

SPATIAL DISTRIBUTION OF NON-NATIVE INVASIVE PLANTS FOLLOWING LARGE-  
SCALE WIND DAMAGE AT LARUE PINE HILLS – OTTER POND RESEARCH  
NATURAL AREA, UNION COUNTY, ILLINOIS

by

Anthony J. Romano

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A Thesis

Submitted in Partial Fulfillment of the Requirements for the  
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Approved by:

Dr. Matthew Therrell, Chair

Dr. Justin Schoof

Dr. David Gibson

Graduate School  
Southern Illinois University Carbondale  
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## AN ABSTRACT OF THE THESIS OF

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MAJOR PROFESSOR: Dr. Matthew Therrell

The objective of this study was to determine if a large-scale wind disturbance facilitated the invasion of forest interiors by non-native invasive plant species. The northern portion of LaRue Pine Hills – Otter Pond Research Natural Area in the Shawnee National Forest, of southern Illinois, was severely damaged by high winds during a derecho event on May 8<sup>th</sup> 2009. In the summer of 2011, 53 permanent research plots, as well as 20 additional plots located along roads that form the boundaries of the study site, were surveyed for the presence of 20 non-native invasive plant species. Only three of 53 interior plots (5.6%) contained invasive plant species (*Rosa multiflora*, *Lonicera japonica*, and *Lonicera maackii*). Sixteen of 20 road plots contained a non-native invasive species (80%), and six species were identified (*Dioscorea oppositifolia*, *Lactuca serriola*, *Lonicera maackii*, *Microstegium vimineum*, *Rosa multiflora*, and *Sorghum halepense*). These findings indicate that wind damage does not appear to have facilitated invasion of forest interiors in the first two years following the storm. The spatial distribution of non-native invasive plants in the study area fits the pattern of other studies conducted in southern Illinois with non-native invasive plants associated primarily with forest edges and diminishing in the forest interior despite the opportunity for establishment following the wind disturbance.

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## CHAPTER 1

### INTRODUCTION

Invasive species pose a significant threat to biodiversity worldwide (Lee and Macdonald 1997; Pimentel et al. 2005). Non-native invasive species (NNIS as defined by Alpert et al. 2000) often reduce native species richness and have the potential to drive extinctions of native species (Lesica and Shelly 1996; Powell et al. 2011; Vilà et al. 2011). NNIS have also been shown to alter habitat, disturbance regimes, and ecosystem functionality (D'Antonio and Vitousek 1992; Ehrenfeld 2003; Vilà et al. 2011). In addition to ecological harm there are also tremendous economic costs associated with NNIS, particularly agricultural losses and expenses associated with control efforts. In the United States, this cost has been estimated to be \$137 billion annually (Pimentel et al. 2005). Taken together these ecological issues and economic costs make it apparent that understanding patterns and processes of biological invasions is vital if conservationists and land managers are to effectively constrain detrimental NNIS.

Non-native invasive plants (NNIPs) have been shown to compete for resources and space to the detriment of native communities and frequently create monospecific stands that alter microhabitat characteristics and underlying ecosystem functions (Meekins and McCarthy 1999; Forseth and Innis 2004; Simberloff 2011; Vilà et al. 2011). Within forest communities of the eastern United States, forest interiors with dense overhead canopies are considered to be largely resistant to invasion by most NNIPs due to reduced light levels (Brothers and Spingarn 1992; Yates et al. 2004;



Honu and Gibson 2008). But, NNIPs have been principally associated with forest edges and disturbances (Brothers and Spingarn 1992; Hobbs and Huenneke 1992; Alpert et al. 2000; Christen and Matlack 2009; West et al. 2009). Ecological processes associated with forest edges can facilitate establishment, growth, and spread of NNIPs (Brothers and Spingarn 1992; Cadennaso and Pickett 2001; Meekins and McCarthy 2001; Honu and Gibson 2006). Edges associated with roadways and trails can also act as pathways that funnel propagules of invading species along the linear edges of a forest community (Campbell and Gibson 2001; Christen and Matlack 2009).

Disturbance or a change in the existing disturbance regime (Moles et al. 2012) has also been implicated as an important factor in the spread of NNIPs (Hobbs and Huenneke 1992; Alpert et al. 2000; Lake and Leishman 2004). Disturbances are typically discrete events that alter the structure and resource availability of an ecosystem, community, or population (White and Pickett 1985). Many NNIPs have been characterized as disturbance dependent or early successional species that colonize areas following disturbance events as a result of changes in microhabitat and resource availability (Hobbs and Huenneke 1992; Rejmanek and Richardson 1996; Meekins and McCarthy 1999; Alpert et al. 2000; Davis and Thompson 2000). Whether or not a particular disturbance will promote invasion is highly context specific and dependent on the historic disturbance regime of the system in question as well as the characteristics of the potential invaders (Higgins and Richardson 1998).

Wind damage is a widespread and frequently occurring disturbance in the Eastern Forests of the United States (Canham and Loucks 1984; Peterson 2000; Lorimer 2001). Wind damage to forests can range from a small gap produced by the

tipping or breakage of an isolated tree to catastrophic “blowdowns” thousands of hectares in size (Runkle 1982; Canham and Loucks 1984; Everham and Brokaw 1996; Zhang et al. 1999; Peterson 2000; Woods 2004). Derechos, microbursts, and tornadoes are common causes of wind damages in inland states and hurricane winds can cause extensive damage in forests of coastal states (Bormann and Likens 1979; Peterson 2000; Lorimer 2001).

Large wind disturbance events can open extensive gaps in forest interiors through defoliation, breakage, and wind throw of trees (Everham and Brokaw 1996; Woods 2004). Canopy gaps provide an increase in available light to understory vegetation that can enable germination and growth of plants previously suppressed by canopy coverage (Canham 1988; 1989; Poulson and Platt 1989; Schupp et al. 1989; Woods 2004). Examination of the impacts of large wind disturbance events in temperate forest ecosystems has largely focused on reconstruction of disturbance regime patterns and recovery of dominant canopy species with less attention paid to the response of understory vegetation or NNIP species (e.g. Canham and Loucks 1984; Everham and Brokaw 1996; Peterson and Pickett 1995; Zhang et al. 1999; Peterson 2000).

Studies in tropical and sub-tropical forests affected by wind damage from hurricanes and cyclones have shown that NNIPs can benefit from these large disturbance events. Lorence and Sussman (1986) found that cyclone damage may accelerate invasion of forests by non-native plants on Mauritius. Similar results were found in both Jamaican and Australian forests following severe wind damage from tropical storms (Bellingham et al. 2005; Murphy et al. 2008). In the North America,

NNIPs have been shown to respond strongly to wind damage following hurricanes in both Florida and Maryland (Horvitz et al. 1995; 1998; Snitzer et al. 2005).

The May 8<sup>th</sup> 2009 super-derecho provided an excellent opportunity to determine if Midwestern forest communities are similarly vulnerable to invasion following regional scale wind disturbances. A derecho is a long lasting windstorm associated with bands of rapidly moving thunderstorms and downburst clusters that produce sustained severe winds (Johns and Hirt 1987; Coniglio et al. 2011).

Originating from a thunderstorm system that developed in western Kansas, the May 8<sup>th</sup> 2009 super-derecho was unusually intense and produced severe winds over a remarkably large geographic extent (Coniglio et al. 2011). Because of its unusual intensity and large geographic extent, it has been classified as a “super-derecho” by some meteorologists and climatologists (Israel 2010; Weisman et al. 2012). When it finally dissipated the storm system had travelled over a thousand miles (spawning multiple tornadoes across several states) in a 24 hour period (Coniglio et al. 2011). The super-derecho produced sustained straight-line winds greater than 120kmph that were recorded in multiple locations as well as isolated gusts over 160kmph (Coniglio et al. 2011). The most severe winds occurred in southeastern Kansas, southern Missouri, and southern Illinois (Coniglio et al. 2011). In southern Illinois this event resulted in widespread severe canopy damage to portions of the Shawnee National Forest.

The purpose of this study is to determine if the 2009 super-derecho event facilitated the recruitment or establishment of NNIP species into the forest interior of LaRue Pine Hills - Otter Pond Research Natural Area. To make the determination the following questions are addressed:

1. Are there significant differences in the abundance of NNIPs in wind damaged forest interiors as compared to adjacent undisturbed forest?
2. Are there significant differences in the abundance of NNIPs along forest edges as compared to the forest interior?

The concept of invasibility describes why some plant communities are more susceptible to colonization by NNIPs than others (Hutchinson and Vankat 1997). The results of this study may further the understanding of how allogenic disturbances, of unusual size and intensity, potentially contribute to invasibility of forest communities. The results of this study may also prove useful to land managers engaged in controlling NNIPs by indicating what habitats are particularly prone to invasion.

#### *A note on terminology*

Invasive species have been defined in numerous ways and this has led to recent debates in the scientific community over terminology (Richardson et al. 2000; Brown and Sax 2004; Colautti and MacIsaac 2004; Cassey et al. 2005; Lockwood et al. 2007). This paper will follow Alpert et al. (2000) which defines an invasive species as “one that both spreads in space and has negative effects on species already in the space that it enters.” This paper will also follow their definition of non-native species, which are those species that have been transported by humans to a region where they do not naturally occur (Alpert et al. 2000). Following those definitions it is important to note that it is possible for a species to be non-native and non-invasive as well as native *and* invasive. However, non-native invasive species generally pose the greatest threat to intact ecosystems (Alpert et al. 2000), and as such they are the focus of this research.

## CHAPTER 2

### LITERATURE REVIEW

Humans have played an important role in driving biological invasions around the world by transporting organisms across natural barriers to dispersal (Mack and Lonsdale 2001). Natural long-distance dispersal relies on the dispersal ability of the organism itself whereas the current global rise of biological invasion events has resulted from human mediation (Cassey et al. 2005). Anthropogenic dispersal of organisms and the subsequent colonization of new regions by these organisms differ from natural colonization events because of the greater geographical extent and shorter timescale of anthropogenically driven colonizations (Cassey et al. 2005). Introductions of NNIS may occur intentionally (e.g. the introduction of agricultural crops to new regions) but accidental introductions frequently occur when non-native species “stow away” on other goods that are transported across natural dispersal barriers.

Accidental introductions of plants are common and may result from contaminants contained in shipments of agricultural or horticultural material (Mack 2004). Use of solid shipping ballast was historically an important vector for plant invasions (Mack 2004). In the United States, many non-native plant species were intentionally introduced for agricultural and horticultural purposes and have since escaped cultivation and become problematic invaders of native ecosystems (Mack and Lonsdale 2001; Reichard and White 2001). Some of the most problematic NNIPs in the United States were introduced as ornamentals and were later widely used by federal agencies (such as the U.S. Soil Conservation Service) for soil erosion control efforts (Reichard and White

2001; Forseth and Innis 2004). State wildlife agencies unaware of the potential negative impacts of these species, aggressively planted NNIPs such as Japanese honeysuckle (*Lonicera japonica* Thunb.) to provide wildlife forage (Schierenbeck 2004). However, not all non-native plant species will become invasive and pose a threat to native communities. This has led to attempts to identify common traits of invasive plants that may explain why some species become problematic and others do not. In other words, why are some plants more invasive than others?

### *Invasiveness*

Researchers have identified several life history characteristics that promote the success of NNIPs over their native counterparts. In an extensive literature review Alpert et al. (2000) identified characteristic traits found in plant species considered to be highly invasive. In general, plants with broad native ranges and those which exhibit rapid dispersal are among the most likely to be highly successful invaders (Alpert et al. 2000). Plants with a broad native range may be considered “generalists” species, which are able to establish in a wider variety of environmental conditions than more specialized species. Rapid dispersal allows highly invasive plants to quickly spread and establish in new areas. Traits associated with rapid dispersal include: rapid maturation, long fruiting periods, large seed quantity, small seed size, prolonged seed viability, and transport by wind or animals (Rejmanek and Richardson 1996; Alpert et al. 2000). These reproductive traits have led to the generalization that NNIPs are early successional or pioneer species that rapidly invade disturbed areas (Rejmanek and Richardson 1996).

A more recent study of trait differences between NNIPs and native species revealed significant differences across six categories of performance related traits including: Fitness, growth rate, leaf-area allocation, physiology, shoot allocation, and size (Van Kleunen et al. 2010). These broad categories included more specific traits such as photosynthetic rates, leaf construction costs, leaf area index, nitrogen use efficiency and water use efficiency among others (Van Kleunen et al. 2010). Many of these traits promote rapid growth of individuals, which may enable NNIPs to out compete native species for light and soil resources as well as space.

Phenotypic plasticity is also considered an important factor that promotes invasiveness. Species with high phenotypic plasticity are able to alter their morphology and development based on ambient environmental conditions such as resource availability (Alpert et al. 2000). *Lonicera japonica*, a non-native highly invasive species prevalent throughout the United States provides an excellent example of a species with high phenotypic plasticity. *Lonicera japonica* alters its growth form depending on habitat and is capable of growing as a twinning vine (eventually overtopping and smothering shrubs or trees) or can alternatively grow as a spreading mat up to 1.5m deep when no climbing structures are present (Schierenbeck 2004; West et al. 2009). The leaves of *L. japonica* are facultatively deciduous in response to cold or drought and will increase in specific leaf area under shaded conditions (Schierenbeck 2004). *Lonicera japonica* will also increase biomass allocation to leaves under herbivory treatments (Schierenbeck 2004). The phenotypic plasticity of *L. japonica* has in part enabled its success across a wide range of environmental conditions world-wide. Meta-analysis across 75 invasive and non-invasive species pairs has shown phenotypic plasticity to be significantly

higher in NNIPs than in their non-invasive counterparts (Davidson et al. 2011). NNIPs showed greater plasticity in their response to increased resource availability but non-invasive species responded just as well to conditions with limited resources (Davidson et al. 2011). Interestingly the greater plasticity of NNIPs in response to increased resources was not always correlated to increased fitness and further study is necessary (Davidson et al. 2011). Other authors have recently suggested that NNIPs may not possess greater phenotypic plasticity than native or non-native non-invasive species and it would appear that this topic still an unresolved issue in invasion ecology (Palacio-López and Gianoli 2011).

