



# N-mixture models for population estimation: Application in spotted lanternfly egg mass survey

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## ABSTRACT

Population density and structure are critical to nature conservation and pest management. Traditional sampling methods such as capture-mark-recapture and catch-effort can't be used in situations where catching, marking, or removing individuals are not feasible. N-mixture models use repeated count data to estimate population abundance based on detection probability. They are widely adopted in wildlife surveys in recent years to account for imperfect detection. However, its application in entomology is relatively new. In this paper, we describe the general procedures of N-mixture models in population studies from data collection to model fitting and evaluation. Using *Lycorma delicatula* egg mass survey data at 28 plots in seven sites from the field, we found that detection probability ( $p$ ) was negatively correlated with tree diameter at breast height (DBH), ranged from 0.516 [95 % CI: 0.470–0.561] to 0.614 [95 % CI: 0.566–0.660] between the 1st and the 3rd sample period. Furthermore, egg mass abundance ( $\lambda$ ) was positively associated with basal area (BA) for the sample unit (single tree), with more egg masses on tree of heaven (TOH) trees. More egg masses were also expected on trees of other species in TOH plots. Predicted egg mass density (masses/100 m<sup>2</sup>) ranged from 5.0 (95 % CI: 3.0–16.0) (Gordon) to 276.9 (95 % CI: 255.0–303.0) (Susquehannock) for TOH plots, and 11.0 (95 % CI: 9.00–15.33) (Gordon) to 228.3 (95 % CI: 209.7–248.3) (Burlington) for nonTOH plots. Site-specific abundance estimates from N-mixture models were generally higher compared to observed maximum counts. N-mixture models could have great potential in insect population surveys in agriculture and forestry in the future.

## 1. Introduction

Accurate and reliable information on population size, structure, and distribution is essential to the monitoring, conservation, and management of animal species. However, detecting all individuals of a species in a given place and time is usually not possible. As one of the most widely utilized approaches in population studies, the capture-mark-recapture method uses recapture frequency of marked individuals to evaluate population abundance (Pollock, 1981; Chao, 2001; Funk et al., 2003; Bailey et al., 2004), while the catch-effort (removal sampling) method compares declining catch size during sequential captures to measure initial population size (Schnute, 1983; Bruce, 1995; Chao and Chang, 1999; Petranka and Murray, 2001). However, catching, marking, identifying, and removing a large amount of individuals over wide ranges is labor intensive and logistically difficult. To avoid these, occupancy models use site occupancy status when unmarked individuals at fixed sites are recorded through standard monitoring procedures (e.g., point

count, call survey, distance sampling) (Buckland et al., 1993; Rodda and Campbell, 2002; Pellet and Schmidt, 2005; MacKenzie et al., 2006). However, imperfect detection with zero inflation (disproportionate number of absences) resulting from species traits (e.g., conspicuousness, behavior, life history, rarity), individual characteristics (e.g., sex, age, distance to the observer), or survey itself (e.g., effort, observer experience, weather, method, time of the day, season in the year) renders traditional data analysis (e.g., Poisson regression, generalized linear model with a Poisson error distribution) ineffective for these models (Mazerolle et al., 2007; Wenger and Freeman, 2008; Sólymos et al., 2012).

N-mixture model is a hierarchical model that estimates detection probability ( $p$ ) and mean abundance ( $\lambda$ ) with spatially and temporally varying covariates using repeated counts of animals at fixed sample units. It assumes that the population is demographically closed, individuals are not counted at more than one sample unit, all individuals within the same sample unit have the same probability of being detected

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(or its heterogeneity can be explained by survey or site characteristics), and all sample units have the same probability of being occupied (or its heterogeneity can be explained by site characteristics) (Royle, 2004). It explicitly separates abundance from detection during the process (Martin et al., 2011). It also differs from the repeated measures design by estimating individual-level instead of site-level detection probability (Dénes et al., 2015). Count data are treated as Poisson distributed variables whereas individual detections are treated as binomial random events (Royle and Dorazio, 2008). N-mixture models have become a standard tool in population studies in recent years (Royle et al., 2005; Kéry et al., 2005; Graves et al., 2012; Gomez et al., 2018).

