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The effect of treefall gaps on the spatial distribution of three invasive plants in a mature upland forest in Maryland^{1,2}

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Abstract. Invasive plants impact native plant and animal species, communities, and ecosystems. We explore the role of treefall gaps in facilitating invasive species growth. We measured the frequency and density of different life stages of three invasive species: *Rubus phoenicolasius*, *Berberis thunbergii*, and *Rosa multiflora* in an eastern deciduous mature forest. Gaps were important for the establishment, growth, and reproduction of *R. phoenicolasius*, growth of *R. multiflora* and reproduction of *B. thunbergii*. We present several hypotheses as to why we observed a species-specific response of invasive plants to treefall gaps, including propagule rain as a driver of invasive plant establishment.

Key words: canopy gaps, disturbance, invisibility

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Invasive plants make up a large subset of invasive species; the United States alone harbors over 1,500 plants that are invasive (Vitousek *et al.* 1996). Invasive plants impact native plant and animal species, communities, and ecosystems (Vila *et al.* 2011). These impacts make it important to understand the factors that promote exotic plant invasion.

One of the most prominent factors that influence invasion is invasibility (Williamson 1996), defined as the intrinsic susceptibility of an area or region to invasion (Lonsdale 1999). Invasibility is hypothesized to be higher in areas where there is a surge of available resources (Davis, Grime, and Thompson 2000). Such areas include disturbances, as they increase the flux of resources which can then be

utilized by invasive plants (Davis *et al.* 2000, With 2002), although evidence that disturbance promotes plant invasion is mixed (Moles *et al.* 2012). In forested areas, canopy disturbances (*i.e.*, treefall gaps) are a facilitator of exotic plant invasion (*e.g.*, Hutchinson and Vankat 1997, Eschtruth and Battles 2009, Burnham and Lee 2010, Gorchov *et al.* 2011). Canopy disturbance promotes invasion by creating gaps that reduce competition, enabling poorer competitors to colonize (*e.g.*, Henry and Swan 1974, Forcier 1975, McClure and Lee 1993). Competition reduction includes higher light availability to understory plants and an increase in bare ground exposure (Denslow 1987, Webb 1999).

HYPOTHESES AND PREDICTIONS. Our hypothesis was that treefall gaps promote plant invasion. We predicted that invasive plant density would be higher in gaps versus nongap areas. We predicted that seedling recruitment and establishment would be restricted to gap areas, although established plants might be able persist in closed canopy. We also predicted that fruit production would be limited to gap areas. We predicted that the density of invasive plant species would be positively associated with gap size, due to greater resource availability in larger gaps.

Methods. STUDY SITE. This study took place in a 16-ha forest dynamics plot established in 2007 at the Smithsonian Environmental Research Center (SERC), about 10 km southwest of Annapolis, MD, on the western shore of the Chesapeake Bay. The boundaries of the square plot are 38.887 to 38.891°N and 76.562 to 76.557°W. The plot is in the coastal plain physiographic province and has a substrate of deep sediments; elevation is 0.2–12.0 m with a slope averaging $8.4^\circ \pm 7.2^\circ$. Precipitation averages 1068 mm annually; the mean temperature is 13.2°C (Anderson-Teixeira *et al.* 2014).

This plot is part of a network of plots for the Center for Tropical Forest Science (CTFS), a global forest study system. The Center utilizes 47 forest plots for studying forest science and ecosystems, climate change, forest management, and policy (Anderson-Teixeira *et al.* 2014).

This SERC plot is comprised primarily of upland deciduous forest, developed on what was likely a pasture abandoned in the late 1800s (G. Parker, personal communication). Prominent trees in the overstory of the upland forest are *Liriodendron tulipifera*, *Carya* spp., *Quercus* spp., *Fagus*

grandifolia, and *Liquidambar styraciflua*. Understory trees include *Cornus florida*, *Carpinus caroliniana*, *Acer rubrum*, and *Ilex opaca*, along with the shrubs *Viburnum dentatum* and *Lindera benzoin* (Parker, O'Neill, and Higman 1989). Bordering this mature upland forest is floodplain forest dominated by *Fraxinus* spp., *Platanus occidentalis*, and *Ulmus americana* (SERC 2012). Mean basal area is 40.8 m² ha⁻¹ and above-ground biomass is 381 Mg ha⁻¹ (G. Parker, personal communication).

