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Multiscale assessment of oviposition habitat associations and implications for management in the spotted lanternfly (*Lycorma delicatula*), an emerging invasive pest

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Abstract

1. Control of incipient invaders—established invasive species in the early stages of spreading—can be inhibited by incomplete knowledge of the species' habitat use. By identifying consistent habitat associations for incipient invaders early, control efforts can be more effective. Yet, because habitat associations are the result of multiscale processes, approaches are needed for integrating data collected across scales to identify them.

2. We employed a hierarchical, multiscale approach to identify oviposition habitat associations in the spotted lanternfly (*Lycorma delicatula*), an incipient invasive species of high concern in the United States. We targeted four oviposition habitat spatial scales most likely to be used by lanternflies and the spatial scales of explanatory habitat variables most easily used by managers to locate egg masses to control.

3. Spotted lanternflies exhibited oviposition habitat associations at the landscape, site, and tree scales. Overall, lanternflies oviposited more frequently at sites and on trees with low canopy cover in the surrounding landscape indicating higher use of human-impacted habitat. Additionally, they oviposited more frequently on trees from the Acer genus and in the crowns of larger trees beyond the reach of managers without special equipment. The duration a site had been invaded had opposing effects on oviposition at the site and tree scales.

4. Despite high variation in the number of eggs per egg mass, no habitat variables explained this variation, suggesting more work is needed to understand spotted lanternfly reproductive output.

5. *Synthesis and applications*: Our results indicate that a multiscale approach is needed for spotted lanternfly control with unique strategies for locating egg masses at sites and on trees that vary in invasion duration. Specifically, at younger sites at the invasion edge, managers should expect patchy colonization of sites, yet when a site is colonized, many trees will have egg masses. Comparatively, older sites at the invasion core are more likely to have egg masses present, yet often at a lower density, which may make them difficult to find on individual trees.

> Based on our results, we assert that multiscale investigations of habitat associations would likely inform the control of other incipient invasive species as well.

1 | INTRODUCTION

Because invasive species are being introduced at accelerating rates (Seebens et al., 2017) and are a significant cause of negative ecological and economic impacts (Pyšek et al., 2020), devising strategies for their control is imperative. Incipient invaders—established species in the early stages of spreading—are thought to be the most cost-effective invasion stage to control (Homans & Horie, 2011), yet their control still provides unique challenges. Since incipient invaders are often at low densities and managers have incomplete knowledge of the species' habitat use, searches for them can be long, ineffective, and costly (Mehta et al., 2007). However, if incipient invaders are consistently associated with particular habitat types, the early identification of their habitat associations can enhance management by drastically reducing search efforts and improving success.

In general, *habitat use* refers to the aspects of the habitat species exploit for their needs (Krausman, 1999) and *habitat associations* arise when species consistently use the same type of habitat, often because that habitat provides higher fitness (McLoughlin et al., 2006). Habitat associations are identified when species have higher abundance in consistently used habitats. For incipient invaders, habitat associations may arise when a habitat provides a needed resource. For example, invasive ladybeetles (*Harmonia axyridis*) use oviposition habitats based on the availability of prey for their offspring (Rondoni et al., 2017). Alternatively, if incipient invaders are transported by humans, habitat associations between the species and the habitats associated with their transport may arise. This is the case for several invasive cavity-nesting mosquito species; they are associated with tires in human settlements because they are directly transported in tires to these locations by humans (Lounibos, 2002). Comparatively, when incipient invaders are generalist species and/or experience enemy release, they may use many habitat types, making it difficult to discern clear habitat associations. Instead, as incipient invaders are expanding their range, habitat use as indicated by species abundances may be better explained by the duration a site has been invaded rather than any habitat variables (Strayer et al., 2017).

Regardless of the mechanisms generating them, the processes that underlie habitat associations operate at multiple spatial scales (Mayor et al., 2009). Investigations that employ a hierarchical design where habitat use at multiple, nested spatial scales is explained by habitat variables provide a more complete understanding of habitat associations than investigating single or non-nested scales (Johnson, 1980). In this hierarchical context, habitat associations may arise between habitat use and environmental variables acting at the same and/or broader scales. From a management perspective, hierarchical designs provide useful guidance for enacting management actions for invasive species (Martins et al., 2016). Broad-scale habitat associations indicate the general area where a species may be, while fine-scale associations provide key information for exactly where to find the species to control. Therefore, it is important to conduct multiscale assessments at both the scales at which species use habitat and the scales at which management decisions are made (Brown & Barney, 2021). Despite their utility, multiscale assessments of habitat associations for non-native species are scarce (Froehly et al., 2020; Weaver et al., 2012), partly because they may require different skillsets to collect finer scale data through field studies and broader scale data aggregated through data science methods. Studies that can integrate datasets across scales are poised to provide comprehensive information to direct management efforts.

