# Host Preferences of Spotted Lanternfly and Risk Assessment of Potential Tree Hosts in Managed and Semi-Natural Landscapes

Authors: Kim, Suji, Kuhn, Anna, Raupp, Michael J., and Martinson, Holly

Source: Florida Entomologist, 106(2) : 74-82

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.106.0202

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Florida-Entomologist on 06 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

# Host preferences of spotted lanternfly and risk assessment of potential tree hosts in managed and semi-natural landscapes

*Suji Kim[1], Anna Kuhn[1], Michael J. Raupp[2], and Holly Martinson[1,]**

## Abstract

The spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), is an invasive, polyphagous herbivore native to China which was first detected in Pennsylvania, USA, in 2014. As of spring 2022, *L. delicatula* has spread to 14 states in its introduced range in the eastern US, prompting quarantines, increased surveillance, and new research. Despite known preferences for tree of heaven, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), *L. delicatula* has been reported from over 100 plants for feeding and oviposition. As *L. delicatula* continues to spread, individuals have the potential to encounter new host plants for feeding and new substrates for oviposition. In this study, we investigated oviposition and host plant use by nymphs among common trees, shrubs, and vines at 3 field sites in eastern Pennsylvania to determine whether use of plants differs among plant species and with plant size. We then used our field data and information from the literature to assess the risks to 2 nearby, uninvaded habitats in central Maryland. In repeated visual surveys in Pennsylvania, we found *L. delicatula* egg masses on 10 of 15 plant species, including new observations on *Cercis canadensis* L. (Fabaceae), *Crataegus viridis* L. (Rosaceae), and *Liquidambar styraciflua* L. (Altingiaceae). Egg mass abundance increased strongly with tree size. We found nymphs on 12 plant species, including new observations on *C. viridis*, and nymphal abundance differed significantly among plant species. Applying results from our field surveys and from the literature to currently uninvaded sites, we found high levels of risk for trees in managed and semi-natural settings; the great majority of trees in these inventories are at risk for use by *L. delicatula*, though several plant species have yet to be evaluated for risk. Our work highlights the need for continued research into oviposition and feeding choices as well as the urgency for monitoring and preemptive management at sites near known *L. delicatula* infestations.

Key Words: host plant use; invasive species; *Lycorma delicatula*; risk assessment; sap-feeding herbivore; tree inventory

## Resumen

La mosca-linterna manchada, *Lycorma delicatula* (Blanca) (Hemiptera: Fulgoridae), es un herbívoro polífago invasivo originario de China que se detectó por primera vez en Pensilvania, EE. UU. en el 2014. Desde la primavera del 2022, *L. delicatula* se ha dispersado a 11 estados en su rango invasivo en el este de los EE. UU., lo que provocó cuarentenas, mayor vigilancia y nuevas investigaciones. A pesar de las preferencias conocidas por el árbol del cielo, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), se ha informado que *L. delicatula* se encuentra en más de 100 plantas para alimentación y oviposición. A medida que *L. delicatula* continúa propagándose, los individuos tienen el potencial de encontrar nuevas plantas hospederas para alimentarse y nuevos sustratos para la oviposición. En este estudio, investigamos la oviposición y el uso de plantas hospederas por parte de las ninfas entre árboles, arbustos y enredaderas comunes en 3 sitios de campo en el este de Pensilvania para determinar si el uso de plantas difiere entre especies de plantas y con el tamaño de la planta. Luego usamos nuestros datos de campo e información de la literatura para evaluar los riesgos para 2 hábitats cercanos no invadidos en el centro de Maryland. En estudios visuales repetidos en Pensilvania, encontramos masas de huevos de *L. delicatula* en 10 de 15 especies de plantas, incluidas nuevas observaciones sobre *Cercis canadensis* L. (Fabaceae), *Crataegus viridis* L. (Rosaceae) y *Liquidambar styraciflua* L. (Altingiaceae). La abundancia de masa de huevos aumentó fuertemente con el tamaño del árbol. Encontramos ninfas en 12 especies de plantas, incluidas nuevas observaciones sobre *C. viridis* y la abundancia de ninfas difirió significativamente entre las especies de plantas. Al aplicar los resultados de nuestros sondeos de campo y de la literatura a sitios actualmente no invadidos, encontramos altos niveles de riesgo para los árboles en entornos manejados y seminaturales; la gran mayoría de los árboles en estos inventarios están en riesgo de ser usados por *L. delicatula*, aunque varias especies de plantas todavía no han sido evaluadas por riesgo. Nuestro trabajo destaca la necesidad de continuar la investigación sobre la oviposición y las opciones de alimentación, así como la urgencia del monitoreo y el manejo preventivo en sitios cercanos a infestaciones conocidas de *L. delicatula*.

Palabras Clave: uso de plantas hospederas; especies invasivas; *Lycorma delicadatula*; evaluación de riesgos; herbívoro que se alimenta de savia; inventario de árboles

*Lycorma delicatula* (White) (Hemiptera: Fulgoridae), the spotted lanternfly, is an invasive herbivorous insect first identified in Pennsylvania, USA, in Sep 2014 (Barringer et al. 2015). Since its original detection, this species has spread throughout the mid-Atlantic region, with current infestations in 14 eastern states, prompting quarantines in portions of Connecticut, Delaware, Maryland, New Jersey, Ohio, Penn-

---

[1]Department of Biology, McDaniel College, 2 College Hill, Westminster, Maryland 21157, USA; E-mail: sjk006@mcdaniel.edu (S. K.); ajk012@mcdaniel.edu (A. K.); hmartinson@mcdaniel.edu (H. M.)

[2]Department of Entomology, University of Maryland, Plant Sciences Building, College Park, Maryland 20742, USA; E-mail: mraupp@umd.edu (M. J. R.)

*Corresponding author; E-mail: hmartinson@mcdaniel.edu

sylvania, and Virginia, USA (NY IPM 2022; USDA-APHIS 2022). Long-distance spread has led to isolated detections in at least 2 additional eastern states (Vermont and New Hampshire, USA) (NY IPM 2022). The rapid range expansion and long-distance spread of *L. delicatula* are human assisted, because individuals can hitchhike on vehicles, and egg masses are easily moved on solid objects (Urban 2019). Modeling studies have identified broad areas of habitat suitable for establishment of *L. delicatula* populations, including much of eastern North America, portions of the west coast of the USA, broad areas of Europe, and portions of Australia, South America, and southern Africa (Jung et al. 2017; Wakie et al. 2019). This broad global habitat suitability and propensity for rapid spread have led to expectations of increased economic and ecological impacts of this species in the future.