Our study area was 9 of the 16 ha that was comprised of contiguous upland forest (Fig. S1). On the eastern side of the 9 ha study area, a buffer zone of 800 m² was excluded because it was completely covered by standing water. In the southeast corner of the 9 ha, a creek runs south to north (Fig. S1). Adjacent and southeast of the creek was an area (approx. 7,800 m²) also determined to be floodplain based on elevation < 2.5 m, relative to the lowest area in a 2011 digital elevation model (DEM; Anne Arundel County 2011), which was censused in this study, but excluded from many of the analyses (Fig. S1). We surveyed four of the hectares in the summer of 2011, and the remaining five in the summer of 2012.

The northwest corner of the 9 ha study area is located just south of a younger stand that was logged from the fall of 2006 through the spring of 2007 (G. Parker, personal communication, November 2012; Fig. S1). The logging made this stand highly invasible, and by 2011 it had high densities of several invasive plant species.

There are two roads in the study area: a gravel road in the northeast corner of hectare 4, and a one-lane paved road (Fig. S1). The northwest corner of the study area, north of the gravel road, was part of the logged stand, so data from these plots were excluded from many of the analyses.

We utilized an existing 10 m grid of PVC pipes to divide the study area into 2 × 2 m subplots.

STUDY SPECIES. Three invasive plant species of interest were chosen based on their high frequency in this stand: *Rubus phoenicolasius*, *Berberis thunbergii*, and *Rosa multiflora*; the ecology of these species is reviewed in Klinczar (2014). These species have been present in the study area or its vicinity for > 45 yr. All three species are native to East Asia.

Rubus phoenicolasius was present in the 1960s at SERC; however, it was restricted along roads.

About 20 years ago, it started to spread into the 16 ha forest site (D. Whigham, personal communication, April 2014). This species has higher growth and survival in high light, and is therefore found in habitat edges and forest gaps (Spencer 2002a, Swearington *et al.* 2002). Gorchov *et al.* (2011) showed that, although canopy gaps are needed for this species' establishment and fruiting in mature forest, they are not necessary for persistence.

Berberis thunbergii was established in forests immediately adjacent to SERC, and invaded the 16-ha forest about 35 years ago (D. Whigham, personal communication, April 2014). *Berberis thunbergii* is a shrub that requires high sunlight for seedling establishment, but mature plants can be found in dense canopy areas. This species can invade and form dense patches in fields, deciduous forests, and roadsides (Randall and Marinelli 1996, as cited by Silander and Klepeis 1999). Fruit production is high in areas of high light (Silander and Klepeis 1999).

Rosa multiflora has been established in the SERC forest and along the roads for over 45 years (D. Whigham, personal communication, April 2014). *Rosa multiflora* can invade mature forests but has higher growth and reproduction in areas such as thickets, edges, and riparian areas that have more sunlight (Robertson, Robertson, and Tague 1994). This plant is a shrub, but does have the ability to climb trees (Steavenson 1946, Banasiak and Meiners 2009).

Seeds of all three species are dispersed by vertebrates (Kern 1921, as cited by Silander and Klepeis 1999; Amrine and Stasny 1993; Nuzzo 1997; Otani 2003).

FIELD METHODS. In each subplot, we counted the number of individuals of each of the three focal species for each of three life history classes: single-stem sterile, multistem sterile, and fertile individuals. This distinction was made because these parameters are representative of relative age, as plants will progress from a single-stemmed plant to a multistemmed plant, and then become fertile. We pooled fertile and multistem sterile *R. multiflora* individuals into one multistem group for analyses, because only three fertile individuals occurred in the whole study area. For five of the hectares, a seedling life history class for *B. thunbergii* was also identified. Plants of all life history stages were considered distinct individuals (ramets) based on a 10 cm distance between shoots. For *R. multiflora* and *B. thunbergii*, the tallest plant in each subplot

was identified and measured. This was not done for *R. phoenicolasius* because stems are not erect.