Here, we conduct a hierarchical, multiscale assessment of habitat associations in the spotted lanternfly (*Lycorma delicatula*), an incipient invasive species of high concern in the US (Dara et al., 2015). Native to China, the spotted lanternfly planthopper was first documented in the U.S. in Pennsylvania in 2014, and as of 2021, it has expanded its range to nine additional states in the Mid-Atlantic region (NYSIPM, 2021). Its reproduction is univoltine: females lay wax-covered egg masses on trees in the autumn, which hatch into nymphs the following spring and then transition to adults in late summer (Liu, 2019). Control efforts currently target adult, nymph, and egg stages, yet because egg masses can be difficult to detect, identifying oviposition habitat associations would help to inform management efforts substantially.

Spotted lanternflies may have oviposition habitat associations driven by preferred resources and/or dispersal, or alternatively, oviposition habitat use may be better explained by the duration a site is invaded. Spotted lanternflies are generalist phloem-feeders and have been documented on over 150 plant taxa (Barringer & Ciafré, 2020). Yet, their most frequently used host plant species, like *Ailanthus altissima*, are weedy or ornamental species that are common in human-dominated habitats. Additionally, spotted lanternflies disperse with human assistance within their invaded range (Urban et al., 2021). Both their host plant usage and dispersal modality may generate positive associations with human-dominated habitats. Finally, as spotted lanternflies have spread outward from their initial introduction site, they may follow recurring boom and bust population dynamics exhibited by other invasive species (Strayer et al., 2017). If so, the duration a site has been colonized may explain habitat use in addition to or better than habitat variables.

We use a hierarchical design to identify variables influencing multiscale oviposition habitat use from the landscape to egg mass scale (Figure 1). We integrate data science methods with traditional field methods to generate explanatory variables at two spatial scales likely to influence spotted lanternfly habitat associations that are also easily used by managers. Finally, we discuss how the multiscale nature of our results has clear implications for spotted lanternfly control and management.

2 | MATERIALS AND METHODS

We analysed spotted lanternfly oviposition habitat use across four hierarchical scales: oviposition at sites across Pennsylvania (landscape-scale), oviposition on trees within a site (site-scale), oviposition within a tree (tree-scale) and eggs within an egg mass (egg mass scale; Figure 1). Hereafter, we use 'scale' to refer to the different scales of these response variables of spotted lanternfly habitat use and 'level' to refer to the scales of explanatory variables (McGarigal et al., 2016).

Our oviposition response variables for the four scales came from two surveys. The first was a large, multiagency survey of egg masses at 141,984 sites across Pennsylvania (hereafter 'statewide survey'; Figure 2a), and we used these data for the landscape-scale analysis. For the finer three scales, we used data from an in-depth survey of 66 sites sampled from the 'core' (longest invaded sites) to the 'edge' (newer invaded sites) of the invaded range in southeastern Pennsylvania (hereafter 'core-to-edge survey'; Figure 2b).

Below, we describe our data collection and multiscale analyses on these two datasets. Explanatory variables were scaled to facilitate comparison of their estimated effect sizes among models at each scale. Analyses were conducted using R programming for statistics version 4.1.1 (R Core Team, 2021). Model diagnostics were run for each model using the "simulateResiduals" function from the DHARMa package (Hartig, 2020). Collinearity among variables (variance-inflation) was checked using the "vif" function from the car package (Fox & Weisberg, 2019). This research did not require

ethical approval for research on animals. No licences or permits were needed to conduct the surveys; however, appropriate permissions were obtained from private property owners as needed.
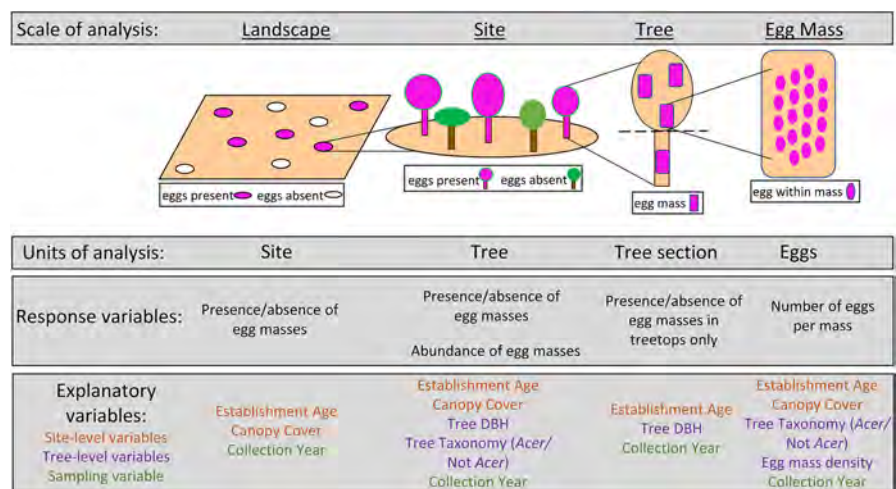
2.1 | Statewide survey