Individuals of *L. delicatula* damage plants directly by feeding on phloem, leading to puncture wounds, loss of photosynthate, and sap exudation, with reports of direct damage contributing to plant mortality in grape vineyards (*Vitis* spp.) (Lee et al. 2019; Urban 2019). Feeding also leads to indirect damage, because honeydew and exuded sap both facilitate the growth of sooty mold, which blocks photosynthesis when it grows on green plant tissues (Dara et al. 2015; Urban 2019). Economic losses are currently of greatest concern for grapes (Lee et al. 2019; Urban 2019; Leach & Leach 2020a), although tree fruits, hops, nursery stock, and forestry also have been identified as potentially at risk for direct and indirect economic losses (Harper et al. 2019; USDA-APHIS 2019). Plant diseases are not known to be vectored by *L. delicatula* (Urban 2019; Brooks et al. 2020), and individuals do not bite humans or other animals, but *L. delicatula* is a notable nuisance pest in residential landscapes. Adult insects can be found in high densities on trees and shrubs in these landscapes; adults often fly in large aggregations in the autumn, and individuals produce copious amounts of honeydew (Urban 2019).

*Lycorma delicatula* is known as a feeding generalist, with observations on over 100 plant species across its native and invasive range, with particular affinity for tree of heaven, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae) (Dara et al. 2015; Liu 2019). Although lists of potential host plants assembled from the literature are available for *L. delicatula* (Barringer et al. 2015; Dara et al. 2015; Liu 2019; Avanesyan & Lamp 2020; Barringer & Ciafré 2020), quantitative information on host use remains incomplete and appears to depend in part on host availability (Liu 2019). When herbivores are introduced to new ranges, predicting host plant use can be challenging (Bertheau et al. 2010; Pearse & Altermatt 2013). Different assemblages of plants may be present in the native and invaded ranges, and preferences for plants shared across the global range of the species may not be consistent. Even for polyphagous species, use of plants typically is non-uniform and may change across ontogeny, may depend on the locally available plants, or may be a function of plant species abundance or geographic provenance (Mason et al. 2011; Martinson et al. 2016, 2020).

Although adults of *L. delicatula* exhibit strong preference for *A. altissima* (Barringer et al. 2015; Liu 2019), egg masses are oviposited on a variety of substrates, including live plants, landscape materials, and vehicles (Liu 2019; Urban 2019). Nymphs are highly mobile, move within and among plants, and likely feed on several host plant species (Kim et al. 2011; Jung et al. 2017; Urban 2019; Avanesyan & Lamp 2020; Nixon et al. 2020, 2022). Factors that determine female oviposition preference and the use of plants by nymphs remain unclear but are important in understanding risks and developing management strategies for *L. delicatula* (Urban 2019). In addition to plant species, plant size may play a role in oviposition and feeding, with larger plants expected to support higher abundances of insect herbivores because of the greater availability of resources (Marques et al. 2000; Whitfeld et al. 2012).

In this study, we investigated egg mass locations and nymphal host plant use at 3 sites in eastern Pennsylvania. We assessed patterns of egg mass and nymphal abundance with respect to plant species and plant size, focusing on trees, shrubs, and vines, because woody plants constitute most known host plants (Barringer & Ciafré 2020). We then applied this information and information from the literature to predict threats to 2 currently uninvaded sites in central Maryland. In doing so, we hope to demonstrate that a combination of local tree inventories and information about *L. delicatula* host plant use can be used to assess future risks. As *L. delicatula* continues to spread in the mid-Atlantic region, understanding risks to locations likely to be infested will be a key to developing a priori management strategies.

## Materials and Methods

### PENNSYLVANIA FIELD SURVEYS

We conducted field surveys for *L. delicatula* egg masses and nymphs at 3 locations in eastern Pennsylvania (Table 1). Sites were selected to represent a range of management types and based on access to a variety of plants commonly found in managed landscapes. Each site was visited twice during early summer 2019. At each site, species of trees, shrubs, and vines were selected for study if multiple individuals could be surveyed during a visit. To the greatest extent possible, the sampled plants were a representative subset of the available plants, though complete plant inventories were unavailable. Plants were identified with a local field guide (Cope 2001), and plant locations were mapped with GPS (Garmin, Olathe, Kansas, USA). Tree size was measured as diam at breast height (at 1.3 m), and shrub size was measured as basal diam (Pocket Diameter Tape, Forestry Suppliers, Inc., Jackson, Mississippi, USA). Vine sizes were not measured; vines and plants that were inaccessible were excluded from the analysis of plant size. Although several herbaceous plant species have been identified as host plants for *L. delicatula* (Avanesyan & Lamp 2020), most plants thus far identified as oviposition and feeding hosts are woody (Barringer & Ciafré 2020), and herbaceous plants were outside the scope of our work.

Counts of *L. delicatula* egg masses and nymphs were timed, and survey duration was scaled to plant size to allow for greater search time on plants with larger surface area (as in Lee et al. 2014). Plants < 10.16

**Table 1.** Locations of field surveys in Pennsylvania for *Lycorma delicatula* egg masses and nymphs.

| Site | Location | Dates Visited | Property Description |
|---|---|---|---|
| Arboretum | Pottstown<br>(40.155280°N, 75.681684°W) | 11 Jun 2019<br>21 Jun 2019 | Managed, private site with ornamental plantings and semi-natural areas |
| Roadside | Pottstown<br>(40.130027°N, 75.690873°W) | 11 Jun 2019<br>21 Jun 2019 | Unmanaged, public site surrounding an access road, with edgy vegetation bordering a forest parcel |
| Residential | Barto<br>(40.352830°N, 75.586844°W)[a] | 21 Jun 2019<br>1 Jul 2019 | Managed, private site with ornamental plantings and a wooded section |

Note: To protect privacy, residential coordinates are provided for a nearby intersection.

cm (< 4 in) in diam, including all vines, were surveyed for 1 min, plants 10.16 to 20.32 cm (4 – 8 in) were surveyed for 2 min, plants 20.32 to 30.48 cm (8 – 12 in) were surveyed for 3 min, and plants greater than 30.48 cm (> 12 in) were surveyed for 4 min. Surveys were conducted between 11:00 A. M. and 5:30 P. M. and included all plant material from the ground to 2 m in height, including trunks and low-hanging branches. The number of egg masses observed on a plant was assessed as the maximum egg mass count across the repeated surveys, because no new egg masses would have been laid between surveys. Egg mass counts included egg masses from the survey yr and previous yr and therefore represent the cumulative use of the plant for oviposition over time. Nymphs were counted, and the occurrence of instars (1st or 2nd, 3rd, and 4th) was recorded. No adults were observed in the Pennsylvania field surveys.

