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RESEARCH ARTICLE

The Impact of Treefall Gaps on the Species Richness of Invasive Plants

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Invasive plant species pose a threat to biodiversity worldwide. Ecological disturbances, such as those created by fallen trees, create conditions in which invasive plant species can establish and thrive. This study investigated whether treefall gaps have higher richness of invasive plant species than other areas within forests and potentially serve as a source for the spread of invasive species. A nine-hectare area of mature deciduous forest at the Smithsonian Environmental Research Center (SERC) near Edgewater, MD, was censused for invasive plant species during the summers of 2011 and 2012. The area was divided into 2m x 2m subplots, and the presence or absence of invasive plant species was recorded for each subplot. Gaps were defined as areas in which there was no canopy cover above 10m. The species richness of invasive plants in gap and non-gap areas was analyzed using ArcGIS. No significant association between invasive plant species richness and treefall gaps was found. However, there was a positive association between coarse woody debris cover and invasive plant species richness.

INTRODUCTION

One of the leading causes of native species loss is the introduction and spread of invasive species (Pimental, Lach, Zuniga, & Morrison, 2000). Invasive species are species found in geographic regions where they do not naturally occur and whose introduction results in economic or environmental harm (Pimentel et al., 2000). Invasive plant species change the environment they invade and interact with local species, thus impacting native species by reducing biodiversity, altering habitats, competing with native species, and potentially having a negative impact on ecosystem services (Pejchar and Mooney 2009).

Many non-native and exotic species are introduced into the United States each year through accidental transport on ships, planes, cars, and by other modes of transportation. Others are imported and brought in for land management, pest control, landscaping, food, pets, and horticultural purposes. If the introduced species "escapes," the results can be detrimental to the local environment. Measures taken to prevent non-native plant invasions cost the United States around $20 billion per year in losses in agriculture, livestock, and natural resources (Pimentel et al., 2000). While a number of characteristics enhance the invasiveness of a plant, the potential for an area to be invaded depends upon a number of factors including propagule pressure and invasibility (Sandlund, Schei, & Viken , 2001). Propagule pressure is the number of growing plant parts that arrive, colonize, and have the potential to establish at particular sites (Lonsdale, 1999). Invasibility is the susceptibility of an area to the colonization and establishment of a nonnative species and is determined by a number of factors, in cluding the assemblage of the native community, the amount of disturbance, and the resistance of the native plants in that area to disturbance (Davis, Thompson, & Grime, 2005; Lonsdale, 1999; Moles et al., 2012).

One type of disturbance which may impact the establishment and survival of invasive plants is gaps that are created by treefalls. A treefall gap is the open space beneath the canopy resulting from the death of one or more trees, or a large portion of a tree (Runkle, 1984). Conditions within a treefall gap can differ greatly from those in surrounding areas and can even differ within the gap itself (Barik, Pandey, Tipathi, & Rao, 1992). Gaps are heterogeneous as a result of changes in microenvironment (temperature, moisture, and light) and structural changes resulting from roots, crowns, and boles of fallen trees (Barik et al., 1992). These alterations in microenvironmental conditions may impact the plants that are able to reestablish in a particular area and enable previously suppressed species to grow and flourish (Brokaw 1982). While it is known that disturbed conditions can allow invasive plant species to colonize an area, less is known about the potential role of treefall gaps in promoting invasive species spread.

It is thought that gaps promote the regeneration of shade-intolerant plants and thus add to the species richness of forested areas by providing an opportunity for establishment of plants that require the conditions temporarily provided by the gap (Barik et al., 1992). Treefall gaps create bare patches in which no litter or debris is present on the soil surface, increase the ability of light to penetrate an area, reduce competition, and create a change in microclimate. All of these factors could enable invasive plant species to invade an area (Gorchov, Thompson, O'Neill, Whigham, & Noes, 2011). Canopy gaps, along with propagule pressure, have been found to be useful predictors of plant invasion (Eschtruth & Battles, 2009). A study on the relationship between canopy gaps and the establishment of *Frangula alnus* (colloquially known as

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glossy buckthorn) in New Hampshire found that this invasive shrub was much more prevalent in gap areas than in non-gap areas of the forest (Burnham & Lee, 2010). Gorchov et al. (2011) found that *Rubus phoenicolasius*, or wineberry, was able to utilize the disturbance caused by treefalls to establish in the gaps and then persist even after the canopy had closed. Treefall gaps have also been shown to promote the reproduction of other invasive species, such as *Berberis thunbergii* (Klinczar 2014).

