survival

Source	*SS*	*DoF*	*MS*	*F*	*p*
Intercept	15.58345	1	15.58345	52.58402	0.000779
Block	0.86783	5	0.17357	0.58567	0.714301
Treatment	0.11250	1	0.11250	0.37963	0.564766
Error	1.48177	5	0.29635		
Time	2.58401	2	1.29201	31.28424	**0.000050**
Time*Block	0.91347	10	0.09135	2.21184	0.113314
Time*Treatment	0.06875	2	0.03438	0.83240	0.463035
Error	0.41299	10	0.04130		

Table 4-1. Repeated measures ANOVA results for the probability of survival of three amphibians species to August (*L. sphenocephalus* and *A. americanus* only), September, October, and April capture occasions within paired invaded and native enclosures across seven (*L. sphenocephalus* and *A americanus*) or six (*N. viridescens*) locational blocks.

Habitat alterations following *M. vimineum* invasion			
Structural	*Predatory (μ)*	*Prey (g)*	*Abiotic*
Increased complexity	Increased spider persistence	Decreased prey density	Increased soil pH, moisture, temperature

Life history of model species and responses to invasion			
	A. americanus	*L. sphenocephalus*	*N. viridescens*
Size at metamorphosis *(Range)*	Tiny 0.039 to 0.222 g	Large 0.299 to 1.041 g	Small 0.098 to 0.355 g
Growth *(mean % mass increase of survivors; avg time since metamorphosis)*	Very high 940%; 55 days	Medium 57% native, 46% invaded; 28 days	Very low 6.5%; 38 days
*Foraging strategy**	Active (as juveniles)	Sit-and-pursue	Intermittent (rainfall)
*Abiotic susceptibility**	Low; high water absorption abilities, epidermal water channeling, bladder resorption, AVT sensitivity, etc	Medium; limited water absorption abilities, higher rates of evaporative water loss	Low; enhanced water absorption, epidermal water channeling, bladder resorption, AVT sensitivity, high acidity tolerance, etc
Response to plant invasion *(ratio of daily, treatment-specific g and/or μ values)*	Short-term, post metamorphic increase in mortality $\mu_{\text{invaded}} = 5.2*\mu_{\text{native}}$	Reduced post-metamorphic growth rates $g_{\text{invaded}} = 0.72*g_{\text{native}}$	None
Probable cause of observed effect	Increased top-down pressure from lycosid spiders	Reductions in prey abundance, decreased sighting distance	Not applicable

Table 4-2. Summary of environmental effects of *M. vimineum* invasion, model consumer characteristics, consumer responses to invasion, and the probable drivers behind these influences. Post-metamorphic growth was calculated for individuals surviving to the first capture period; the time between release and recapture is an average, which varied based on the release date, the capture date, and the survival of the multiple cohorts that were released. Short-term comparisons of μ in invaded and native habitats were based on daily mortality rates of metamorphic toadlets during 7-day short-term mortality and foraging trials. *Taken from Wells (2007)

CHAPTER 5

GENERAL CONCLUSIONS AND POTENTIAL FURTHER RESEARCH

Plants produce basal resources, influence abiotic habitat properties, drive biogeochemical cycling, and affect the physical architecture of ecosystems. Given this, changes in plant communities, including those resulting from exotic invasion, are likely to have far reaching impacts on taxa across multiple trophic levels. The majority of studies seeking to quantify the impact of plant invasion on native species have focused either on competitive changes in the distribution of other plant species, belowground influences on microflora or, more rarely, effects on invertebrate herbivores (Kourtev et al. 2002, Levine et al. 2003, Carvalheiro et al. 2010). Fewer studies have also quantified invertebrate detritivores across invasion fronts. However, the influences of invasion are unlikely to be confined to these groups. For example, since the majority of higher trophic-level taxa derive some, if not the majority, of their energy from detrital pathways, plant effects on detritivores are likely to influence these consumers. I discovered some evidence of bottom-up effects of plant invasion on predator growth; however, other species were apparently unaffected. I also demonstrated that largely overlooked effects of plant invasion on the structural complexity of a habitat can significantly alter the strength of interactions among native species. Specifically, in this system plant invasion led to the increased persistence of lycosid spiders, which intensified predation rates on newly metamorphosed amphibians. Outside the context of invasions, the effects of habitat architecture on trophic interactions is well-documented and widely accepted, so I propose that the contextually-mediated effect of plant invasion is a relatively common mechanism by which plant invasions may affect resident communities. However, I also demonstrated that consumer responses to such effects can vary interspecifically, as species utilizing different life history strategies are known to differ in their prioritization of growth and survival, leading to differential influences of ecosystem change on these related species. This dissertation therefore represents a unique achievement in understanding the impacts of plant invasion by integrating both engineering and trophic effects of plant invasion with native consumer life history traits to detail both the causes and effects of influences by invasion on native consumers.