All data analysis was conducted in R (R Core Team 2022). Our overall approach was to investigate whether plant size (as diam at breast height or basal diam in cm) or plant species were important determinants of *L. delicatula* egg mass and nymphal abundances in the Pennsylvania field surveys, using linear mixed-effects models (lme4 package) (Bates et al. 2015). For egg mass abundance, we assessed whether the maximum egg mass count on a plant (square root transformed to better meet model assumptions) was a function of the fixed effects of plant size and species, with survey site as a random effect. For nymphs, we assessed whether nymphal abundance (square root transformed) depended on plant size, plant species, and date, with survey site and individual plant as random effects. For the analysis of both the egg masses and nymphs, we compared models with and without a term using maximum likelihood ratio chi-square tests to derive the most parsimonious model (Crawley 2007).

## RISK ASSESSMENT IN MANAGED AND SEMI-NATURAL SETTINGS

Using data from the Pennsylvania field surveys and published reports of host plant use, we then assessed the extent to which *L. delicatula* would pose a risk to the woody plants present in 2 settings in Carroll County, located in north-central Maryland. Recent establishment of *L. delicatula* populations in many of the counties in central and northern Maryland, along with climatic suitability throughout the mid-Atlantic region (Wakie et al. 2019), indicate that risk of *L. delicatula* to locations throughout Carroll County, Maryland, is high. We therefore assessed risk of *L. delicatula* impacts at the main campus of McDaniel College in Westminster, Maryland (39.586327°N, 77.000360°W), and the McDaniel Environmental Center, a 55-acre semi-natural property in nearby New Winsor, Maryland (39.527894°N, 77.042380°W). These 2 sites allowed us to work in locations similar to those we surveyed in Pennsylvania in that they both included managed and unmanaged areas and assemblages of native and introduced plants common in the region.

A subset of trees on McDaniel College's campus and at the McDaniel Environmental Center were identified and mapped in Jun and Jul 2019. The college campus is managed and park-like, with ornamental plantings near academic and residential buildings and semi-natural habitats around a golf course (Fig. 1A). We conducted a partial tree inventory of the campus and included a random set of both ornamental and semi-natural regions to develop a robust risk assessment for *L. delicatula*. The McDaniel Environmental Center contains a variety of habitat types, including agriculture, old fields, forest patches, ponds, and small access roads (Fig. 1B). At the McDaniel Environmental Center, the tree inventory focused on trees within 1 m of forest edges. Though our survey at the McDaniel Environmental Center was constrained to edge habitats, forest edges represent an important habitat for a favored host plant, *A. altissima*, and surveys in vineyards in Pennsylvania have documented strong edge effects for *L. delicatula* (Leach & Leach 2020b).

For each species in the tree inventories, we determined risk in the following manner. Plant species described in the literature as being used for oviposition or as hosts for nymphs or adults were designated in our inventories as "known risk." Plant species used for oviposition or as a nymphal

**Fig. 1.** Sites of partial tree inventories for *Lycorma delicatula* risk assessment at (A) McDaniel College in Westminster, Maryland, and (B) the McDaniel Environmental Center in New Windsor, Maryland. At the college, trees were selected randomly and included ornamental plantings near academic and residential buildings and trees in semi-natural habitats around the golf course. At the McDaniel Environmental Center, trees were surveyed at forest edges.

host in our Pennsylvania field surveys but not yet reported elsewhere in the literature were designated as "of new concern." Finally, plant species in the campus or McDaniel Environmental Center tree inventories but not yet evaluated or reported as hosts from the literature were designated as "unknown risk." Literature used for assessing risk included Dara et al. (2015), Barringer and Ciafré (2020), and Liu et al. (2020).

## Results

### PENNSYLVANIA FIELD SURVEYS

We investigated the presence and abundance of *L. delicatula* egg masses and nymphs on a total of 15 species of trees, shrubs, and vines in our Pennsylvania surveys (Table 2). The surveys included 55 unique plants, most of which (69.1%) were visited twice, for a total of 93 timed surveys. We found a total of 174 *L. delicatula* egg masses and 460 nymphs in our 179 min of field surveys. Egg masses were present on 10 of the 15 plant species we surveyed, and nymphs were present on 12 plant species (Table 2). Notably, our observations of egg masses on eastern redbud, *Cercis canadensis* L. (Fabaceae) and sweetgum, *Liquidambar styraciflua* L. (Altingiaceae), and egg masses and nymphs on green hawthorn, *Crataegus viridis* L. (Rosaceae) are, to the best of our knowledge, newly recorded host plants for *L. delicatula* (Table 2).

Sites differed substantially in the composition of plants and the use of these plants by *L. delicatula*. Far more egg masses were observed at the residential site (160 egg masses) than the arboretum (14 egg masses), and no egg masses were observed at the roadside site (Fig. 2). Nymphal abundance also was highest at the residential site (214 nymphs), followed by the arboretum (159 nymphs) and the roadside (87 nymphs (Fig. 2). Overall, the highest proportion of egg masses across all the surveys was observed on sugar maple, *Acer saccharum* Marshall (Sapindaceae) at the residential site, and the highest proportions of nymphs across all the surveys were found on black walnut, *Juglans nigra* L. (Juglandaceae) and ornamental rose, *Rosa* sp. (Rosaceae) at the residential site; on beebee tree, *Tetradium daniellii* (Bennett) T. G. Hartley (Rutaceae) at the arboretum, and *A. altissima* at the roadside site (Fig. 2).

The most parsimonious model for egg mass abundance included only the effect of plant size (square root transformed maximum egg mass abundance per plant; Likelihood ratio test, LRT $\chi^2 = 15.388$; df = 1; $P < 0.0001$), and egg mass abundance increased as a function of plant size (Fig. 3A). In contrast, nymphal abundance tended to be lower on larger trees, though the relationship between nymphal abundance and plant size was not retained for the final model (square root transformed nymphal abundance; LRT $\chi^2 = 2.522$; df = 1; $P = 0.112$) (Fig. 3B).