For each subplot, we assessed canopy height. For each of four canopy strata (0–2 m, 2–5 m, 5–10 m, and above 10 m) we assessed if at least 25% of the area above each subplot was covered (denoted by a 1) or uncovered (denoted by a 0) by leafy branches of woody vegetation. This was done using the aid of a telescoping pole, which extended to 8 m, and a densitometer, which allowed for an aerial view directly above the subplot.

DATA ANALYSIS. For analysis, we used ArcGIS 10.1 (ESRI 2012) and the statistical environment R (R Core Team 2012), utilizing RStudio 2.15.1 (2012; RStudio, Inc., Boston, MA). For data exportation out of ArcGIS into Excel, we used Geospatial Modeling Environment 0.7.2.1 (Bever 2009–2012). The subplot points did not have spatial coordinates (they were unprojected) when they were input into ArcGIS, and had to be georeferenced to subplot centroids using the spatial adjustment tool in ArcGIS. For this we used the 10 m grid plot centers locations, which had been calculated by SERC research staff from the 10 × 10 m grid that was surveyed using a Topcon Total Station CTS-2 (Topcon Positioning Systems Inc. Itabashi, Tokyo, Japan) to the nearest centimeter.

Assessing Treefall Gaps. We used a 10 m canopy height threshold to distinguish treefall gap areas (Runkle 1992, Wright *et al.* 2003, King and Antrobus 2005). First, each 2 × 2 m subplot was classified as low canopy (1) or high canopy (2) based on whether canopy cover was scored as present for the > 10 m height class. This classification method led to some isolated subplots that were assessed as high canopy but surrounded by low canopy area, as occurs when a subcanopy tree remains standing in a treefall gap. These isolated subplots would not be shaded sufficiently to result in nongap conditions. Similarly, a subplot under low canopy does not necessarily experience gap conditions if the conditions surrounding it are high canopy. Therefore, we created more contiguous gap and nongap areas by considering not only the canopy height of the subplot, but also the canopy height of adjacent subplots. We assigned subplots to be gap or nongap based on the median canopy class (1 or 2) for the subplot and the eight neighboring

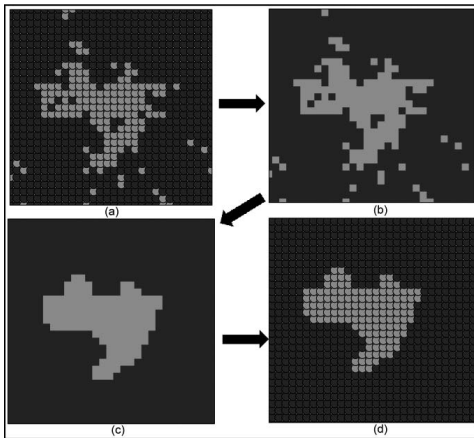


FIG. 1. The process of using the focal statistics tool to convert values of low canopy (gray) and high canopy (black) to gap (gray) and nongap (black). Raw data (a) is rasterized (b). The focal statistics tool employed a 3×3 square (nine neighboring 2×2 m subplots) to calculate the median of each subplot. The results in raster form (c) and converted back into point form (d).

subplots using the focal statistics tool in ArcGIS (Price 2012, fig. 1; Klinczar 2014).

We used a second, independent method to determine gap locations based on a 1 m light detection and ranging (LiDAR) dataset acquired in the spring of 2004 by the Maryland Department of Natural Resources (DNR; Klinczar 2014). These data were processed by the Maryland DNR to create a canopy height model, which has the height of the canopy at a 1×1 m scale. From this layer, we rescored canopy height in each 2×2 m subplot to reflect high and low canopy based on the same 10 m height threshold as the field data. To assign subplots to gap and nongap areas, we again used the median canopy class for the subplot and the eight neighboring subplots using the focal statistics tool.

For many of the analyses, we used field data and LiDAR data to represent gaps present in 2011–2012 and 2004, calling them field gaps and LiDAR gaps, respectively (Fig. 2a, 2b). From the intersection of these two data layers we distinguished three categories of gaps: persistent gaps (Fig. 2c), which consisted of subplots that were classified as gaps in both layers; current gaps (subplots that were gaps in 2011–2012, but not 2004); and old gaps (gaps in 2004, but not 2011–2012).