While a number of studies have examined the impact of gaps on individual invasive plant species, the authors are aware of no studies examining the impact of treefall gaps on invasive plant species richness. In a previous study that took place at the Smithsonian Environmental Research Center (SERC), exotic species richness in 1m2 plots was found to be higher in younger forests than in older forests (Parker, Richie, Lind, & Maloney, 2010). The researchers hypothesized that this was a result of older forests having lower light availability, less recent disturbances, and more limited dispersal of propagules (Parker et al., 2010). The objective of this study was to examine invasive plant species richness in gaps, contributing to a larger study on the impact of treefall gaps on the establishment and spread of invasive plant species in eastern temperate forests. We hypothesized that treefall gaps provide ideal conditions for invasive plant establishment and recruitment due to the changes in microenvironmental conditions in gap areas. Based on this hypothesis, we predicted that gaps would have a higher richness of invasive plants than surrounding non-gap areas.

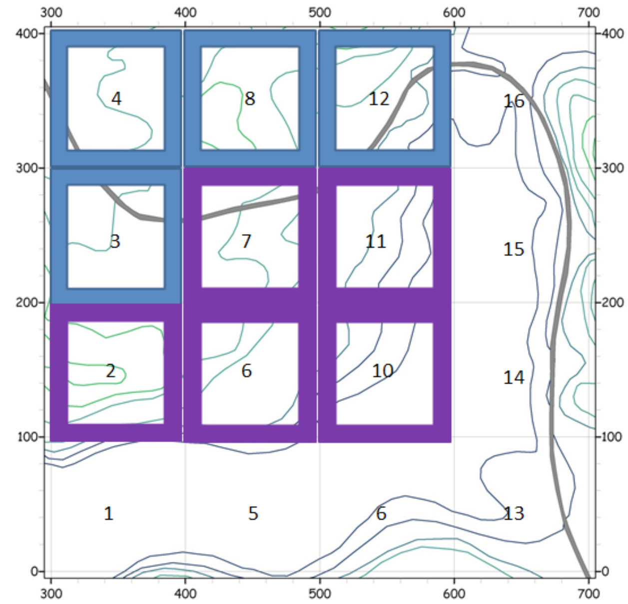

Figure 1. Topographic map of the 16-hectare CTFS/SIGEO plot at SERC. The plots censused in 2011 are outlined in blue, those studied in 2012 are outlined in purple, and the road that goes through the study area is depicted as a gray line. North of hectares 4 and 8 is a logged forest. A wetland area is present in hectares 1, 5, 6, and 13-16 (Figure created by N. Angeli).

MATERIALS AND METHODS

Study Site

This study took place at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland. The 16-hectare plot located at SERC is a mixture of floodplain and mature secondary forest. The canopy is composed of about 40 tree species and around 150 different understory plant species, including invasive species such as wineberry and Japanese honeysuckle (*Lonicera japonica*) (Parker et al., 2010). The site is impacted by a one-lane road that passes through the northern part of the study area. Additionally, an area to the north was logged in 2006-2007 and now has fruiting plants of many invasive species. Seven of the 16 hectares are located in floodplain and were excluded from this study, resulting in a nine hectare square of primarily upland forest study area (Fig. 1).

Each of the 9 hectares had previously been surveyed and every 10m distance was marked by PVC pipe in order to divide each hectare into one hundred 10m x 10m plots. Each of these plots was divided into 2m x 2m subplots, resulting in 22,500 total subplots that were censused over the course of two consecutive summers, from late May to late July in 2011 and 2012. Estimates of canopy cover, bare ground, coarse woody debris, and the invasive plant species present were recorded for each subplot.