Egg mass abundance varied considerably among surveyed plants, but the effect of plant species was not retained in the final model (LRT $\chi^2 = 13.578$; df = 9; $P = 0.138$) (Fig. 4A). Again, the pattern for nymphs differed from that of egg masses, and nymphal abundance varied significantly among plant species (LRT $\chi^2 = 49.352$; df = 9; $P < 0.0001$) (Fig. 4B), with the highest average abundances on *A. altissima* (AIL), *Rosa* sp. (ROS), *J. nigra* (JUG), and *T. daniellii* (TET). The final model for nymphal abundance included only the effect of plant species; the effect of date was non-significant (LRT $\chi^2 = 1.956$; df = 3; $P = 0.582$) and was removed during model simplification.

### RISK ASSESSMENT IN MANAGED AND SEMI-NATURAL SETTINGS

We surveyed a total of 307 trees at the McDaniel College campus and the McDaniel Environmental Center representing a range of ornamental plantings and trees in semi-natural habitats. The partial tree inventory of the college campus included a greater number of tree species (15 species) compared to the McDaniel Environmental Center (6 species) (Table 3). The campus included 12 species known to be used by *L. delicatula* for oviposition and feeding, making up 86% of the trees surveyed. We identified 1 species on the campus that may be of new concern as a host for *L. delicatula*, the commonly planted native sweet gum tree (*L. styraciflua*), based on our Pennsylvania field surveys. The diverse tree community on the campus also included 2 species (*Quercus palustris* Munchh. and *Gleditsia tricanthos* L. [both Fagaceae]) that previously have not been assessed or reported for *L. delicatula* host plant status. In contrast, the semi-natural habitats surveyed at the McDaniel Environmental Center contained far more trees of species known to be host plants or oviposition substrates for *L. delicatula*, in-

**Table 2.** Presence and total counts of egg masses (EM) and nymphs (Nym) of *Lycorma delicatula* among surveyed plants, with the total number of each species surveyed (N). Literature accounts of plants used for feeding and oviposition also are indicated, as are new records of host plant use from this study.

| | | | | | Instars[a] | | | |
|---|---|---|---|---|---|---|---|---|
| Plant scientific name | Plant code | *N* | EM | Nym | 1st – 2nd | 3rd | 4th | Literature context |
| *Acer saccharum* | ACE | 7 | 71 | 7 | X | | | Pennsylvania[c] |
| *Ailanthus altissima* | AIL | 6 | 0 | 104 | | X | X | Pennsylvania, Korea[c,d] |
| *Amelanchier* sp. | AME | 6 | 1 | 11 | X | X | | Pennsylvania[e] |
| *Cercis canadensis* | CER | 4 | 23 | 0 | | | | Current study |
| *Crataegus viridis* | CRA | 6 | 5 | 3 | X | | | Current study |
| *Fagus grandifolia* | FAG | 4 | 6 | 4 | X | X | | Pennsylvania[c,d] |
| *Juglans nigra* | JUG | 12 | 14 | 121 | X | X | X | Korea[c] |
| *Liquidambar styraciflua* | LIQ | 2 | 13 | 0 | | | | Current study |
| *Liriodendron tulipifera* | LIR | 6 | 0 | 5 | | X | | Pennsylvania[c,d] |
| *Pinus strobus* | PIN | 5 | 30 | 1 | X | | | Pennsylvania, Korea[e] |
| *Prunus avium* | PRU | 2 | 9 | 0 | | | | Pennsylvania[d] |
| *Rosa* sp. | ROS | 5 | 0 | 66 | | X | X | Korea[c] |
| *Rubus* spp.[b] | RUB | 12 | 0 | 26 | X | X | | Pennsylvania[e] |
| *Tetradium daniellii* | TET | 8 | 2 | 77 | X | X | | Korea[c] |
| *Vitis* sp. | VIT | 8 | 0 | 35 | X | X | | Pennsylvania, Korea, China[c] |
| Totals | | 93 | 174 | 460 | | | | |

[a]Presence of instars is recorded with an "x"; [b]*Rubus* spp. were a mix of *R. allegheniensis* and *R. occidentalis*; [c]Dara et al. (2015); [d]Liu et al. (2020); [e]Barringer and Ciafré (2020).