Presence/Absence of Invasive Plants in Gap vs. Nongap Areas. Once the gaps were properly

delineated, we determined if each life history stage of each of the three focal species had a higher frequency in gaps than would be expected by chance alone. Separate sets of analyses were done for field gaps and LiDAR gaps. For each of these sets, only subplots in upland forest were examined, and we did separate analyses for each life history stage of each species. In each of these 18 analyses, we ran a Monte Carlo simulation using a Bernoulli distribution, assigning values for the life history stage being present (1) or absent (0; Klinczar 2014). For each simulation, the probability of the Bernoulli distribution was equal to the frequency of this life history stage across all subplots (*i.e.*, the proportion of subplots with at least one individual of that life history stage, and the number of observations (n) was equal to the number of subplots ($n = 19,230$). (For *B. thunbergii* seedlings, n was equal to 10,284 subplots because these were only surveyed in a portion of the study area.) For each observation, a value (0 or 1) was drawn randomly from this Bernoulli distribution. We separately drew a gap (1) or nongap (0) subplot from the dataset, which contains all of the gap and nongap values for both field and LiDAR gaps (4.70% of subplots in the field dataset were gaps, and 2.67% of subplots in the LiDAR dataset were gaps). These two draws (presence/absence of species life history stage; gap/nongap) were paired together to determine how many subplots that were in gaps had this life history stage present in this simulation. The total number of subplots that had this life history stage present was also summed. Each simulation was run 4,000 times, which was the maximum number of simulations that could be processed at one time. From these 4,000 runs, we constructed a frequency distribution for the proportion of subplots with this life history stage that occurred in gaps due to chance alone. The observed proportion of this life history stage that was in gaps was compared to this distribution to determine the probability of obtaining that proportion, or a greater proportion, by chance alone.

Density in Gaps vs. Nongap Areas. We used the zonal statistics spatial analysis tool in ArcGIS to calculate the mean density of each life history stage of each invasive species in the four types of gap conditions based on the intersection of the LiDAR and field gap data layers: old gaps, current gaps, persistent gaps, and nongaps. We determined the standard error for each mean density; however,

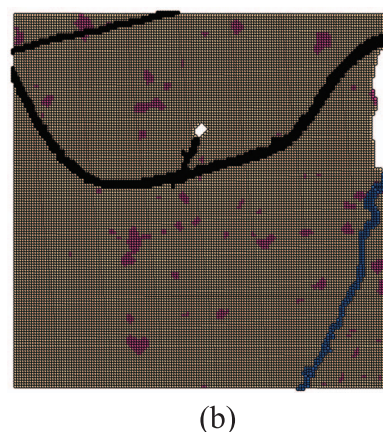
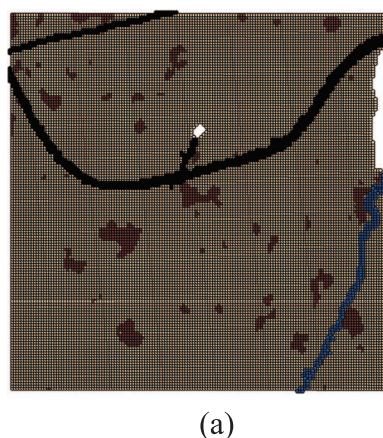


FIG. 2. Gap delineations for (a) 2011–2012 field gaps (brown); (b) 2004 LiDAR gaps (pink); and (c) old gaps (pink), current gaps (brown), and persistent gaps (green). Persistent gaps represent subplots that were gaps in both the 2004 LiDAR data and the 2011–2012 field data. For all figures, nongap areas are represented in tan. The creek (blue) runs through

we could not run parametric tests due to the lack of spatial independence of the subplots.

Density and Gap Size. We investigated the impact of gap size on invasive plant density separately for field gaps and LiDAR gaps. For each analysis, each individual gap was designated as a separate zone. We determined the mean density of each life history stage of each species in each individual gap using the zonal statistics tool in ArcGIS. For each life history stage of each of the three invasive plant species, the plot of density versus gap size was best fit with a logarithmic function, so linear regression with log-transformed gap areas was used to determine if there was a significant positive relationship between density and gap.