Chapter 2 of this dissertation presents a novel investigation of all of the potential pathways through which resources produced by an exotic plant can influence energy availability within affected habitats and quantifies the degree to which this energy contributes to that utilized by a native predator. Few studies have investigated the effects of plant invasion on energy availability within affected habitats, despite the fact that primary production by plants is critical to the functioning of ecosystems. Energy resources from autotrophic production can reach food webs in a variety of ways, including herbivory via "green" food webs, as well as through litter and belowground inputs (e.g. via root exudation) into detrital, or "brown" pathways. Invasion typically alters the quality, quantity, and timing of these inputs, and may further influence the bioavailability of these resources through influences on belowground C cycling or detritivore community composition. These plants may therefore be expected to alter energy flow to native consumers through a variety of mechanisms. My finding that resources produced by *M. vimineum* are utilized by the forest floor predator *Anaxyrus (Bufo) americanus* in proportion to their presence in litter inputs to detrital food webs establishes that exotic production is an important source of energy for native consumers, thereby demonstrating the presence of a trophic link to native consumers that, in this case, is likely independent of herbivorous pathways. Another novel finding from work associated with this dissertation is that root exudates from this exotic plant are rapidly incorporated into belowground microbial communities and subsequently utilized by aboveground predators. Although the importance of root exudates to soil respiration and detrital communities has been established in native systems (Pollierer et al. 2007), the potential for nonindigenous exudates to serve as an energy source for native consumers had not been previously established. While the influences of changes in belowground food webs on aboveground communities have recently received increasing attention, the majority of food web studies seeking to connect belowground with aboveground processes have focused on plant-mediated effects on herbivore populations (Wardle 2002, Hines et al. 2006) or the influences of subsidies from detrital food webs on the suppression of herbivore populations via a "resource shunt", in which detrital subsidies increase the abundance of generalist predators, leading to cascading implications for plant growth (Wise et al. 1999, Halaj and Wise 2002). However, focusing attention on the consequences of detrital alterations for herbivorous food webs has generally impeded recognition of the fact that detritus is the dominant mechanism through which autotrophic production enters food webs (Polis and Strong 1996, Moore et al. 2004, Sanders and Platner 2007) and may therefore provide a key resource for native consumers that operates independently to herbivory. Accordingly, this dissertation presents evidence that detrital pathways may serve as more than an additional subsidy for generalist predators, but an important source of trophic resources through which even nonindigenous production supports native communities. Additional work in this system also demonstrated that *M. vimineum* is consumed by certain native invertebrate herbivores, a pathway that had not been previously described for this plant (Bradford et al. 2010). These investigations have thereby detailed numerous pathways through which native consumers utilize nonindigenous resources produced by this plant. However, through the enumeration of detrital invertebrates within these habitats I also demonstrated that the dominant microarthropod order in these systems, the Acari, are less abundant within invaded habitats. Additionally, invasion by this plant appears to drive a priming effect, in which carbon turnover rates increase following invasion. I therefore hypothesize that changes in decomposition processes, which could be contributed to by abiotic habitat changes that I documented in association with invasion as well as increased inputs of labile carbon from root exudation, may result in altered production of invertebrates from detrital food webs. This has the potential to drive bottom-up effects within invaded systems and, in fact, we found evidence that the growth of a sit-and-wait forest floor predator was significantly lower in invaded habitats. Further research is needed to explore the relationship between biogeochemical processes and invertebrate production from detrital food webs. As rapid cycling systems are thought to be associated with copiotrophic decomposer communities with lower substrate affinities and limited connections to aboveground food webs, it is possible that priming effects negatively impact invertebrate production aboveground, however, I did not directly establish a mechanistic explanation for these effects. Nevertheless, this work is novel in its demonstration that bottom-up effects of invasion in this system are more likely to operate through whole-scale changes in detrital community composition rather than through the sequestration of nonindigenous production, as resources produced by this exotic plant are readily utilized by native consumers, albeit most frequently through detrital channels.

