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THE EFFECTS OF THE SPOTTED LANTERNFLY ON ANT AND LAND SLUG POPULATIONS IN EASTERN PENNSYLVANIA

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Official Honors Thesis

Honors College, University of Vermont

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Abstract. Invasive species pose a significant threat to ecosystems. The spotted lanternfly (*Lycorma delicatula*), an invasive species in the northeastern USA, consumes plant phloem and produces sugary honeydew, which in turn is often covered by sooty mold. Honeydew is a high-value resource for ants that fuels worker activity and competitive interactions, and as such the presence of *L. delicatula* has the potential to impact the diversity and composition of ant communities. Furthermore, the presence of sooty mold and the honeydew itself provides additional resources for land slugs, important seed predators and a prey item for many predators. To test for an effect of *L. delicatula* invasion on ant and land slug populations, I collected invertebrate samples using pitfall traps at four locations in Pennsylvania, two within and two outside of the current range of *L. delicatula*, during the summers of 2020 and 2021. Principal component analysis identified distinctive community compositions associated with the presence of *L. delicatula*, most strongly differentiated by the high incidence of *Aphaenogaster picea* and low incidence of *Camponotus chromaiodes* at locations outside the current range of *L. delicatula*. *Aphaenogaster* species in the *rudis* species complex, including *A. picea*, are important seed dispersers and are known to be yielding in interspecific interactions, while *C. chromaiodes* is known to be more aggressive. These data suggest that the presence of *L. delicatula* may favor ant species which exhibit high interspecific aggression and can dominate the additional food sources it provides. Additionally, land slug abundance was significantly higher at locations infested by *L. delicatula*. Thus, two additional avenues were identified by which *L. delicatula* can exert a cascading effect on the Pennsylvania forest ecosystem.

Introduction

Invasive species are nonnative or native species harmful to native systems. The presence of invasive species often foundationally disrupts key native organisms, leading to a change in how energy and nutrients move through the ecosystem (Charles and Dukes, 2008). In the United States, this impact is no longer theoretical. Invasive species are the third leading cause of loss of biodiversity in the United States, following closely behind anthropogenic habitat destruction and degradation (Wilcove et al., 1998). In addition, the rate at which new invasive species appear has only been increasing for the past several centuries, and shows no signs of slowing now or in the foreseeable future (Seebens et al., 2017). Based on this information, it must be assumed that the threat of invasive species will continue to rise in the coming decades, especially if measures are not taken to mitigate damages. For these reasons, understanding invasive species and their impacts is vital in the prevention of long-term or permanent damage to natural systems and human lives. This study contributes to that goal by examining the impacts of the invasive spotted lanternfly (*Lycorma delicatula*).

Lycorma delicatula is a species of planthopper (infraorder Fulgoromorpha) native to regions of South/Southeast Asia, and was first found with established populations in North America in Pennsylvania, USA, in 2014. Since then, unrestricted by natural population checks, *L. delicatula* numbers have rapidly expanded (Cornell College of Agriculture and Life Sciences, 2022; NYDEC, 2018). As an invasive species in North America, *L. delicatula* follows a different ecology and phenology than it would in its natural range. In South/Southeast Asia, *L. delicatula* is strongly associated with a particular host plant: the tree-of-heaven (*Ailanthus altissima*) (Barringer and Ciafre, 2020). Tree-of-heaven has been present in North America since the 18th century, originally as a purposefully-introduced ornamental plant. Since then, tree-of-heaven has become common across the North American continent (Sladonja et al., 2015). However, *L. delicatula* appears not to prefer tree-of-heaven as strongly in North America as in South/Southeast Asia. Instead, *L. delicatula* can survive on a great variety of North American plant species (Barringer and Ciafre, 2020). In the USA, *L. delicatula* egg masses are largest in cherry trees, and while feeding, early-instar *L. delicatula* prefer multiflora rose and black walnut, while later instars and adults prefer the tree-of-heaven and summer grape (Liu, 2019). This host-plant flexibility has enabled *L. delicatula* to colonize a large variety of habitats in the Northeastern USA, where it has become an insidious pest (Harper et al., 2019; Cornell College of Agriculture and Life Sciences, 2022). In Pennsylvania alone, *L. delicatula* damage to agriculture, particularly in nurseries, vineyards, and Christmas tree farms, is expected to cost the state economy 42.6 million dollars annually. Pennsylvania forestry will also be impacted, with an expected annual loss of 152.6 million dollars (Harper et al., 2019). A plant-sucking insect, *L. delicatula* consumes phloem, and secretes copious amounts of a sugar-rich liquid, called honeydew, as a digestive by-product (Leach and Leach, 2020; Liu, 2019; NYDEC, 2018). *Lycorma delicatula* infestations in Pennsylvania lead to an excessive buildup of honeydew, resulting in, among other effects, extensive growth of sooty mold in affected areas (NYDEC, 2018).

The presence of honeydew and sooty mold has the potential to drive widespread shifts in eastern Pennsylvania forest food webs, including organisms situated at a variety of trophic levels. Ants are key invertebrate predators consistently found at high trophic levels, and can reliably be used as indicators of overall ecosystem conditions, including detecting invasive species and examining ecosystem changes (Otonetti et al., 2008; Tillberg et al., 2005;

Underwood and Fisher, 2006). Positioned at a lower trophic level, land slugs are an exceedingly abundant omnivore of eastern North American forest systems, and play an important role as both a consumer of fungi and plants and a prey item of predatory invertebrates and vertebrates (Beyer and Saari, 1978; Chichester and Getz, 1973; Luff, 1974; Oberholzer and Frank, 2003; South, 1992). In this way, the effects of *L. delicatula* on ants and land slugs could influence the entire eastern Pennsylvania forest food web, from the producer foundation to the apical consumers.