N-mixture models have been widely used in wildlife surveys such as small vertebrates (Ficetola et al., 2018), Italian wall lizard (*Podarcis siculus* (Rafinesque) [Squamata: Lacertidae]) (Sacchi et al., 2022), Nile crocodile (*Crocodylus niloticus* (Laurenti) [Crocodylia: Crocodylidae]) (Lyet et al., 2016), black rhinoceros (*Diceros bicornis* L. [Perissodactyla: Rhinocerotidae]) (Kidwai et al., 2019), African lion (*Panthera leo* (L.) [Carnivora: Felidae]) (Belant et al., 2016), sloth bear (*Melursus ursinus* (Shaw) [Carnivora: Ursidae]) (Chaudhuri et al., 2022), white-tailed deer (*Odocoileus virginianus* (Zimmermann) [Artiodactyla: Cervidae]) (Keever et al., 2017; Christensen et al., 2021), and marsh tit (*Poecile palustris* (L.) [Passeriformes: Paridae]) (Neubauer et al., 2022). Its application in population survey in entomology, however, is relatively new to the best of our knowledge except that by Keller and Hoover (2023).

The spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoroidea), a pest of tree of heaven (TOH) (*Ailanthus altissima* (Mill.) Swingle [Sapindales: Simaroubaceae]) from China (Zhou, 1992), was recently introduced to Pennsylvania (Barringer et al., 2015; Dara et al., 2015). It completes one generation a year and overwinters as egg masses on various substrates (Supplemental Text 1). Current distribution of this pest in the United States include 17 states from Massachusetts to Indiana and New York to North Carolina (NYSIPM, 2024). As a polyphagous pest, it also feeds on grapevines (*Vitis* spp. [Vitales: Vitaceae]) and >100 other plant and tree species (Dara et al., 2015; Liu, 2019; Barringer and Ciafré, 2020), posing a significant threat to the multibillion-dollar fruit, nursery, landscape, and hardwood industries in the United States (USDA APHIS, 2018).

To survey for *L. delicatula* egg mass population in the field, infested trees were either felled (Liu and Hartlieb, 2020; Keller et al., 2020) or visually inspected from the ground for part (Liu, 2019, 2020; Keller et al., 2020) or the entire tree (Liu and Hunter, 2021; Keller and Hoover, 2023). However, accuracy of these estimates has not been tested as egg masses are unevenly distributed in the forests with excessive zero detections on many of the trees surveyed (Liu and Hunter, 2021). In this paper, we describe the application of N-mixture models in the population study of *L. delicatula* based on repeated counts on its egg masses by following general procedures for data collection, model fitting, and evaluation. We believe this new approach will help alleviate problems associated with imperfect detection through the examination of model assumptions and identification of impactful covariates for both detection and abundance. It could have broad utility in general population surveys for species conservation and pest management in agriculture and forestry.

## 2. Materials and methods

### 2.1. General procedures for N-mixture modeling

To collect data for N-mixture models, a fixed sample unit (e.g., a spot, tree, or known area) is selected to ensure that the population is closed and individuals within the units can be detected independently during the survey. The target species (life stage) in each sample unit is surveyed by repeatedly counting over a period of time across all study sites. Survey results can be fitted in different mixture models for detection probability with various spatial and temporal covariates. The best supported model for detection can then be used to select abundance models

with their own set of covariates. Abundance for a sample unit is calculated based on the best supported model, with model selection often based on Akaike Information Criteria (AIC). Possible distributions for abundance in the models include Poisson, negative binomial, and zero-inflated Poisson (ZIP). Goodness-of-fit for each model can be evaluated by Pearson's Chi-square, Least Squares, or Freeman-Tukey test (Fig. 1A). Abundance at the plot level can be estimated by area expansion when the sample unit is part of a known area (e.g., fixed-radius plot). Site-specific population density is the average of estimated abundance of multiple plots at each site.