Canopy Cover Estimate and Height Class

An 8m telescoping pole was extended above the center of each subplot in order to determine whether leaf cover was present at each of four height class categories (0-2m, 2-5m, 5-10m, and above 10m). A densitometer was used to confirm that the pole was perfectly vertical and to constrain the observer's view to the area directly above the subplot. If woody plant leaves covered > 25% of the vertical projection of the subplot within a height class, it was denoted with a value of one, while absence of leaf cover was denoted by a zero. Thus a plot in which there was no cover would receive a score of 0000 while one in which there was cover in all four height classes was scored as 1111. Each subplot was given a canopy height class score ranging from one to five based on the height of the highest class with foliage (Table 1).

Bare Ground, Coarse Woody Debris, Wet Ground, and Road Estimate

To estimate bare ground, road, wet ground, and coarse woody de-

Category Description	Height Class
No Cover (0000)	1
Cover from 0-2m (1000)	2
Cover 2-5m and below (0100, 1100)	3
Cover 5-10m and below (1110, 0110, 0010)	4
Cover 10m and below (0001, 0011, 0111, 1111)	5

Table 1. Canopy cover and derived height class.

Cover Class	Percent Cover
1	<1
2	1-4
3	5-9
4	10-25
5	26-50
6	51-75
7	76-91
8	92-96
9	97-99
10	>99

Table 2. The cover class system used to determine road, bare ground, and coarse woody debris estimates for each 2m x 2m subplot.

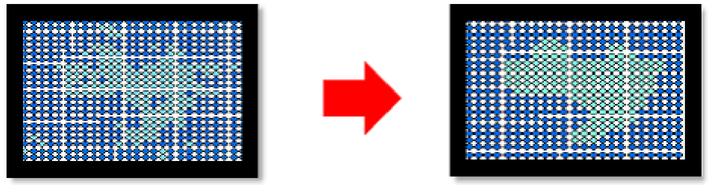

Figure 2. Example of gap delineation using focal statistics. The left image depicts a 20m x 46m area from hectare 3 with each subplot scored as low canopy (light green) and high canopy (blue). The resulting image on the right, which depicts the median values for each subplot, shows one contiguous gap (light green).

Invasive Plant Species	Frequency in 2m x 2m Subplots (this study)	Frequency in 1m x 1m Plot (Parker et al. 2010)
Lonicera japonica (Japanese honeysuckle)	41	49
Berberis thunbergii (Japanese barberry)	9	2
Rubus phoenicolaisus (Wineberry)	6	34
Rosa multiflora (Multiflora rose)	5	30
Celastrus orbiculatus (Oriental bittersweet)	4	-
Ligustrum vulgare (Wild privet)	1	-
Microstegium vimineum (Japanese stiltgrass)	1	23
Hedera helix (English ivy)	0.3	3
Eleagnus umbellata (Autumn olive)	0.1	-

Table 3. Frequency of each invasive plant species per 2m x 2m subplot for this study and 1m x 1m quadrants for Parker et al. (2010)

bris in each subplot, a modified Daubenmire cover class system (Daubenmire, 1959) was used (Table 2).

Invasive Plant Species Census, Richness, and Frequency

The presence of invasive plant species was recorded in each sub plot, including those listed in Table 3. Species richness was determined for each subplot by counting the number of distinct invasive plant species present. The frequency of each invasive plant species was calculated from the invasive plant presence/absence data.

DATA ANALYSIS

All subplots containing road and wet ground were excluded from the species richness and frequency calculations, leaving 22,206 subplots in the analysis.

Spatial Analysis

The invasive plant species richness and canopy height class data from Excel (Microsoft 2003) was imported into ArcMap 10.1, a GIS (Global Information System) software program developed by Esri Corporation (ESRI 2012). The invasive plant species richness data was then used to create a feature class and then a raster layer in ArcMap.

Gaps were defined by a 10m threshold (Runkle 1982; Wright, Mullur-Lanau, Condit, & Hubbell, 2003). Subplots with canopy present above 10m were given a value of two in GIS and those with no canopy present above 10m were given a value of one. The median value of each subplot and its eight surrounding subplots (e.g., a 3m x 3m square with the target subplot at the center) was calculated using focal statistics in ArcGIS (Fig. 2). This operation enabled us to delineate contiguous gap areas and remove isolated subplots of high canopy within gaps or low canopy not within a gap. The result was a GIS feature layer of gaps represented by 2x2 m subplots with median scores of one.