Honeydew is a favorite energy source for ants, and access to large volumes of carbohydrates, as is supplied by honeydew, can drastically change ant behavior and colony processes. Ants with a carbohydrate-heavy diet show increased reproduction, have larger colonies, possess increased activity, aggression, and foraging efficacy, and are more effective at socially resisting fungal infection (Grover et al., 2007; Kay et al., 2014; McGlynn and Parra, 2016; Wittman et al., 2018). Furthermore, a supply of carbohydrates can be a point of interspecific competition for ants, and the more aggressive species tend to dominate sugar resources and reap all of the corresponding rewards (Buczowski and Bennet, 2008; Wilder et al., 2013). In eastern US forest, this would particularly apply to ants of the genus *Camponotus*, *Crematogaster*, and *Prenolepis* (Stuble et al., 2013). Additionally, invasive ant species, such as *Nylanderia flavipes* and *Tetramorium caespitum*, unrestricted by co-evolved competition and environmental limitations, typically have an advantage in interspecific encounters (Buczowski and Bennet, 2008; Ellison et al., 2012; Grover et al., 2007; Rowles and Silverman, 2009; Savage et al., 2011). Logically, this leads to a system in which the combination of highly competitive nonnative or native ants and invasive honeydew-producing insects results in the ants causing enhanced or uncharacteristic ecological impacts. This may include the local expulsion of less competitive ant species such as *Aphaenogaster*, without which many species of myrmecochorous plant would lose a primary seed disperser (Ellison et al., 2012; Handel et al., 1981; Lubertazzi, 2012; Stuble et al., 2013).

In addition to the top-down trophic impacts provided by ants, the large amount of sooty mold which develops on honeydew has the potential to impact land slugs, a lower trophic position. Around sixteen species of land slug inhabit Northeastern North America, most of which are highly generalist feeders, consuming fungi, plant and animal detritus, microscopic invertebrates, algae films, plant seeds, and plant tissues (Chichester and Getz, 1973). Land slugs may also feed directly on honeydew when given the chance, creating an additional factor through which *L. delicatula* can impact land slug populations (Naskrecki and Nishida, 2007). Changes in land slug populations could have a significant direct impact on local plants, due to the fact that land slugs are important seed predators and plant grazers. Land slug population is strongly correlated with the total seed predation in an area, and herbivory by slugs can markedly decrease local plant populations and diversity (Alizadeh and Hitchmough, 2020; Buschmann et al., 2005; Miczajkaab et al., 2019). Additionally, land slugs are an abundant and important prey item for a wide variety of invertebrate and vertebrate predators, including ground beetles of the genus *Pterostichus* and a wide variety of bird species (Luff, 1974; Oberholzer and Frank, 2003; South, 1992). Overall, a sudden increase in land slug population due to honeydew and sooty mold produced by *L. delicatula* could have far-reaching effects the ecosystem at large.

In this study, I tested the hypotheses that the presence of *L. delicatula* (H1) selects for interspecifically competitive ant species and (H2) increases resource availability for land slugs. During the summers of 2020 and 2021, I used pitfall traps to sample invertebrate communities to compare areas in eastern Pennsylvania infested by *L. delicatula* to areas which remain free of *L.*

delicatula. I predicted that, in the presence of *L. delicatula*, the relative abundance of interspecifically competitive ant species would increase, ant species diversity would decrease, and land slug abundance and total biomass would increase.

Methodology

Field Locations

Invertebrate sample collection was conducted in two types of area in eastern Pennsylvania, USA: areas with *L. delicatula* presence, and areas without. Areas infested by *L. delicatula* were represented by two locations: Crow's Nest Preserve and Stone Hills Preserve (Figure 1). Areas free of *L. delicatula* were represented by two locations within Bear Creek Preserve; one in the larger Shades Creek Parcel, and one in the smaller Dry Land Hill Parcel.