Production of allelopathic compounds may also contribute to the success of NNIPs. Allelopathy refers to interference between plants where secondary compounds produced by one species negatively affect the growth and fitness of other species (Inderjit and del Moral 1997). Callaway and Ridenour (2004) proposed the “novel weapons hypothesis” wherein NNIPs have a particularly powerful allelopathic effect because native species did not coevolve with the invading species and are thus more susceptible to the allelopathic substances a non-native invader produces. It may be difficult to prove that native species are more susceptible to non-native *foreign* allelopathic compounds, but there is evidence that allelopathy is important to the success of several highly invasive non-native plants.

Originating from eastern Asia, the knotweeds (*Fallopia* sp.) are a group of aggressive NNIPs shown to produce secondary chemicals that may inhibit growth of other plants (Vrchoťova and Sera 2008). Murrell et al. (2011) found that the presence of *Fallopia x bohemica* (Chrtek & Chrtková) J. P. Bailey. reduced the abundance of native



forbs. However, addition of activated carbon to the soil significantly reduced the suppressive effect (Murrell et al. 2011). Activated carbon absorbs organic compounds and can neutralize allelopathic chemicals, which suggests that *Fallopia x bohemica* suppressed native forbs through allelopathic interference (Murrell et al. 2011). Allelopathic interference is not limited to direct plant-to-plant interactions.

Garlic mustard (*Alliaria petiolata* (Bieb.) Cavara and Grande.), native to Europe and central Asia and a common invader of forest communities in North America, produces allelopathic chemicals that may suppress germination of mycorrhizal fungi as well as seeds of plants dependent on mutualisms with mycorrhizal fungi (Roberts and Anderson 2001). This may enable *A. petiolata* to form dense monospecific stands and locally exclude mycorrhizal dependent plants. Mycorrhizal fungi in *A. petiolata*'s native range appear to be only weakly affected by the compounds it produces, which lends support to the "novel weapons hypothesis" (Callaway et al. 2008).

It is likely impossible to determine which species will become invasive based on traits alone. Even lists of general traits provide little predictive power and potential NNIPs may possess different combinations of traits that enable their success in novel environments. The specific traits of a potential NNIP must be suitable for novel environment in which it is introduced, and some environments may be more readily invaded than others.

### *Invasibility*

Early studies looking at the geographic distribution of NNIS recognized a few global patterns. Elton (1958) was among the earliest ecologists to note that islands

appeared to harbor more NNIS than similarly sized mainland regions, and this pattern has since been supported empirically (Lonsdale 1999). Elton (1958) also noted that temperate environments appeared to have greater numbers of NNIS than tropical environments. Additionally, new world countries appeared to harbor more NNIS than old world countries (DiCatri 1989). Such patterns led to the notion that some environments are intrinsically more susceptible to invasion by non-native species than others. The term invasibility describes the susceptibility of an environment to invasion and research has been directed towards understanding what factors may contribute to high invasibility (e.g. Hutchinson and Vankat 1997; Lonsdale 1999; Stohlgren et al. 2003). Research would later suggest that the global patterns discussed above are artifacts of global trade patterns and associated introductions of non-native species rather than reflections of inherent invasibility (Lockwood et al. 2007). Nevertheless, the concept of invasibility persists, but is best thought of as an emergent property of an environment dependent on both abiotic resources and biotic interactions that may fluctuate over time (Davis et al. 2000).

### *Biotic Resistance*

In addition to abiotic factors, NNIS must overcome biotic resistance (often in the form of competition or predation) in order to establish in a novel environment. Again, Elton (1958) was at the forefront and proposed that species rich environments would be less vulnerable to invasion from NNIS because all available niche space would have been filled and invading species would be competitively excluded from the environment. This hypothesis has received support from small scale studies (Naeem et

al. 2000; Kennedy et al. 2002). Naeem et al. (2000) found that higher native diversity increased crowding, decreased available light and soil nutrients, and reduced the success of NNIPs. Likewise, Kennedy et al. (2002) found that increased native diversity increased crowding and reduced establishment and success of NNIPs.

However, studies operating at larger scales have contradicted Elton's hypothesis and shown that at the global scale species rich locations are just as, if not more, invaded than species poor locations (Lonsdale 1999; Stohlgren et al. 2003). One intuitive explanation is that environments that promote high diversity of native species are also likely to promote a high diversity of non-native introduced species. In other words conditions that promote high native diversity are also likely suitable for the invading species provided that they can overcome interspecific interactions at the local scale such as competition (Lonsdale 1999; Lockwood et al. 2007). Competitive interactions can be important at the local level for determining which species will be able to establish at a particular site because individuals will directly compete for available resources. Davies and colleagues (2005) showed that in some situations physical factors that influence plant establishment (e.g. soil depth, soil nitrogen, aspect, etc.) do not vary at small spatial scales. As a result, there is low beta diversity (species diversity across space) and high competition between individuals for available resources. At larger spatial scales the physical conditions can vary considerably and the influence of competitive interactions is dwarfed by larger scale patterns of resource heterogeneity. At larger scales, species responses to resource gradients throughout the environment are more important in determining the spatial distribution of species than competition and as a result beta diversity tends to be higher (Davies et al. 2005).

The greater the resource heterogeneity in an environment the greater the number of species, both native and non-native, that can establish therein (Davies et al. 2005). This may account for the apparent positive correlation between native species diversity and NNIS diversity at global and regional scales. Higher habitat heterogeneity may be positively correlated with species diversity, which would include native and NNIPs. How important biotic resistance through competitive exclusion is at the local scale or at particular sites is still unclear. Levine et al. (2004), through meta-analysis, showed that competition may have an influence on seedling establishment of NNIPs but was generally not enough to completely exclude invaders from a given environment. The authors suggest that biotic resistance through competitive exclusion may serve only as a check on the presence of NNIPs but not a complete barrier to establishment (Levine et al. 2004).

Another component of biotic resistance that has received considerable attention in the field of invasion ecology is predation. Initially, the “enemies release hypothesis” suggested that NNIS would escape the specialist herbivores and pathogens of their native range and this may enable their success in a novel environment (Maron and Vilà 2001). Native pests and predators may preferentially graze on native species as opposed to NNIPs. This may increase the fitness of NNIPs by direct release from herbivory as well as reallocation of resources from defense to growth. This may eventually lead to selection of genotypes with increased allocation of resources to plant growth, the so called “evolution of increased competitive ability hypothesis” (Blossey and Notzold 1995). There is some evidence that non-native plants may experience release from herbivory. Lake and Leishman (2004) found that both NNIPs and non-

native non-invasive plants experience significantly lower herbivory than native species. This suggests however, that herbivory release alone is not enough for a non-native species to become a problematic invader (Lake and Leishman 2004). While a non-native plant may escape specialists pests or herbivores it may not be released from generalists herbivores at all, and native herbivores can effectively reduce invasion (Levine et al. 2004). Morrison and Hay (2011) found that four out of five generalist herbivores from North and South America preferentially selected NNIPs over native species. A recent study has also found that NNIPs incur similar damage and have similar performance compared to native species when in the presence of herbivores which suggests that enemy release may not be particularly important to the success of NNIPs (Chun et al. 2010).

The importance of propagule pressure should also be considered in regards to biotic resistance and ecosystem invasibility. D'Antonio et al. (2001) indicated that the number of propagules required to successfully invade an ecosystem is proportional to the biotic resistance encountered by the introduced species. If biotic resistance is low in a given environment then the total number of propagules required for successful establishment of a NNIP would also be low (D'Antonio et al. 2001). If biotic resistance is high then the required number of propagules would also be high. The authors argue that as long as propagule pressure is sufficient biotic resistance would be incapable of excluding NNIPs from the environment (D'Antonio et al. 2001). Hutchinson and Vankat (1997) found that proximity to a seed source was a primary variable that contributed to the invasibility of a forest in southwestern Ohio. In a field study, Van Holle and Simberloff (2005) tested the importance of native species diversity, physical

disturbance, and propagule pressure on the abundance of NNIPs in a southwestern Virginia forest. Their results indicated that propagule pressure was the only factor that successfully predicted the survival of NNIPs in experimental plots over time (Van Holle and Simberloff 2005). While biotic resistance may act to reduce the invasibility of an environment it would appear that propagule pressure may be the most important factor in determining success of NNIPs (Lockwood et al. 2005).

### *The role of disturbance*

Many NNIPs have been characterized as disturbance dependent or early successional species that colonize areas following disturbance events as a result of changes in microhabitat and resource availability (Hobbs and Huenneke 1992; Rejmanek and Richardson 1996; Meekins and McCarthy 1999; Alpert et al. 2000; Davis and Thompson 2000). Daehler (2003) found that NNIPs are not necessarily better competitors than native species but that frequent physical disturbances may be enabling success of many NNIP species. Disturbance can be considered a mechanism that may increase the invasibility of an environment by causing resource fluxes that provide new opportunities for invading species (Davis et al. 2000). Disturbances can take on many forms (natural or anthropogenic in origin) and can occur with varying intensity and return intervals. Instances of disturbance facilitating invasion by NNIP species abound and several examples are provided in the following passages. Hull and Scott (1982) found that cover of *Lonicera japonica* was ubiquitous following debris avalanches in a Virginia forest. Creation of shrub layer canopy gaps produced an increase in the abundance of *Alliaria petiolata* in a northern Kentucky forest (Luken et

al. 1997). Hobbs and Atkins (1988) found that physically disturbing soil and addition of nutrients promoted the establishment of NNIPs in Australian woodland and shrub communities. Likewise, physical disturbance and nutrient addition increased the abundance of NNIPs in riparian zones and along stormwater outlets (Lake and Leishman 2004).

In a classic review paper, Hobbs and Huenneke (1992) found that fire, grazing, soil disturbance, and nutrient inputs all had the potential to facilitate establishment of NNIPs. Fire disturbance has been widely studied and recognized for its importance in shaping species composition across a variety of ecosystems (e.g. Abrams 1992; Lorimer 2001). D'Antonio (2000) found that depending on the ecosystem and plant species involved, fire could promote NNIPs. However, other studies have shown that fire may reduce the numbers of NNIPs in an ecosystem (Smith and Knapp 1999) and use of prescribed fire has successfully reduced colonization by certain NNIS (DiTomaso et al. 2006). Contradictory findings on the role of disturbance and invasibility have led some authors to suggest that it may not be disturbance per se that facilitates invasion but rather changes to historic disturbance patterns than results in increased invasibility (Daehler 2003; Moles et al. 2012). For instance, in riparian habitats, alterations to historic flood regimes have enabled the spread of woody NNIPs (Busch and Smith 1995). In grass dominated sites of southwestern British Columbia, MacDougall et al. (2005) found that dominance of NNIPs was likely due to long-term fire suppression rather than competitive effects. Recent meta-analysis has tested the hypothesis that alteration to a disturbance regime is more important than disturbance itself (Moles et al. 2012). The authors found that changes to historic disturbance

regimes were better predictors of invasion than simply disturbance (Moles et al. 2012). There does not appear to be a clear pattern that will determine if disturbance drives an invasion or will increase the abundance of NNIPs already present in an environment (Lockwood et al. 2007). It is clear that whether or not a particular disturbance will promote invasion is highly context specific and dependent on the historic disturbance regime of the system in question as well as the characteristics of the potential invaders (Higgins and Richardson 1998).

#### *Wind disturbance in forests*

Like all disturbances, wind disturbance varies in intensity, spatial and temporal scale, and the frequency of return (Foster et al. 1998; Peterson 2000; Lorimer 2001). Small scale wind disturbances produce individual tree falls within a forest or in some cases several trees may be blown down creating a larger canopy gap within a relatively small area (Woods 2004). New canopy gaps typically occupy less than one percent of a given forest patch per year (Runkle 1982). Canopy gaps provide an increase in available light to understory vegetation, which can enable germination and growth of plants previously suppressed by canopy coverage (Canham 1988; Canham 1989; Poulson and Platt 1989; Schupp et al. 1989; Woods 2004). Tree throw also produces disturbed bare soil (Stephens 1955; Whitmore 1989), which may facilitate colonization by early successional species including NNIS (Hobbs and Huenneke 1992). Biological residuals may be important colonizers of a canopy gap such as buried seeds, seedlings, and saplings (Connell 1989). Other colonizers must disperse into the gap from nearby areas (Schupp et al. 1989). Small canopy gaps will typically close quickly



through growth of neighboring trees that were not damaged and also through release of shade tolerant saplings (Woods 2004; Everham and Brokaw 1996). In both small and large canopy gaps species diversity increases and stems show accelerated growth (release) into larger size classes (Runkle 1982). Whitmore (1989) identified the roles of pioneer and climax forest species in which pioneer species quickly colonize new openings in the canopy and are later replaced by shade tolerant climax species over longer periods of time. Shade intolerant species may be dependent on larger canopy gaps and may occur in less density in small canopy openings (Brokaw and Scheiner 1989). Frequency of gaps may be more important to shade tolerant species than gap size because of their ability to withstand long periods of suppression under closed canopies (Canham 1989). Responses of individual species to canopy gaps will vary geographically as a result of spatial heterogeneity in associated tree species, understory species, and abiotic factors (Poulson and Platt 1989; Veblen 1989).

Catastrophic wind disturbance events occur with less frequency but can open extensive gaps in forest interiors through defoliation, breakage, and wind throw of trees (Everham and Brokaw 1996; Turner et al. 1997; Woods 2004). These events may also create networks of smaller canopy gaps across a forest patch at much higher frequencies than typical background disturbance levels (Lorimer 1989). In the United States, return intervals of large regional scale wind disturbances can range from 500 to over 1000 years in northern hardwood forests (Canham and Loucks 1984; Zhang et al. 1999) to a matter of decades in hurricane affected coastal states (Pimm et al. 1994). Despite long return intervals, large wind disturbances can account for significant proportions of successional stands in temperate hardwood forests (Canham and

Loucks 1984; Lorimer 1989; Zhang et al. 1999).