To examine the relationship between gaps and invasive plant species richness, the invasive plant species richness layer was overlaid on the gap layer in GIS. The gap and non-gap assignments of subplots were exported into Excel, enabling us to determine the distribution of species richness values (0, 1, etc.) for all gap subplots and for all non-gap subplots. These values were then converted to two cumulative frequency distributions (species richness of gap subplots, species richness of non-gap subplots) and a Kolmogorov-Smirnov two-sample test (Sokal & Rohlf, 1995) was used to determine if these two cumulative distributions were

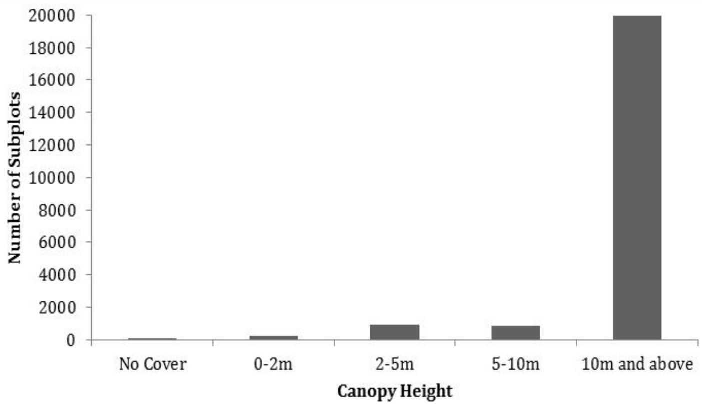

Figure 3. Frequency of subplots of each canopy height class. The bars represent the count of 2m x 2m subplots with no canopy cover or a canopy height of 0-2m, 2-5m, 5-10m, or ≥10m.

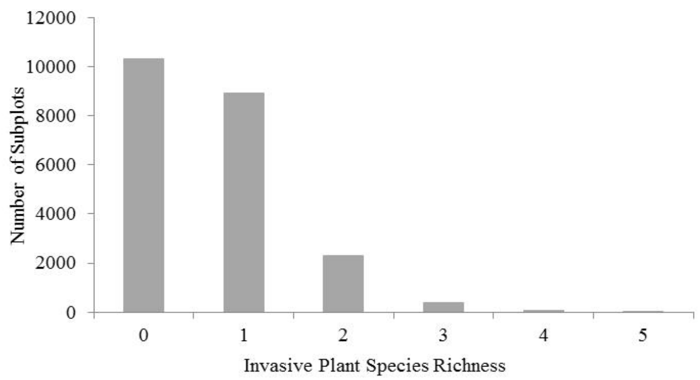

Figure 4. Number of subplots with each level of each invasive plant species richness. The number of 2m x 2m subplots with an invasive species richness of 0, 1, 2, 3, 4, or 5.

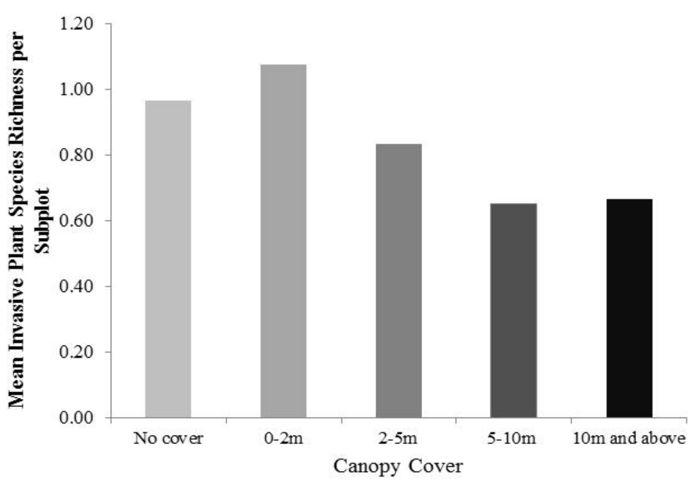

Figure 5. Mean invasive plant species richness per subplot stratified by canopy height class. The mean invasive plant species richness for the 2m x 2m subplots within the no canopy cover, 0-2m, 2-5m, 5-10m, and ≥10m canopy cover classes.