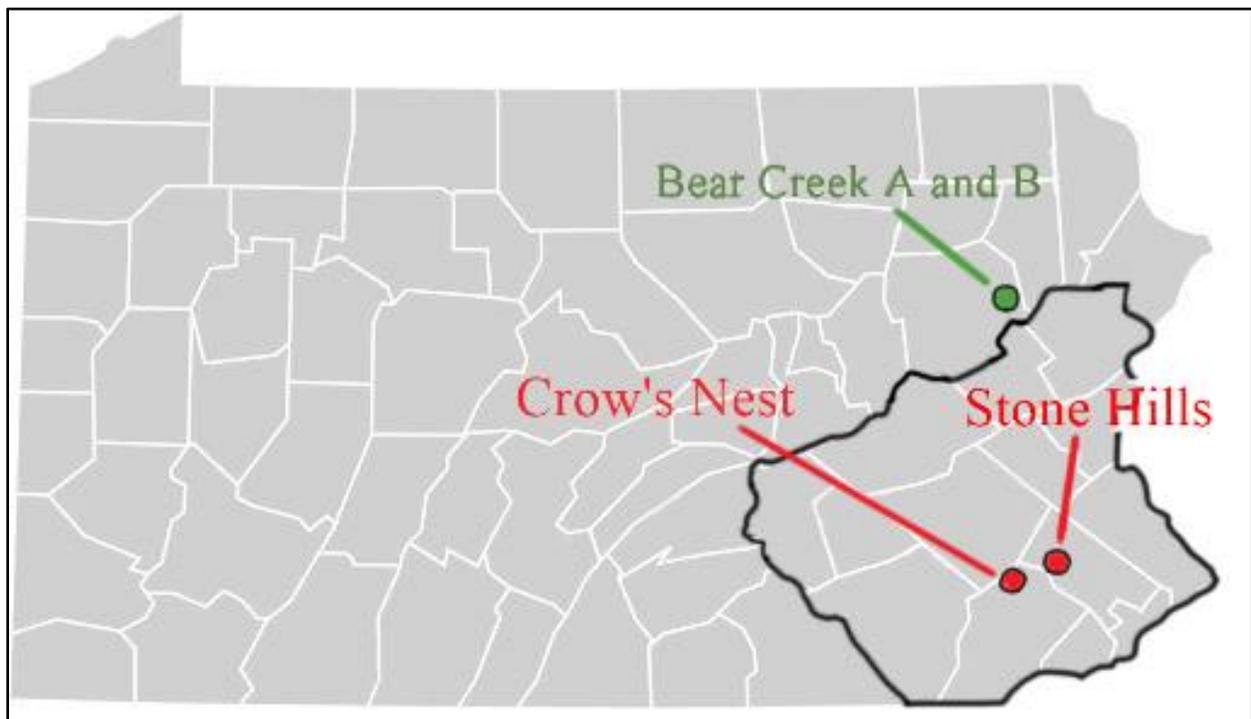


Figure 1. Relative positions of sampling locations within Pennsylvania, USA. Green = *L. delicatula* absent, Red = *L. delicatula* present. The 2020 range of *L. delicatula* is outlined in black.

Crow's Nest Preserve (henceforth referred to as CN) is located in Elverson Borough, Chester County, PA, and consists of 712 acres of mixed farmland and Appalachian oak forest (Natural Lands, 2022; Rhoads and Block, 2005). *Lycorma delicatula* was first detected on CN property in 2017, with abundance peaking in 2018 and continually declining through 2019, 2020, and 2021 (D. Barringer, personal communication, 2022). Manual removal of juveniles, adults, and egg masses has been intermittently implemented at CN as a form of *L. delicatula* population control (D. Barringer, personal communication, 2022). Research conducted within the CN

property was permitted by Preserve Manager Daniel Barringer (dbarringer@natlands.org). Stone Hills Preserve (henceforth referred to as SH) is located in Schwenksville Borough, Montgomery County, PA, about 15 miles northeast of CN, and consists of 13 acres of Appalachian oak forest (Natural Lands, 2022). *L. delicatula* was first detected on SH property ca. 2017, with abundance highest during 2018 and 2019 (D. Groff, personal communication, 2022). There have been no *L. delicatula* population control attempts on SH property (D. Groff, personal communication, 2022). Research conducted within the SH property was permitted by Preserve Manager Darin Groff (dgroff@natlands.org). Bear Creek Preserve (henceforth referred to as BC; BCA refers to the Shades Creek parcel, while BCB refers to the Dry Land Hill parcel), is located in Bear Creek Village Borough, Luzerne County, PA, about 100 miles North of CN and SH, and consists of 3,565 acres of mixed Appalachian oak forest and Northern hardwood forest divided into two parcels (Natural Lands, 2022; Rhoads and Block, 2005). As of winter 2022, no *L. delicatula* presence has been detected on BC property (J. Saltmer, personal communication, 2022). Research conducted within the BC property was permitted by Preserve Manager Joshua Saltmer (jsaltmer@natlands.org).

Field Sites

A number of sites were selected within each location by choosing random coordinate points. Ten CN, six SH, eight BCA, and eight BCB sites were established, with an average of 0.34 km between sites within locations. All CN sites were established south of Harmonyville Road. At each site, two pitfall traps were constructed, each one foot from the center of the site and 180° from each other. Pitfall traps were constructed by placing a 16oz plastic drinking cup into the ground so that the edge sat just below the surface. These were filled halfway with a 1:3 ratio mixture of propylene glycol and water. A small piece of corrugated plastic was positioned ~2.5cm over the cups to act as a roof against rain. Finally, a 1ft x1ft piece of chicken wire was secured over the traps to prevent access by vertebrates. The contents of the pitfall traps were collected once every two weeks during the summers of 2020 and 2021, between June 19th and August 21st. The contents of a single trap collected at a single occasion constitutes one sample. On each collection occasion, local *L. delicatula* abundance was assayed by counting all *L. delicatula* individuals at or below eye level of the observer, about 1.68 meters, within a ground-level 3.66m x 3.66m quadrat centered on the site. Any presence of honeydew or sooty mold buildup within the quadrat was also noted.

Sample Analysis

Each sample was sorted and all land slugs and ants were removed. All ants were identified to species using the dichotomous key system in *A Field Guide to the Ants of New England* by Ellison et al., 2012. As eusocial organisms with centralized nesting locations, relative abundance of ant species at a single site can be misleading. Therefore, ant species abundance data was converted to incidence data for use in further analyses.

For each sample, the number of land slugs was tallied, then desiccated in a drying oven at 38°C until all moisture was removed (48 hours). A dry mass of the pooled sample was obtained

to the nearest thousandth of a gram and divided by the number of slugs to yield the mean slug mass per sample.

Statistical Analyses

Statistical analyses were conducted using R version 4.0.5.

The incidence of *L. delicatula* at sampling occasions was analyzed using a two-way ANOVA with Tukey's multiple comparisons tests. Assessments were made on the differences between area types (presence/absence of *L. delicatula*), the differences between study years (2020 and 2021), the interaction effect of area type and year, and the effect of location (BCA, BCB, CN, and SH) nested within area type.

To summarize ant community composition, the relative incidences of ant species as decimal proportions for each site at each location for 2020 and 2021 were entered into a principal component analysis (PCA). The PCA reduces the dimensionality of the ant incidence data and allows a simplified and uncorrelated view of the underlying patterns of variation. A two-way ANOVA was utilized to assess differences in PC 1 and PC 2 values between area types.