Vegetation type, height, and topographic position all play an important role in determining the spatial pattern of forest damage following a powerful wind event (Foster and Boose 1992; Turner et al. 1997; Zhang et al. 1999). Deciduous hardwood trees may be more resistant to wind damage than coniferous trees (Foster and Boose 1992; Everham and Brokaw 1996), while height, age, and crown characteristics can also increase susceptibility to wind damage (Everham and Brokaw 1996; Peterson 2000). Topographically exposed positions such as ridgetops and westerly aspects may also experience greater damage than sheltered locations (Foster and Boose 1992; Everham and Brokaw 1996; Zhang et al. 1999). Physical damage to the canopy may have minimal effects on understory species (Hughes and Fahey 1991; Peterson and Pickett 1995; Peterson 2000). As a result, cover of herbaceous species typically increases rapidly due to increased light levels but these changes may only be short lived as mid-successional species close gaps and reduce light levels once more (Hughes and Fahey 1991; Peterson and Pickett 1995).

In a review of over a hundred studies on catastrophic wind damage Everham and Brokaw (1996) identified four major modes of forest recovery, which are: regrowth, release, recruitment and repression. In larger gaps the authors suggest that recruitment may be the most important recovery mechanism and characterize it as recruitment of plants into damaged areas by long-range dispersal of seeds (wind) as well as recruitment from within the soil seed bank. Repression is the suppression of some plant species by others (such as vines) that may grow more quickly and shade out seedlings (Everham and Brokaw 1996). The authors also suggest that if wind disturbance causes

a high degree of structural damage then increased coarse woody debris coverage may actually suppress recruitment of seedlings. Turner et al. (1998) suggested that the centers of large disturbed areas may experience greater recovery through recruitment and release while regrowth and repression may be more dominant along the edges of a disturbance.

### *Derechos*

Convectively induced thunderstorms can produce powerful downbursts that are the result of strong downdrafts that descend to the surface and then spread out laterally, forming a front of high winds at the leading edge of the storm (Hjemfelt 2007). Supercell thunderstorms (distinguishable by the presence of a rotating updraft) and groups of thunderstorms known as mesoscale convective systems may produce clusters of downbursts that cause damage over hundreds of square kilometers (Hjemfelt 2007). Derechos are downburst clusters that produce sustained severe winds potentially in excess of 100kmph over a large spatial extent (Johns and Hirt 1987; Coniglio et al. 2011). Derechos occur frequently in the United States with an average of 21 events per year over an 18-year period (Ashley and Mote 2005). Derechos occur most frequently during the warm-season from May to August with the highest monthly frequency occurring in May (Ashley and Mote 2005). Regions with high derecho frequency include an area from the southern Great Plains that extends eastward to the southern Mississippi Valley and an area in the upper-Midwest extending to the Ohio Valley region (Johns and Hirt 1987; Ashley and Mote 2005). Areas of maximal derecho frequency occur in northeastern Oklahoma, western Kentucky and northwestern

Tennessee, and the Ohio Valley region (Ashley et al. 2005). Atmospheric conditions are often favorable for the formation of derecho series in which multiple derecho events occur in the same region over a short period of time (Ashley et al. 2005). Between 1994 and 2003 over 62% of derecho events were associated with a derecho series indicating the high possibility of repeated severe wind events in a given region (Ashley et al. 2005).

Strong derechos have resulted in extensive blowdowns in northern hardwood forests of the United States. In July of 1995, 392,000ha of forest in Adirondack Park of New York were impacted by a derecho, which resulted in 15,300ha being classified as heavily damaged with canopy loss between 60 and 100% (Robinson and Zappieri 1999). Over 8,000ha of forest in Colorado and 4,000ha of forest in Michigan were severely damaged by derecho winds in 1997 (Peterson 2000). The Boundary Waters Canoe Area of northern Minnesota was impacted by a large derecho event in July of 1999 that resulted in 150,000ha being severely damaged (Hjelmfelt 2007). While the return interval of catastrophic wind at a particular location may be long, it has been estimated that approximately one very large derecho (hundreds of km<sup>2</sup>) occurs each year in the United States (Brooks and Doswell 1993), and they are clearly capable of influencing forest vegetation dynamics (Peterson 2000).

#### *Wind disturbance facilitates invasion*

Previous studies on catastrophic wind damage to forests have generally focused on recovery of dominant tree species following the disturbance events but there are important implications for NNIPs that occupy the understory. Many NNIPs are early

successional species and are often associated with disturbance (Meekins and McCarthy 2001; Alpert et al. 2000; Hobbs and Huenneke 1992). Some NNIPs have also been shown to be both shade tolerant and highly competitive in high-light environments (Schierenbeck 2004; West et al. 2009). Given that large scale wind damage can dramatically increase light levels reaching the forest floor (Everham and Brokaw 1996) these events may produce conditions that enable NNIPs to establish and dominate the early successional period. Large canopy disturbance can often leave the understory vegetation relatively undamaged (Hughes and Fahey 1991; Darwin et al. 2004; Woods 2004). If NNIPs are already present in the understory when a large wind event disturbs the forest canopy they may then be in a position to become the dominant species through the mechanisms of release and repression in which fast growing extant plants suppress the growth of juveniles and seedlings following the disturbance event (Everham and Brokaw 1996).

In many cases recruitment from the soil seed bank may be the dominant mechanism of succession following a large disturbance event (Everham and Brokaw 1996; Turner et al. 1998). NNIPs have been shown to persist in the soil seed bank deep within forest interiors (Honu and Gibson 2008; Honu et al. 2009). Following an extensive wind disturbance these persistent seeds may then germinate in newly suitable light conditions and have an advantage over native understory plants whose seeds may not be present in the soil seed bank in the same abundance as the NNIPs (Honu and Gibson 2008; Honu et al. 2009). Also, if a time lag in seed availability occurs due to high winds stripping seeds off of plants the soil seed bank may be the dominant mechanism of recruitment (Everham and Brokaw 1996), which again may

offer NNIPs an advantage.

Previous studies of the response of NNIPs to wind damage have been centered on hurricanes and other tropical cyclones. Lorence and Sussman (1986) found that cyclone damage may accelerate invasion of forests by NNIPs on Mauritius. Similarly, invasion of forests in the blue mountains of Jamaica by *Pittosporum undulatum* Vent., an evergreen tree native to Australia, was accelerated by wind damage from hurricanes (Bellingham et al. 2005). NNIPs also responded strongly to canopy disturbance following Cyclone Larry in 2006, which damaged large swaths of Australian rainforest (Murphy et al. 2008). The authors suggested that NNIPs will be important in the early successional sere and some NNIS may potentially have long-term impacts on future forest structure and species composition (Murphy et al. 2008).

In North America, Horvitz et al. (1995, 1998) compared the abundance of native to NNIPs in wind damaged areas following hurricane Andrew which struck Florida in 1992. Their results indicated that NNIS exceeded native plants in both cover and frequency and that vines (both native and non-native) played an important role in recovery following hurricane damage (Horvitz et al. 1995, 1998). Vines grew quickly and composed a high percentage of the vegetation coverage following hurricane Andrew and may have suppressed seedlings of other plants (Horvitz et al. 1998). They also found that recruitment from the soil seed bank was of high importance in the successional process following the storm (Horvitz et al. 1998). Canopy openness was also directly correlated with the abundance of NNIPs and areas that received higher levels of canopy disturbance were more prone to invasion (Horvitz et al. 1998). More recently, Snitzer et al. (2005) found that NNIPs, in Maryland, responded strongly to

increased light levels following canopy damage from Hurricane Ivan in 2003. These studies have shown that large scale wind damage has the potential to increase the invasibility of forest communities by dramatically increasing light that reaches the forest floor.

*Invasion in Eastern Forests: The importance of edge effects*

A forest edge is an ecotone (transitional habitat) that forms the boundary between two ecosystems (crop-field and forest margins being one example) and the changes in ecological processes around these edges are known as “edge effects” which may penetrate into undisturbed forest interiors (Leopold 1933; Murcia 1995). Edge effects include, but are not limited to, changes in microclimate (solar radiation, air temperature, air moisture, soil moisture, soil temperature, wind speed, and litter density), abundance and distribution of species, and interactions between species (Saunders et al. 1991; Murcia 1995; Harper and Macdonald 2001; Honu and Gibson 2006). The distance that edge effects penetrate into forest interiors is known as the “distance of edge influence” (DEI) and numerous studies have identified varying DEIs (e.g. Murcia 1995; Harper and Macdonald 2001).

Forest edges have been identified as essential habitat and also dispersal points of NNIPs into intact forest interiors (Cadenasso and Pickett 2001; Brothers and Spingarn 1992; Yates et al. 2004). One of the reasons for this is that edge habitats and associated DEIs exhibit microhabitat features that are favorable for NNIPs (Alpert et al. 2000). Brothers and Spingarn (1992) found that closed canopy cover of old growth forest in Indiana reduced encroachment into forest interiors by NNIPs. Their findings

have since been supported by numerous studies that show the abundance of NNIPs declining rapidly along a forest edge to interior gradient (e.g. Yates et al. 2004; Honu and Gibson 2006; Christen and Matlack 2009). NNIPs that are shade tolerant or late successional can readily invade forest interiors (Martin et al. 2009). However, dense sub-canopies in the shrub layer may effectively reduce establishment and long term survival of shade tolerant NNIPs (Cole and Weltzin 2005; Schramm and Ehrenfeld 2010). *Microstegium vimineum* (Trin.) A. Camus. is an important NNIP prevalent in Eastern Forests that is capable of invading closed canopy forest interiors. Cole and Weltzin (2005) found that ambient light levels under closed overstory canopy were approximately 20% and that dense shrub layer canopies of *Asimina triloba* L. (Pawpaw) reduced light levels to 6% of ambient light levels (1% of full sunlight). Survival and biomass accumulation of *M. vimineum* seedlings were significantly lower in plots under *A. triloba* canopy than in unshaded plots (Cole and Weltzin 2005). Similarly, Schramm and Ehrenfeld (2010) found that thickets of *Lindera benzoin* L. (Spicebush) reduced survivorship and created patchiness in infestations of *M. vimineum* under close canopy forests. Despite the ability of some species to invade forest interiors edge habitat still plays an important role in forest invasibility.

Edge structure can influence the seed flux of NNIPs (as well as native plants) into forest interiors. Cadenasso and Pickett (2001) compared seed flux into forest interiors between a control and an experimentally thinned forest edge. Seed traps were then placed along transects that extended from the forest edge to the interior, and the results indicated that a much greater number of seeds crossed into the forest interior in the thinned treatment zone and that seeds also penetrated farther into the forest in the



thinned zone (Cadenasso and Pickett 2001). Their findings suggest that the thick vegetation of forest edges can act as a barrier that prevents seed flux into forest interiors and may help reduce the impacts of newly created edges once the vegetation has grown in and effectively closed large openings (Cadenasso and Pickett 2001). This functional aspect of forest edges may limit the propagule pressure of NNIPs in forest interiors.

NNIPs are not restricted to moving perpendicularly from the forest edge into forest interiors and much of their establishment and spread in a region may be attributed to movement *along* edges (Christen and Matlack 2009). In Ohio, Christen and Matlack (2009) examined the abundance of NNIPs along roadways as compared to adjacent forest interiors. Of the seven NNIPs encountered all were in greater abundance along roads (Christen and Matlack 2009). Multi-flora rose (*Rosa multiflora* Thunb.) was found to be the only plant in their study that had established in forest interiors (Christen and Matlack 2009). Additionally, a seed sowing experiment that compared germination of NNIPs in plots along roadways to plots within forest interiors found that roadways experienced greater germination rates (Christen and Matlack 2009). These findings indicate that roads provide long stretches of continuous habitat that can enable establishment and spread along forest margins (Christen and Matlack 2009). NNIPs may also spread along roadways due to increased seed transportation along the road corridor. Open roadways would conceivably be conducive to wind dispersal and animals also utilize roads for movement and as a result may disperse seeds parallel to forest interiors (Cadenasso and Pickett 2001; Christen and Matlack 2009). Trails are another component of forest fragmentation that can act in a similar

fashion to roads. While many forest trails are narrow dirt paths they may still exhibit microclimate changes such as reductions in canopy cover and an associated increase in light levels that may favor NNIPs (Campbell and Gibson 2001). Trails in protected forest environments also penetrate deeper into forest interiors and may act as pathways of spread into areas that NNIPs may not otherwise have been able to reach.

#### *Previous studies in Southern Illinois*

Despite the large body of literature dedicated to the study of NNIPs only a handful of studies have taken place in the natural areas of Southern Illinois. Working in the Touch of Nature Environmental Center, located eight miles south of Carbondale, IL, Yates et al. (2004) compared the heights and densities of three NNIPs (*Rosa multiflora*, *Lonicera japonica*, and *Eleagnus umbellata* Thunb.) along linear forest edges and forest interiors. Height and density of all three species declined from transects along the forest edge to the interior transects. *L. japonica* (an abundant species in southern Illinois) had the highest densities in both edge and interior locations (Yates et al. 2004). Microclimate factors along forest edges, particularly, light availability was suggested as the primary cause for increased height and density of these invaders (Yates et al. 2004).

Oriental bittersweet (*Celastrus orbiculatus* Thunb.) was also found to be associated with forest edges (in this case road edges) in Giant City State Park located just south of the Touch of Nature Environmental Center (Pande et al. 2007). The authors used linear regression models to predict locations of this non-native invasive vine, and found that insolation, proximity to roads, and soil characteristics were all

associated with the presence of Oriental bittersweet (Pande et. al. 2007). The authors also indicate that land use history of Giant City State Park may explain current distributions. Much of Giant City was once agricultural homesteads that have since undergone successional changes to vegetation and that legacy of human disturbance may have facilitated invasion by *C. orbiculatus* (Pande et al. 2007).