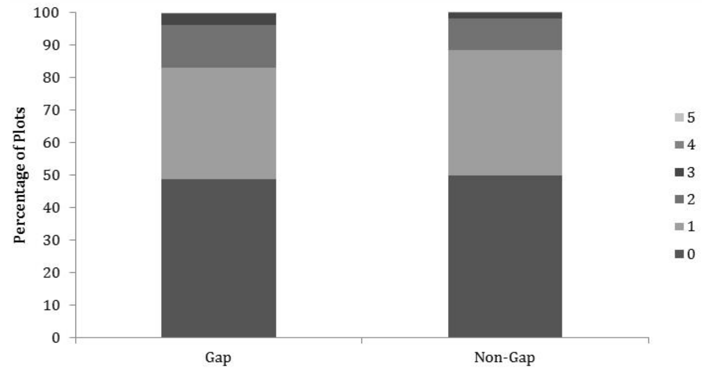

Figure 6. Percentage of gap and non-gap plots within each invasive plant species richness category. The bars represent gap and non-gap plots, respectively, stratified by the percentage of all gap and non-gap 2m x 2m subplots having a species richness of 0, 1, 2, 3, 4, or 5.

significantly different. Whether species richness at the subplot level differed between plots with more or less coarse woody debris (26-100% vs. 0-25% cover) was also tested using a Kolmogorov-Smirnov two-sample test (Sokal & Rohlf, 1995).

Gap Size Determination

The area of each gap polygon created using GIS was measured by converting the gaps from raster to polygons. The gaps were then split into three size classes: small (< 200m^2), medium (200-400m^2), and large (> 400m^2) (Runkle & Yetter, 1987).

RESULTS

Invasive Plant Species Richness and Frequency per Subplot

The mean invasive plant species richness per subplot was 0.68 and the maximum number of invasive plant species encountered in a subplot was five. The four most frequent invasive plant species were *L. japonica*, *Berberis thunbergii*, *R. phoenicolasius*, and *Rosa multiflora* (Table 3).

Frequency of Subplots of each Canopy Height Class and Invasive Species Richness

The majority (95%) of the subplots had canopy cover present above 10m (Fig. 3). No invasive plants were observed in 50% of the subplots and relatively few subplots (approximately 12%) had an invasive plant species richness of two or higher (Fig. 4).

Mean Invasive Plant Species Richness per Subplot and Canopy Class

Subplots with canopy cover present only in the 0-2m height class had the highest invasive plant species richness, surpassing subplots with no canopy cover. Subplots with no canopy cover had greater invasive plant species richness than subplots with canopy cover above two meters (Fig. 5).

Invasive Species Richness in Gaps and Non-Gaps

Non-gap subplots had a slightly higher percentage of subplots with an invasive species richness of one, while gap subplots had slightly more subplots with an invasive species richness of two, three,

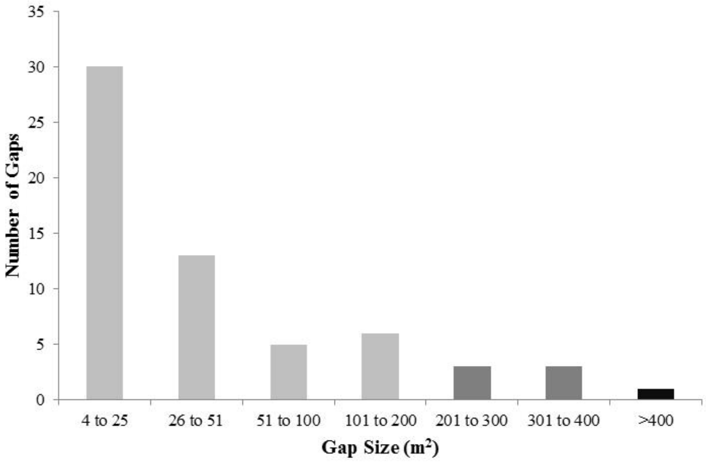

Figure 7. Number of gaps of each size class. Light gray, dark gray, and black bars represent small, medium, and large gap size classes, respectively.