This dissertation also presents novel evidence that the dominant effects of *M. vimineum* invasion on certain native species actually result from alterations in habitat structure that accompany autogenic ecosystem engineering by this plant. The potential for changes in structural complexity to affect consumers is well-established, as these effects have been shown to influence basic functions such as movement (Rieder et al. 2010), foraging (Brownsmith 1977, Crist and Wiens 1994), and escape behaviors (Mattingly and Jayne 2005). The role of ecosystem engineers on the modification of trophic interactions, in particular, is known to be a significant issue with potentially large effects (Jones et al. 1997). Implications of structural changes for native species have therefore been demonstrated in cases of anthropogenic disturbance (Hawlena and Bouskila 2006), plant succession (Bultman et al. 1982), and habitat degradation (McCormick 2009). However, the mechanisms through which structural implications of plant invasion influence native consumers within affected communities have only rarely been investigated (Pearson 2009, Byers et al. 2010, Pearson 2010). My finding that the dominant effect of an invasive plant on the forest floor predator *A. americanus* occurs through top-down effects, via the modification of an existing trophic connection with another native species, highlights the significance of plant invasion as a driver of physical habitat modification and the importance of addressing the mechanisms behind effects on consumer communities. While many studies have focused on correlating invasions with decreases in native diversity or abundance, studies such as the one presented in Chapter 3 that address the mechanisms behind these effects are rare (Crooks 2002). Additionally, conducting these correlative studies on mobile species may underestimate effects of invasion, as changes in abundance may be associated with habitat selection rather than changes in habitat quality; for example, Nagy et al. (2011) found that amphibians are more abundant in areas invaded by *M. vimineum,* but here I have demonstrated that the survival of one of the species they investigated is actually lower within affected habitats due to these engineering effects. Admittedly, although the food web dynamics of nearly every ecosystem are likely to be influenced by ecosystem engineers (Jones et al. 1997), the level of complexity associated with these processes can make unraveling the mechanisms behind these effects difficult. However, these processes are critical to the maintenance of food webs, which form the core of biotic ecosystem components (Schmitz 2010) and some of the effects they initiate are relatively predictable. As habitat alterations continue to occur at an unprecedented rate, developing an understanding of the mechanisms that drive effects on native species may increase our ability to make generalizations about the nature of these influences across ecosystems. Although the majority of studies on the influences of ecosystem engineers focus on bottom-up effects initiated by habitat provisioning (Crooks 2002), here I found that these bottom-up provisioning effects resulted in increased survival of intraguild predators, but eventually culminated in increased top-down pressure on their shared prey. Top-down effects were thereby the dominant mechanism through which these contextual effects were found to influence another native species, *A. americanus*. I expect that intraguild predation is a trophic link that is exceptionally likely to respond to alterations in habitat structure resulting from plant invasion, and that top-down pressures resulting from such processes have the potential to drive more immediate, significant effects on native species than bottom-up effects (Miyashita and Takada 2007). Studies seeking to illuminate the effects of invasion that fail to account for the structural implications are therefore likely to underestimate the influences of this process on native communities. Given my results and the established importance of habitat structure, I expect that plant invasion commonly affects native consumers indirectly through contextually-mediated modifications of preexisting trophic relationships.