Results. INVASIVE PLANT FREQUENCIES. Among all 2×2 m subplots in the 9 ha study area, the frequencies of the three focal invasive species were as follows: *B. thunbergii*, 8.51%; *R. phoenicolasius*, 6.65%; and *R. multiflora*, 5.04%. When only subplots within the upland forest were analyzed, the frequencies were: *B. thunbergii*, 9.49%; *R. phoenicolasius*, 9.47%; and *R. multiflora*, 5.15%.

UPLAND VS. FLOODPLAIN DENSITIES. One of the three focal invasive species, *R. multiflora*, had higher densities in the floodplain area than in the upland area (Fig. S2). *Rubus phoenicolasius* had a higher density in the upland area, and *B. thunbergii* density was about the same in the upland and floodplain areas. All subsequent analyses involved only the upland forest and excluded the northwest extreme of the plot that was within the logged stand.

DELINEATION OF GAPS. Gap delineation indicated that in the 2011–2012 upland study area, 4.66% of the subplots were field gap subplots, and 95.34% were nongap subplots (Fig. 2a). Analysis of 2004 LiDAR data indicated that 2.67% of the subplots were in gaps, and 97.33% were in nongap areas

the SE corner. The one-lane road (black) runs through the plot, and the gravel road (black) runs through the NW corner of the plot, representing the boundary to the logged forest, north of the gravel road. On the eastern side of this 9 ha study area, an area of about 800 m^2 was excluded because it was completely covered in standing water (white). In addition, there is a tower near the center of this study area (white), which was fenced off and therefore excluded from the survey.

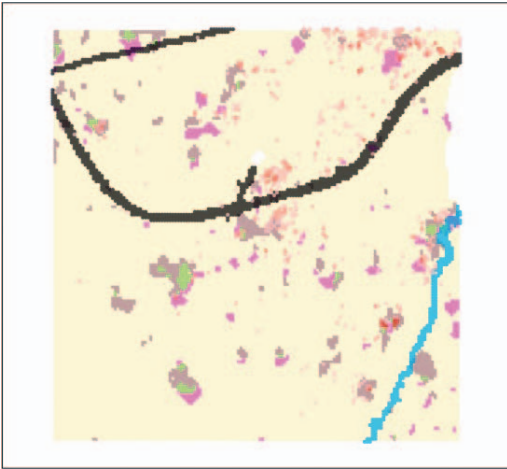


FIG. 3. Map showing density (per subplot) of fertile *R. phoenicolasius* in the 9 ha study area. Subplots where fertile individuals were present are represented in red, with the intensity of the color corresponding to density. Current gaps (brown), old gaps (pink), persistent gaps (pink) and nongaps (tan) are represented. The road (black) and creek (blue) area also shown.

(Fig. 2b). Gaps ranged in size from 8 m² to 532 m² for the field data and 8 m² to 288 m² for the LiDAR data. When these two data layers were combined, only 0.59% of the subplots were gaps in both (*i.e.*, persistent gaps). The remaining area was comprised of current gaps (4.07%), old gaps (2.08%), and nongaps (93.26%; Fig. 2c).

FREQUENCY OF INVASIVE SPECIES IN GAPS VS. NONGAPS. Each of the three life history stages of *R. phoenicolasius* was more frequent in gaps than expected by chance alone, based on the Monte Carlo simulations of a Bernoulli distribution (Table 1); this was true for both field gaps (Fig. S3a–c) and LiDAR gaps (Fig. S4a–c). This association with gaps is illustrated for fertile *R. phoenicolasius* (Fig. 3). For *B. thunbergii*, only fertile individuals were more frequent in gaps than expected by chance, and this was only true for LiDAR gaps (Fig. S4d; Table 1), though not field gaps (Fig. S3d; Table 1). Multistem sterile, single-stem sterile, and seedlings were not more frequent in field or LiDAR gaps (Fig. S3e–g; Fig. S4e–g; Table 1). For *R. multiflora*, the multistem life history stage was more frequent than expected by chance in field gaps (Fig. S3h), but less frequent in LiDAR gaps (Fig. S4h; Table 1). Single-stem

sterile *R. multiflora* individuals were not associated with gaps (Fig. S3i; Fig. S4i; Table 1).