Using iNEXT version 2.0.20, estimation of ant species diversity based on sampling effort was conducted by creating species accumulation curves for 2020 and 2021 for each location with 95% upper and lower confidence intervals. The presence or absence of a species in a particular sample represented a single sampling unit. Differences between species accumulation curves within each year were assessed by analyzing overlap of the 95% upper and lower confidence intervals at the minimum number of sampling units collected at any location that year.

Total land slug biomass per sample and mean mass per land slug were analyzed using a two-way ANOVA with Tukey's multiple comparisons tests. Number of land slugs collected per sample, being count data, was analyzed using a negative binomial generalized linear model (Walker, 2018). For these three land slug variables, assessments were made on the differences between area types, the differences between years, the interaction effect of area type and year, and the effect of location nested within area type.

Results

Lycorma delicatula was observed six times out of 40 sampling occasions (Pr = 0.150) at CN in 2020, including a range of one to 13 individuals (Figure 2). Observed abundance at CN decreased in 2021, with only one *L. delicatula* observation, consisting of one individual, out of 50 sampling occasions (Pr = 0.020). Observed *L. delicatula* abundance at SH followed a similar pattern, with two observations including one individual each made out of 24 sampling occasions (Pr = 0.083) in 2020, and no observations being made in 2021. No *L. delicatula* observations were recorded at any BCA or BCB sites during 2020 and 2021. The main effect of area type showed no significant difference in the frequency of *L. delicatula* observance between areas infested by *L. delicatula* and to areas free of *L. delicatula* (ANOVA; $F_{(1, 282)} = 3.580$, $p = 0.06$). However, the main effect of year revealed that observations were significantly more frequent in 2020 compared to 2021 ($F_{(1, 282)} = 3.918$, $p = 0.05$). Additionally, the interaction effect between area type and year was significant ($F_{(1, 282)} = 3.918$, $p = 0.05$), specifically between 2020 and

2021 within areas infested by *L. delicatula* (Tukey HSD; $p = 0.03$). Finally, the effect of location nested in area type showed no significant differences (ANOVA; $F_{(2, 283)} = 1.407$, $p = 0.25$)

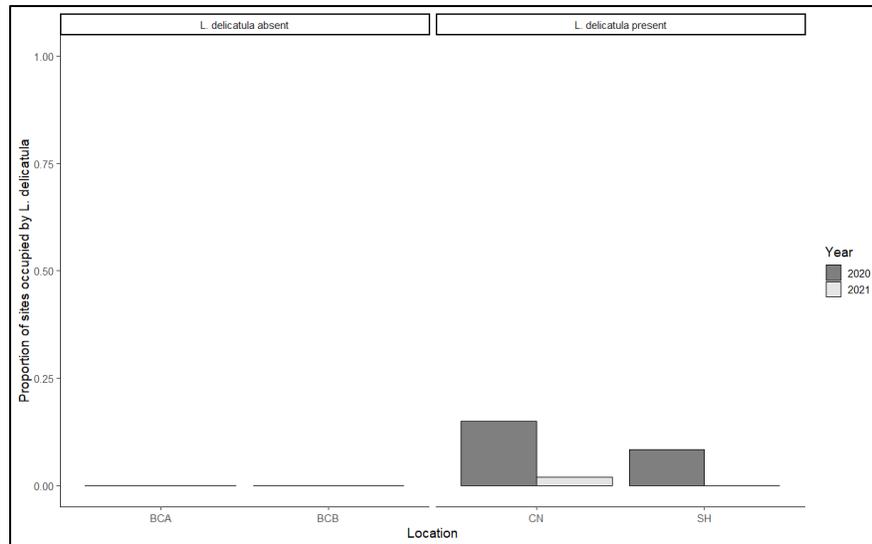


Figure 2. The proportion of sampling occasions at which *L. delicatula* was found at the four locations (BCA, BCB, CN, and SH) during 2020 and 2021.

Principal component analysis of ant species proportion data revealed that the first two principal components accounted for 55.7% of the variance in species composition (Figure 4). Principal component 1 (PC 1) accounted for 37.3% of variance, with the highest contributing species being *Aphaenogaster picea* with a positively associated contribution of $Pr = 0.738$ and *Camponotus chromaiodes* with a negatively associated contribution of $Pr = 0.217$ (Figure 5). Principal component 2 (PC 2) accounted for 18.4% of variance, with the highest contributing species being *Camponotus chromaiodes* with a negatively associated contribution of $Pr = 0.392$, *Formica neogates* with a positively associated contribution of $Pr = 0.230$, *Camponotus pennsylvanicus* with a positively associated contribution of $Pr = 0.155$, *Aphaenogaster picea* with a negatively associated contribution of $Pr = 0.134$, and *Lasius flavus* with a positively associated contribution of $Pr = 0.457$.

between SH and BCA/B. Locations free of *L. delicatula* (BCA and BCB) both held relatively high and very similar values for both PC 1 and PC 2. Areas free of *L. delicatula* held significantly higher PC 1 (ANOVA; $F_{(1, 42)} = 47.812$, $p < 0.001$) and PC 2 (ANOVA; $F_{(1, 42)} = 23.174$, $p < 0.001$) values compared to areas infested by *L. delicatula*.