In Chapter 4 I present evidence that the responses of native consumer to invasion are not necessarily consistent, but may vary interspecifically even among related, sympatric species. Determining whether plant invasion will similarly affect native species has become ever more important as invasion continues to represents an increasingly ubiquitous driver of anthropogenic change. This study is therefore important in that it both illustrates the effects of plant invasion on a group that has been traditionally overlooked in this context (the amphibians; recently reviewed by Martin and Murray 2011) and highlights the fact that interspecific and ontogenetic variation in response to these effects is likely. However, I also demonstrate that the nature of these effects could be predicted by accounting for the metamorphic syndrome of the species in question. Metamorphosis is a common strategy that allows species to strategically balance two environments with variable predation risk and resource availability (Werner 1986). Stable strategies have developed in association with this transition, such that post-metamorphic behaviors and associated risks are thought to be compensatory to the timing of metamorphosis. Although previous research and modeling exercises incorporating interspecific variation in metamorphic strategies have traditionally focused on optimizing responses to changes in predation pressure, food availability, or abiotic stressors during the larval stage, with the goal of maximizing metamorph size or improving the timing of departure from this environment (Wilbur and Collins 1973, Johansson et al. 2001, Day and Rowe 2002), the influences of such effects in the secondary habitat of these species have received little attention in the context of metamorphic strategy. Research on terrestrial life stages, meanwhile, has focused principally on the influence of intraspecific variability on post-metamorphic performance. However, while intraspecific flexibility in the size at and timing of metamorphosis often reflects the plasticity of individuals in response to proximate drivers, such as predation risk and resource availability within the larval environment (Higginson and Ruxton 2010), and do, in fact, frequently have carry-over effects on post-metamorphic performance (Chelgren et al. 2006), this variation is a reflection of larval environment quality rather than an indication of disparate strategies for success within the secondary habitat (Higginson and Ruxton 2010). In this dissertation work, I confirmed that intraspecific carry over effects of the larval environment influence species performance (as an individual's survival probability increased with size at metamorphosis for both *A. americanus* and *Lithobates sphenocephalus*), but I also demonstrated that there was significant interspecific variation in post-metamorphic susceptibilities to environmental change. When exposed to an invasion-driven gradient of predation pressure and trophic resource availability, the nature of observed effects on species performance (i.e. growth rates and mortality probabilities) aligned with what is predicted by theoretical modeling exercises, thereby providing novel support for these predictions as well as a potentially valuable management tool that may improve our ability to predict the nature of native species responses to habitat change.

Due to the multifaceted roles that plants play in ecosystems, the implications of plant invasion are likely to be complex and far-reaching. In the course of this dissertation work, I have demonstrated that invasion by *M. vimineum* drove a multitude of complex effects on abiotic habitat characteristics, energy flow, and species interactions within affected habitats. I have also demonstrated complex consumer responses to invasion, such that closely related, sympatric species may differ in both the nature and strength of their responses to these changes. However, despite the apparent compounded complexity of these effects and responses, there are underlying rules that, when revealed, rendered such effects relatively predictable. It is my hope that this work will reinforce that environmental change can influence native species through a multitude of mechanisms, but that closer investigation of these effects will frequently reveal that these responses can be predicted by established ecological theories.

That being said, in science there are no good answers that don't raise more questions, and the same is true here.

Limitations and open issues

There is no question that the complexity of ecosystems makes it difficult to draw clear conclusions; unraveling this complexity should be a priority if we are to understand the nature of biotic interactions (Schmitz 2010). This dissertation illuminated the nature of consumer responses to environmental change through the integration of multiple trophic levels, but behind each of these transfers there is additional, unresolved complexity. Therefore, in many ways, this dissertation raises more questions than it answers. The relationship between autotrophic inputs and the production of invertebrates from detrital food webs, whether reductions in prey availability or the alteration of habitat structure are more effective at driving bottom-up effects in this system, how bottom-up and top-down effects interact via behavioral modifications to affect consumer performance, whether cascading top-down effects of increased predator pressure are sufficient to affect processes that could stimulate bottom-up effects (such as biogeochemical cycling)… For each step, there are multiple questions.

How biogeochemical processes influence consumers

Rates of nutrient cycling are generally believed to influence resource availability for consumer populations, as copiotrophic and oligiotrophic decomposers are thought to exhibit differential substrate affinities, potentially resulting in "leakier" biogeochemical cycling within systems that exhibit rapid nutrient turnover. However, the influences of belowground cycling rates on terrestrial detrital food webs are poorly understood. Instead, the majority of investigations focus on how nutrient availability influences herbivore communities via influences on plant growth (e.g. Forkner and Hunter 2000). This disconnect between nutrient availability and the production of invertebrate trophic resources from belowground food webs reflects a prevailing disregard of detrital production as an important source of energy for aboveground consumers that may operate independently to herbivorous food webs (Wardle 2002). As detrital food webs rely upon microfloral communities that drive decomposition, processes that influence belowground nutrient cycling may be expected to drive bottom-up effects in terrestrial food webs.