### 2.2. Application to *L. delicatula* egg mass count data

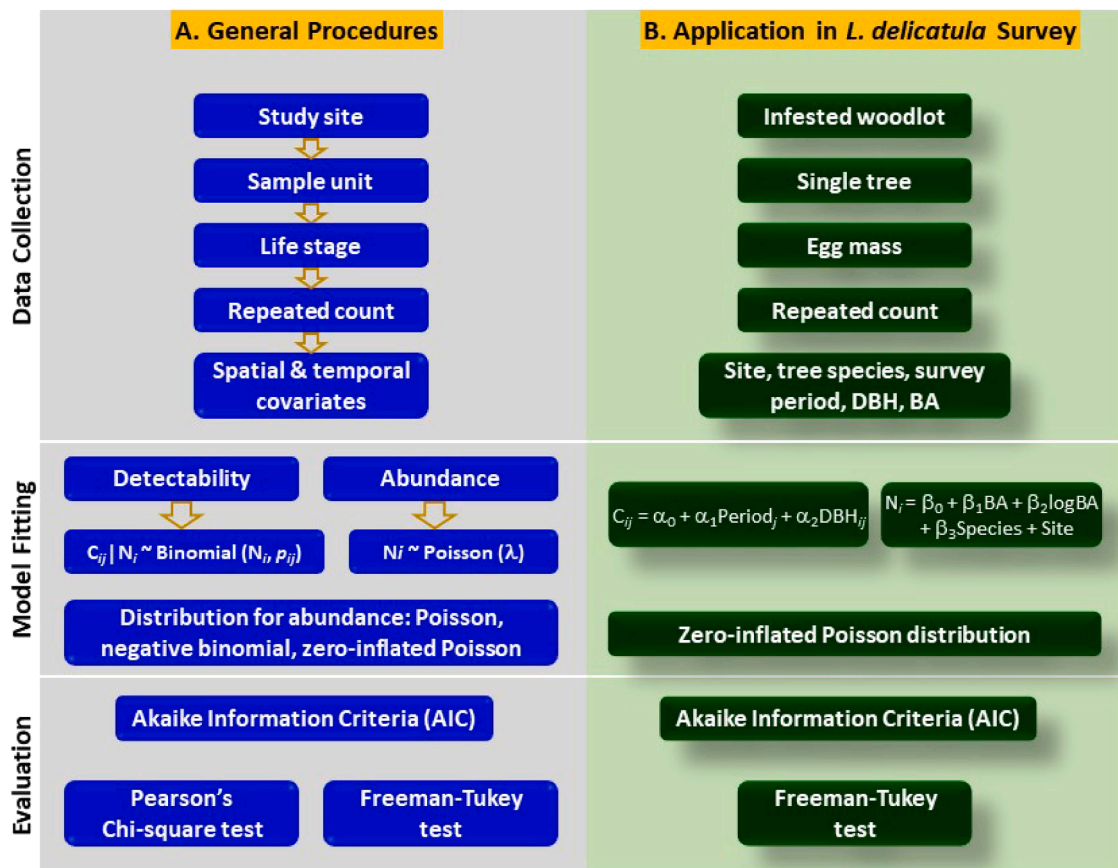
Data used in this application consist of three repeated counts of *L. delicatula* egg masses on 181 trees in 28 100-m<sup>2</sup> fixed-radius (= 5.65 m) circular plots at seven study sites in Pennsylvania and New Jersey (Supplemental text 2, 3, Table S1, Fig. S1) from late March to early May in 2021. Single trees were selected as the sample units since the number of egg masses on each tree would not change and no egg mass would be detected on two different trees during each survey. Field counting was carried out by the same two observers following the egg mass survey protocol each time (Supplemental text 4). Covariates considered include tree DBH (diameter at breast height) and survey period for detection probability; tree species (TOH vs others), BA (basal area), and study site for abundance on trees of all species; and BA, plot type (TOH plot vs nonTOHplot) and study site for abundance on trees other than TOH. Egg mass counts from two extremely large trees with a DBH > 70 cm were excluded from the analysis to avoid disproportional impact of tree size from them. Plot-level naïve estimates were based on unadjusted raw counts that used the highest observed egg mass count (among the three surveys) for each tree. Estimates of egg mass density (masses/100 m<sup>2</sup>) from maximum counts (Nmax) and N-mixture models (Nmix) were calculated for each plot. Site-specific comparison between them was based on mean density/plot and coefficient of variation (100 × standard deviation/mean).