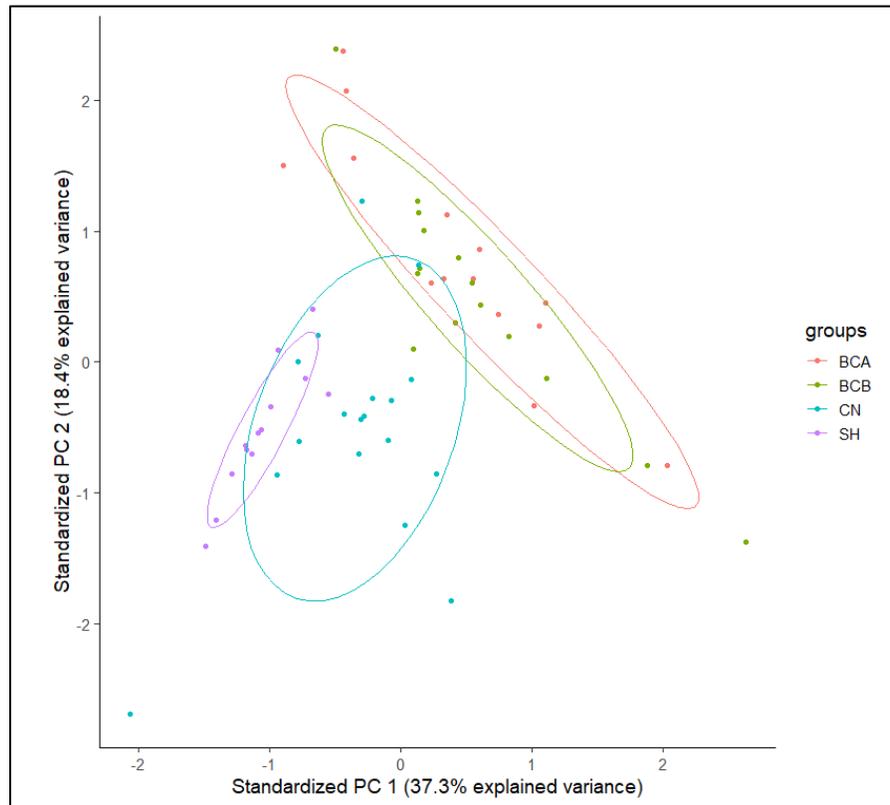


Figure 6. Ant principal component analysis, showing the PC 1 and PC 2 values of sampling sites at BCA, BCB, CN, and SH. Each site is represented by two points, for 2020 and 2021. The ellipses are drawn to encompass the normal data while excluding outlier points.

For 2020, BCB, CN, and SH followed similar ant species accumulation curves, peaking at 13 species in 42 sampling units, 15 in 36, and 13 in 35, respectively (Figure 3). BCA in 2020 differed from the rest of the locations, reaching the lower value of only 5 species in 47 sampling units. At 31 sampling units, BCB, CN, and SH all shared overlapping 95% confidence intervals, while the 95% confidence interval of BCA fell outside those of the other three locations.

For 2021, BCA, BCB, CN, and SH all followed similar species accumulation curves, peaking at 15 species in 72 sampling units, 16 in 76, 17 in 76, and 15 in 59, respectively. At 61 sampling units, BCA, BCB, CN, and SH all shared overlapping 95% confidence intervals.

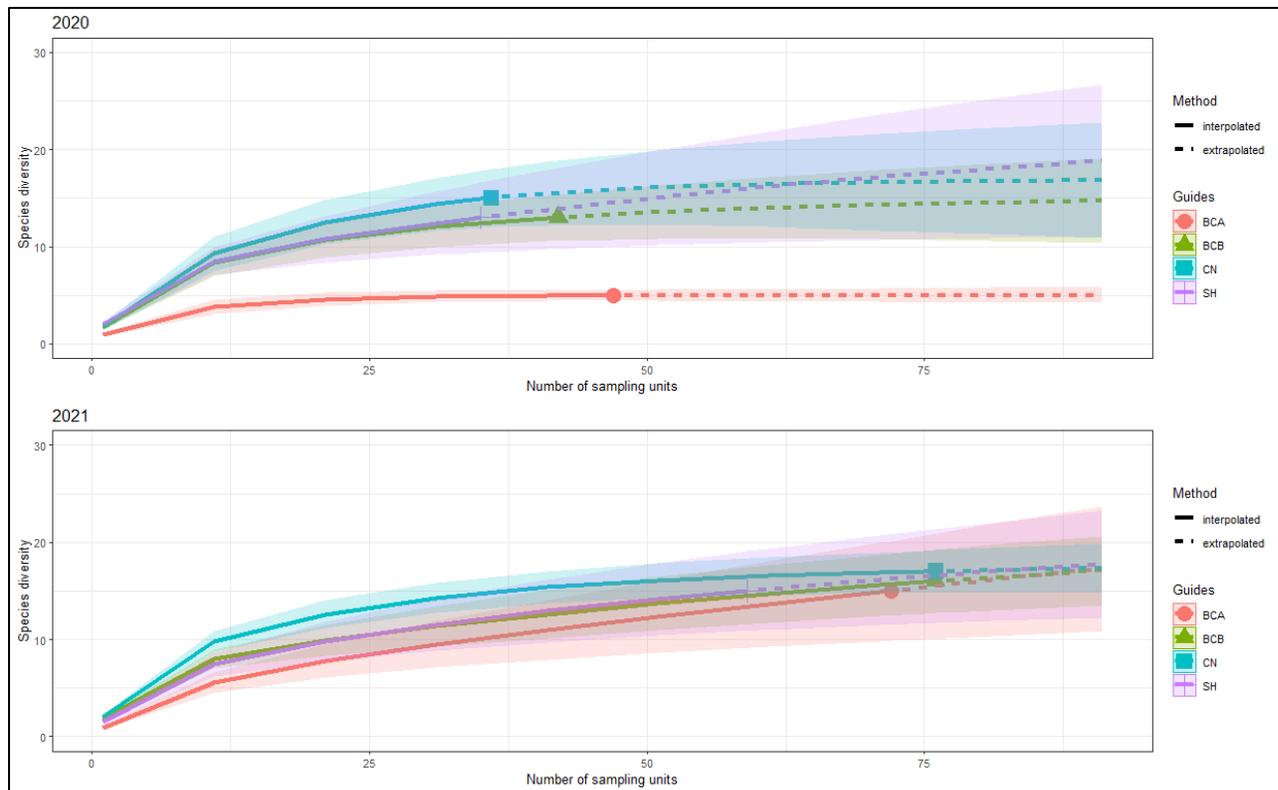


Figure 3. Species accumulation curves for all four locations (BCA, BCB, CN, and SH) for 2020 (top) and 2021 (bottom), showing interpolated and extrapolated values and shaded regions corresponding to the 95% confidence interval.