Bacterial vs. fungal pathways

A confounding factor that generally impedes our ability to predict the implications of altered detrital inputs for the production of aboveground invertebrates is the fact that decomposition occurs through two distinct pathways, one of which is based on fungal decomposers while the other is bacterial-based (Wardle 2002). While fungal decomposition generally results in hyphal growth, which occurs externally to the soil water matrix, bacteria operate within soil water. As such, fungal resources can be directly consumed by arthropods, while bacterial microflora remain largely confined within the soil water matrix. Although microarthropods such as predaceous mites may join these food web pathways together, the number of trophic transfers required to convert bacterial resources to prey that is detectable by microarthropod predators may contribute to inefficient aboveground invertebrate production within bacterial-based detrital food webs. Since bacterial decomposition is generally associated with higher nutrient availability and more rapidly cycling systems (Wardle et al. 2004, but see Fierer et al. 2007), the effects of a shift in the dominant detrital pathway are frequently confounded with alterations in nutrient availability. However, shifts between fungal and bacterial based decomposition pathways are a relatively frequent consequence of anthropogenic habitat change (Moore 1994, Bardgett and McAlister 1999), so the implications of this process for aboveground consumers is worthy of investigation and may improve our ability to predict whether specific habitat alterations will drive bottom-up effects on consumers that rely on detrital food webs.

The role of root exudates as a driver of environmental change following plant invasion

Up to 20% of photoassimilate is released from live roots into soil as exudates (Hutsch et al. 2002), and this process has demonstrated potential to drive priming effects (Kuzyakov 2010). The process of plant invasion may be expected to dramatically alter inputs of labile carbon into belowground detrital food webs, especially in systems where an invasive plant moves into habitats in which the native plant community is relatively depauperate, such as those studied here. However, the ways in which altered root exudation patterns influence carbon dynamics in invaded systems has not been addressed, despite observations that plant invasion is frequently associated with changes in decomposition rates (Ehrenfeld 2003, Ashton et al. 2005) or carbon dynamics (Ehrenfeld 2003, Strickland et al. 2010, 2011). Additionally, the role that these root exudates may play in supporting aboveground consumers has received little attention, despite evidence that decomposers are highly reliant upon this resource (Pollierer et al. 2007). As plants are known to use root exudation to increase decomposition rates and thereby increase the availability of nutrients in the surrounding soil (Hamilton and Frank 2001), it is possible that high-nutrient, fast growing invasive plants are particularly dependent upon root exudates in order to facilitate nutrient uptake. If this is the case the effects of root exudation on detrital food webs may be especially pronounced in invaded systems.

Bottom-up effects: Prey availability vs. structural complexity

Decreased prey availability can result in resource limitation for predator populations and, as such, the decreases in leopard frog growth rates that were observed within invaded habitats may be a consequence of the lower prey densities. However, reductions in sighting distance could also contribute to this effect in stationary species, as increases in structural complexity have been associated with decreased foraging efficiency among sit-and-wait predators (Crowder and

Cooper 1982). Therefore, structural changes alone may be sufficient to initiate bottom-up influences on leopard frog growth, even when prey densities remain consistent. Future investigations could easily determine whether increases in structural complexity alone can play a role in reducing the foraging success of this species.

Bottom-up effects: Interactions between growth and predation risk

Body size often plays a large role in predation risk, with vulnerability to gape limited and size-selective predators varying as a function of prey size. Like many predators, lycosid spiders are size selective, taking prey from 0.01 to 1.3 times their own mass (Moulder and Reichle 1972, Schmitz et al. 1997). Increased top-down pressure from this group as a consequece of plant invasion has been observed, but size at metamorphosis and growth rates are likely to play a role in mediating the strength and duration of this risk (Werner 1986). This dissertation demonstrated that small (~0.09g) metamorphic American toads are suceptible to increased top-down pressures in invaded habitats, exhibiting significant reductions in short-term survival. Theory predicts that rapid growth is incentivized in species that enter a novel environment at a small size in order to reduce the duration of "predation windows" that result from increased suceptibility to predation during this time (Almany and Webster 2006), and American toads embody this principle, exhibiting a mean mass increase of 940% between release and recapture (~55 days). If small body size is associated with increased vulnerability to predation in this system, ontogenetic changes in susceptibility to this risk would be expected as individuals grow. This was observed, as by six weeks post-metamorphosis toads no longer experienced increased mortality in invaded habitats, and I could not establish the presence of significant, long-term influence of invasion on survival. However, in systems where both bottom-up and top-down effects are possible, the duration of this "predation window" could be extended due to lower growth rates in impacted habitats. In this way, bottom-up effects could manifest as top-down effects, as slower-growing individuals are exposed to predation risk for a longer period of time. This interplay between growth and predation risk is likely to be a common occurrence that confounds our understanding of the relative importance of growth and survival, and therefore deserves further exploration.