Field data from individual trees (sample units) were organized by survey period, site, plot, species, DBH, and BA (Supplemental Data 1). Survey period and DBH were used in model selection for detection probability; whereas site, plot, species, and BA were used to fit abundance models (Supplemental Material Text 5). All models were analyzed in R 4.2.3 with the *unmarked* package (Fiske and Chandler, 2011) using the ZIP distribution with progressively higher K-values to ensure relatively consistent parameter estimates (Royle 2004; Kéry, 2018). Competing models were compared to each other with the best model selected based on the lowest AIC (Burnham and Anderson, 2002). For the top model in each data set evaluated, goodness-of-fit was assessed by using the parametric bootstrap and the Freeman-Tukey test (n = 1,000 samples) based on the *fitstats* function in *unmarked* (R Core Team, 2023).

## 3. Results and discussion

All top models displayed adequate fit based on Freeman-Tukey statistics (Table 1). The top detection model (Table 1A) predicted egg mass detection probability to increase with progressive sample periods, but decrease with DBH. Detection probability for an egg mass on an average tree (DBH = 16 cm) increased from 0.516 [95 % CI: 0.470–0.561] in the 1st sample period to 0.614 [95 % CI: 0.566–0.660] by the 3rd sample period. On the other hand, an increase of 20 cm in tree DBH resulted in an 18.7 % decrease of detection probability for a given egg mass (Fig. 2).

Egg mass abundance was positively associated with tree BA when either all species (Table 1B) or only species other than TOH were considered (Table 1C). Higher egg mass counts were predicted for TOH than other species ( $\beta_{\text{TOH}} \pm \text{SE} = 0.374 \pm 0.064$ ) (Fig. 3). Similarly, trees of other species in TOH plots were predicted to have higher egg mass counts than those in nonTOH plots ( $\beta_{\text{TOH plot}} \pm \text{SE} = 0.201 \pm 0.065$ )