DENSITY OF INVASIVE SPECIES IN OLD AND NEW GAPS. *Rubus phoenicolasius* had a higher density in gaps than nongaps (Fig. 4a). Specifically for fertile plants, the highest density was in persistent gaps, with current gaps having the second highest density. Multistem plants had higher densities in all three gap zones compared to nongap areas. Single-stem plants occurred at a very low density, making it difficult to discern a pattern.

Berberis thunbergii did not differ greatly in density between gap and nongap areas (Fig. 4b). Multistem sterile plants were at somewhat higher densities in current gaps than in the other zones. The other life history stages had densities too low to detect patterns.

For multistem *R. multiflora*, density was higher in current gaps, but lower in old and persistent gaps, compared to nongap areas (Fig. 4c). Density of single-stem individuals was too low to assess density differences.

DENSITIES OF INVASIVES AND GAP SIZE. The only significant relationship between density of a life history stage of a focal species and gap size was the positive relationship between fertile *R. phoenicolasius* and log-transformed size of current gaps, which was fit with a linear regression (Fig. 5). All other relationships were not significant (Klinczar 2014).

Discussion. **IMPORTANCE OF TREEFALL GAPS.** The gap hypothesis was at least partially supported for each of the three study species. Despite these significant effects of gaps, neither reproduction nor distribution was confined to gaps for any of the study species.

Gaps were important for recruitment, growth, and reproduction of *R. phoenicolasius*, as frequencies and densities of each of the three life history stages was higher in gaps than in nongaps. Our findings that persistent gaps had the highest density of fertile individuals, and current gaps the second highest, supports the hypothesis that gaps are important for fruit production. Established *R. phoenicolasius* individuals do not need much light for persistence (Gorchov *et al.* 2011), which likely explains why old gaps retain high densities of sterile plants.

Reproduction of *B. thunbergii* was associated with old gaps (areas that were in gap conditions in

Table 1. Results of the Monte Carlo simulations used to determine if each life history stage of each invasive plant species has a higher frequency in upland forest gaps than expected by chance for both field (2011–2012) gaps and LiDAR (2004) gaps. Subplot frequency is the observed proportion of subplots where this life history stage was present. Observed proportion in gaps represents the number of gap subplots where this life stage was present/the total number of subplots where this life stage was present. The simulated mean (\pm SD) in gaps represents the mean from the Monte Carlo simulation for each life stage, based on its observed frequency and the observed proportion of subplots that were in gaps; the frequency distribution for each simulation is provided in Fig. S3. Significance tests ($* = P < 0.05$, $** = P < 0.01$) were based on the percentage of the simulated frequency of each life history stage in gaps that was greater than or equal to the observed frequency in gaps.

		Field Gaps		LiDAR Gaps	
	Subplot Frequency	Observed Proportion in Gaps	Simulated Mean in Gaps	Observed Proportion in Gaps	Simulated Mean in Gaps
Fertile <i>R. phoenicolasius</i>	0.032	0.153**	0.047 \pm 0.009	0.069**	0.027 \pm 0.006
Multi-stem Sterile <i>R. phoenicolasius</i>	0.045	0.114**	0.047 \pm 0.007	0.059**	0.027 \pm 0.005
Single-stem Sterile <i>R. phoenicolasius</i>	0.013	0.121**	0.047 \pm 0.015	0.078**	0.027 \pm 0.010
Fertile <i>B. thunbergii</i>	0.004	0.047	0.047 \pm 0.028	0.071*	0.027 \pm 0.020
Multi-stem Sterile <i>B. thunbergii</i>	0.069	0.045	0.047 \pm 0.006	0.028	0.027 \pm 0.004
Single-stem Sterile <i>B. thunbergii</i>	0.018	0.042	0.047 \pm 0.011	0.028	0.027 \pm 0.008
Seedling <i>B. thunbergii</i>	0.003	0.037	0.047 \pm 0.028	0.037	0.027 \pm 0.025
Multi-stem <i>R. multiflora</i>	0.040	0.064	0.047 \pm 0.008	0.014	0.027 \pm 0.005
Single-stem Sterile <i>R. multiflora</i>	0.012	0.049	0.047 \pm 0.016	0.036	0.027 \pm 0.010