The role that horses may play in dispersing NNIPs along trails was investigated in three natural areas (Trail of Tears State Forest, Jackson Hole Ecological Area, and Jackson Hollow Ecological Area). Campbell and Gibson (2001) surveyed the vegetation and collected horse dung along trails. They found that density of NNIPs was highest near trails as compared to forest interiors. They also found that many non-native seeds are viable following transport through horse digestive tracts. *Kummerowia striata* (Thunb.) Schindl. and *Prunella vulgaris* L. were the only NNIPs found both in the vegetation as well as germinating from horse dung samples (Campbell and Gibson 2001). They suggest that horses, browsing on NNIPs in agricultural fields or on existing NNIPs along forest trails, may then transport seeds throughout the forest system (Campbell and Gibson 2001). This study indicates that trails may act as mechanisms for dispersal of NNIPs in Southern Illinois.

West et al. (2009) investigated three shale barren communities in Union County, IL to determine microhabitat associations of NNIPs. Only three species were present at all three sites (*Lonicera japonica*, *Torilis japonica* (Houtt.) DC., and *Rosa multiflora*). NNIPs were found in a wide variety of environmental conditions. Soil characteristics were found to be the most important variables, and surprisingly high light levels and low canopy coverage were not significant (West et al. 2009). NNIPs in these shale

barrens were also considered to be occupying transitional habitat and that many of the significant variables they measured were characteristic of forest edge habitat (West et al. 2009). West et al. (2010) found that *L. japonica* is likely associated with barrens edges where forest is encroaching and areas where canopy has been removed.

Working in three Research Natural Areas in Shawnee National Forest (Baker Bluff, Dennison Hollow, and Panther Hollow) Honu and Gibson (2006) examined microhabitat differences from forest edges to interiors to determine their influence on the distribution of NNIPs. Three types of abrupt edges were used in the study (crop-forest, hay-forest, and road-forest). Across all three sites canopy cover increased and the amount of available light decreased from forest edge to interior. Canopy cover appeared to be the most important microhabitat variable associated with NNIPs.

*Lonicera japonica* and *Allium vineale* L. were classified as gap-adapted species and were associated with canopy openness. The abundance of both species decreased from forest edge to forest interior and it was suggested that canopy openness of less than 15% may minimize the occurrence of these species in forest interiors (Honu and Gibson 2006).

Honu and Gibson (2008) performed a study at three research natural areas (RNAs) in Shawnee National Forest looking for patterns in the understory vegetation, seed rain, and seed bank from forest edges to forest interiors. They identified native and NNIP species in transects that extended from forest edges to forest interiors (Honu and Gibson 2008). They also utilized seed traps to quantify seed rain and later tested collected seeds for viability (Honu and Gibson 2008). Additionally, soil cores were taken to determine the abundance of viable native and NNIPs in the soil seed bank

(Honu and Gibson 2008).

Their results indicated that species richness of both native and NNIPs declined from forest edge to forest interiors and that none of the NNIPs persisted in the vegetation beyond 30m from the forest edge (Honu and Gibson 2008). Of the native species present in the vegetation, only 57% were present in the soil seed bank (Honu and Gibson 2008). The species richness of the seed rain also declined from the forest edge to interior (Honu and Gibson 2008). Within the soil seed bank, NNIPs were significantly more abundant than native species and it is suggested that they possess greater dormancy than native species as well as delayed germination (Honu and Gibson 2008). NNIPs are believed to exist within forest only sporadically and in associations with disturbance events but this may be enough to allow them to accumulate in the seed bank and remain dormant until released by a disturbance (Honu and Gibson 2008).

The results of this study were well supported by the work of Honu and colleagues (2009) in which species richness in the vegetation and soil seed bank in eight RNAs in Shawnee National Forest were examined. Utilizing sampling plots that ranged from 10m to 730m from the nearest forest edge they identified all species in the sampling plots and also took soil cores to examine the seed bank (Honu et al. 2009). They found that the soil seed bank was clearly acting as a reserve for NNIPs as they had greater persistence than native plant seeds (Honu et al. 2009). However, only one NNIPs was present in both the vegetation and the soil seed bank of the sampling plot, Japanese stilt-grass (*Microstegium vimineum*), and they go on to suggest that NNIP seeds in the soil may have been dispersed into the forest from established plants in

edge habitats and then remain dormant in the seed bank until disturbance such as treefall changes environmental conditions enough to make germination possible (Honu et al. 2009). Additionally, they found *Lactuca serriola* L. deep in forest interiors, up to 730m away from forest edges, and this seems to support their assertion of seed dormancy and release by disturbance events (Honu et al. 2009).

## CHAPTER 3

### THE STUDY SITE

Established in 1991, The LaRue Pine Hills - Otter Pond Research Natural Area is a 1,046.6ha specially designated portion of the Shawnee National Forest, located on the western edge of Union county near Wolf Lake, Illinois (Figure 1) (United States Department of Agriculture 1991). It is located in the southern portion of the Ozark Natural Division (Schwegman 1973). The topography consists of exposed limestone bluffs (up to 50m in some locations) and xeric ridges adjacent to the Mississippi floodplain (Basset 1925). The xeric ridge tops are dissected by steep ravines (Figure 2) with upper slopes of six to 12 percent over steeper slopes of 30 to 70 percent at lower slope positions (Miles et al. 1979). The limestone bluffs are capped with chert formations (Basset 1925) and the soils of the ridge tops are composed of Alford silt loam (Miles et al. 1979). Soils comprising upper slopes are Alford silt loam and Goss soils comprise the lower slope positions (Miles et al. 1979). Soils at the bases of ravines are classified as Elsah silt loam (Miles et al. 1979).

The area was classified as Western Mesophytic Forest by Braun (1950), and the LaRue Pine Hills has long been recognized for its high diversity of plant species with over 1,100 species of vascular plant reported by Mohlenbrock and Voigt (1965). Gleason (1906) attributed the occurrence of unique flora in extreme upland and lowland sites to a temperature inversion effect that occurs along the Ozark region of southern Illinois.

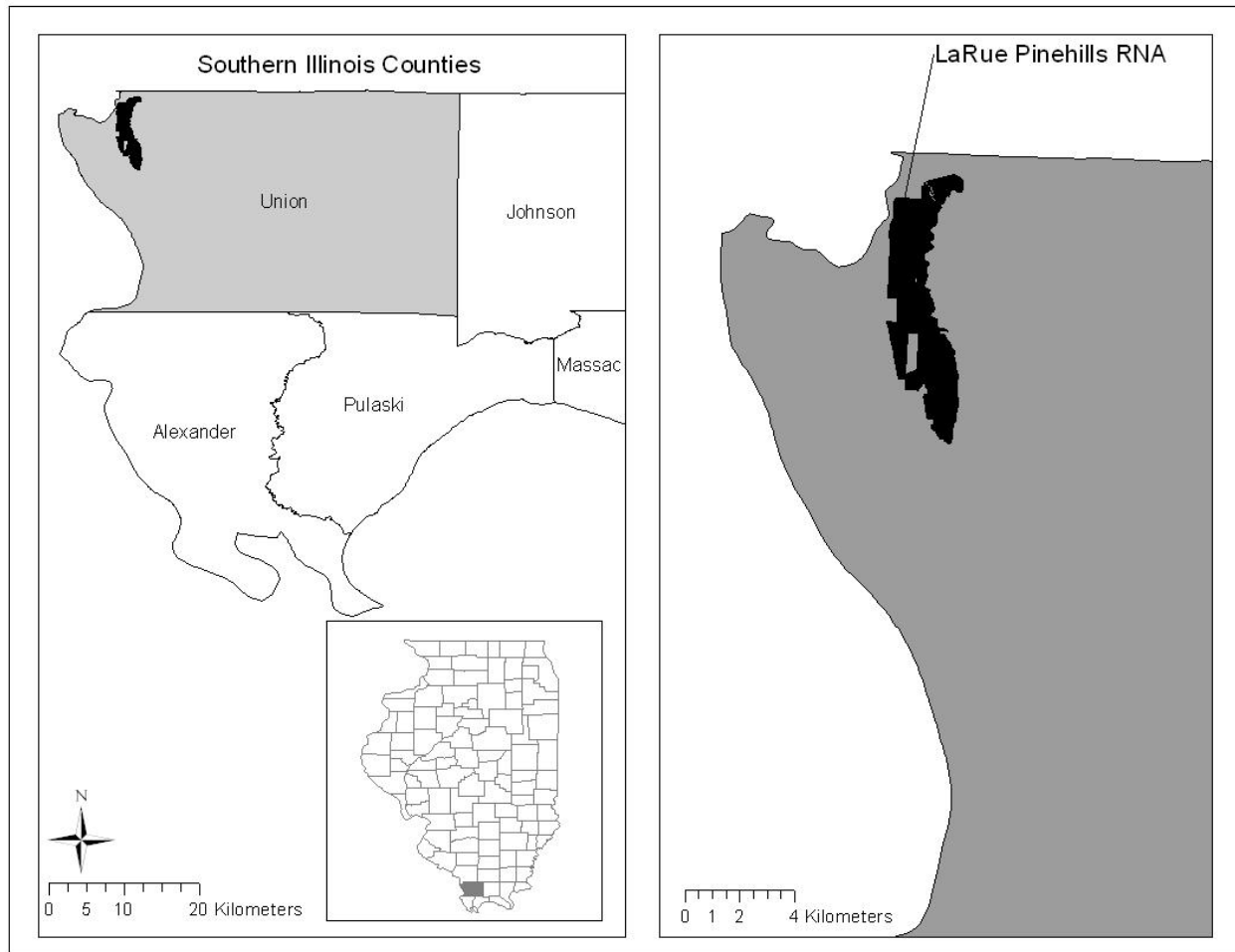


Figure 1. Map of the study area in southern Illinois. LaRue Pine Hills RNA is located in the northwestern corner of Union County and is adjacent to the Mississippi River floodplain, which forms the western boundary of Union County.





Figure 2. The northern portion of LaRue Pine Hills RNA is highlighted in yellow. The lowland floodplain habitat is divided from the forest habitat by the Snake Road. High bluffs and steep ravines characterize the woodland habitat east of the Snake Road. Pine Hills Road forms the eastern boundary of the RNA.

SucHECKI (1999) described the upland forest of the RNA as consisting of White oak (*Quercus alba* L.) and Black oak (*Quercus velutina* Lam.) with some stands of Shortleaf pine (*Pinus echinata* Mill.). Ravines provide habitat for mixed mesophytic species including maple (*Acer* L.), hickory (*Carya* Nutt.), beech (*Fagus* L.), ash (*Fraxinus* L.), tulip tree (*Liriodendron tulipifera* L.), cucumber tree (*Magnolia acuminata* L.) mulberry (*Morus* L.), wild black cherry (*Prunus serotina* Ehrh.), and elm (*Ulmus* L.) (SucHECKI 1999). The following community types are listed in the RNA establishment record: Xeric upland, dry upland, dry-mesic upland, mesic upland, mesic floodplain, wet-mesic floodplain, and wet floodplain forest (USDA, 1991). SucHECKI (1999) also notes the presence of loess hill prairie, limestone glade, limestone cliff, shrub swamp, and pond communities. More recently, SucHECKI and Gibson (2008) reported a large decline of *Cornus florida* L. (Flowering dogwood) due to dogwood anthracnose. However, in a companion study, Holzmueller et al. (2009) found that *C. florida* increased 4% in plots under a prescribed burn treatment. The authors also reported tremendous increases in density of *Asimina triloba* (316%) and *Sassafras albidum* (Nutt.) Nees. (494%) following burn treatment. The May 8<sup>th</sup>, 2009 derecho impacted the northern portion of LaRue Pine Hills resulting in a patchwork of heavily damaged areas along with zones of relatively little structural damage to canopy trees (Figure 3).

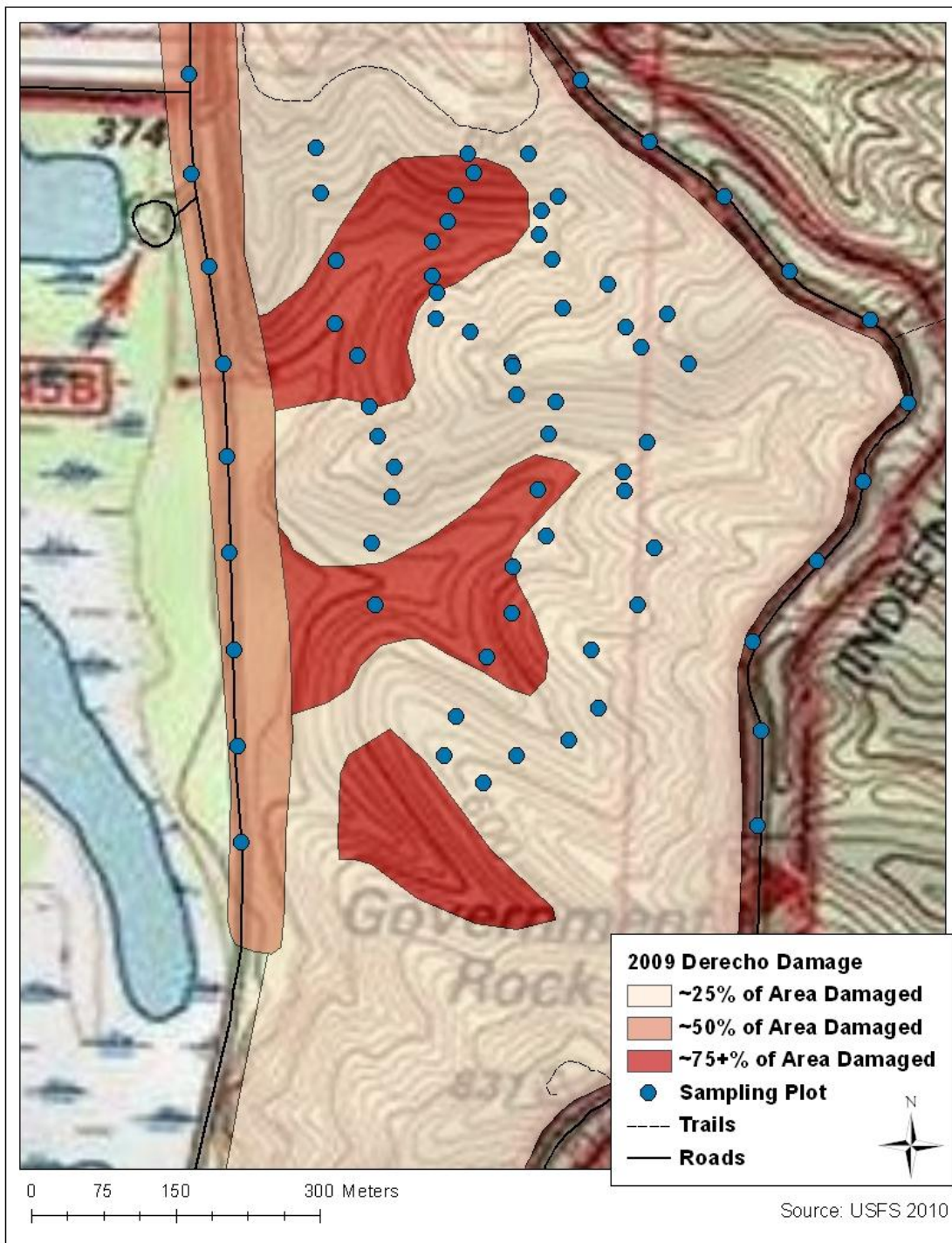


Figure 3. Derecho damage at LaRue Pine Hills RNA. Heavy damage (75%) corresponds to ravines and in some cases extends to ridgetops. Moderate damage (50%) occurs along the western boundary road, and large areas of light damage (25%) occur throughout the northern portion of the site. Blue dots indicate 73 sampling plots used in this study.