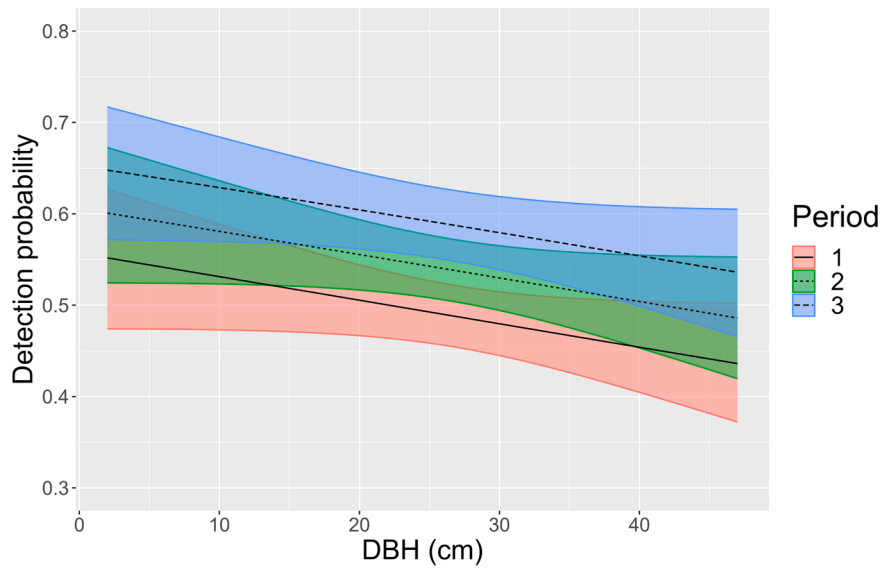


**Fig. 1.** Guidelines for population estimation with N-mixture models based on repeated count data: A) general procedures and B) application in *L. delicatula* survey.  $N_i$  - population abundance at sample unit  $i$ ,  $C_{ij}$  - count at sample unit  $i$  during survey  $j$ ,  $p_{ij}$  - detection probability at sample unit  $i$  during survey  $j$ .  $\lambda$  - density per sample unit. Sample unit can be a point, distance, habitat, or an area as long as population within the unit is demographically closed and individuals are not counted at more than one unit. Site-specific population density or total abundance can be estimated by area expansion if the sample unit is a known area (e. g., fixed-radius plot) or part of it. Spatial and temporal covariates (e.g., time, weather, plot type, method, observer) are used to explain potential heterogeneity in detectability and abundance. Distribution for abundance depends on raw data, model selection is determined by Akaike Information Criteria (AIC), and Goodness-of-fit can be evaluated by Pearson's chi-square or Freeman-Tukey test. DBH - diameter at breast height. BA - basal area.