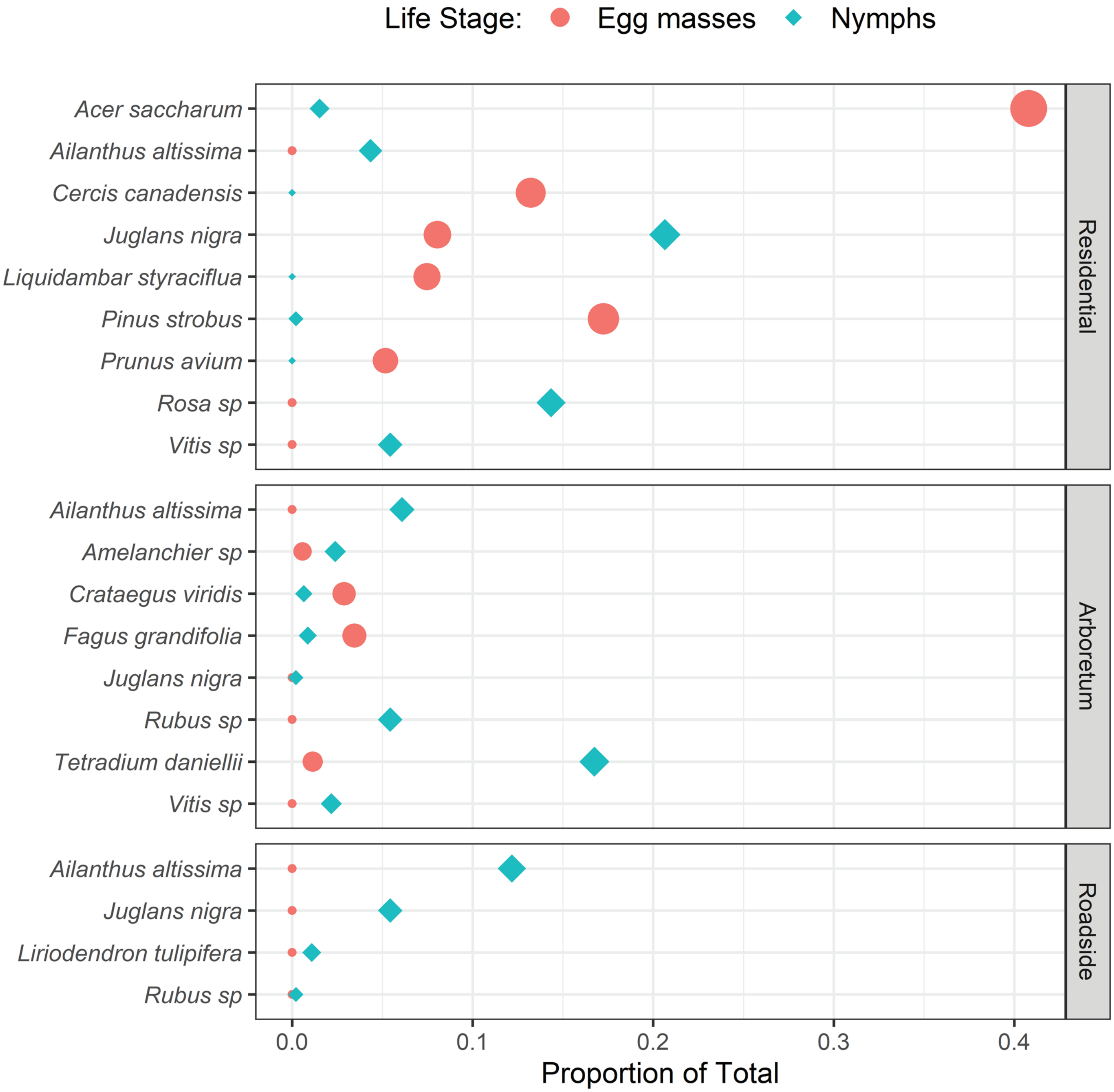

**Fig. 2.** Plant composition and the distribution of *Lycorma delicatula* egg masses and nymphs among plants varied among residential (top), arboretum (middle), and roadside sites (bottom) in the Pennsylvania field surveys. Plotted are the abundances of egg masses as the proportion of all egg masses observed in the study (orange circles) and the abundances of nymphs as the proportion of all nymphs observed in the study (blue diamonds), with symbol size scaled to proportional abundance.

cluding *A. altissima* and *J. nigra*; all together, trees of known risk made up 98.6% of the trees surveyed at the McDaniel Environmental Center.

## Discussion

*Lycorma delicatula* is a major new threat to natural environments and agriculture, and is a significant nuisance pest in its invaded ranges (Dara et al. 2015; Lee et al. 2019). Since its first detection in Pennsylvania in 2014 (Barringer et al. 2015), the list of plants used as oviposition substrates or for feeding by nymphs and adults has continued to grow and now includes over 100 species from various geographic provenances (Barringer & Ciafré 2020). As populations continue to spread and these insects move into new sites with varying environmental conditions and varying plant communities, the list of plants susceptible to oviposition, feeding, and damage is likely to expand. Continued investigations into host plant use and oviposition substrates certainly will be a key to developing effective monitoring and management strategies throughout the invaded range of *L. delicatula*.

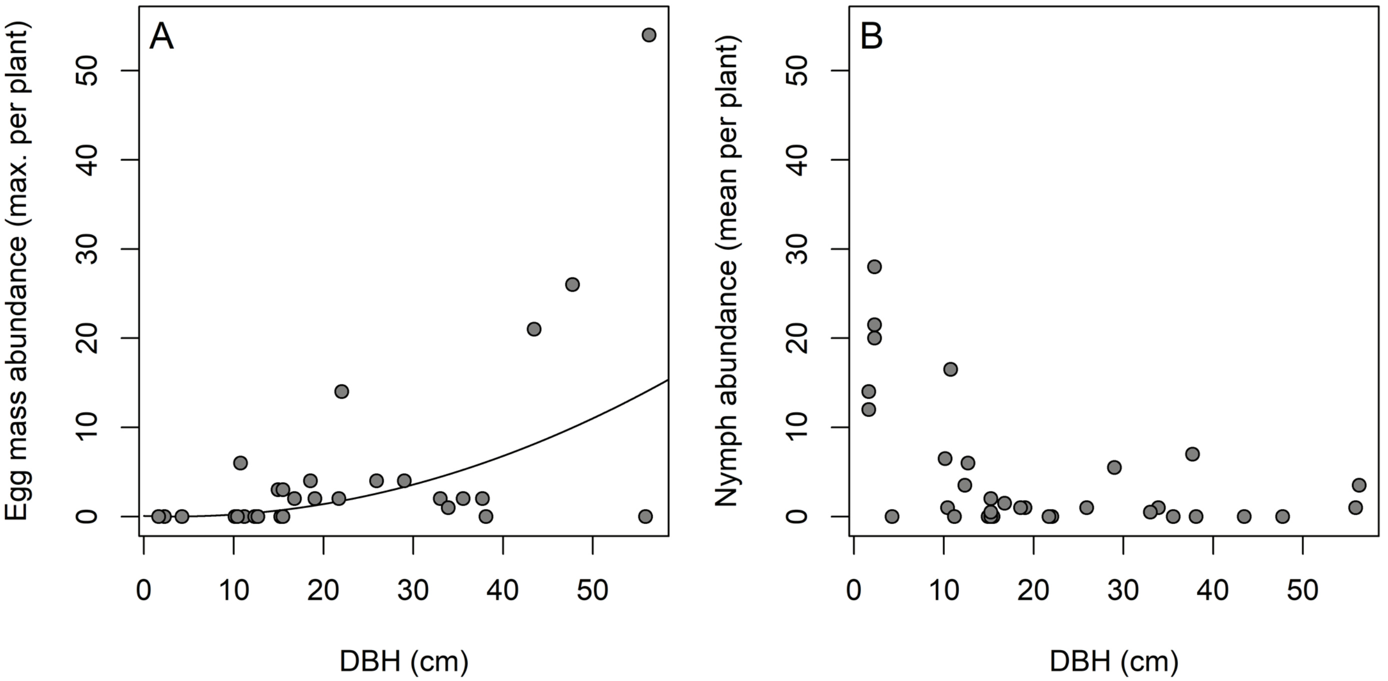

**Fig. 3.** Plant size (as diam at breast height, DBH, in cm) differentially affected the abundance of *Lycorma delicatula* egg masses and nymphs in the Pennsylvania field surveys. (A) Egg mass abundance was an increasing function of plant size. Points are maximum egg mass counts per plant, and the line depicts the back-transformed model-estimated effect of plant size. (B) Nymphal abundance (plotted as average nymphal abundance per plant but analyzed as raw count data) tended to decrease with plant size.