## CHAPTER 4

### METHODS

Fifty-three permanent research plots were surveyed for the presence of NNIPs. Established in 1991, the plots are circular with a 0.04ha area ( $400 \text{ m}^2$ ) and radius of 11.28m (Holzmueller et al. 2009). Initial plot locations were selected along three transects to sample upper, middle, and lower slope positions, with differing aspects. Plot site selection also included ridge tops and ravine bottoms. Within each plot 44  $1 \text{ m}^2$  quadrats were established along four transects from the plot center extending to plot edges. Transects were chosen using a stratified random protocol in which a random azimuth was selected and the first transect established along it. The second transect was placed perpendicularly to the initial transect and this was repeated for the third and fourth transect. This method prevented overlap of quadrats near the plot center (Figure 4). Eleven  $1 \text{ m}^2$  quadrats were utilized to avoid overlap of the 11.28m radius but it also reduced the effective sampling area to a 0.038ha circular sub-plot ( $380.13 \text{ m}^2$ ) within the larger 0.04ha plot. The total sampled area amounts to 11.5% of a  $380.13 \text{ m}^2$  subplot (Mueller-Dombois and Ellenberg 1974). Each quadrat was surveyed for a targeted list of 20 NNIP species (Table 1). These plant species are known to be highly invasive and present throughout Shawnee National Forest (USDA 2010a). Priority was given to species under active management programs by the United States Forest Service, The Nature Conservancy, and the River to River Cooperative Weed Management Area.

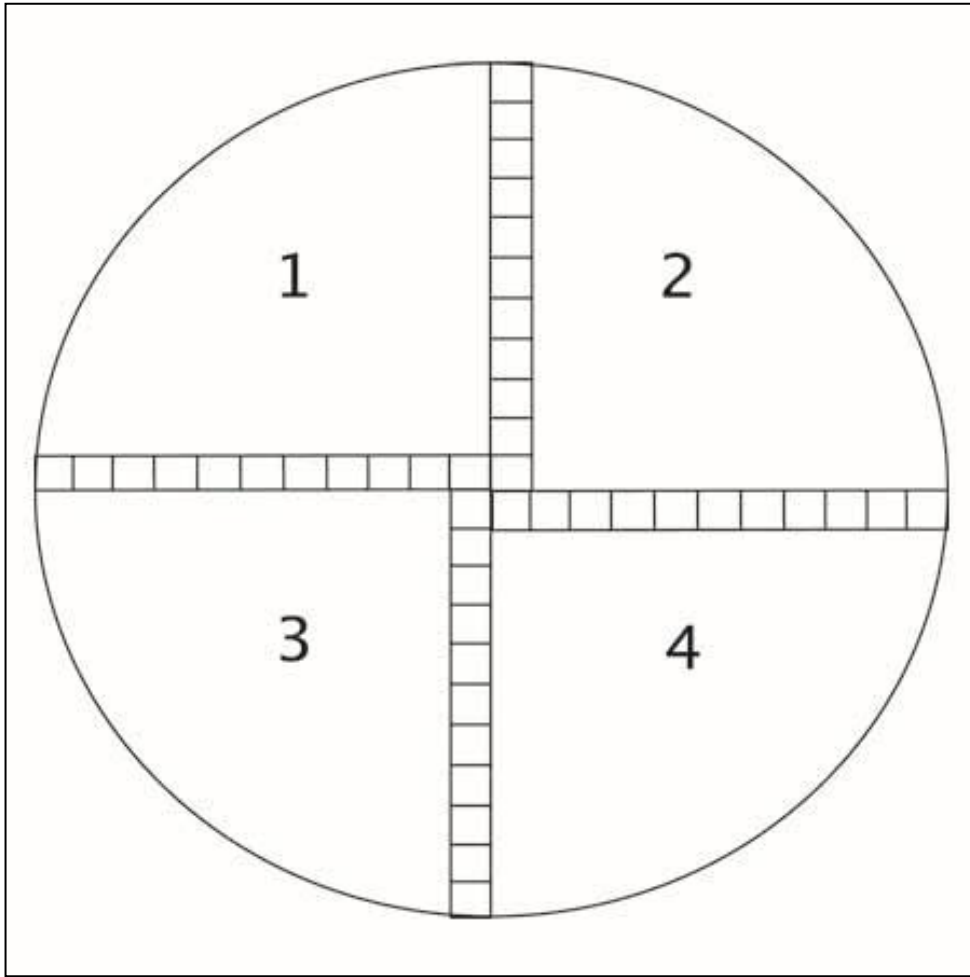


Figure 4. Quadrat layout within circular forest interior plots.



Table 1. Twenty surveyed non-native invasive plants.

Scientific Name	Common Name
<i>Ailanthus altissima</i> (Mill.) Swingle.	Tree of Heaven
<i>Alliaria petiolata</i> (Bieb.) Cavara and Grande.	Garlic Mustard
<i>Barbarea vulgaris</i> R. Br.	Garden Yellowrocket
<i>Berberis thunbergii</i> DC.	Japanese Barberry
<i>Celastus orbiculatus</i> Thunb.	Oriental Bittersweet
<i>Dioscorea oppositifolia</i> L.	Chinese Yam
<i>Elaeagnus umbellata</i> Thunb.	Autumn Olive
<i>Fallopia japonica</i> (Houtt.) Ronse Decraene.	Japanese Knotweed
<i>Heracleum mantegazzianum</i> Sommier & Levier.	Giant Hogweed
<i>Humulus japonicas</i> Sieb. & Zucc.	Japanese Hops
<i>Lactuca serriola</i> L.	Prickly Lettuce
<i>Lespedeza cuneata</i> (Dum.-Cours.) G. Don.	Sericea Lespedeza
<i>Lonicera japonica</i> Thunb.	Japanese Honeysuckle
<i>Lonicera maackii</i> (Rupr.) Maxim.	Amur Honeysuckle
<i>Microstegium vimineum</i> (Trin.) A. Camus.	Japanese Stiltgrass
<i>Polygonum perfoliatum</i> L.	Mile-a-Minute Weed
<i>Pueraria lobata</i> (Willd.) Owhi.	Kudzu
<i>Rosa multiflora</i> Thunb.	Multiflora Rose
<i>Securigera varia</i> (L.) Lassen.	Crown Vetch
<i>Sorghum halepense</i> L.	Johnson Grass

*Barbarea vulgaris* (Gardenrocket) and *Lactuca serriola* (Prickly lettuce) were included because they had previously been found at LaRue Pine Hills (Honu et al. 2009). The presence or absence of each NNIP species was recorded in each quadrat and used to calculate relative frequency of occurrence for each plot (Mueller-Dombois and Ellenberg 1974). Density was recorded through counts of individual rooted stems and summed across each quadrat for each species (Mueller-Dombois and Ellenberg 1974). Additionally, the percent canopy cover of each NNIP species was estimated using a modified Daubenmire Scale, which consists of seven categories corresponding to a range of cover (Daubenmire 1959; Mueller-Dombois and Ellenberg 1974; Abrams and Hulbert 1987). Midpoints of canopy coverage estimates were averaged across all quadrats for each species in each plot (Daubenmire 1959).

Each plot was sampled twice, once in June 2011 and again in August 2011, and maximum values for individual rooted stem counts and canopy cover estimates were used in analysis (Abrams and Hulbert 1987). Voucher samples of each NNIP species found in the vegetation were deposited in the Southern Illinois University Carbondale, Plant Biology Herbarium.

Canopy damage estimates to the LaRue Pine Hills RNA were provided by the United States Forest Service and were mapped using ArcMap 10.0 (ESRI 2010; USDA 2010b). Additionally, structural damage estimates to dominant trees were generated for each plot following the derecho in 2009 (P. Suchecki, pers. comm. 2010). Structural damage ranged from no signs of visible damage to complete loss of all dominant trees within a plot (Figures 5, 6, and 7). Overhead canopy coverage is associated with physical damage and also serves as an indirect measure of light availability.

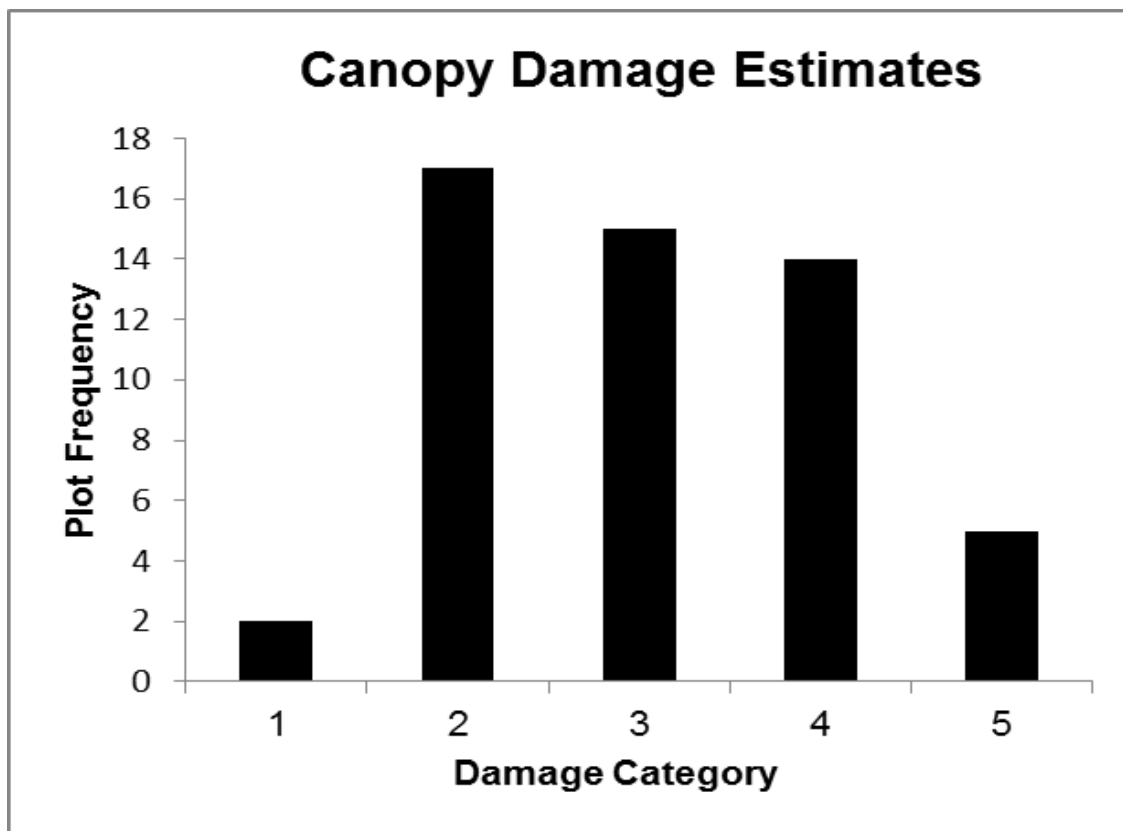


Figure 5. The number of plots located in each damage category based on physical damage to mature canopy trees. Damage Categories: 1=no damage, 2=some limb damage, 3=some trees down, 4=many trees down, 5= total loss of trees.





Figure 6. An example of a sampling plot (Plot 103) with category 1 wind damage.



Figure 7. An example of a sampling plot (Plot 311) with category 5 wind damage.

Overhead canopy coverage was estimated using a hemispherical densiometer (Lemmon 1956). Overhead canopy coverage was estimated from the plot center as well as the sixth quadrat (from the center) along each transect. The average of these estimates was used as a plot level value. The Euclidean distance (meters) from each plot center to the nearest road or trail was determined using the “Near” function in ArcGIS 10.0 (ESRI 2010).

An additional 20 plots (Figure 3) were established along the roads that form the eastern and western boundary of the study site. Eleven plots were placed on the eastern road and nine plots placed along the western road. Plots were spaced at 100m intervals and each plot consisted of a 10m x 2m transect that was divided into 20, 1m<sup>2</sup> quadrats. The locations of road plots were recorded using a Global Positioning System device and the presence or absence of each invasive species was recorded for each quadrat. Relative frequency of occurrence of each NNIP was then calculated for each plot (Mueller-Dombois and Ellenberg 1974). Overhead canopy cover measurements were taken in road plots using a hemispherical densiometer within four quadrats of each plot (Lemmon 1956). The average of those estimates was used as a plot level value.