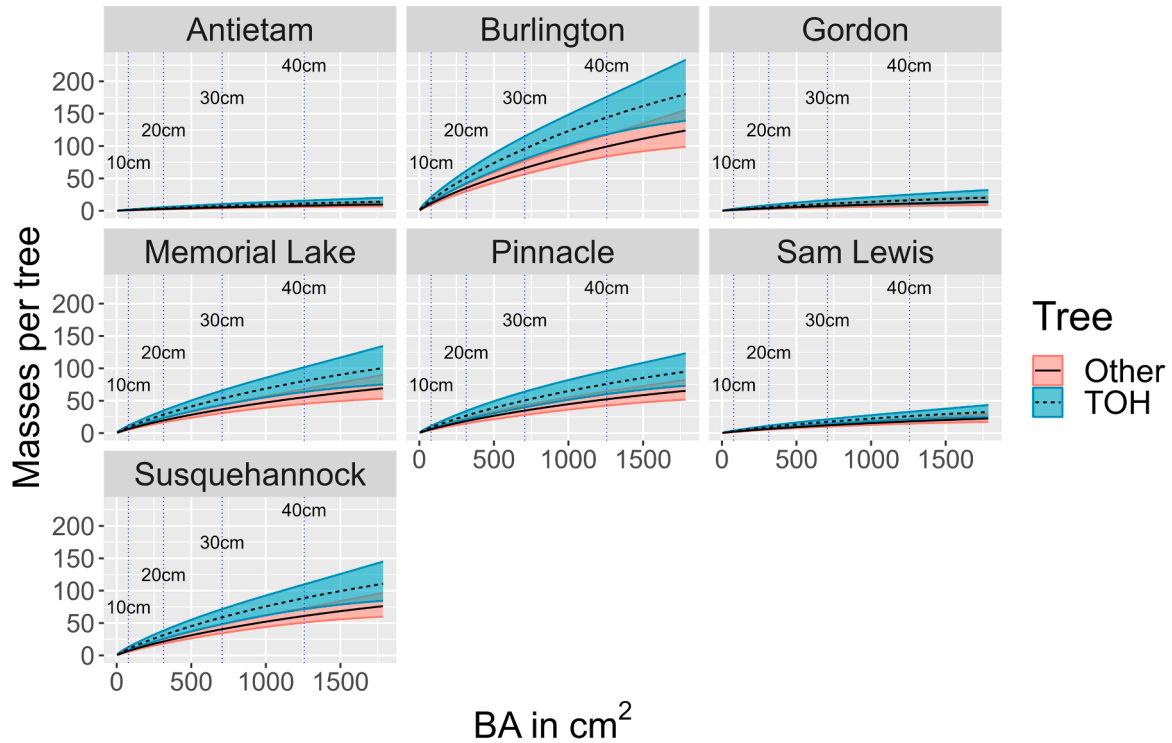
**Table 1**

Model selection results. (A) Detection models with egg mass count per tree, using observations from all trees. Covariates considered: Tree diameter (DBH), Period-specific detection (Period), Period 3 (P3) based on the assumption that detection is identical for periods 1 and 2, but different in period 3. (B) Abundance models with egg mass count per tree, using observations from trees of all species. Covariates considered: Tree basal area (BA), non-linear response for BA (logBA), Tree species (TOH vs other species), Site-specific abundance estimates (Site). (C) Abundance models with egg mass count per tree, using trees other than TOH. Covariates considered: BA, logBA, Plot type (TOH plot vs nonTOH plot), Site. Model selection based on number of parameters (nPars), Akaike's Information Criterion (AIC), the difference from the model with the lowest AIC (delta), model weights (AICwt), cumulative model weights (cumWt), and p-value for Freeman-Tukey tests (F-T GOF).

		nPars	AIC	delta	AICwt	cumWt	F-T GOF
<b>A. Detection probability, analysis with all trees</b>							
$\lambda(\text{BA}+\text{logBA}+\text{TOH}+\text{Site})$	$p(\text{Period}+\text{DBH})$	8	3148.38	0.00	0.650	0.65	p = 0.634
" "	$p(\text{Period})$	7	3149.64	1.26	0.349	1.00	
" "	$p(\text{P3}+\text{DBH})$	8	3170.75	22.37	<0.001	1.00	
" "	$p(\text{P3})$	7	3172.07	23.69	<0.001	1.00	
" "	$p(\text{DBH})$	7	3197.87	49.5	<0.001	1.00	
" "	$p(\cdot)$	6	3199.29	50.92	<0.001	1.00	
<b>B. Abundance, analysis with trees of all species</b>							
$\lambda(\text{BA}+\text{LogBA}+\text{TOH}+\text{Site})$	$p(\text{Period}+\text{DBH})$	8	3148.38	0.00	0.999	1.00	p = 0.634
$\lambda(\text{BA}+\text{LogBA}+\text{Site})$	" "	7	3177.54	29.16	<0.001	1.00	
$\lambda(\text{BA}+\text{Site})$	" "	6	3390.75	242.37	<0.001	1.00	
$\lambda(\text{TOH}+\text{Site})$	" "	6	3427.95	279.57	<0.001	1.00	
$\lambda(\text{Site})$	" "	5	3483.41	335.03	<0.001	1.00	
<b>C. Abundance, analysis with trees other than TOH</b>							
$\lambda(\text{BA}+\text{LogBA}+\text{TOH plot}+\text{Site})$	$p(\text{Period}+\text{DBH})$	8	2554.95	0.00	0.970	0.97	p = 0.168
$\lambda(\text{BA}+\text{LogBA}+\text{Site})$	" "	7	2562.2	7.25	0.027	1.00	
$\lambda(\text{BA}+\text{Site})$	" "	6	2741.55	186.59	<0.001	1.00	
$\lambda(\text{TOH plot}+\text{Site})$	" "	6	2809.75	254.8	<0.001	1.00	
$\lambda(\text{Site})$	" "	5	2811.19	256.24	<0.001	1.00	



**Fig. 2.** Detection probability by tree diameter (DBH) during the first (solid trendline), second (dotted trendline), and third (dashed trendline) sampling periods. Shaded areas represent 95 % confidence bands.



**Fig. 3.** Predicted egg mass abundance by basal area (BA) for individual trees of TOH (dotted trendline) and other species (solid trendline) by site. Vertical dotted lines mark tree diameters (DBH) corresponding to basal areas (BA). Shaded areas represent 95 % confidence bands.