Total land slug biomass per sample ranged from zero to 3.5 grams (Figure 7-A). The main effect of area type revealed total land slug biomass to be significantly greater in areas infested by *L. delicatula* compared to areas free of infestation (ANOVA; $F_{(1, 423)} = 65.825$, $p < 0.001$). Additionally, the main effect of year revealed greater land slug biomass per sample in 2020 compared to 2021 (ANOVA; $F_{(1, 423)} = 51.468$, $p < 0.001$). The interaction effect between area type and year was also significant (ANOVA; $F_{(1, 423)} = 75.312$, $p < 0.001$), specifically between 2020 and 2021 within areas infested by *L. delicatula* (Tukey HSD; $p < 0.001$). Finally, the effect of location nested within area type was significant (ANOVA; $F_{(2, 423)} = 4.645$, $p = 0.01$). Locations CN and SH were significantly different than BCA (Tukey HSD; $p < 0.001$ and $p = 0.002$, respectively) and BCB (Tukey HSD; $p < 0.001$ and $p = 0.001$, respectively), whereas there was no significant difference between CN and SH (Tukey HSD; $p = 0.06$) or between BCA and BCB (Tukey HSD; $p = 1.00$).

Number of land slugs per sample ranged from zero to 87 (Figure 7-B). The main effect of area type revealed number of land slugs per sample to be significantly greater in areas infested by *L. delicatula* compared to areas free of infestation (ANOVA; $F_{(1, 427)} = 444.51$, $p < 0.001$). Additionally, the main effect of year revealed number of land slugs per sample to be significantly greater in 2020 compared to 2021 (ANOVA; $F_{(1, 426)} = 17.33$, $p < 0.001$). The interaction effect between area type and year was also significant (ANOVA; $F_{(1, 425)} = 4.58$, $p = 0.03$). Finally, the effect of location nested within area type was significant (ANOVA; $F_{(2, 423)} = 18.34$, $p < 0.001$).

Mean land slug biomass ranged from 0.003 to 0.142 grams (Figure 7-C). The main effect of area type revealed mean land slug biomass to be significantly greater in areas free of *L. delicatula* compared to infested areas (ANOVA; $F_{(1, 152)} = 28.786$, $p < 0.001$). Additionally, the main effect of year revealed greater mean land slug biomass in 2020 compared to 2021 (ANOVA; $F_{(1, 152)} = 45.410$, $p < 0.001$). The interaction effect between area type and year was also significant (ANOVA; $F_{(2, 152)} = 5.645$, $p = 0.02$), specifically between 2020 and 2021 within areas infested by *L. delicatula* (Tukey HSD; $p < 0.001$). Finally, the effect of location nested in area type showed no significant differences (ANOVA; $F_{(2, 152)} = 1.154$, $p = 0.32$)