To assess oviposition habitat use at the landscape scale, we used data from spotted lanternfly surveys at sites across Pennsylvania by the Pennsylvania Department of Agriculture (PDA) and the United States Department of Agriculture (USDA). At each site, these agencies recorded the presence/absence of spotted lanternflies and egg masses during the 2018–2019 and 2019–2020 seasons (hereafter 'collection year 2018' and 'collection year 2019', respectively). The surveyed sites varied substantially in size and habitat type, yet were predominantly clusters of accessible trees on maintained properties that the agencies had permission to access. Although 141,984 sites were surveyed, many sites had no spotted lanternfly present because the agencies surveyed beyond the edge of the invasion range. To restrict the dataset to only sites within the invaded range, we defined the invaded range by creating a 0.1 km grid across the state and analysed only those sites contained in grid cells where at least one site had an established spotted lanternfly population. This grid size corresponds to the distance that spotted lanternfly adults have been recorded dispersing during the mating and egg laying season (Wolfin et al., 2019). This filtering resulted in 7363 sites within 4016 grid cells that contained at least one site with an established lanternfly population (Figure 2a).

2.2 | Core-to-edge survey

We sampled egg masses at 66 sites spanning the invasion core to edge (Figure 2b) in southeastern Pennsylvania for two reproductive seasons: November 20, 2018 to May 17, 2019 ('collection year 2018') and November 14, 2019 to March 9, 2020 ('collection year 2019'). Across the two collection years, 24 sites were sampled during both years, 28 sampled in 2018 and 14 sampled in 2019. To maintain consistency with

FIGURE 1 Hierarchical, multiscale study design showing the four scales of oviposition habitat use response variables, the unit of analysis, and the site- and tree-level explanatory variables used in our analyses. DBH, diameter at breast height.
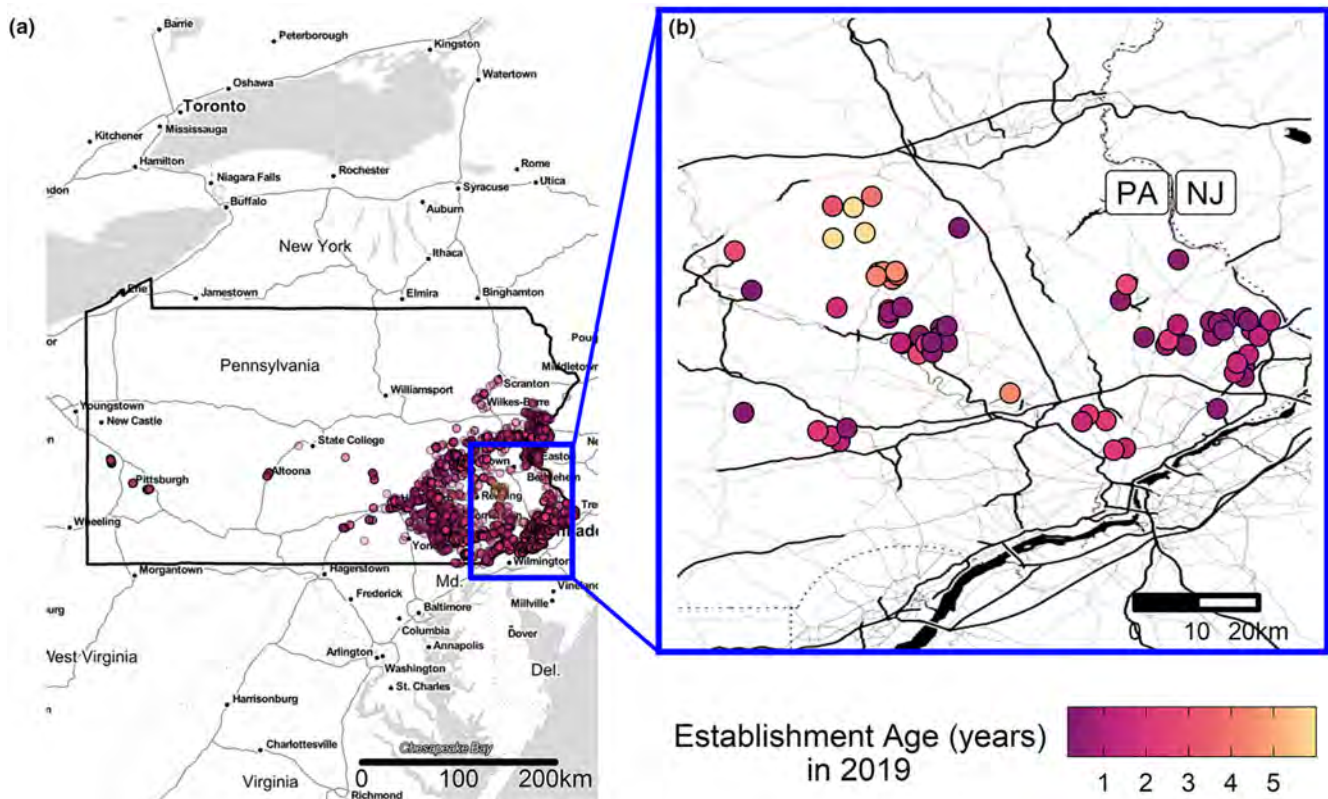
FIGURE 2 Multiscale oviposition habitat selection by the invasive spotted lanternfly was assessed using data from two surveys: (a) A statewide survey recorded the presence/absence of eggs at 7363 sites across Pennsylvania. (b) A core-to-edge survey of 66 sites within southeastern Pennsylvania recorded egg mass abundance and eggs per mass on multiple trees within sites. In both surveys, sites varied in the number of years spotted lanternfly was established at sites (establishment age—site shading).