Though limited in temporal and geographic scope, our study found similar patterns in favored oviposition and host plant use compared with field studies in other locations in Pennsylvania. Specifically, we found that nymphal abundance in our timed surveys differed significantly among potential host plants, with highest nymphal abundances on *A. altissima*, *Rosa* sp., *J. nigra*, and *T. daniellii* (Fig. 4B). These top nymphal hosts correspond well with favored host plants from the recent literature (Dara et al. 2015; Lee et al. 2019; Liu 2020). Additional host plants used by nymphs in our study (*Acer saccharum* Marshall [Sapindaceae], *Amelanchier* sp. Medik. [Rosaceae], *Fagus grandifolia* Ehrh. [Fagaceae], *Liriodendron tulipifera* L. [Magnoliaceae], *Pinus strobus* L. [Pinaceae], *Prunus avium* L. [Rosaceae], *Rubus* spp. L. [Rosa-

**Table 3.** Risk assessment and counts of trees in partial tree inventories at the McDaniel College campus in Westminster, Maryland, and the McDaniel Environmental Center (MEC) in New Windsor, Maryland. Risk categories are based on literature reports (Known risk: Dara et al. 2015; Barringer & Ciafré 2020; Liu et al. 2020), new data from the current study (Of new concern), or no known reports (Unknown risk) for *Lycorma delicatula* egg masses and nymphs.

| Location | Risk category | Tree species | Count |
|---|---|---|---|
| Campus (*n* = 86) | Known risk (86%) | *Quercus montana* | 16 |
| | | *Juglans nigra* | 11 |
| | | *Acer saccharum* | 9 |
| | | *Pinus strobus* | 9 |
| | | *Liriodendron tulipifera* | 8 |
| | | *Zelkova serrata* | 5 |
| | | *Prunus avium* | 4 |
| | | *Acer palmatum* | 3 |
| | | *Cornus* sp. | 3 |
| | | *Fraxinus americana* | 3 |
| | | *Ailanthus altissima* | 2 |
| | | *Quercus rubra* | 1 |
| | Of new concern (4.7%) | *Liquidambar styraciflua* | 4 |
| | Unknown risk (9.3%) | *Quercus palustris* | 7 |
| | | *Gleditsia tricanthos* | 1 |
| MEC (*n* = 221) | Known risk (98.6%) | *Ailanthus altissima* | 97 |
| | | *Juglans nigra* | 60 |
| | | *Acer saccharum* | 39 |
| | | *Sassafras albidum* | 17 |
| | | *Liriodendron tulipifera* | 5 |
| | Of new concern (1.4%) | *Liquidambar styraciflua* | 3 |

ceae], and *Vitis* sp. Bunge [Vitaceae]) also correspond with literature reports and support the conclusion of a broad host range for nymphs (Kim et al. 2011; Song et al. 2018; Lee et al. 2019). We also report early instar nymphs on green hawthorn (*Crataegus viridis* L. [Rosaceae]), which is a new nymphal record for *L. delicatula*. We suggest further investigation into whether these common, native understory trees are true feeding hosts, potentially by using DNA gut analysis (Avanesyan & Lamp 2020) and by assessing the frequency of nymphal feeding on these trees at other sites.

Egg mass abundance also varied considerably among individual plants in our study (Fig. 4A). In contrast to the clear differences in nymphal abundances among plant species, egg mass abundances did not vary significantly among plant species. This lack of influence of host plant species on oviposition patterns is perhaps unsurprising given the incorporation of both living and non-living substrates for oviposition (Urban 2019). In addition, egg mass abundances may be influenced by factors we did not assess directly in this study. Notably, sites varied in both plant composition, abundance, and invasion history. Addition-