Soil samples were collected from 20 plots in order to investigate the presence of NNIPs in the seed bank. Ten plots were randomly chosen from both road and interior forest plots. Of the interior plots sampled, five were classified with category 1 wind damage and five were classified with category 5 wind damage. One 6cm deep soil core was taken with a soil probe (approximately 15cm<sup>3</sup>) from the center of 20 quadrats (a stratified pattern was used in interior plots that contained 44 quadrats) within each

plot and then pooled to create a sample of approximately 305cm<sup>3</sup> per plot. Soil samples were collected in July of 2011 and stored at 4.5°C for 15 weeks (Honu et al. 2009). The germination study took place at the Southern Illinois University Carbondale Horticulture Research Center. Soil samples were spread over a mixture of potting soil and vermiculite in plastic germination trays and arranged randomly in a greenhouse (Honu et al. 2008; 2009). Large debris such as stones or small wood fragments were removed. Five trays containing only potting soil and vermiculite were arranged randomly with the trays containing soil samples to serve as a control (Honu et al. 2008; 2009). Samples were watered daily and monitored on a weekly basis. Every two weeks emerging seedlings were tallied, seedlings were removed from germination trays when they were either positively identified as a target NNIP or identified as a species not on the list of 20 target species. If no seedlings emerged for more than two weeks the soil sample was stirred to expose any ungerminated seeds (Honu et al. 2009). The germination study was terminated in March of 2012.

## CHAPTER 5

### RESULTS

The spatial pattern of NNIPs and wind damage from the 2009 super-derecho is depicted in Figure 8. Approximately 124.5ha of LaRue Pine Hills were damaged in the 2009 super-derecho. Of those, 92.2ha experienced canopy loss of 25% or less. Areas of approximately 50% canopy damaged comprised 17.4ha and 14.9ha experienced severe damage of 75% canopy loss or greater. Areas of continuous severe damage correspond to bottomland areas between ridges and in some cases extend upslope to encompass ridge tops. The western road experienced 50% canopy loss along the length of the study site, and areas of lesser wind damage (25% canopy loss or less) covered the remainder of the study site.

#### *Interior Plots*

Target NNIPs were present in three of 53 plots surveyed (5.6%; Table 2). Species recorded were *Rosa multiflora*, *Lonicera japonica*, and *Lonicera maackii*. All plots containing NNIPs had sustained loss of at least some canopy trees from the 2009 super-derecho with physical damage estimates ranging from Category 3 (in one plot) to Category 4 (2 plots). No NNIPs were found in plots that sustained little or no canopy damage. Additionally, no NNIPs were found in the most heavily damaged plots in which all dominant trees had been thrown or broken. Overhead canopy cover estimates for all plots ranged from 54.4% to 99.8% with a mean of 90.3% and median of 93.3%.



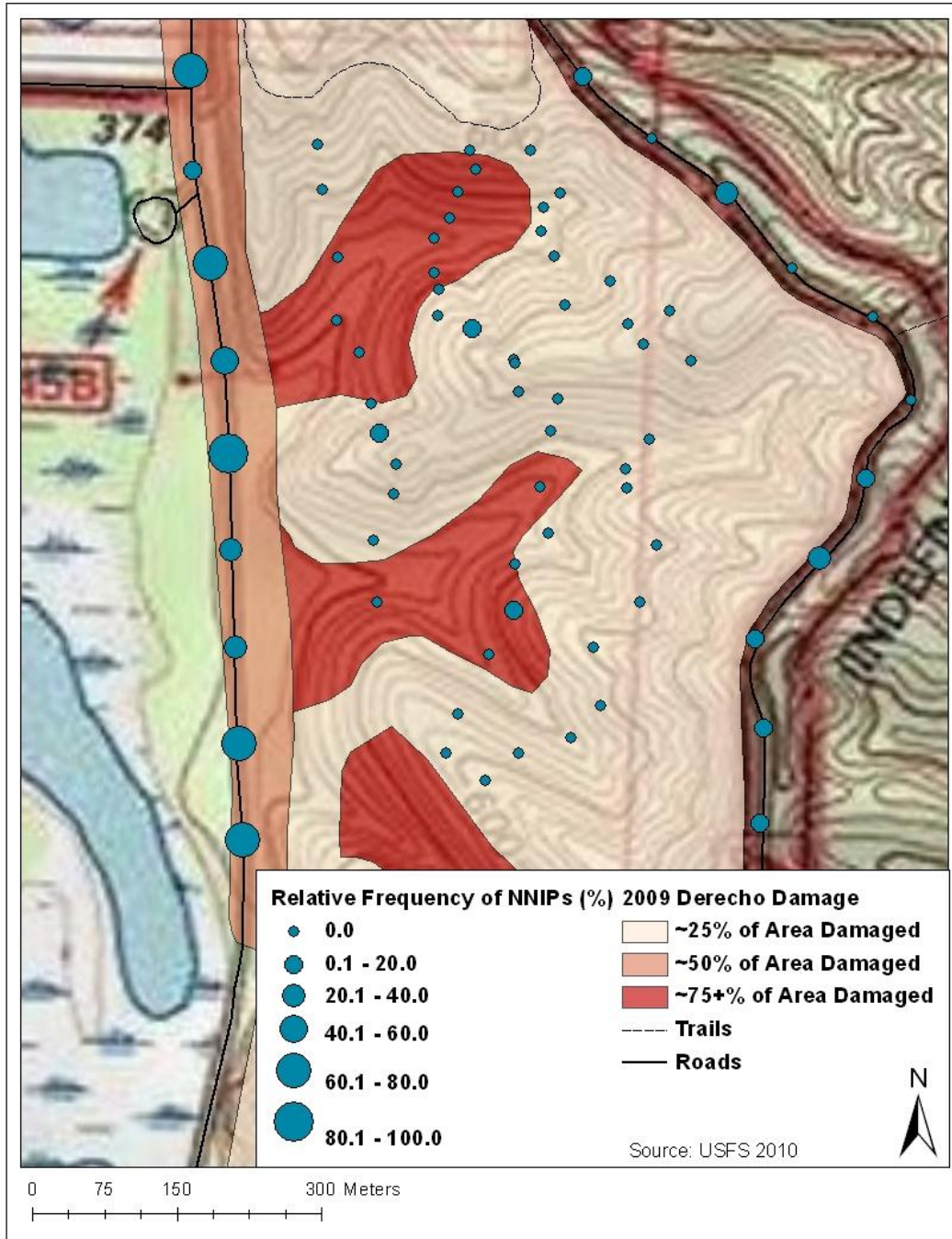


Figure 8. The relative frequency of all NNIPs within each plot and the extent of storm damage as estimated by the United States Forest Service. Zones of severe damage correspond to bottomland areas located between ridges. Relative frequency of NNIPs was considerably higher in road plots than in the forest interior plots. NNIPs were recorded in three of 53 surveyed interior plots. NNIPs were recorded in 16 of 20 surveyed road plots.

Table 2. Summary of findings in interior forest plots. *L. japonica* occurred with the greatest in plot frequency (15.9%) and *L. maackii* was the only species to occur in more than one interior plot. Despite high estimates of physical damage immediately following the 2009 super-derecho, the overhead canopy cover was high (>85%) in all plots containing a NNIP.

Species	Plot occurrences	Frequency all plots (%)	Max frequency within plot (%)	Max damage estimate	Max canopy cover (%)	Max distance to edge (m)
<i>Rosa multiflora</i>	1	1.8	2.2	4	94.3	252.0
<i>Lonicera japonica</i>	1	1.8	15.9	4	88.3	209.8
<i>Lonicera maackii</i>	2	3.7	2.2	4	89.9	209.8

Canopy coverage estimates for plots containing NNIPs ranged from 88.4% to 95.4%. *Rosa multiflora* was found furthest from a forest edge (road or trail) at a distance of 252m. *Lonicera japonica* appeared with the greatest relative frequency inside an individual plot (15.9%) while *Lonicera maackii* had the greatest relative frequency across all plots (3.7%). *Lonicera maackii* was also the only species to appear in more than one plot. However, its relative frequency at individual plots was low (2.2%). Given the low presence of NNIPs individual rooted stem counts and cover estimates were not included in this analysis.

#### *Road Plots*

NNIP species were present in 16 of 20 plots surveyed (80%; Table 3). Road plots contained greater diversity of NNIPs than interior plots with six species recorded including: *Dioscorea oppositifolia*, *Lactuca serriola*, *Lonicera maackii*, *Microstegium vimineum*, *Rosa multiflora*, and *Sorghum halepense*. Road plots also showed greater within plot species richness than forest interior plots (Figure 9). Five road plots contained two or more NNIP species compared to only one interior plot containing multiple species. *Microstegium vimineum* was the most frequently observed species. It occurred in 10 of 20 plots surveyed (50%) with a maximum individual plot frequency of 90% (18 of 20 quadrats). *Microstegium vimineum* was most frequent along the western road and only appeared in one plot on the eastern road. The second most frequently recorded species was *L. serriola*, which was recorded in six plots (30% relative frequency) and a max relative frequency in an individual plot of 35%.

Table 3. Summary of findings in road plots. Six species were recorded in road plots. *M. vimineum* was the most frequently occurring species across all plots and also occurred with the greatest frequency in an individual plot. \*Mean canopy cover refers to the average overhead canopy cover for plots containing a given species.

Species	Plot occurrences	Relative frequency all plots (%)	Max frequency within plot (%)	Mean canopy cover (%)*
<i>Dioscorea oppositifolia</i>	1	5.0	20.0	90.3
<i>Lactuca serriola</i>	6	30.0	35.0	54.2
<i>Lonicera maackii</i>	1	5.0	5.0	91.9
<i>Microstegium vimineum</i>	10	50.0	90.0	64.2
<i>Rosa multiflora</i>	1	5.0	25.0	57.0
<i>Sorghum halepense</i>	4	20.0	65.0	68.9



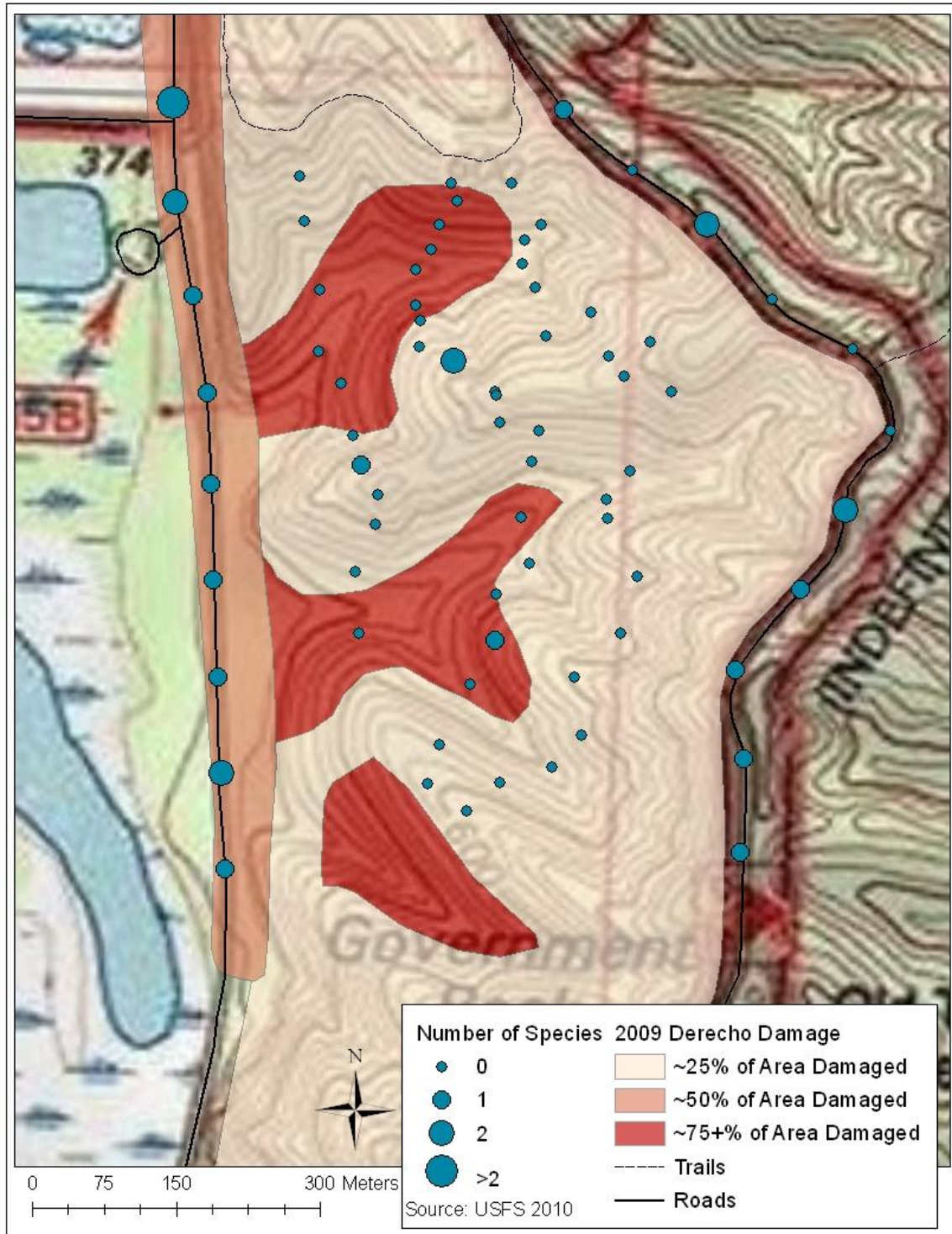


Figure 9. Indicates the species richness of NNIPs per plot. Road plots typically had higher species richness with several plots containing multiple species while only one interior forest plot contained more than a single species.

*Sorghum halepense* occurred with a relative frequency of 20% and a maximum relative frequency for an individual plot of 65%. *Dioscorea oppositifolia*, *Lonicera maackii*, and *Rosa multiflora* were only recorded once among road plots (relative frequency of 5%). *Lonicera japonica* was the only species recorded in the forest interior that was not also recorded in the road plots. NNIPs occurred in all plots surveyed on the western road (100% relative frequency) and in seven of 11 plots surveyed on the eastern road (63.6% relative frequency). Overhead canopy cover estimates for road plots ranged from 22.1% to 95.5% with a mean of 61.1% and a median value of 64.4%.