the statewide survey methods, sites in our core-to-edge survey were clusters of trees predominantly at maintained properties such as residential areas and public parks. Trees within our clusters were no more than 10 m from another surveyed tree, and we selected sites with a minimum of five trees per cluster (mean trees/site = 13, range = 5–22). To ensure we sampled across the invasion gradient, sites were selected by first identifying regions on a map that likely differed in invasion duration and we selected several candidate properties within each region. Once on the ground, we sampled only the properties that were accessible and fulfilled our site and tree cluster criteria. Beyond these criteria, we did not target or exclude specific tree species or sizes; however, a few individual trees were excluded due to inaccessibility.

At each site, we recorded oviposition at three scales: site, tree and egg mass (Figure 1). At the site scale, we conducted exhaustive visual searches for egg masses on tree trunks and branches with the naked eye and recorded the number of egg masses per tree. At the tree scale, we recorded if egg masses on a tree were only in the treetops beyond the reach of managers without special equipment (>2 m) or distributed across the trunk and treetops. At the egg mass scale, we collected at least five egg masses per tree from different parts of the tree (i.e. minimum of 25 egg masses per site) and counted the number of eggs per egg mass with a dissecting microscope. All trees in the survey were identified to species and spanned a range of diameter at breast height (DBH) of 3.6–300 cm (mean = 36.21 cm, SD = ±34.49).

2.3 | Derived site-level explanatory variables

We predicted that spotted lanternfly oviposition should be positively associated with human-dominated habitats due to the availability of resources and/or dispersal modes. We used canopy cover surrounding each site as a proxy for human-dominance of sites. Given that our study area is in the forested temperate biome, low canopy cover is not a natural feature and mostly represents forest loss due to human activities, namely urban development. We calculated canopy cover in 500 m buffers surrounding each site, which is greater than the recorded dispersal distance of adult lanternflies (100 m; Wolfin et al., 2019) and is thus a conservative approximation of the maximum possible habitat available to lanternflies in their lifetime preceding oviposition. Canopy cover was the average pixel value within the buffer of the Global Forest Cover Change (GFCC) Tree Cover dataset computed using Google Earth Engine at 30 m resolution (Sexton et al., 2013) and ranged from 2.48%–69.65% (statewide survey) and 5.65%–54.76% (core-to-edge survey).

We also predicted that spotted lanternfly oviposition could be negatively correlated to a site's establishment age—the duration a site has had an established population of lanternfly. We estimated the establishment age of each site by spatially interpolating the presence/absence of spotted lanternfly at any life stage from data collected by PDA and USDA across PA for each year between 2015 and 2019 (Supporting

Information 1, Section 1). From our interpolation method, the minimum value for any site was zero and the maximum value was 5 years, indicating the certainty of spotted lanternfly being established throughout the 5 years considered, 2015–2019 (Figure 2). Using this method, we calculated establishment ages for sites from both survey datasets. For the sites that were sampled both collection years, we used the corresponding establishment age of the site for the year when the data were collected as explanatory variables in our statistical models.

2.4 | Landscape scale analysis

For our landscape scale analysis, we explored habitat associations across sites in the statewide survey. We tested the effect of surrounding canopy cover, establishment age and collection year on egg mass presence at sites with a logistic regression ("glm" in the stats package). We included collection year to account for unexplained year-to-year variation that may influence oviposition and accounted for spatial autocorrelation among sites using the "autocov_dist" function from the spdep package (Bivand, 2022; Dormann et al., 2007).