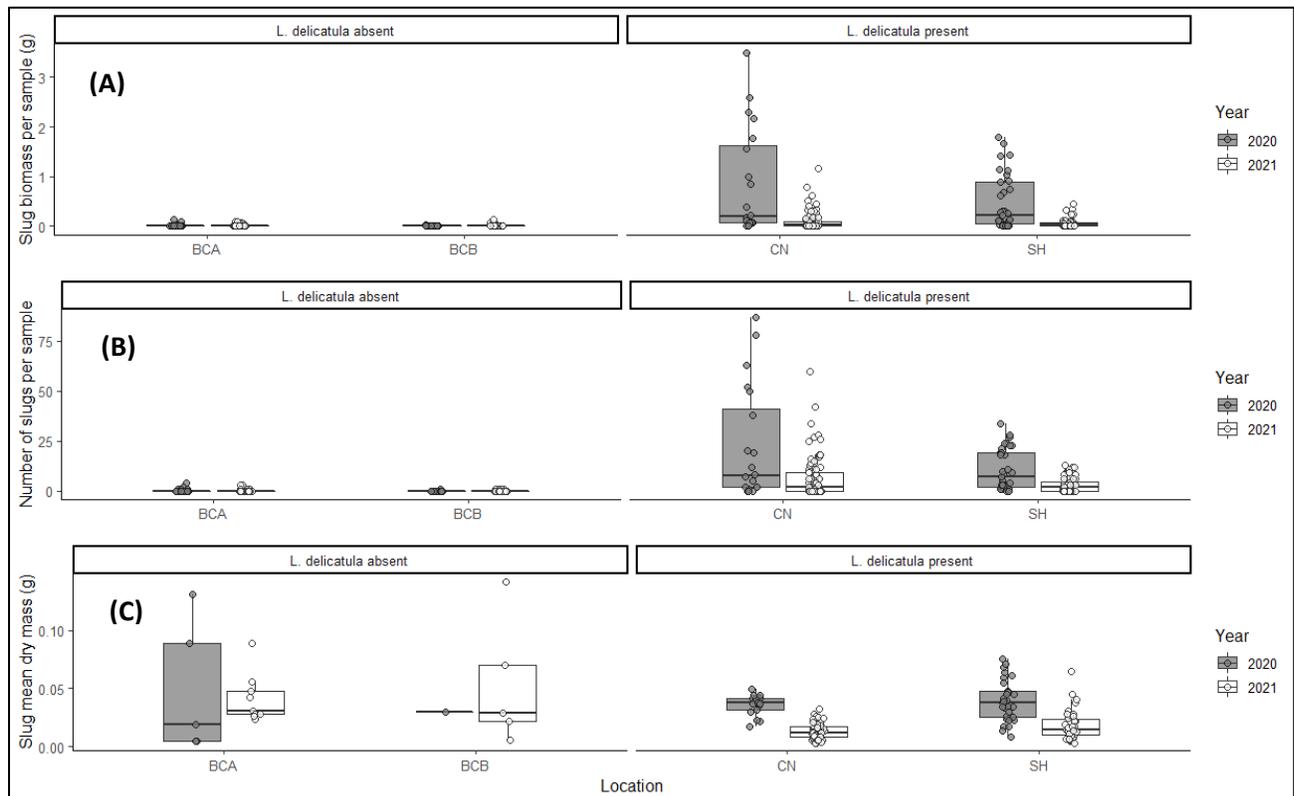


Figure 7. Box plots with individual data points showing land slug data, including (A) the amount of land slug dry mass collected per sample, (B) the number of land slugs collected per sample, and (C) the mean dry mass of a single land slug, all for each location (Bear Creek A, Bear Creek B, Crow's Nest, and Stone Hills) and year (2020 and 2021).

Discussion

Understanding the impacts of invasive species is essential if long-term negative effects are to be avoided. The planthopper *Lycorma delicatula*, a recently-introduced invader of the eastern United States, sucks plant phloem and produces large volumes of sugar-rich honeydew (Cornell College of Agriculture and Life Sciences, 2022; NYDEC, 2018). The combination of this honeydew and the sooty mold which grows upon it constitutes a new resource available to many invertebrates. High carbohydrate consumption in ants leads to heightened reproduction, colony size, and aggression, among other effects, and increased food availability for land slugs

may lead to an increase in the population of an important prey item and seed predator (Grover et al., 2007; Kay et al., 2014; McGlynn and Parra, 2016; Wittman et al., 2018; Miczajkaab et al., 2019; Luff, 1974; Oberholzer and Frank, 2003; South, 1992). My results are weakly supportive of H1 and highly supportive of H2. I predicted that, in the presence of *L. delicatula*, the relative abundance of interspecifically dominant ant species would increase, ant species diversity would decrease, and land slug abundance and total biomass would increase. My results suggest that the presence of *L. delicatula* may favor a particular ant community structure which emphasizes competitively dominant species, however not to the extent that overall ant species diversity is discernably reduced. Additionally, my results suggest that the presence of *L. delicatula* provides the resources for increased land slug abundance. As such, invasion by *L. delicatula* may drive changes in eastern Pennsylvania forest invertebrate communities.

Observation of *L. delicatula* in Pennsylvania forest was sporadic, even in the areas they were known to occur. Actual observation of *L. delicatula* at field sites was low, with the highest frequency of sightings being 15% of sampling occasions at CN in 2020 (Figure 2). Other locations and years were still lower. Additionally, I noted no buildup of honeydew or sooty mold at any site during either year. These deviations from expectations may be due to the random nature of site selection in this study largely missing the host species favored by *L. delicatula*. In the USA, *L. delicatula* egg masses are largest in cherry trees, early-instar individuals are found at highest density on multiflora rose and black walnut, and later instars and adults possess the highest densities on tree-of-heaven and summer grape (Liu, 2019). The distinct possibility remains that these focal host species were absent from the majority of my study sites. Thus, the apparently low frequency of *L. delicatula* occurrence observed in this study may not be indicative of overall *L. delicatula* abundance, the effects of which may extend further than the locale of individual host plants. Regardless, the significantly greater observation of *L. delicatula* at infested locations in 2020 compared to 2021 aligns with reports of relative *L. delicatula* populations provided by the relevant preserve managers (D. Groff, personal communication, 2022; D. Barringer, personal communication, 2022). As such, it appears that populations of *L. delicatula* were higher at infested study locations in 2020 compared to 2021.

The presence of *L. delicatula* may create an environment favorable to competitively dominant ant species. The relative incidence of ant species was significantly different in areas infested by *L. delicatula* compared to non-infested areas (Figure 6). Locations without *L. delicatula* (BCA and BCB) were characterized by a high incidence of an ant species known to be yielding in interspecific interactions, *Aphaenogaster picea*, and a low incidence of a competitively dominant species, *Camponotus chromaiodes*, whereas locations infested by *L. delicatula* (CN and SH) lacked this characteristic (Figure 5; Figure 6) (Warren et al., 2020; Lubertazzi, 2012; Lynch et al., 1980; Stuble et al., 2011, Clark and Singer, 2018). At the same time, via another explanation of variance, locations free of *L. delicatula* were characterized by a high incidence of both competitively yielding and dominant species, respectively represented by *Formica neogagates* and *Camponotus pennsylvanicus*, and a low incidence of both competitively yielding and dominant species, respectively represented by *Aphaenogaster picea* and *Camponotus chromaiodes* (Stuble et al., 2011; Clark and Singer, 2018). Furthermore, ant species known to be highly competitively dominant, including *Crematogaster lineolata* and *Prenolepis imparis*, as well as the non-natives *Nylanderia flavipes* and *Tetramorium caespitum*, were not found to characterize any area or location, despite being regularly identified in samples (Stuble et al., 2011; Lynch et al., 1980; Ellison et al., 2012). These results constitute a weak correlation

between *L. delicatula* presence and an emphasis on competitively dominant ant species, consistent with my hypotheses and predictions. Alternatively, patterns in variance could be explained by other variables, such as the simple geographic distribution of ant species. *Aphaenogaster picea* is a species most commonly associated with conifer forest and mixed deciduous forest (Ellison et al., 2012). As such, it would be expected that *A. picea* has a proportionally higher incidence at BCA and BCB, locations dominated by Appalachian oak forest and Northern hardwood forest, and a proportionally lower incidence at CN and SH, locations dominated by Appalachian oak forest, farmland, and suburbia (Rhoads and Block, 2005). However, if entirely due to presence of *L. delicatula*, this correlation could have far-reaching implications for the ecosystem at large. *Aphaenogaster*-species ants are keystone seed distributors for numerous myrmecochorous plants in Pennsylvania forest, including a substantial portion of herb species, such as snow trillium (*Trillium nivale*) (Lubertazzi, 2012; Handel et al., 1981). Alterations to the abundance of *Aphaenogaster* species, including *A. picea*, could have a significant impact on myrmecochorous plant abundance and distribution.