Behaviorally-mediated effects: Increased foraging activity due to decreased prey density

Sensitivity to reductions in prey abundance often varies as a function of foraging strategy (Werner and Anholt 1993, Resetarits and Chalcraft 2007). The species observed here display a range of foraging strategies; leopard frogs are sit-and-pursue predators (Dole 1965), juvenile toads are active foragers (Werner 1986), and efts emerge to forage intermittently, primarily during rain events (DeVore pers obs, Wells 2007). As prey availability decreases, theory predicts that optimal foraging speeds should increase, providing a foraging advantage to organisms that forage actively (Werner and Anholt 1993). In accordance with this prediction, we observed that growth rates of metamorphic toads were not affected by reductions in prey availability associated with plant invasion, but that the growth of leopard frogs was reduced in these habitats, likely because the active foraging technique utilized by American toads increased their resilience to changes in prey density. However, there is further potential for intraspecific variation in foraging activity in response to altered prey densities, and these changes in prey behavior can simultaneously influence both foraging success and predation risk (Denno et al. 2002). If toads increased their foraging activity in order to compensate for decreased prey availability, the reductions in survival that were observed in invaded habitats could also be a consequence of increased exposure to sit-and-wait predators such as the lycosid spiders that were observed within these environments. Therefore, alterations in toad behavior may result in bottom-up influences of invasion manifesting via increased top-down predatory pressure.

Behaviorally-mediated effects: Decreased foraging activity due to predation risk

Prey behavior is a mitigating factor in predation risk (Denno et al. 2002). As ground-dwelling lycosid spiders are sit-and-pursue predators that rely on visual cues to identify prey (Moulder and Reichle 1972, Schmitz 2010), species that limit movement are unlikely to be observed by this species. Accordingly, there was no evidence that increases in lycosid spider persistence within invaded habitats led to increased predation on the sit-and-pursue predator *L. sphenocephalus.* Spider predation of this species was observed nearly exculsively within pitfall traps, where the cryptic behavior and rapid escape techniques utilized by this species are likely to be ineffective. However, as reductions in foraging effort have been demonstrated in response to increased predatory pressure (Abrams and Rowe 1996), behavioral adaptations to predation risk may have also contributed to the reductions in growth observed in invaded habitats. We did not monitor activity within this species, and we therefore cannot discount the possibility that even this relatively inactive predator made fewer foraging movements within invaded habitats. It is therefore possible that it is increases in predator presence, rather than decreases in prey abundance, that drives reductions in growth rates in this species by influencing foraging decisions (Madison et al. 1999, Maerz et al. 2001)

Diet breadth

Diet breadth can also significantly influence sensitivity to bottom-up effects (Jiang and Morin 2005, Carvalheiro et al. 2010). As *A. americanus* preys heavily on chitinous invertebrates, especially ants (Clarke 1974, Flowers and Graves 1995)—a strategy that has been shown to reduce time spent functioning under a negative energy balance (Huey et al. 2001)—growth in this species may be related to ant density rather than the overall abundance of potentially edible prey items (Suarez and Case 2002). The aboveground density of the family Formicidae observed within enclosures utilized in this dissertation was highly variable and not influenced by invasion (95.9% increase to ~96m^{-2}, p=0.747; n=6), and toads were observed seeking out this resource, actively approaching ant colonies that were disturbed during sampling activities. Although diet specialization is often associated with increased vulnerability to environmental change (Suarez and Case 2002), in this case a generalist foraging strategy may render *L. sphenocephalus* more sensitive to decreases in overall prey abundance that are not problematic for a species that specializes on an unaffected resource base. Ant specialization may therefore be another strategy through which *A. americanus*, a species that prioritizes post-metamorphic growth, increases its growth potential.