2.5 | Site scale analysis

For our site-scale analysis, we explored which variables affected oviposition across trees within the sites sampled in our core-to-edge survey. We included the site-level establishment age and canopy cover variables due to their possible association with oviposition on trees. Since tree size and tree taxonomy may influence oviposition habitat use (Liu, 2019; Liu & Hartlieb, 2020), we included tree DBH and tree species as tree-level variables. However, our dataset encompassed 32 tree species from 23 genera, which was more categories than we had statistical power to test. Therefore, analysed oviposition preference at the genus level (Beyer et al., 2010) and found spotted lanternfly oviposited on the genus *Acer* at a higher frequency than its availability at sites (Supporting Information 1, Section 2). Accordingly, we grouped all genera into *Acer*/not *Acer* categories and use this as our binary tree taxonomy variable in subsequent analyses to test the strength of the preference for tree taxonomy relative to other environmental variables influencing habitat use.

Our models for the site-scale analysis to explain variation in oviposition on trees within sites included the explanatory variables: establishment age, canopy cover, collection year, tree size (DBH) and tree taxonomy (*Acer*/not *Acer*). Given the high number of trees we sampled with zero egg masses, we conducted our site-scale analysis in two parts. First, we tested the effect of the explanatory variables on the presence/absence of egg masses on trees using a binomial generalized linear mixed model (GLMM) with site as a random effect ("glmer" in lme4, Bates et al., 2015). Only data from collection year 2019 were used because trees without eggs were not recorded in collection year 2018. Then, using only the subset of the trees in our dataset that exhibited oviposition activity (i.e. excluding trees with zero egg masses),

we fit a second model testing the effect of the explanatory variables on the number of egg masses per tree using a GLMM with a zero-truncated negative binomial error distribution with a *log-link* function (glmmTMB, Brooks et al., 2017) using data from both collection years.

2.6 | Tree scale analysis

For our tree-scale analysis, we explored the effect of the explanatory variables on the distribution of egg masses within a tree because lanternflies may prefer to oviposit in treetops over trunks (Liu & Hartlieb, 2020). Our binary response variable was the presence of egg masses only in the treetops (1) versus presence of egg masses in the treetops and along the trunk (0). We never observed instances of egg masses only on the trunk and not in the treetops when multiple masses were present. This analysis only included trees for which egg masses were present. To explore these patterns, we fit a GLMM with a binomial error distribution and a *logit-link* function, with establishment age, collection year, and tree DBH as the fixed effects and site as a random effect ("glmer" in lme4).

2.7 | Egg mass scale analysis

For our egg mass scale analysis, we focused on explanatory variables that could influence the number of eggs per egg mass: establishment age, canopy cover, collection year, tree taxonomy (*Acer*/not *Acer*) and egg mass density. Egg mass density per tree was included in the model because planthopper density may be negatively correlated with fecundity (Denno & Roderick, 1992; Heong, 1988). Egg mass density was calculated as the number of egg masses per tree scaled by tree DBH and provides a proxy for spotted lanternfly adult and nymph density at our sites (sampled in summer 2019—Table S1; Figure S2; Supporting Information 1, Section 3). To test the effects of the explanatory variables on the number of eggs per egg mass, we fit a GLMM with a negative binomial error distribution ("glmer.nb" in lme4) with a nested random effect of tree ID within site.

3 | RESULTS

3.1 | Survey summaries

For the statewide survey, we examined egg mass presence/absence from 7363 sites across the spotted lanternfly's invaded range in Pennsylvania, 2834 of which had egg masses present. For the core-to-edge survey, during egg collection year 2018, we surveyed 52 sites, 12 of which had ≥1 egg mass present and site and tree scale data (DBH, species) recorded. Across these 12 sites, we collected 183 egg masses from 40 trees (8 species, 6 genera) with an average of 27.52 eggs per egg mass (range 1–95 eggs). For egg collection year 2019, 38 sites were surveyed, 25 of which had ≥1 egg mass present and tree-scale data recorded. We collected egg masses at 19 of these 25 sites; we

collected 280 egg masses from 81 trees (12 species, 8 genera) with an average of 32.84 eggs per egg mass (range: 2–102 eggs).

3.2 | Landscape scale

At the landscape scale, oviposition was higher at sites with older establishment age ($p < 0.001$) and higher at sites with low mean canopy cover surrounding the site ($p < 0.05$, Table 1). Putting this into context, sites with 10% canopy cover had a 10% higher likelihood of having egg masses than sites with 30% canopy cover. Across the three variables tested at the landscape scale, collection year had the strongest effect, reflecting an overall higher probability of oviposition at sites in the 2019 than 2018 season ($p < 0.001$); in 2019, the odds of finding eggs at a site were over seven times higher compared to 2018. The effect of these explanatory variables was estimated after accounting for positive spatial autocorrelation among sites ($p < 0.001$).