(Fig. S2). This trend was supported by naïve occurrence data from the field as we observed 100 % of trees of other species in TOH plots being infested, compared to 67.7 % in nonTOH plots. No predictions were made for Antietam and Gordon as  $\leq 1$  tree of other species were found in the TOH plot.

Estimates of abundance for the best-supported N-mixture model (Table 1B) predicted egg mass densities (masses/100 m<sup>2</sup>) to range from 5.0 (95 % CI: 3.0–16.0) (Gordon) to 276.9 (95 % CI: 255.0–303.0) (Susquehannock) for TOH plots, and 11.0 (95 % CI: 9.00–15.33) (Gordon) to 228.3 (95 % CI: 209.7–248.3) (Burlington) for nonTOH plots. Nmax at those same sites produced lower densities, which ranged

from 2.7–163.7 for TOH plots and 0.0–259.0 for nonTOH plots. As expected, site-specific egg mass density was higher based on Nmix compared to Nmax estimation (Fig. 4). There were no consistent differences in error between them although Nmix estimation had a lower coefficient of variation at four of seven sites with an average difference of -2.3 %.

Differences in detection probability between sample periods (Fig. 2) is likely related to increased familiarity with egg mass locations because of repeated visits to the same trees by the same observers. The inverse relationship between DBH and egg mass detection probability is also anticipated as larger trees generally have more cryptic locations (e.g.,