A comparison between interior and road plots across all species that were recorded (Table 4) shows that relative frequency across all plots as well as within individual plots was higher along roadsides (80% and 90% respectively as compared to 5.6% and 18.2% for interior plots). Likewise, species richness across all plots and within individual plots was also higher along roadsides (6, 4) than in the forest interior (2, 2). The mean and median canopy cover of roadside plots (61.1%, 64.4%) was lower than in the forest interior (90.4%, 93.4%). Maximum canopy cover between road plots (95.5%) and interior plots (99.5%) was similar while minimum canopy cover was lower for road plots (22.1%) compared to interior plots (55.4%).

Table 4. A comparison of interior and road plots across all species. NNIPs were more prevalent along road plots than in forest interior plots. NNIPs also occurred with greater frequency within individual plots. Species richness of NNIPs was also higher in road plots. Canopy cover was lower in road plots as compared to forest interior plots.

	Interior plots	Road plots
Invasive species occurrences	(3/53)	(16/20)
Relative frequency	5.6%	80.0%
Max occurrence in a plot	(8/44)	(18/20)
Max frequency within a plot	18.2%	90.0%
Total species present	2	6
Max species per individual plot	2	4
Mean canopy cover	90.4%	61.1%
Median canopy cover	93.4%	64.4%
Max canopy cover	99.5%	95.5%
Min canopy cover	54.4%	22.1%

### *Seed Bank*

Across all sampled plots, 277 seedlings emerged in the germination trays. No target NNIPs seedlings emerged from the soil samples. Considerably more seedlings emerged from soil samples taken from road plots (245 total) as compared to forest interior plots (32 total; Table 5). Within interior forest plots total seedling emergence was similar for both low damage category plots (15) and high damage category plots (17). No seedlings germinated in control trays.

Table 5. Totals of emerging seedlings from road and interior plots (lower portion of table depicts totals from high and low damage categories). More seedlings emerged from road plots than the forest interior. Seedling emergence was similar across high and low damage categories. No NNIPs emerged in germination trays.

Road Plots	Seedlings	Interior Plots	Seedlings
ph1	28	104	5
ph2	31	106	1
ph7	36	109	6
ph9	24	112	3
Ph11	35	206	3
sn1	24	209	3
sn2	18	219	2
sn5	18	301	5
sn8	16	303	1
sn9	15	304	3
Mean	24.5		3.2
Totals	245		32
Total across all plots	277		
Low Damage Plots	Seedlings	High Damage Plots	Seedlings
104	5	109	6
106	1	112	3
301	5	206	3
303	1	209	3
304	3	219	2
Mean	3		3.4
Total	15		17

## CHAPTER 6

### DISCUSSION

This study sought to determine if the extent of wind damaged from the 2009 super-derecho was related to the frequency of NNIPs in forest interiors. Low numbers of NNIPs were found in plots containing moderate to high levels of damage to canopy trees, and no NNIPs were found in plots with low or zero physical damage from the 2009 super-derecho. However, NNIPs were only found in three out of 53 interior plots and that is insufficient evidence to suggest that canopy gaps associated with wind damage from the 2009 super-derecho are driving recruitment of NNIPs in forest interiors at LaRue Pine Hills RNA. The absence of NNIPs in wind damaged forest interiors at LaRue Pine Hills is somewhat surprising given evidence that NNIP establishment can be facilitated by disturbance events that alter resource availability (Hobbs and Huenneke 1992; Alpert et al. 2000; Lake and Leishman 2004; Christen and Matlack 2009). These findings differ from previous studies on catastrophic wind where NNIPs were shown to respond favorably to damage produced by tropical cyclones (Lorence and Sussman 1985; Horvitz et al. 1998; Snitzer et al. 2005).

Instead, the spatial pattern of NNIPs at LaRue Pine Hills is consistent with findings of other studies in Southern Illinois and the Eastern Forests of the United States. These studies have shown that NNIPs are primarily associated with forest edges (Brothers and Spingarn 1992; Campbell and Gibson 2001; Meekins and McCarthy 2001; Yates et al. 2004; Honu and Gibson 2006; 2008; Pande et al. 2007; Christen and Matlack 2009). The presence of NNIPs diminishes rapidly from forest

edges to forest interiors, and beyond 50m the presence of NNIPs is often minimal (Brothers and Spingarn 1992; Yates et al. 2004; Honu and Gibson 2006; Honu and Gibson 2008; Christen and Matlack 2009). Small populations and scattered individuals may occur deep within forest interiors, beyond areas associated with edge habitat (Brothers and Spingarn 1992). These occurrences are often considered ephemeral with plants that are often stunted and incapable of reproduction (Brothers and Spingarn 1992). Yates et al. (2004) found examples of *Eleagnus umbellata*, *Lonicera japonica*, and *Rosa multiflora* existing at distances of 195m to 495m from forest edges. NNIPs growing in forest interiors were noted to be smaller than their counterparts in edge habitats at the same sites, possibly indicating reduced vigor (Yates et al. 2004). Honu and colleagues (2009) also found NNIPs capable of penetrating deep into forest interiors of Shawnee National Forest with *Lactuca serriola* found 730m from the nearest forest edge.

Similar results were found in this study. *Lonicera japonica*, *Lonicera maackii*, and *Rosa multiflora* were found at a range of 157m to 252m from the forest edge. These populations were small and in the case of *R. multiflora* and *L. maackii* consisted of only a few individuals with *L. japonica* having a slightly higher relative frequency within an individual plot. Roadside plots at LaRue Pine Hills showed both higher diversity and higher relative frequency of NNIPs. Three species were found in forest interiors and six species found along forest edges. NNIPs occurred in 5.6% of plots in forest interiors compared to 80% of plots along forest edges.

Plots along the western road had a high frequency of NNIPs and also suffered significant canopy damage from the super-derecho. However, because of the strong

association of NNIPs with forest edges, it is not possible to attribute the high frequency of NNIS at this location to wind damage (Brothers and Spingarn 1992; Campbell and Gibson 2001; Meekins and McCarthy 2001; Yates et al. 2004; Honu and Gibson 2006; Pande et al. 2007; Honu and Gibson 2008; Christen and Matlack 2009).

Available light decreases from the forest edge to forest interiors, and the association between edges and light availability has been implicated in promoting NNIPs (Brothers and Spingarn 1992; Murcia 1995; Meekins and McCarthy 2001; Christen and Matlack 2009). Forest edge plots at LaRue Pine Hills had lower canopy cover than forest interior plots, and this may explain the greater diversity and frequency of NNIPs in those plots. Interior plots that sustained heavy losses of overstory trees (Category 5), from high winds in the 2009 super-derecho, could have high canopy coverage (up to 96.98%) because of the presence of dense sub-canopies of tree saplings. Blowdown events can often leave understory vegetation relatively intact and forests may then undergo advanced regeneration in which suppressed tree seedling and saplings are released upon opening of the overhead canopy (Everham and Brokaw 1996; Woods 2004). Biological residuals following disturbance events can have a significant impact on successional patterns (Turner et al. 1998). Rapid growth of surviving saplings and development of a dense sub-canopy may have effectively suppressed (through shading) the germination and growth of NNIPs germinating from the seed bank or from newly arriving seeds. The increased available light reaching the forest floor, from canopy gaps, may have been quickly reduced prior to the arrival and establishment of NNIPs. Dense understory canopies of woody shrubs have been found to suppress germination and survivorship of *Microstegium vimineum* a NNIS otherwise



capable of invading closed canopy forests (Cole and Weltzin 2005; Schramm and Ehrenfeld 2010). Similar processes may be occurring at LaRue Pine Hills and effectively limiting invasion. The increased available light (and related low canopy cover) along roadside edges, has likely been higher for much longer periods of time than two-year old canopy gaps caused by the 2009 super-derecho and therefore been more favorable for the species considered here. Additionally the seed dispersal corridor function of roads may also account for the increased frequency of NNIPs along forest edges at LaRue Pine Hills (Christen and Matlack 2009).

These findings may suggest that biological resistance (through competition for light) has enabled LaRue Pine Hills to withstand the large scale disturbance without appreciable invasion of canopy gaps in forest interiors (Levine et al. 2004). It is also possible that a lack of propagule pressure from NNIPs has prevented their successful invasion of forest interiors and newly opened canopy gaps (Lonsdale 1999; D'Antonio et al. 2001; Lockwood et al. 2005). The presence of NNIPs (along with natives) in the seed rain and seed bank decreases as one moves from forest edge to forest interior which in part accounts for their reduced numbers in the vegetation along the same gradient (Honu and Gibson 2008; Honu et al. 2009). Additionally, the functional role of forest edges, identified by Cadenasso and Pickett (2001) reduces the distances that seeds can disperse into a forest interior because the complex and dense physical structure of forest edges act as barriers to seed dispersal.

This study found that a similar process may be occurring at LaRue Pine Hills RNA. Considerably more seedlings germinated from soil collected in road plots than from soil collected in forest interior plots. It is also worth noting that all of the NNIP

species found in the forest interior plots at LaRue Pine Hills are bird dispersed, which may have enabled those species to reach forest interiors easier than wind dispersed species trapped by forest edges (Cadenasso and Pickett 2001).

That none of the NNIPs considered in this study germinated from soil samples is surprising given that 7 species were identified in the vegetation. Road plots had a high frequency of NNIPs including *Microstegium vimineum*, which is known for establishing persistent seed banks (Gibson et al. 2002), so it is especially surprising that no NNIPs germinated from road plot soil samples. It is possible that the density of NNIPs in the seed bank was low and that the sampling protocol was inadequate to detect their presence. Future seed bank studies of NNIPs at LaRue Pine Hills may consider taking a larger number of soil samples as well as a larger volume of soil per sampling plot. Additionally, investigation of the seed rain from forest edge to interior would help researchers quantify propagule pressure in forest interior canopy gaps.

## CONCLUSION

This study has illustrated that NNIPs did not appear to have invaded forest interiors at LaRue Pine Hills in the first two years following large scale wind damage from a super-derecho in May 2009. The spatial pattern of NNIPs appears to fit previous studies in the region with higher diversity and frequency of NNIPs occurring along roadside forest edges and fewer occurrences in forest interiors. Given the significant negative ecological impacts of NNIPs, it is imperative that land managers effectively and efficiently respond to invasions. The most efficient and cost effective way to prevent impacts of NNIPs is to remove or limit their spread while populations are small (Rejmanek 2000). However, such actions require rapid identification of a growing infestation. Long term monitoring provides one means of detecting encroachment by NNIPs. In the case of LaRue Pine Hills, removal of NNIPs found in three forest interior plots may limit establishment of NNIPs in the forest interior. Without prior knowledge of the frequency and abundance of NNIPs at this site, this study relied on the current presence NNIPs for comparison between areas across a gradient of wind damage. Further studies could survey plots for all non-native species not just the 20 NNIPs considered here. Additionally, surveys of all vegetation within plots are required to better determine the proportion of vegetation comprised by native versus non-native species. Such information would enable further understanding of processes occurring in forest understories following damage to overhead canopies.

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## APPENDIX

## APPENDIX

Table 6. Indicates GPS coordinates of each plot, richness of NNIS, and within plot frequency of NNIPs.

Plot	X	Y	Number of Invasive Species	Invasive Frequency (%)
101	284838	4162519	0	0.00
102	284845	4162500	0	0.00
103	284826	4162476	0	0.00
104	284817	4162449	0	0.00
105	284802	4162428	0	0.00
106	284802	4162392	0	0.00
107	284807	4162375	0	0.00
108	284805	4162348	0	0.00
109	284841	4162334	2	18.18
110	284884	4162302	0	0.00
111	284886	4162298	0	0.00
112	284889	4162269	0	0.00
113	284930	4162261	0	0.00
114	284923	4162228	0	0.00
115	284911	4162170	0	0.00
116	284920	4162122	0	0.00
117	284886	4162090	0	0.00
118	284884	4162042	1	2.27
119	284858	4161996	0	0.00
120	284826	4161934	0	0.00
121	284814	4161893	0	0.00
201	284902	4162519	0	0.00
202	284932	4162475	0	0.00
203	284915	4162460	0	0.00
204	284912	4162435	0	0.00
205	284926	4162410	0	0.00
206	284937	4162359	0	0.00
207	284984	4162384	0	0.00
208	285003	4162339	0	0.00
209	285046	4162353	0	0.00
210	285019	4162318	0	0.00
211	285068	4162301	0	0.00
213	285025	4162219	0	0.00
214	285000	4162189	0	0.00
215	285002	4162169	0	0.00
216	285032	4162109	0	0.00
217	285015	4162050	0	0.00
218	284967	4162004	0	0.00
219	284974	4161943	0	0.00
220	284944	4161910	0	0.00
221	284889	4161894	0	0.00
222	284855	4161865	0	0.00



Table 6. Continued.

Plot	X	Y	Number of Invasive Species	Invasive Frequency (%)
301	284681	4162526	0	0.00
302	284685	4162479	0	0.00
303	284701	4162408	0	0.00
304	284700	4162343	0	0.00
305	284724	4162310	0	0.00
306	284736	4162256	0	0.00
307	284745	4162225	1	2.27
308	284762	4162194	0	0.00
309	284760	4162163	0	0.00
310	284738	4162114	0	0.00
311	284742	4162050	0	0.00
ph1	284956	4162595	1	5.00
ph2	285003	4162532	0	0.00
ph3	285082	4162475	2	25.00
ph4	285154	4162396	0	0.00
ph5	285247	4162335	0	0.00
ph6	285302	4162259	0	0.00
ph7	285242	4162180	2	20.00
ph8	285208	4162095	1	35.00
ph9	285135	4162011	1	15.00
ph10	285143	4161919	1	15.00
ph11	285140	4161820	1	5.00
sn1	284549	4162602	4	65.00
sn2	284551	4162498	2	5.00
sn3	284570	4162402	1	75.00
sn4	284584	4162300	1	60.00
sn5	284588	4162205	1	90.00
sn6	284591	416210	1	30.00
sn7	284595	4162003	1	40.00
sn8	284599	4161903	2	80.00
sn9	284603	4161803	1	70.00

Table 7. Rooted stem counts of NNIPs in interior forest plots.