3.3 | Site scale

At the site-scale, we found qualitatively similar patterns for the two models exploring the effects of the explanatory variables on egg mass presence and abundance, with stronger effects on egg mass presence. Site-level canopy cover had the strongest effect in the models, with higher egg mass presence ($p < 0.001$) and abundance ($p < 0.01$) on trees at sites with low surrounding canopy cover (Table 1). Specifically, the probability of finding egg masses on trees was 50% higher at sites with 10% versus 30% canopy cover. The tree-level variable *Acer*/not *Acer* was the next strongest variable with higher egg mass presence ($p < 0.001$) and abundance ($p < 0.001$) on trees from the *Acer* genus. The odds of finding egg masses on *Acer* trees were 10 times higher than on non-*Acer* trees, and the abundance of egg masses was on average over four times higher on *Acer* compared to other trees. Finally, site-level establishment age had the third-strongest effect such that egg mass presence ($p < 0.01$) and abundance ($p < 0.05$) on trees was higher at more recently invaded sites with lower establishment ages. This means that site-level establishment age has opposite effect on oviposition habitat use when considered at the site (negative effect size) and landscape scales (positive effect size).

3.4 | Tree scale

At the tree-scale, only tree DBH explained the likelihood to oviposit in the treetops versus in the entire tree, with trees with larger DBH being more likely to have eggs laid only in the treetop ($p < 0.001$, Table 1). For example, the likelihood of eggs being laid only in the treetops was almost 20 times higher for a tree with a DBH of 50 cm compared to a tree with a DBH of 10 cm.

3.5 | Egg mass scale

At the egg mass-scale, no site-level or tree-level variables explained variation in numbers of eggs per egg mass. The number of eggs per mass was only affected by collection year with significantly higher numbers of eggs per mass in collection year 2019 ($p < 0.001$, Table 1). There was also no evidence for density-dependent effects on the number of eggs per egg mass ($p = 0.324$, Table 1).

4 | DISCUSSION

Using a hierarchical, multiscale design, we identified several habitat associations for spotted lanternflies at the landscape, site, and tree scales, which have important implications for spotted lanternfly management strategies. In addition, we found that the duration spotted lanternflies have been established at a site was also a predictor of habitat use, regardless of the habitat type. Remarkably, despite high variation in the number of eggs per egg mass, none of the habitat variables we tested explained this variation, indicating more work is needed to identify drivers of spotted lanternfly reproductive output.

Oviposition habitat use at the broadest scales—landscape scale (oviposition at sites) and site-scale (oviposition on trees within sites)—was explained in part by the site-level explanatory variables, canopy cover and establishment age. Oviposition was associated with lower canopy cover in the 500 m radius surrounding the site at both scales and is consistent with our predication that spotted lanternfly oviposition is associated with human-dominated habitats. While the correlative nature of our study does not indicate a clear mechanism, the management implications are clear. Managers should target lower canopy cover areas when searching for egg masses. Indeed, at both the landscape and site scales, we found a much higher likelihood of finding egg masses at sites with 10% versus 30% canopy cover. While our sites covered an appreciable range of canopy cover across our study area and represent sites where spotted lanternfly are likely to occur, there are two important caveats. First, low canopy cover could be associated different land uses like agriculture or urban development. In our system, agriculture is minimal, yet further studies exploring the effects of specific land cover types on habitat use are necessary. Second, since we did not sample densely forested sites, our results cannot be used to infer habitat use at the highest end of the canopy cover gradient. We did not sample these sites because based on our experience and anecdotal evidence from colleagues, lanternfly use of forest interiors is rare, but future studies should confirm these predictions.

Mechanistically, spotted lanternfly's association with lower canopy cover habitats could be driven by selecting habitats that provide preferred host plants and/or dispersal. In the context of selecting habitats that provide host plants, oviposition habitat selection in insects may be due to females choosing oviposition habitats that best guarantee offspring success, or it may be a consequence of females choosing a habitat that is best for them at the time of

TABLE 1 Results from each model of oviposition habitat use at different spatial scales.

Model scale	Response variable	R^2	Term	Estimate	Standard error	Statistic	p-Value
Landscape	Presence/absence of egg masses at sites	0.200	(Intercept)	−2.521	0.108	−23.457	**<0.001**
			Establishment age	0.229	0.035	6.465	**<0.001**
			Canopy cover	−0.142	0.059	−2.412	**<0.05**
			Collection year (2019)	2.049	0.061	33.439	**<0.001**
			Spatial autocovariate	0.978	0.071	13.753	**<0.001**
Site	Presence/absence of egg masses on trees	0.489	(Intercept)	9.674	2.256	4.283	**<0.001**
			Establishment age	−1.510	0.545	−2.770	**<0.01**
			Canopy cover	−6.864	1.974	−3.477	**<0.001**
			Tree DBH	−0.206	0.350	−0.588	0.556
			Tree taxonomy (not *Acer*)	−2.380	0.432	−5.507	**<0.001**
Site	Abundance of egg masses on trees	0.365	(Intercept)	6.379	0.985	6.478	**<0.001**
			Establishment age	−0.755	0.321	−2.348	**<0.05**
			Canopy cover	−2.744	0.920	−2.984	**<0.01**
			Collection year (2019)	−0.280	0.288	−0.974	0.330
			Tree DBH	−0.074	0.419	−0.177	0.859
			Tree taxonomy (not *Acer*)	−1.482	0.286	−5.189	**<0.001**
Tree	Presence/absence of egg masses in tree tops	0.443	(Intercept)	−4.234	0.859	−4.932	**<0.001**
			Establishment age	0.006	0.369	0.016	0.987
			Collection year (2019)	0.640	0.586	1.091	0.275
			Tree DBH	5.062	1.092	4.637	**<0.001**
Egg Mass	Number of eggs per egg mass	0.089	(Intercept)	3.383	0.136	24.950	**<0.001**
			Establishment age	−0.045	0.040	−1.122	0.262
			Canopy cover	0.011	0.111	0.097	0.923
			Collection year (2019)	0.196	0.052	3.771	**<0.001**
			Tree taxonomy (not *Acer*)	−0.046	0.057	−0.806	0.420
			Egg mass density	−0.035	0.036	−0.986	0.324