2004, but had closed by 2011/2012), but not current gaps (which were closed canopy forest in 2004). While mature plants can persist under the canopy (Silander and Klepeis 1999), it is possible that individuals only begin to reproduce if they receive high light for several years, a condition met in some old gaps. The absence of fertile *B. thunbergii* in current gaps could be due to the limited time that the shrubs within these gaps would have been exposed to light, presumably insufficient time to mature and produce fruits. Alternatively, the association of fertile *B. thunbergii* with old gaps may be due to nutrient flux rather than light. Peak nutrient availability in soils of gaps may be years after canopy opening, due to slow decomposition of coarse woody debris (McGee *et al.* 2007). For *B. thunbergii* there was no evidence that seedling establishment or growth of established individuals was enhanced by gaps.

Gaps were important for growth of *R. multiflora*, based on our findings that the frequency and density of multistem, but not of single-stem *R. multiflora* were higher in current gaps. The hypothesis that gaps promote *R. multiflora* growth also leads us to predict that persistent gaps would also have a high density of multistem plants, but this was not observed. Conceivably, the low density of *R. multiflora* in persistent gaps was due to competition from *R. phoenicolasius*, which had high density in persistent gap subplots. However, *R. phoenicolasius* was present in only 25% of persistent gaps, and therefore cannot be the explanation for the low density of *R. multiflora* in persistent gaps. Furthermore, density of *R. multiflora* was not negatively associated with gaps that had high densities of *R. phoenicolasius*. While gaps promoted *R. multiflora* growth, they were not important for reproduction. None of the three fertile individuals in our study area were in