Plot	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>	<i>Rosa multiflora</i>
101	0	0	0
102	0	0	0
103	0	0	0
104	0	0	0
105	0	0	0
106	0	0	0
107	0	0	0
108	0	0	0
109	26	2	0
110	0	0	0
111	0	0	0
112	0	0	0
113	0	0	0
114	0	0	0
115	0	0	0
116	0	0	0
117	0	0	0
118	0	0	8
119	0	0	0
120	0	0	0
121	0	0	0
201	0	0	0
202	0	0	0
203	0	0	0
204	0	0	0
205	0	0	0
206	0	0	0
207	0	0	0
208	0	0	0
209	0	0	0
210	0	0	0
211	0	0	0
213	0	0	0
214	0	0	0
215	0	0	0
216	0	0	0
217	0	0	0
218	0	0	0
219	0	0	0
220	0	0	0
221	0	0	0
222	0	0	0

Table 7. Continued.

Plot	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>	<i>Rosa multiflora</i>
301	0	0	0
302	0	0	0
303	0	0	0
304	0	0	0
305	0	0	0
306	0	0	0
307	0	2	0
308	0	0	0
309	0	0	0
310	0	0	0
311	0	0	0

Table 8. Percent cover estimates of NNIPs in forest interior plots.

Plot	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>	<i>Rosa multiflora</i>
101	0	0	0
102	0	0	0
103	0	0	0
104	0	0	0
105	0	0	0
106	0	0	0
107	0	0	0
108	0	0	0
109	1.25	0.85	0
110	0	0	0
111	0	0	0
112	0	0	0
113	0	0	0
114	0	0	0
115	0	0	0
116	0	0	0
117	0	0	0
118	0	0	0.35
119	0	0	0
120	0	0	0
121	0	0	0
201	0	0	0
202	0	0	0
203	0	0	0
204	0	0	0
205	0	0	0
206	0	0	0
207	0	0	0
208	0	0	0
209	0	0	0
210	0	0	0
211	0	0	0
213	0	0	0
214	0	0	0
215	0	0	0
216	0	0	0
217	0	0	0
218	0	0	0
219	0	0	0
220	0	0	0
221	0	0	0
222	0	0	0

Table 8. Continued.

Plot	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>	<i>Rosa multiflora</i>
301	0	0	0
302	0	0	0
303	0	0	0
304	0	0	0
305	0	0	0
306	0	0	0
307	0	0.35	0
308	0	0	0
309	0	0	0
310	0	0	0
311	0	0	0

Table 9. Relative frequency (% of quadrats surveyed) of NNIS within each plot.

Plots	<i>Dioscorea oppositifolia</i>	<i>Lactuca serriola</i>	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>
101	0.00	0.00	0.00	0.00
102	0.00	0.00	0.00	0.00
103	0.00	0.00	0.00	0.00
104	0.00	0.00	0.00	0.00
105	0.00	0.00	0.00	0.00
106	0.00	0.00	0.00	0.00
107	0.00	0.00	0.00	0.00
108	0.00	0.00	0.00	0.00
109	0.00	0.00	15.91	2.27
110	0.00	0.00	0.00	0.00
111	0.00	0.00	0.00	0.00
112	0.00	0.00	0.00	0.00
113	0.00	0.00	0.00	0.00
114	0.00	0.00	0.00	0.00
115	0.00	0.00	0.00	0.00
116	0.00	0.00	0.00	0.00
117	0.00	0.00	0.00	0.00
118	0.00	0.00	0.00	0.00
119	0.00	0.00	0.00	0.00
120	0.00	0.00	0.00	0.00
121	0.00	0.00	0.00	0.00
201	0.00	0.00	0.00	0.00
202	0.00	0.00	0.00	0.00
203	0.00	0.00	0.00	0.00
204	0.00	0.00	0.00	0.00
205	0.00	0.00	0.00	0.00
206	0.00	0.00	0.00	0.00
207	0.00	0.00	0.00	0.00
208	0.00	0.00	0.00	0.00
209	0.00	0.00	0.00	0.00
210	0.00	0.00	0.00	0.00
211	0.00	0.00	0.00	0.00
213	0.00	0.00	0.00	0.00
214	0.00	0.00	0.00	0.00
215	0.00	0.00	0.00	0.00
216	0.00	0.00	0.00	0.00
217	0.00	0.00	0.00	0.00
218	0.00	0.00	0.00	0.00
219	0.00	0.00	0.00	0.00
220	0.00	0.00	0.00	0.00
221	0.00	0.00	0.00	0.00
222	0.00	0.00	0.00	0.00

Table 9. Continued.

Plots	<i>Dioscorea oppositifolia</i>	<i>Lactuca serriola</i>	<i>Lonicera japonica</i>	<i>Lonicera maackii</i>
301	0.00	0.00	0.00	0.00
302	0.00	0.00	0.00	0.00
303	0.00	0.00	0.00	0.00
304	0.00	0.00	0.00	0.00
305	0.00	0.00	0.00	0.00
306	0.00	0.00	0.00	0.00
307	0.00	0.00	0.00	2.27
308	0.00	0.00	0.00	0.00
309	0.00	0.00	0.00	0.00
310	0.00	0.00	0.00	0.00
311	0.00	0.00	0.00	0.00
ph1	0.00	0.00	0.00	0.00
ph2	0.00	0.00	0.00	0.00
ph3	0.00	0.00	0.00	0.00
ph4	0.00	0.00	0.00	0.00
ph5	0.00	0.00	0.00	0.00
ph6	0.00	0.00	0.00	0.00
ph7	0.00	0.00	0.00	0.00
ph8	0.00	35.00	0.00	0.00
ph9	0.00	15.00	0.00	0.00
ph10	0.00	15.00	0.00	0.00
ph11	0.00	5.00	0.00	0.00
sn1	20.00	30.00	0.00	0.00
sn2	0.00	0.00	0.00	5.00
sn3	0.00	0.00	0.00	0.00
sn4	0.00	0.00	0.00	0.00
sn5	0.00	0.00	0.00	0.00
sn6	0.00	0.00	0.00	0.00
sn7	0.00	0.00	0.00	0.00
sn8	0.00	5.00	0.00	0.00
sn9	0.00	0.00	0.00	0.00

Table 9. Continued.

Plots	<i>Microstegium vimineum</i>	<i>Rosa multiflora</i>	<i>Sorghum halepense</i>
101	0.00	0.00	0.00
102	0.00	0.00	0.00
103	0.00	0.00	0.00
104	0.00	0.00	0.00
105	0.00	0.00	0.00
106	0.00	0.00	0.00
107	0.00	0.00	0.00
108	0.00	0.00	0.00
109	0.00	0.00	0.00
110	0.00	0.00	0.00
111	0.00	0.00	0.00
112	0.00	0.00	0.00
113	0.00	0.00	0.00
114	0.00	0.00	0.00
115	0.00	0.00	0.00
116	0.00	0.00	0.00
117	0.00	0.00	0.00
118	0.00	2.27	0.00
119	0.00	0.00	0.00
120	0.00	0.00	0.00
121	0.00	0.00	0.00
201	0.00	0.00	0.00
202	0.00	0.00	0.00
203	0.00	0.00	0.00
204	0.00	0.00	0.00
205	0.00	0.00	0.00
206	0.00	0.00	0.00
207	0.00	0.00	0.00
208	0.00	0.00	0.00
209	0.00	0.00	0.00
210	0.00	0.00	0.00
211	0.00	0.00	0.00
213	0.00	0.00	0.00
214	0.00	0.00	0.00
215	0.00	0.00	0.00
216	0.00	0.00	0.00
217	0.00	0.00	0.00
218	0.00	0.00	0.00
219	0.00	0.00	0.00
220	0.00	0.00	0.00
221	0.00	0.00	0.00
222	0.00	0.00	0.00



Table 9. Continued.

Plots	<i>Microstegium vimineum</i>	<i>Rosa multiflora</i>	<i>Sorghum halepense</i>
301	0.00	0.00	0.00
302	0.00	0.00	0.00
303	0.00	0.00	0.00
304	0.00	0.00	0.00
305	0.00	0.00	0.00
306	0.00	0.00	0.00
307	0.00	0.00	0.00
308	0.00	0.00	0.00
309	0.00	0.00	0.00
310	0.00	0.00	0.00
311	0.00	0.00	0.00
ph1	0.00	0.00	0.05
ph2	0.00	0.00	0.00
ph3	0.00	25.00	0.15
ph4	0.00	0.00	0.00
ph5	0.00	0.00	0.00
ph6	0.00	0.00	0.00
ph7	20.00	0.00	0.05
ph8	0.00	0.00	0.00
ph9	0.00	0.00	0.00
ph10	0.00	0.00	0.00
ph11	0.00	0.00	0.00
sn1	20.00	0.00	0.65
sn2	30.00	0.00	0.00
sn3	75.00	0.00	0.00
sn4	60.00	0.00	0.00
sn5	90.00	0.00	0.00
sn6	30.00	0.00	0.00
sn7	40.00	0.00	0.00
sn8	80.00	0.00	0.00
sn9	70.00	0.00	0.00

Table 10. Environmental measures of forest interior plots.

Plot	Elevation (m)	Damage estimate	Overhead Canopy Coverage (%)	Edge Distance (m)
101	177	3	96.15	28.67
102	173	3	90.02	46.31
103	167	1	96.26	72.91
104	154	2	96.10	100.67
105	140	2	98.70	124.02
106	142	2	96.20	159.30
107	147	2	94.23	175.34
108	155	2	96.31	202.37
109	167	4	88.35	209.79
110	185	3	86.27	240.38
111	195	3	92.25	244.48
112	191	4	85.70	273.61
113	188	3	92.51	271.91
114	165	4	79.82	298.03
115	152	2	97.87	275.40
116	163	2	96.05	243.82
117	156	3	95.94	263.20
118	173	4	94.33	251.99
119	143	3	92.20	263.72
120	149	4	97.50	230.09
121	169	4	87.00	217.02
201	188	2	94.75	32.24
202	175	3	96.62	85.15
203	163	4	91.89	90.46
204	140	2	95.79	113.16
205	144	2	95.01	141.25
206	170	4	80.08	193.17
207	177	4	80.50	146.88
208	188	5	92.20	166.14
209	212	4	82.79	123.86
210	213	5	96.98	166.83
211	228	4	82.94	140.41
213	176	3	91.42	215.45
214	161	3	97.35	214.85
215	167	3	93.92	200.99
216	186	2	93.50	141.41
217	190	3	92.67	128.17
218	188	5	82.74	163.94
219	184	4	94.96	158.08
220	173	3	84.66	193.58
221	173	4	86.74	250.81
222	187	5	73.64	256.16

Table 10. Continued.

Plot	Elevation (m)	Damage estimate	Overhead Canopy	
			Coverage (%)	Edge Distance (m)
301	177	2	97.03	49.34
302	150	2	96.41	96.47
303	121	2	99.48	132.36
304	116	1	98.33	121.99
305	122	2	93.18	141.57
306	132	3	93.24	149.65
307	142	3	89.91	157.19
308	153	2	93.86	173.01
309	163	2	96.41	170.15
310	145	4	94.74	146.87
311	127	5	54.44	149.18

Table 11. Additional environmental measures of forest interior plots.

Plot	Litter Coverage (%)	Bare Soil Coverage (%)	Woody Debris Coverage (%)	Vegetation Coverage Height <1m (%)
101	61.5	29.5	1.5	23.2
102	58.8	27.8	7.5	31.6
103	48.7	30.0	1.0	21.9
104	76.3	6.2	2.3	31.7
105	59.9	19.8	6.2	30.6
106	81.8	8.4	0.8	31.1
107	88.9	2.7	2.1	42.8
108	91.8	2.0	1.2	62.7
109	87.3	1.9	3.3	74.4
110	84.0	2.6	3.4	62.2
111	87.2	1.3	4.8	50.4
112	63.1	20.2	11.8	27.9
113	51.4	34.8	1.5	19.6
114	66.3	12.3	12.7	47.5
115	78.8	3.5	5.6	19.2
116	88.0	1.8	1.3	17.8
117	84.7	1.0	11.0	21.9
118	85.2	0.9	12.7	64.5
119	83.1	9.8	3.1	58.4
120	78.5	2.2	9.5	37.6
121	86.5	1.6	5.4	60.5
201	52.8	30.4	2.6	24.7
202	69.7	10.6	15.7	35.6
203	84.3	0.9	11.2	31.5
204	78.8	8.7	4.9	25.0
205	81.2	1.3	18.0	21.1
206	79.9	9.1	10.8	61.0
207	73.5	7.7	21.2	70.5
208	78.3	4.7	13.5	34.8
209	84.1	2.7	17.3	56.4
210	80.6	2.5	15.7	27.4
211	51.7	29.7	17.9	14.9
213	76.3	11.4	16.7	34.9
214	67.9	19.6	12.8	48.4
215	87.6	5.4	3.6	70.1
216	59.9	33.5	1.6	28.5
217	79.3	8.5	10.8	50.7
218	80.7	3.9	17.9	66.4
219	72.6	1.7	27.4	13.1
220	87.0	6.7	4.9	65.6
221	77.3	12.9	9.5	20.3
222	80.9	7.1	12.9	78.6

Table 11. Continued.

Plot	Litter Coverage (%)	Bare Soil Coverage (%)	Woody Debris Coverage (%)	Vegetation Coverage Height <1m (%)
301	91.0	5.1	0.9	29.1
302	94.8	0.6	1.9	55.6
303	90.2	2.7	1.5	30.8
304	91.0	3.9	4.3	64.0
305	74.1	2.6	18.1	21.8
306	88.3	1.5	7.5	30.8
307	86.8	1.5	5.0	55.6
308	93.7	1.3	0.7	40.3
309	75.9	8.7	7.4	18.3
310	82.3	4.1	15.3	46.2
311	50.1	14.5	38.3	77.9

Table 12. Overhead canopy coverage estimates of road plots.

Plot	Canopy Coverage (%)
ph1	50.41
ph2	64.06
ph3	57.04
ph4	89.67
ph5	76.80
ph6	37.02
ph7	77.64
ph8	36.89
ph9	64.71
ph10	66.40
ph11	38.12
sn1	90.25
sn2	91.88
sn3	95.52
sn4	90.90
sn5	94.48
sn6	23.89
sn7	22.07
sn8	29.15
sn9	25.97