The presence of *L. delicatula* does not reduce ant species diversity via increased interspecific competition. In total, 30 ant species were collected across the four locations, including ground-nesting, wood-nesting, and arboreal species (ex. *Lasius flavus*, *Camponotus pennsylvanicus*, and *Crematogaster lineolata*, respectively) (Figure 5) (Ellison et al., 2012). Also found were two species of non-native ant, *Nylanderia flavipes* and *Tetramorium caespitum*. I predicted ant species diversity would decline in the presence of *L. delicatula* due to competitively dominant ant species monopolizing the sugar resource provided by *L. delicatula*, thus increasing the colony size and aggression of those species and pushing out other species that are unable to compete (Grover et al., 2007; Kay et al., 2014; McGlynn and Parra, 2016; Wittman et al., 2018; Buczkowski and Bennet, 2008; Wilder et al., 2013). In 2020, both locations infested by *L. delicatula* (CN and SH) and one of the locations free of *L. delicatula* (BCB) possessed highly similar species diversity values, and in 2021, all four locations were highly similar (Figure 4). The divergence of these results from the prediction may be due to the longevity of ant queens and colonies. *Lycorma delicatula* is a relatively new invader, appearing in Pennsylvania in 2014 and first detected at CN and SH in 2017 (Cornell College of Agriculture and Life Sciences, 2022). The four years between 2017 and 2021 is well within the lifespan of many ant queens, some of which can live for decades (Keller, 1998). Therefore, there may be a discernable delay of many years between the appearance of *L. delicatula* in a region and an associated decline in ant species diversity, even if the relative abundance of ant species changes more rapidly. Notably, in 2020, BCA possessed a significantly lower species diversity compared to the other three locations, less than half that of any other location during 2020 or 2021. BCA is a location free of *L. delicatula*, and as such this divergence from the other three locations is due to a factor external to the effects of *L. delicatula*. From April 5th, 2021 onward, Bear Creek Preserve, which encompasses both BCA and BCB, became closed to the public on Mondays for trail maintenance and preserve management (Natural Lands, 2021). Ant species diversity decreases in the presence of anthropogenic disturbance, and the combined effect of reduced foot traffic and increased preserve management may explain the lower species diversity values at BCA in 2020 compared to 2021 (Lach et al., 2010; Sanford et al., 2009; Underwood and Fisher, 2006).

The presence of *L. delicatula* provides resource support for high land slug populations. For both 2020 and 2021, areas free of *L. delicatula* maintained consistently low values for both slug biomass and abundance, whereas areas infested by *L. delicatula* showed significantly higher

values for both variables (Figure 7). However, slugs were significantly larger in non-infested areas. These results suggest that increases in total slug biomass were primarily driven by increasing slug abundance, not mean slug size. Furthermore, in areas infested by *L. delicatula*, land slug abundance, total biomass, and mean biomass were all significantly higher during 2020 compared to 2021, whereas this pattern was not present at locations free of *L. delicatula*. This pattern is consistent with the *L. delicatula* observation proportions found by this study and the reports of relative *L. delicatula* abundance from the CN and SH Preserve Managers (Figure 2) (D. Groff, personal communication, 2022; D. Barringer, personal communication, 2022). These results suggest that the presence of *L. delicatula* increases land slug abundance and therefore biomass, and establish a correlation between the presence of *L. delicatula* and increased land slug abundance. Again, similar to the patterns observed in ant species composition, these data could alternatively be explained by environmental variables external to the effects of *L. delicatula*, such as forest type. However, if causal, this correlation could have far-reaching implications for the ecosystem at large. An abundance of land slugs equates to increased prey availability for a variety of invertebrate and vertebrate predators, including many species of beetle and bird (Luff, 1974; Oberholzer and Frank, 2003; South, 1992). Additionally, land slug abundance is strongly correlated with total seed predation and they are important herbivores (Alizadeh and Hitchmough, 2020; Buschmann et al., 2005; Miczajkaab et al., 2019). As such, increased land slug abundance could result in changes to plant systems. Overall, an increase in land slug abundance due to the presence of *L. delicatula* could drive widespread changes in both producer and consumer community structures.

Altogether, these data reinforce the importance of preventing widespread invasion of *L. delicatula* in the eastern United States by providing evidence for impacts on key invertebrate groups. Besides these direct effects on ant and slug populations, there is the potential for a variety of cascading effects on lower trophic levels. In addition to phloem-feeding behavior, this study has identified two additional avenues by which *L. delicatula* can influence plant communities: promotion of land slug abundance and disruption of myrmecochorous seed dispersal. I suggest further study be performed examining plant species diversity, relative abundance, and seed dispersal and survival rates between locations infested by *L. delicatula* and those which remain free of infestation. Additionally, a causal investigation of the correlation between *L. delicatula* presence and land slug abundance, possibly involving field examination of slug diet, could assist in our understanding of this effect. Finally, an examination of ant populations at set locations before and after invasion by *L. delicatula* could clarify the ant species diversity and community composition results of this study by eliminating confounding environmental variables such as forest type.

This study contributes to the rapidly growing body of literature examining *L. delicatula* in the United States. By increasing our understanding of *L. delicatula* and its effects, management programs can be better informed and more effective.

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