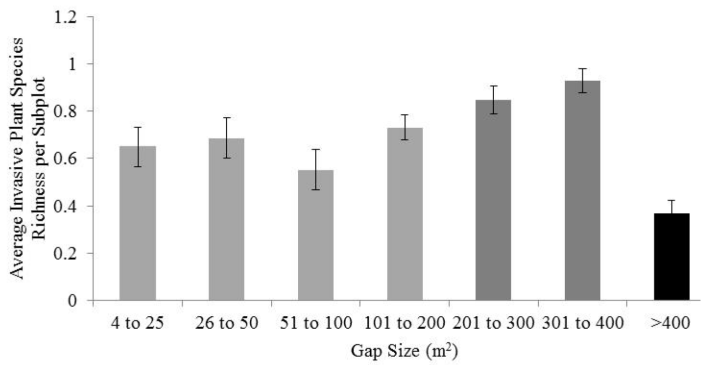

Figure 8. Mean invasive plant species richness per subplot stratified by gap size. Error bars show the standard error of richness values for all subplots in each size class. Light, medium, and dark gray bars indicate gaps in the small (<200m^2), medium (200-400m^2), and large (>400m^2) size classes, respectively.

and four (Fig. 6). The four subplots that contained five invasive species, the maximum encountered in a subplot, were all non-gap subplots. However, around 95% of subplots surveyed were non-gap plots. These differences in invasive species richness between gap and non-gap subplots were not significant (D = 0.036, $D_{.05}$ = 0.041, $p > 0.05$).

Gap Size and Invasive Plant Species Richness

There were many more small gaps (< 200m^2) than medium gaps (200-400 m^2), and only one large gap (> 400 m^2) (Fig. 7). The highest mean invasive plant species richness was found in medium-sized gaps (Fig. 8). There was lower mean invasive plant species richness in small gaps and the lowest mean invasive plant species richness was found in the large gap (Fig. 8).

Spatial Distribution of Invasive Plant Species Richness

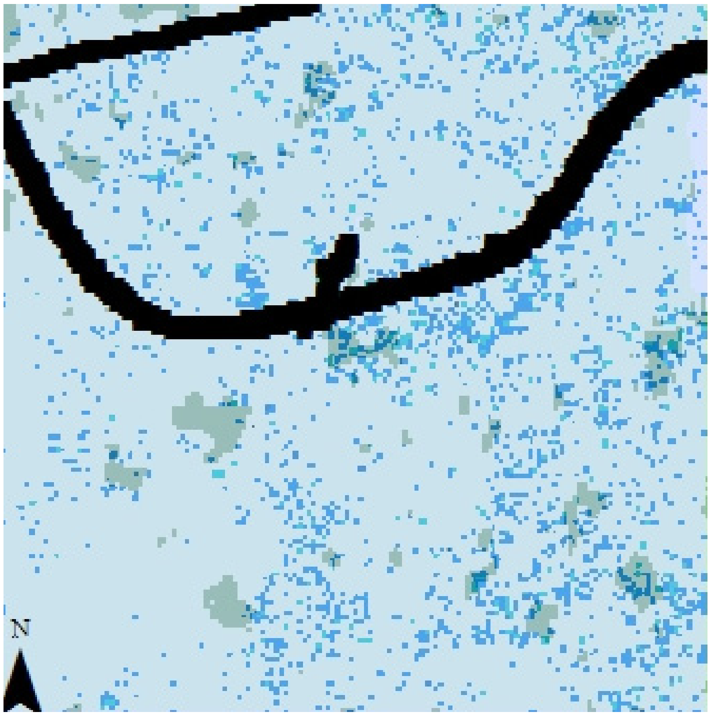

Figure 9. GIS image of the nine-hectare study area showing invasive species richness and canopy gaps. The gaps are represented as shaded gray areas while non-gap areas appear in a very light blue. Areas with higher invasives species richness are depicted by darker blue and those with lower invasive species richness are represented by lighter blue. The roads are depicted as black lines.