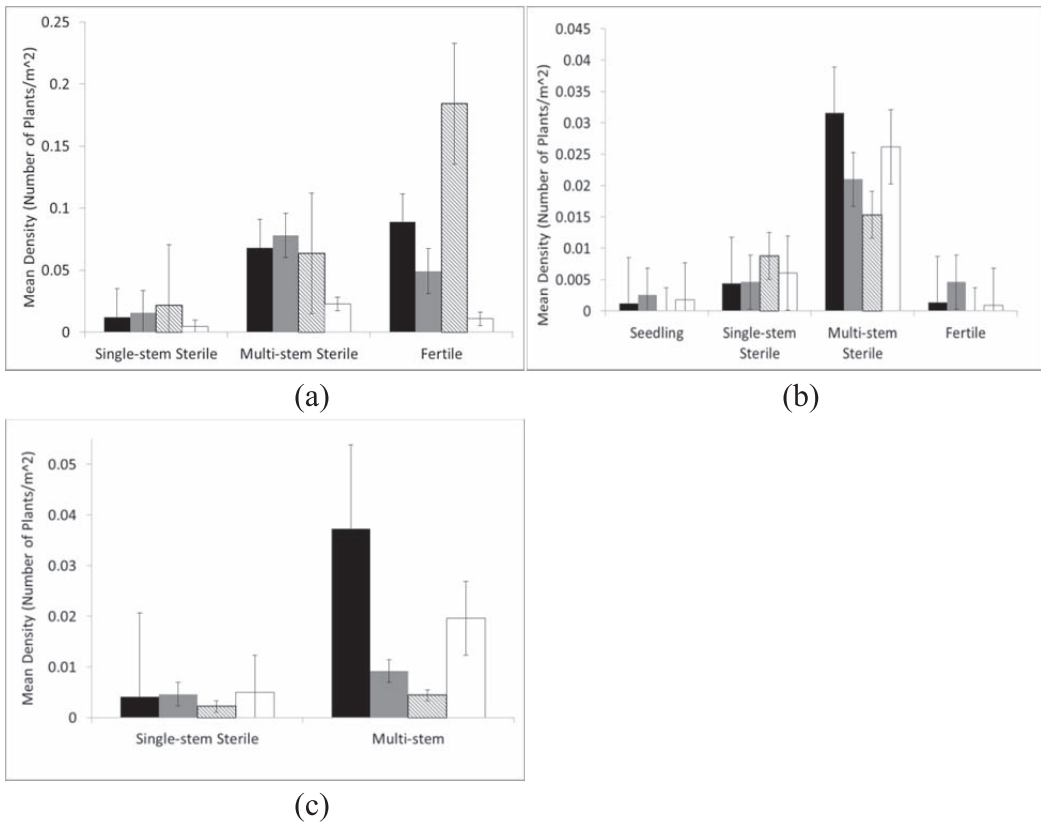


FIG. 4. Mean (+ SE) subplot density of each life history stage of (a) *Rubus phoenicolasius*, (b) *Berberis thunbergii*, and (c) *Rosa multiflora* in upland forest for current gaps (black), old gaps (gray), persistent gaps (diagonal stripe), and nongaps (white).

gaps, suggesting that the gaps in this study area may not have enough incident light for reproduction (Ambler *et al.* 1965). The fact that two of these three fertile plants were found in the floodplain area suggests that edaphic conditions

are more important than high light for fruit production, at least in our study area. Edaphic conditions were also likely important for establishment and growth, as *R. multiflora* density was greater in the floodplain than in our upland focal area, consistent with previous reports associating this species with riparian zones and some wetlands (Robertson 1994, Spencer 2002b).

Gap size did not have a very significant effect on invasive plant density, as fertile *R. phoenicolasius* was the only life history stage to have a relationship with gap size, and only for current gaps. Furthermore, this positive effect of gap size on fertile *R. phoenicolasius* density was not that strong ($R^2 = 0.14$). The reason that other life history stages of the focal invasive species were not significantly denser in larger gaps may be due to low power of the regression; there were very few large gaps, and each species was absent in many of the gaps.

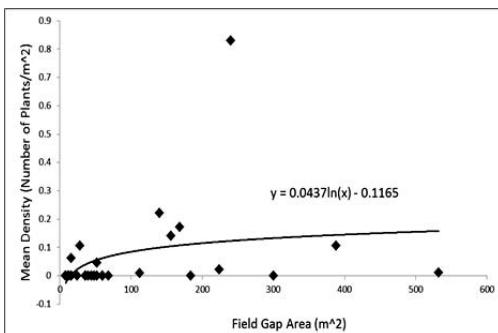


FIG. 5. The relationship of mean density of fertile *Rubus phoenicolasius* versus gap area for field gaps. The regression of density on log-transformed gap area was significant ($F_{1,36} = 0.378$, $R^2 = 0.143$, $P = 0.019$).

There is evidence that the distribution of these invasive plant species was also influenced by propagule rain (Williamson 1996, Lockwood, Cassey, and Blackburn 2009). For *R. multiflora*, the floodplain was likely the major source of propagules, as two of the only three fertile plants were found there. Distance from the floodplain was a significant predictor of log-transformed density of *R. multiflora* within the upland forest, with greater densities closer to the floodplain (Klinczar 2014). Similarly, density of *R. phoenicolasius* showed a significant negative regression on distance to the one-lane paved road (Klinczar 2014), a likely source of propagules given the high density (0.06 plants/m²) of fertile *R. phoenicolasius*, in close proximity (1–5 m) to the road. While not as high as the density of fertile *R. phoenicolasius* in persistent gaps (0.18 plants/m²), it is about the same as the density in current gaps (0.09) and old gaps (0.05), and much higher than in nongaps (0.01).

Conclusion. In conclusion, treefall gaps are important to the spatial distribution of invasive plants in a mature upland forest. For *R. phoenicolasius*, gaps are important for recruitment, growth, and reproduction. *Berberis thunbergii* fruit production is dependent on gaps, but seedling establishment and growth of established plants is not. Gaps are important for *R. multiflora* growth, but not reproduction. In order to more completely understand the relative importance of canopy gaps to the invasion of exotic plant species, the contributions of propagule rain (Eschtruth and Battles 2009) and disturbance to the litter and soil strata (Marshall and Buckley 2008) should be simultaneously investigated.

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