Density-mediated vs. nonconsumptive effects

Predator-induced mortality can occur through both direct consumption of prey or through fear-based, non-consumptive effects. These non-consumptive effects are often especially pronounced when the predator in question utilizes sit-and-wait or sit-and-pursue techniques, such as those utilized by lycosid spiders (Preisser et al. 2007). Whereas increases in direct mortality are typically directly related to increases in predator densities, the nonconsumptive influences of predation risk on prey survival can be nonlinear (Krivan and Schmitz 2004, Trussell et al. 2011). Therefore, through nonconsumptive effects, relatively minor increases in predator densities may drive strong responses in prey populations. However, possible influences of nonconsumptive effects of spider presence on amphibian populations have not been investigated. As nonconsumptive effects can be strong drivers of prey survival, potential driving greater influences than direct mortality (Schmitz et al. 2004), this possibility should be addressed. Other studies have used spiders with glued chelicerae to replicate the presence of a predator while preventing the direct consumption of prey (Schmitz et al. 1997), and this system could benefit from the same approach in order to determine whether toads exhibit similar responses.

Ontogenetic changes in consumer susceptibilities

It is possible that relative susceptibility of the amphibians studied here to bottom-up and top-down pressures varies ontogenetically. As we only monitored amphibian growth and survival for one year, we cannot be sure that the influences observed on metamorphic and juvenile life stages will continue into adulthood. In fact, this seems unlikely, especially in the case of the American toad, as this species prioritizes rapid growth through active diurnal foraging as a juvenile, but is a sit-and-wait nocturnal predator as an adult (Lillywhite et al. 1973). It therefore seems likely that the adult life stage of this species would be more sensitive to bottom-up effects than the top-down influences that affected it during the metamorphic life stage. In this way, the effects of environmental changes such as plant invasion on consumers within these habitats could vary between life stages.

Variation in habitat quality

Although this dissertation presents evidence that invasion generally degrades habitat suitability for *A. americanus* and *L. sphenocephalus,* I also discovered evidence of significant, pronounced variability in habitat quality between locational blocks. This variation occurred despite the fact that all sites were situated within intact, forested systems, typically within floodplain habitat. Although many studies that account for the availability of suitable habitat do so very broadly, often lumping together all habitat that is “forested” or “agricultural”, I have found that even within much narrower habitat classifications there is great variability in habitat suitability. Additionally, I found that the effects of locational block could vary significantly by year. This provides evidence that this significant, underlying variation in habitat quality may vary over time, and raises the possibility that comparisons of habitat quality may yield disparate results through time. Further investigations into what characteristics predict habitat quality for these species are warranted.

Reproductive output

The maximization of fecundity is the ultimate driver behind many adaptations; for species in which body size influences reproductive output the maximization of this parameter frequently requires the incorporation of both survival probabilities and growth rates. In the case of amphibians low energetic requirements mean that reductions in prey capture seldom have immediate consequences for amphibian survival, however, size variation at reproduction is frequently correlated with reproductive output in this group (Werner and Anholt 1993, Wells 2007). Reductions in growth stemming may therefore have consequences for future population recruitment by decreasing reproductive output. In this way, processes that influence amphibian growth could drive population-level effects. In this dissertation we observed both lower survivorship of metamorphic American toads and lower growth rates in southern leopard frogs. However, short-term survival reductions in metamorphic toads did not lead to long-term influences on survival to the following year, implying that these populations may be relatively robust to the degree of survival reductions observed in invaded habitats. If this is the case, the long term effects of *M. vimineum* invasion on amphibian populations may be more pronounced in the case of the southern leopard frog, whose reduced growth in invaded habitats could translate to reduction in reproductive output. Modeling efforts could help to determine which species is more likely to be impacted at the population level by invasion of *M. vimineum* into terrestrial habitats utilized by these species and further illuminate the trade-offs between survival and growth inherent in the life history strategies of these two related consumers.

Spider/amphibian intraguild predation

Intraguild predation is common in many ecosystems and may play a role in stabilizing both predator and prey populations (Rudolf 2007). This dissertation presents data that establishes lycosid spiders as a significant predator of a metamorphic amphibian, the impact of which has likely been traditionally underestimated. Predation of amphibians upon spider populations has also been established (Clarke 1974). However, the role of intraguild predation between these forest floor consumers has not been investigated. As they alternate between predators and prey, the influences of amphibians and spiders upon each other may vary ontogenetically, leading to complex interactions between these predators.

Structure vs. inputs

As plants serve as both basal resources and autotrophic ecosystem engineers, the influences of altered resource availability and changes in habitat structure may be confounded. For example, increased lycosid spider densities are frequently associated with structurally complex habitats, but where this complexity is a result of increased plant growth, bottom-up effects may also contribute to their performance. Although there is evidence that structural complexity is the major driver of lycosid spider densities (Wagner and Wise 1996), the relative importance of bottom-up and structural changes in this study system remain unexplored. The utilization of fake plant material that provides structure but do not contribute to trophic resources could allow us to determine the relative importance of these two effects and ascertain the degree to which structural effects determine the influence of plant invasion.