Abbreviation: DBH, diameter at breast height.
p-Values in bold are significant at the $\alpha < 0.05$ level.

oviposition (Mayhew, 1997). Although we cannot distinguish between these two oviposition habitat selection patterns for spotted lanternfly based on the influence of canopy cover alone, the higher oviposition on *Acer* genus trees we identified in the site-scale analyses may suggest oviposition habitat is based on adult preferences rather than selecting ideal host plants for offspring. *Acer* spp. phenology in our study region aligns better with the adult than nymph stage for feeding. Early instar nymphs preferentially feed on soft tissue such as herbaceous plants and fleshy parts of woody plants (Mason et al., 2020). While nymphs can feed on fleshy leaves of *Acer* species, the nymphs hatch in the spring often before leaf-out in most *Acer* species. Comparatively, adult lanternflies frequently congregate on *Acer* spp. in autumn (Mason et al., 2020), likely as a consequence of the delayed autumnal senescence and prolonged photosynthetic activity that characterizes members of the *Acer* genus relative to other regional tree species. Alternatively, oviposition on *Acer* spp. may reflect its utility as an oviposition substrate rather than a trophic resource due to its relatively smooth bark (Urban, 2020). Like *Acer* spp., *Ailanthus altissima* also has smooth bark and delayed phenology. In our study, *A. altissima* was second

to *Acer* as an oviposition substrate and has been used as an oviposition substrate in other locations within the invaded range (Liu, 2019). Future experimental work should aim to disentangle the effects of phenology from substrate properties on oviposition substrate selection mechanisms.

In addition to spotted lanternfly possibly selecting low canopy cover habitats due to presence of host plants, the association between higher oviposition and lower surrounding canopy cover may also reflect spotted lanternfly's dispersal. All life stages of spotted lanternfly are transported short distances within the invaded range by humans (Urban et al., 2021). Human-assisted dispersal would likely result in them being more tightly associated with human-impacted (i.e. low canopy cover) areas. Identifying the mechanisms underlying the habitat associations we have identified would help to inform management going forward.

Compared to the consistent effect of canopy cover on oviposition at the landscape and site scales, site-level establishment age had opposing effects at these two scales, suggesting divergent search tactics are needed for managers. These opposing effects indicate that sites that have been invaded longer are more likely to

have at least some egg masses present, yet individual trees at sites invaded more recently are more likely to have egg masses present and a higher abundance of egg masses. Although studies of spotted lanternfly population dynamics are ongoing, they may match classic invasion dynamics where newly colonized sites experience a rapid increase in population density and then decline to low densities without ever reaching a point of extinction at the site (Strayer et al., 2017). This boom-and-bust population dynamics pattern would support our finding that older sites are more likely to have eggs present because extinction is rare at old sites and colonization of sites at the invasion edge is patchy. In comparison, our site-scale results suggest that at sites with younger establishment age, spotted lanternflies may have a higher likelihood of ovipositing on a range of trees at a site rather than concentrating their eggs on a few trees, regardless of the tree species.

Collection year also explained significant variation in oviposition with a higher likelihood of oviposition at sites in 2019 (landscape scale) and more eggs per egg mass in 2019 (egg mass scale). While the exact mechanism behind annual variation in reproductive output in spotted lanternflies is not known, annual temperature fluctuations may be responsible for the patterns seen. For example, slight elevations in warming (i.e. 2°C) can increase the number of eggs laid per female in other planthoppers (Manikandan et al., 2015). The yearly average temperature was warmer and precipitation was lower in 2019 compared to 2018 in southeastern Pennsylvania (NCEI, 2019,

2020), so this may have contributed to the seasonal fluctuations we documented.