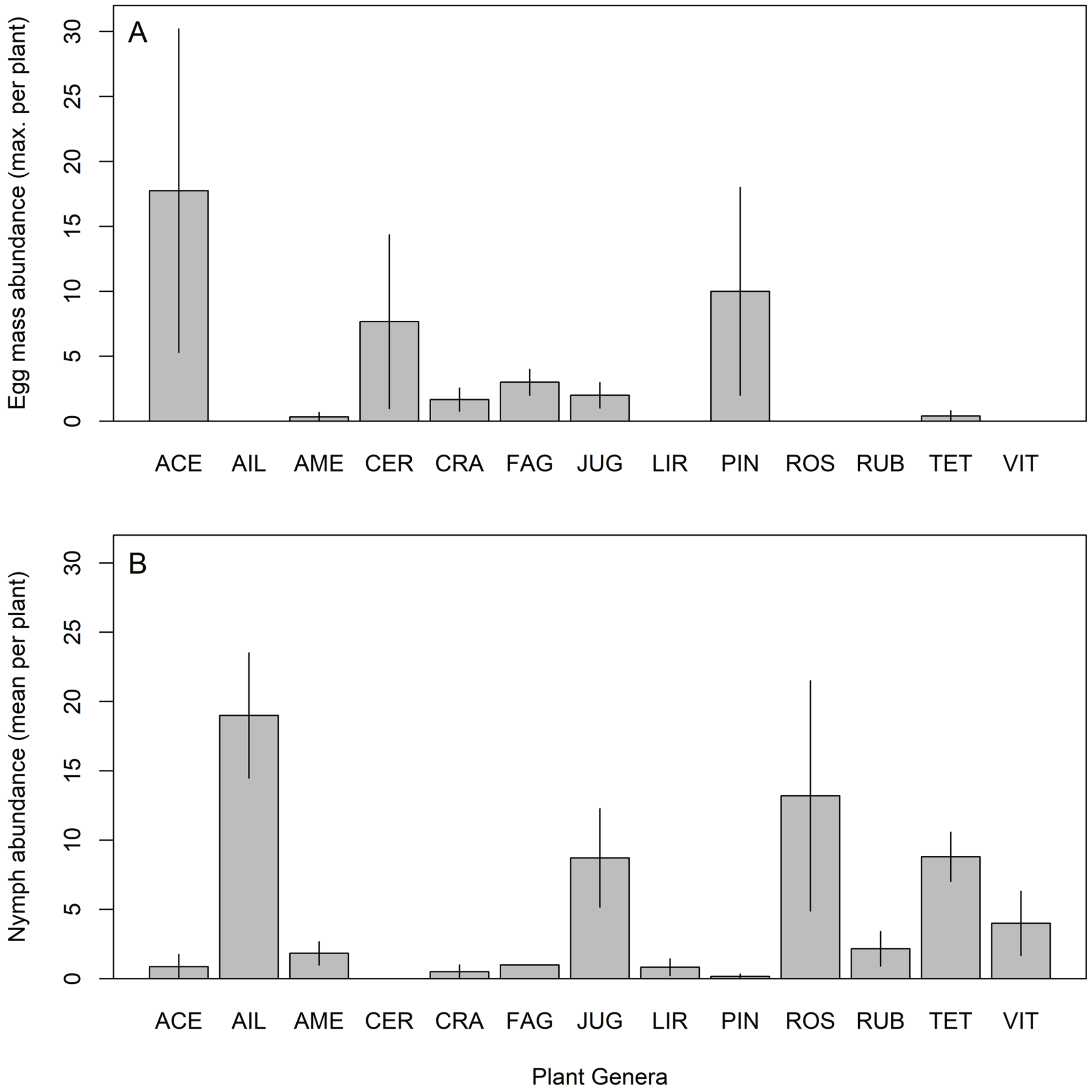

**Fig. 4.** In the Pennsylvania field surveys, egg mass abundance varied greatly (A) but did not significantly depend on plant species, whereas nymphal abundance did (B). Plotted are mean (± 1 SE) maximum egg mass abundance per plant and mean nymphal abundance per plant, as in Figure 3. Abbreviations: ACE (*Acer saccharum*), AIL (*Ailanthus altissima*), AME (*Amelanchier* sp.), CER (*Cercis canadensis*), CRA (*Crataegus viridis*), FAG (*Fagus grandifolia*), JUG (*Juglans nigra*), LIR (*Liriodendron tulipifera*), PIN (*Pinus strobus*), ROS (*Rosa* sp.), RUB (*Rubus* spp.), TET (*Tetradium daniellii*), VIT (*Vitis* sp.).

ally, females may oviposit on plants or structures based on proximity to adult feeding host plants (Liu 2020). We do, however, report here the use of 3 plant species not previously known as oviposition substrates: *C. canadensis*, *C. viridis*, and *L. styraciflua* (Table 2). As with the nymphal assessment above, we suggest these 3 species, all which are common in eastern forests and regularly used as valued native ornamental species in landscape and street tree plantings, be examined at additional sites to evaluate whether their use as oviposition substrates is widespread in the invaded US range.

As more information about oviposition and host plant use for *L. delicatula* becomes available, more effective strategies for surveying and management may become clear. Our work reinforces that targeted investigations on potentially important nymphal hosts during the summer and *A. altissima* and other key aggregation hosts for adults in the fall will be important (Lee et al. 2019; Liu 2020). We also suggest that plant size be taken into consideration for oviposition surveys in the future. In our study, egg mass abundance was an increasing function of plant size (Fig. 3A), with the cumulative use of large trees over time much higher than the use of smaller trees, shrubs, and vines. In habitats with trees of varying sizes, large trees would be clear targets for initial survey efforts. This strong, positive relationship between egg mass abundance and tree size also underscores that herbivorous insects may respond to plant size and other traits associated with resource availability, despite variation in phylogenetic relatedness and secondary chemistry among available plants (Marques et al. 2000; Whitfeld et al. 2012; Castellis et al. 2017).

Based on information from the literature and our Pennsylvania field surveys, we then assessed the extent to which plant communities in nearby, currently uninvaded sites may be at risk for use by *L. delicatula*. At the campus site, our inventory included a diverse set of native and non-native ornamental and wild trees. Similar to studies of risk in natural habitats (Dara et al. 2015), most of these managed trees can be used by *L. delicatula* for feeding or oviposition. Unfortunately, though diverse plantings in campuses and other urban forest settings can help mitigate risks caused by any 1 new pest or pathogen (Raupp et al. 2006), the highly generalized feeding and oviposition habits of *L. delicatula* represent formidable problems for management in both natural and managed settings.

Notably, our tree inventory at the semi-natural site revealed the near ubiquity of at-risk plants, largely because of the dominance of *A. altissima*, *J. nigra*, and *A. saccharum* (Table 3). It should be noted that our tree inventory at the semi-natural site was a partial inventory emphasizing the composition of the forest edge habitats. Thus, the dominance of edge-associated species like *A. altissima* is higher than would be representative of the forest overall. Nevertheless, the high abundance of *A. altissima* in forest edge habitats in our local site and in the mid-Atlantic region overall (McAvoy et al. 2012; Slodonja et al. 2015) indicates that such habitats may be hit hard by *L. delicatula* as it spreads through the region, especially with recent documentation of edge effects in the abundance of *L. delicatula* (Leach & Leach 2020b). Management strategies should include development of tree inventories, monitoring dense stands of *A. altissima* in areas adjacent to established *L. delicatula* populations, and removal of *A. altissima* where possible (Urban 2019).

## Acknowledgments

We thank the Milton Hendrickson Student-Faculty Research Fund, the Jean McDonald Richard Student-Faculty Research Fund, the McDaniel College Department of Biology, and the Charles A. Boehlke, Jr., Engaged Faculty Fellows program for funding. We deeply appreciate the Welkinweir arboretum and Sandi Yanisko for providing access to research sites and for their incredible hospitality. We also are grateful for the 2 peer reviewers whose thoughtful comments helped improve this project.

## References Cited

Avanesyan A, Lamp WO. 2020. Use of molecular gut content analysis to decipher the range of food plants of the invasive spotted lanternfly, *Lycorma delicatula*. Insects 11: 214. doi:10.3390/insects11040215

Barringer L, Ciafré CM. 2020. Worldwide feeding host plants of spotted lanternfly, with significant additions from North America. Environmental Entomology 49: 999–1011.

Barringer L, Donovall L, Spichiger S-V, Lynch D, Henry D. 2015. The first New World record of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). Entomological News 125: 20–23.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Bertheau C, Brockerhoff EG, Roux-Morabito G, Lieutier F, Jactel H. 2010. Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. Ecology Letters 13: 506–515.

Brooks RK, Toland A, Dechaine AC, McAvoy T, Salom S. 2020. The inability of spotted lanternfly (*Lycorma delicatula*) to vector a plant pathogen between its preferred host, *Ailanthus altissima*, in a laboratory setting. Insects 11: 515. doi:10.3390/insects11080515

Castellis E, Morante M, Saura-Mas S, Blasco-Moreno A. 2017. Plant-herbivore assemblages under natural conditions are driven by plant size, not chemical defenses. Journal of Plant Ecology 10: 1012–1021.

Cope EA. 2001. Muenscher's Keys to Woody Plants: An Expanded Guide to Native and Cultivated Species. Cornell University Press, Ithaca, New York, USA.

Crawley MJ. 2007. The R Book. John Wiley & Sons, Ltd. Chichester, United Kingdom.