Reverse successional gradient?

Grass invasions of forest habitats, such as those observed within this dissertation, are relatively rare. Typically, succession results in formerly grass-dominated systems becoming forested. It is possible that the influences of *M. vimineum* on forest ecosystems operate similarly to a reverse successional gradient. Considering the well-studied processes through which succession from a grass-dominated to a forested system influence soil and litter communities, and "reversing" these changes may provide insight into the types of ecosystem changes that can be expected in association with *M. vimineum* invasion.

Potential trophic cascades resulting from increased spider densities

Spiders are important aboveground predators that are dependent upon the detrital food web for resources (Miyashita et al. 2003) and can substantially reduce populations of microbi-detritivores such as collembolans (Wise 2004). Following increases in structural complexity and corresponding reductions in intraguild predation, spiders have the potential to further suppress microbe-detritivore populations (Miyashita and Takada 2007), increasing the probability that a trophic cascade will occur (Finke and Denno 2006). Increased prey suppression associated with these environments not only has the potential to structure prey communities (Finke and Denno 2006), it can also have cascading effects on the detritial food web, ultimately influencing ecosystem properties such as rates of litter decomposition (Lawrence and Wise 2000, 2004). Unfortunately, the complexity of below-ground food webs makes the nature of these influences difficult to predict; for example, spider predation may lower decomposition rates by reducing populations of microbi-detritivorous Collembolans that would otherwise stimulate active fungal decomposition through grazing senescent hyphae and pulverizing leaf material (Lawrence and Wise 2000), or depress decomposition rates by reducing the abundance of active fungi (Wise et al. 1999, Lawrence and Wise 2004). Therefore the effects of aboveground predator accumulation could respectively counteract or contribute to the influences of exotic plant invasion on decomposition processes that have been associated with *M. vimineum* invasion (Ashton et al. 2005) and observed earlier within this dissertation (see Figure 6).

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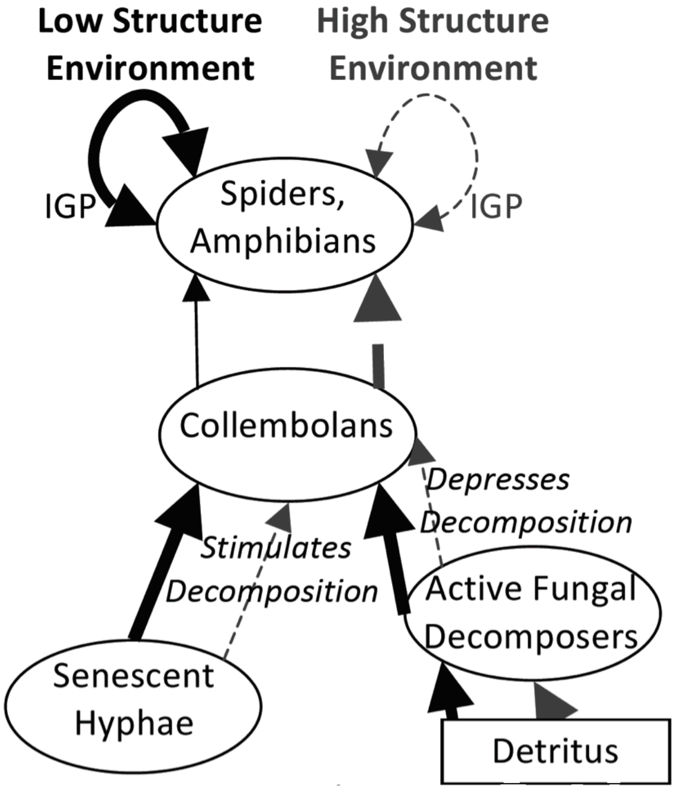

Figure 5-1. Consumptive energy flow in low and high structure environments as driven by structurally-mediated effects on intraguild predation rates that result in the accumulation of predators in structurally complex habitats (left hand solid arrows indicate low structure flows, while high structure is represented by dashed arrows on the right sides). The width of the arrow approximates the relative size of the influence. Impacts on detrital consumption vary depending on the relative strength of the stimulative vs. depressive influences of the collembolans on fungal decomposers.