While some of the gaps had high invasive plant species richness, there was also high invasive plant species richness in some non-gap areas (Fig. 9). While higher invasive plant species richness visually appears to be present in patches, these patches do not ap pear to be closely associated with gaps or roadsides (Fig. 9). The area with the highest invasive plant species richness was the area in the northeastern corner bordered by wetland.

Invasive Species Richness and Coarse Woody Debris

The majority of the subplots in each coarse woody debris cover class had an invasive species richness of 0 (Fig. 10). However, subplots with a higher percentage of coarse woody debris cover had higher invasive plant species richness, with the highest invasive plant species richness being present in subplots with more coarse woody debris cover (Fig. 10). The invasive plant species richness in subplots with ≤ 25% coarse woody debris cover differed significantly from those with > 25% coarse woody debris cover (D = 0.079, $D_{.05}$ = 0.057, $p < .05$).

DISCUSSION AND CONCLUSIONS

Invasive plant species have numerous negative economic and environmental impacts on the areas they invade, and understanding what conditions promote their spread may help to mitigate these negative impacts in the future. Our initial hypothesis was that treefall gaps provide ideal conditions for the establishment and spread of a variety of invasive plant species in deciduous forest. This hypothesis was not supported by the data, as the invasive species richness of subplots in gaps was not significantly greater than those under closed canopy forest. We did, however, find an association between coarse woody debris cover and invasive species richness, indicating that coarse woody debris may promote the spread of invasive plant species into forested areas.

The exotic plant species richness per 2m x 2m subplots in this study ranged from zero to five plant species. A previous study at SERC found that the invasive plant species richness ranged from 0-4in 1m x 1m quadrants (Parker et al., 2010). Overall, species richness did not vary between areas with and without treefall gaps, but invasive plant species richness did appear to be higher in medium-sized (200-400m^2) gaps and subplots with greater coarse woody debris cover (Figs. 4, 6, and 7). Invasive plant species richness did not appear to be higher in areas closer to the logged forest, was higher in subplots closer to the wetland, creek, or road (Fig. 8).

Fallen tree debris and subsequent coarse woody debris could serve as a nutrient source for invasive plants and impact the invasibility of the site. As the debris decays over time, different nutrients are released into the soil through decomposition and made available to invasive plants that can utilize the input of nutrients (Davis, Grime, & Thompson, 2000). As coarse woody debris decays over time, it can serve as a source of nitrogen and phosphorus (Laiho & Prescott, 2004). However, depending upon rate of decay, the composition of the debris, and substrate quality, decades may pass before coarse woody debris becomes a source of nitrogen or phosphorus (Laiho & Prescott, 2004). Thus, the age of gaps also has an effect on nutrient availability from coarse woody debris. Gaps with debris at later stages of decay may add more nutrients to an area and sustain a higher richness of invasive plants. We suggest that treefalls may not initially change local amounts of nitrogen or phosphorus initially, but later elevate nutrients in the soil, thereby promoting invasion.

The frequencies for different invasive plant species reported in this study (Table 3) differ from those found by Parker et al. (2010). In our study, *B. thunbergii* had higher frequency, *L. japonica* had similar frequency, and the other species had much lower frequencies than reported by Parker et al. (2010). These differences may have been due to the location of the plots examined. While all of the plots in this and the 2010 study were located in SERC research forests, the plot locations in the 2010 study were widespread and most were outside the nine-hectare area censused, and thus likely spanned greater environmental variation.