Dara S, Barringer L, Arthurs S. 2015. *Lycorma delicatula* (Hemiptera: Fulgoridae): a new invasive pest in the United States. Journal of Integrated Pest Management 6: 1–6.

Harper JK, Stone W, Kelsey TW, Kime LF. 2019. Potential economic impact of the spotted lanternfly on agriculture and forestry in Pennsylvania. A research report of the Center for Rural Pennsylvania, Harrisburg, Pennsylvania, USA. https://www.rural.pa.gov/download.cfm?file=Resources/PDFs/research-report/Spotted-Lanternfly-2019.pdf (last accessed 6 Feb 2023).

Jung J-M, Jung S, Byeon D-H, Lee W-H. 2017. Model-based prediction of potential distribution of the invasive insect pest, spotted lanternfly *Lycorma delicatula* (Hemiptera: Fulgoridae), by using CLIMEX. Journal of Asia-Pacific Biodiversity 10: 532–548.

Kim J-G, Lee E-H, Seo Y-M, Kim N-Y. 2011. Cyclic behavior of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae) on host plants. Journal of Insect Behavior 24: 423–435.

Leach H, Leach A. 2020a. Seasonal phenology and activity of spotted lanternfly (*Lycorma delicatula*) in eastern US vineyards. Journal of Pest Science 93: 1215–1224.

Leach H, Leach A. 2020b. Characterizing the spatial distributions of spotted lanternfly (Hemiptera: Fulgoridae) in Pennsylvania vineyards. Scientific Reports 10: 20588. https://doi.org/10.1038/s41598-020-77461-9 (last accessed 8 Feb 2023).

Lee D-H, Park Y-L, Leskey TC. 2019. A review of biology and management of *Lycorma delicatula* (Hemiptera: Fulgoridae), an emerging global invasive species. Journal of Asia-Pacific Entomology 22: 589–596.

Lee D-H, Cullum JP, Anderson JL, Daugherty JL, Beckett LM, Leskey T. 2014. Characterization of overwintering sites of the invasive brown marmorated stink bug in natural landscapes using human surveyors and detector canines. PLoS ONE 9: e91575. https://doi.org/10.1371/journal.pone.0091575 (last accessed 8 Feb 2023).

Liu H. 2019. Oviposition substrate selection, egg mass characteristics, host preference, and life history of the spotted lanternfly (Hemiptera: Fulgoridae) in North America. Environmental Entomology 48: 1452–1468.

Liu H. 2020. Seasonal development, cumulative growing degree-days, and population density of spotted lanternfly (Hemiptera: Fulgoridae) on selected hosts and substrates. Environmental Entomology 49: 1171–1184.

Marques ESDA, Price PW, Cobb NS. 2000. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. Environmental Entomology 29: 696–703.

Martinson HM, Raupp MJ, Frank SD. 2020. How urban forest composition shapes the structure and function of arthropod communities, pp. 15–36 *In*

Barbosa P [Ed.], Urban Ecology: Its Nature and Challenges. CABI Press, Boston, Massachusetts, USA.

Martinson HM, Bergmann EJ, Venugopal PD, Riley CB, Shrewsbury PM, Raupp MJ. 2016. Invasive stink bug favors naïve plants: testing the role of plant geographic origin in diverse, managed environments. Scientific Reports 6: 32646. doi: 10.1038/srep32646.

Mason PA, Wilkes SR, Lill JT, Singer MS. 2011. Abundance trumps quality: bi-trophic performance and parasitism risk fail to explain host use in the fall webworm. Oikos 120: 1509–1518.

McAvoy TJ, Snyder AL, Johnson N, Salom SM, Kok LT. 2012. Road survey of the invasive tree-of-heaven (*Ailanthus altissima*) in Virginia. Invasive Plant Science and Management 5: 506–512.

Nixon LJ, Ludwick DC, Leskey TC. 2020. Horizontal and vertical dispersal capacity and effects of fluorescent marking on *Lycorma delicatula* nymphs and adults. Entomologia Experimentalis et Applicata 169: 219–226.

Nixon LJ, Jones SK, Tang L, Urban J, Felton K, Leskey TC. 2022. Survivorship and development of the invasive *Lycorma delicatula* (Hemiptera: Fulgoridae) on wild and cultivated temperate host plants. Environmental Entomology 51: 222–228.

NY IPM. 2022. Confirmed spotted lanternfly locations [online]. New York State Integrated Pest Management Program, Cornell University, Ithaca, New York, USA. https://nysipm.cornell.edu/environment/invasive-species-exotic-pests/spotted-lanternfly/ (last accessed 8 Feb 2023).

Pearse IS, Altermatt F. 2013. Predicting novel trophic interactions in a non-native world. Ecology Letters 16: 1088–1094.

R Core Team. 2022. R: a language for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raupp MJ, Cumming AB, Raupp EC. 2006. Street tree diversity in eastern North America and its potential for tree loss to exotic borers. Arboriculture & Urban Forestry 32: 297–304.

Slandonja B, Sušek M, Guillermic J. 2015. Review on invasive tree of heaven (*Ailanthus altissima* (Mill.) Swingle) conflicting values: assessment of its ecosystem services and potential biological threat. Environmental Management 56: 1009–1034.

Song S, Kim S, Kwon S, Lee S, Jablonski P. 2018. Defense sequestration associated with narrowing of diet and ontogenetic change to aposematic colours in the spotted lanternfly. Scientific Reports 8: 1–11.

USDA-APHIS. 2019. Pest Alert. Spotted lanternfly (*Lycorma delicatula*). APHIS 81-35-024, revised August 2019, https://www.aphis.usda.gov/publications/plant_health/alert-spotted-lanternfly.pdf (last accessed 8 Feb 2023).

USDA-APHIS. 2022. Spotted lanternfly [online]. USDA, Animal and Plant Health Inspection Service. https://www.aphis.usda.gov/aphis/resources/pests-diseases/hungry-pests/slf/spotted-lanternfly (last accessed 8 Feb 2023).

Urban JM. 2019. Perspective: shedding light on spotted lanternfly impacts in the USA. Pest Management Science 76: 10–17.

Wakie TT, Neven LG, Lee WL, Lu Z. 2019. The establishment risk of *Lycorma delicatula* (Hemiptera: Fulgoridae) in the United States and globally. Journal of Economic Entomology 113: 306–314.

Whitfeld TJS, Novotny V, Miller SE, Hrcek J, Klimes P, Weiblen GD. 2012. Predicting tropical insect herbivore abundance from host plant traits and phylogeny. Ecology 93: S211–S222.