Aside from collection year, no other variables we tested explained the substantial variation in the number of eggs per egg mass in our data (1–102 eggs). Lanternfly reproductive biology is currently under investigation, including determining the number of egg masses each female lays and the allocation of resources to egg masses. In insects, habitat quality can affect reproductive output beyond the number of eggs per egg mass, including the size of eggs, occurrence of offspring deformities, and offspring survival (Awmack & Leather, 2002). In addition, insects can adjust egg quality and nutrient allocation to eggs to match environmental conditions and lay higher quality eggs in better habitats (Awmack & Leather, 2002). There was no influence of intraspecific competition (lanternfly density), human-dominated habitats (represented by canopy cover), or establishment age on the number of eggs per mass in our study. Clearly more research is needed to understand variation in lanternfly fecundity.

The multiscale nature of our results suggest explicit management strategies are needed at both the site and tree scales to locate egg masses, in addition to differing strategies at recently established sites at the invasion edge versus long-established sites within the invasion core (Figure 3a). For sites, our data suggest higher variation in the presence of egg masses at younger sites at the invasion edge relative to the core (Figure 3b). At the tree scale, if eggs are present at a site, trees at younger sites are more likely to have egg
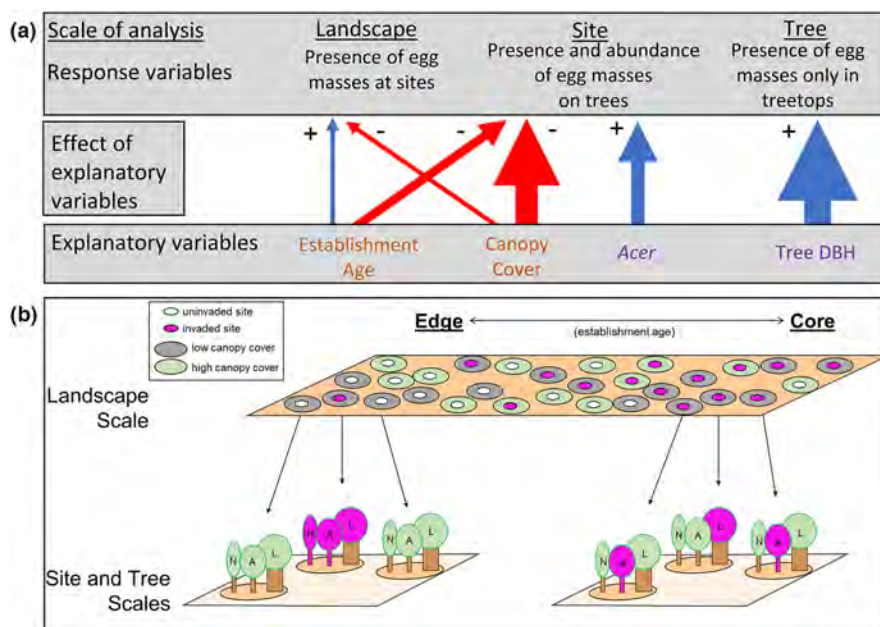

FIGURE 3 (a) Main effects from multiscale models reported in Table 1 that inform management strategies. Width of arrow is proportional to effect size; blue arrows indicate positive effect, red arrows are negative effect of site-level (orange) or tree-level (purple) explanatory variables on multiscale response variables (note: tree taxonomy variable is *Acer* instead of *not Acer* as in Table 1). (b) Pattern of spotted lanternfly oviposition habitat associations (pink shading signifies spotted lanternfly oviposition habitat use) at the landscape and site/tree scales that indicates different search strategies are needed to control spotted lanternfly along the gradient of establishment ages for sites. At the landscape scale, more sites at the core will have eggs present. When eggs are present at a site, more trees at sites at the edge will have egg masses than at the core. Across the gradient, sites with low canopy cover in the surrounding landscape (grey circles) and trees from the *Acer* genus (A) versus other genera (N) will have a higher likelihood of having spotted lanternfly egg masses. In addition, large trees (L) will have a higher likelihood of having egg masses at the top of the trees that are out of reach.

masses than older sites (Figure 3b). In practice, this means older sites are more likely to have egg masses present, but they may be at lower density and possibly harder to find. Comparatively, egg mass densities are likely to be higher and distributed across more trees at younger sites. Across the invasion gradient, we emphasize the need to treat possibly overlooked *Acer* spp., especially in greenspaces and residential areas where *Acer rubrum* is frequently used as an ornamental tree (Mason et al., 2020). We caution that egg masses in larger trees may be inaccessible for mechanical removal because they may be in the tree canopy and other methods may be necessary (Leach et al., 2019).

Finally, while our results clearly demonstrate the need for a multiscale response to management of spotted lanternflies, they are not the only invasive species to exhibit multiscale habitat associations (Froehly et al., 2020; Weaver et al., 2012). We suggest that managers tasked with the control of other incipient invaders consider a multiscale approach.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the *Dryad Digital Repository* https://doi.org/10.5061/dryad.ffbg79d00 (Ramirez et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplemental methods and analyses.

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