While invasive plant species richness was not higher in treefall gap than non-gap areas as we had predicted, other factors may have played a role in the invasive species richness across the site (Fig. 8). Invasive richness in parts of the study area might have been impacted by the propagule pressure from the logged forest located to the north of the site and open areas along the nearby pond. However, invasive species richness adjacent to the logged area was not higher in comparison to other portions of the study area. This agrees with Klinczar's (2014) finding that none of the four most common invasive species were significantly denser near the logged area at this site (Fig. 1). The pond edge at the northeast edge of our study area, as well as the wetland area along the east and southeast, likely served as a propagule sources, as richness tended to be highest in subplots close to these features (Fig. 9). Similarly, Klinczar (2014) found the densities of *L. japonica* and *R. multiflora* to be greater in the wetland area than in the upland portion of the forest. This trend may have been due to more light reaching the understory near the pond and in the wetland, where trees were smaller. Additionally, wetlands and rivers can impact plant invasions by providing areas of disturbance from periods of flooding and drought, changing nutrient availability and water flow (Davis et al., 2000). The road may serve as a seed source of invasive plants and as an area of increased disturbance. We also found that invasive species richness is slightly higher near the road than further into the forest. Klinczar (2014) also showed that one of the four common invasive species, *R. phoenicolasius*, was present in higher densities near the road.

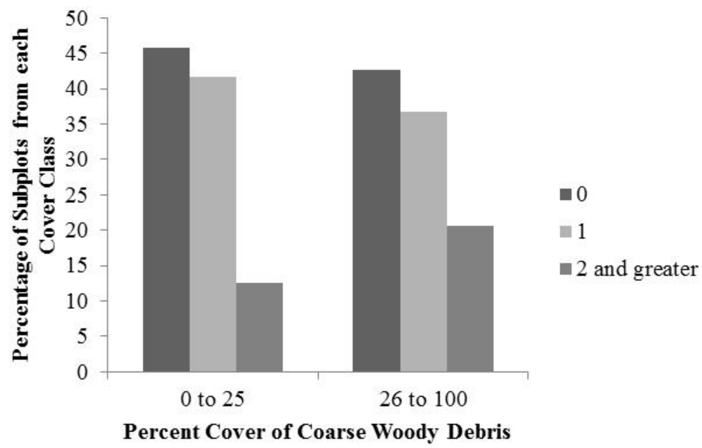

Figure 10. Percentage of subplots with invasive plants species richness, stratified by coarse woody debris cover class. The bars represent the percentage of each 2m x 2m subplot within the 0 to 25 or 26 to 100% cover class of coarse woody debris that had an invasive species richness of 0, 1, or 2 or greater.

Overall, it does not appear that invasive species richness is higher in treefall gaps. However, some gaps did have high invasive plant species richness, while others did not. This difference could be a result of differences in gap age. Older gaps may have more established invasive plant species than younger gaps (Brokaw, 1982).

While invasive plant species richness did not appear to be correlated with treefall gaps, mean invasive plant species richness was highest in medium-sized gaps (200-400m^2) compared to large and small gaps. This could be a result of the amount of light saturation and penetration in gap areas. Larger gaps could have levels of light too high for certain shade-intolerant invasive plants. In fact, certain species may actually be adapted for small gap conditions, while others are adapted for large gap conditions (Denslow et al., 1987). Medium-sized gaps may provide for intermediate light levels that provide enough light for shade-intolerant plant species, but also provide enough shade to support shade-tolerant plant species. The low invasive species richness in gaps could also have been a result of the small subplot size (2m x 2m). Different trends may be seen at a larger spatial scale. Some invasive plant species may be better at colonizing the high-light environment at the "center" of the gap while others might be better able to establish along gap edges. Thus if the entire gap area was examined, the invasive species richness in gaps may be higher than in the areas of the forest with intact canopy.

While gaps did not have significantly higher invasive plant species richness, we also found that invasive plant species richness is greatest in plots with no canopy cover above 2m (Fig. 5). An explanation for this discrepancy could be the differences in the sample size for each canopy height class. Only a few subplots had no canopy cover or no canopy cover above 2m (Fig. 3). Most of the subplots within gaps had canopy heights of 2-10m, and the invasive richness of these subplots was about the same as for those with canopy > 10m (Fig. 5).

We conclude that the presence of gaps was not the major predictor of invasive plant species richness in this deciduous forest. Other aspects of treefalls, such as gap age or the amount of coarse woody debris, may be more important to invasive species than is canopy openness. Understanding the role of gap age and forest/wetland edges may provide valuable answers to how invasive plants spread and establish in forested areas.

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