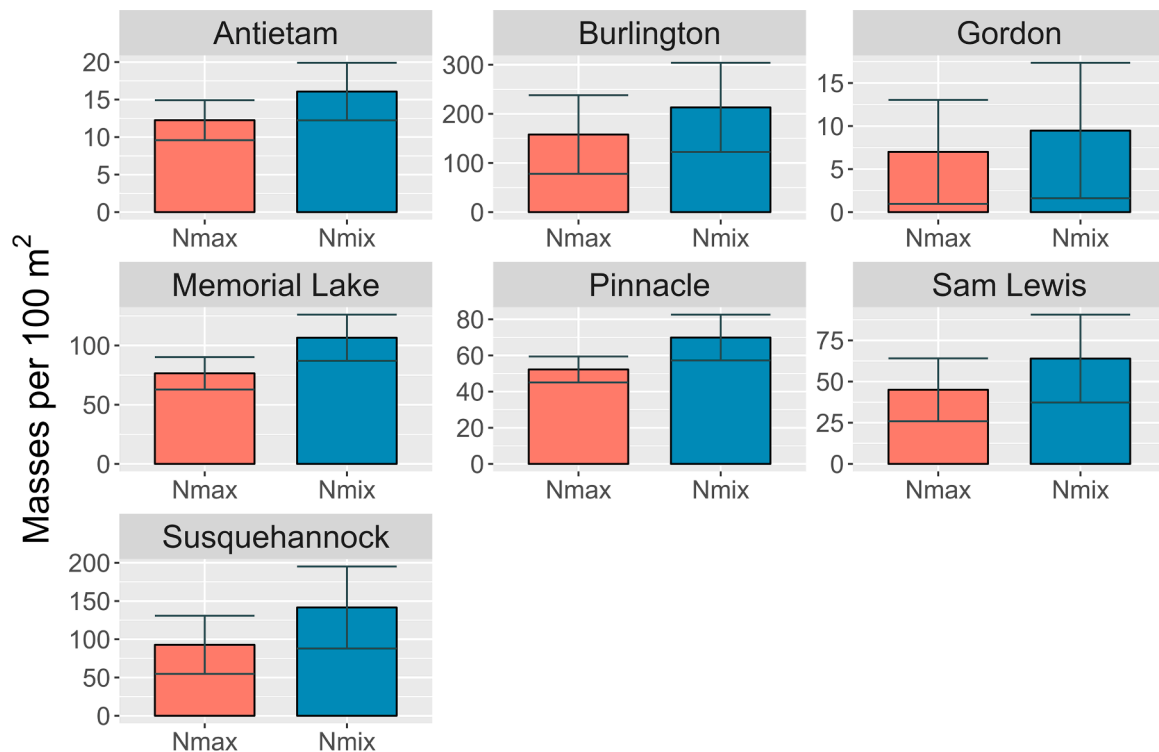


Fig. 4. Site-specific egg mass density (Mean  $\pm$  standard error) per 100 m<sup>2</sup> based on N-mixture models (Nmix) estimates and maximum observed egg mass count (Nmax). There are four 100-m<sup>2</sup> plots at each site, including one TOH and three nonTOH plots.

crotches, cavities, trunk crevices, bark layers) for egg masses to hide compared to smaller trees. Furthermore, more surface areas are available for *L. delicatula* females to lay eggs, resulting in a positive association between predicted abundance (egg mass/tree) and BA (Figs. 3, S2, Liu and Hunter, 2021). Higher egg mass number is expected on TOH than other trees (Fig. 3) since it is the primary host for *L. delicatula* during the initial infestation (Zhou, 1992; Liu, 2022). As a result, other species within the immediate vicinity of TOH trees may be more attractive than those further away as females search for additional substrates to lay eggs (Figs. S1, S2).

Our results are comparable to N-mixture models developed by Keller and Hoover (2023) for *L. delicatula* where a detection probability of 0.522 (95 % CI: 0.401–0.648) was reported based on two egg mass counts (fall and spring) at 75 plots (20  $\times$  5 m). Contrary to our study, none of their model covariates (height, BA, season, and weather) had a significant impact on egg mass detection. By using the plot BA (as opposed to the individual tree BA in the current study) as a covariate, they might not be able to adequately characterize the impact of larger trees as a plot with many small trees could have the same plot BA as the one with a fewer large trees.

Understanding population dynamics of *L. delicatula* in the field is critical to the successful management of this invasive species in North America. The stationary egg mass is an ideal life stage to survey for N-mixture models as population in each sample unit (tree) is closed to recruitment (death, immigration, emigration) for the current generation, and none of them can be counted in two different sample units. This study demonstrates that the assumption of equal detectability could be violated if tree size and sampling period are not considered as covariates. Other conditions such as weather could also affect egg mass detection as lighting conditions change during the day and between different cloud covers. In addition, large branches in the crown could block observer's view from the ground. On the other hand, tree species, BA, plot type all played a role in egg mass abundance on the sample unit (tree). N-mixture models can help account for these covariates while identifying ecological factors that impact population abundance. Model

estimates were higher than maximum egg mass counts at the study sites. Detection and abundance estimates based on sample unit of single tree fitted well with the models. More study is needed to focus on selecting standardized trees of various species and sizes, alternating observers or prolonging survey intervals, and defining impact of distance to TOH trees to minimize potential influences on detection probability and abundance estimates.

Results from this study may pave the way for similar applications in population surveys for other insect species. For example, management decision of the spongy moth (*Lymantria dispar* (L.) [Lepidoptera: Erebiidae]) is typically based on one-time egg mass survey on 100-m<sup>2</sup> fixed-radius plots before egg hatch (Liebhold et al., 1994). Given the similarities in voltinism, overwinter patterns, and types of oviposition substrates used between it and *L. delicatula*, abundance estimates should be improved through repeated egg mass count when factors affecting detectability (e.g., tree species, DBH, crown cover, surveyors, weather, time, season) were characterized in the N-mixture models. Compared to *L. delcatula*, it may have the advantage of possibly satisfying the equal occupancy assumption in addition to independent detection of closed population as egg masses are distributed contiguously in the oak forests (Kolodny-Hirsch, 1986). On the other hand, population estimates of the monarch butterfly (*Danaus plexippus* (L.) [Lepidoptera: Nymphalidae]) (e.g., Kinkead et al., 2019) could be enhanced when the right size of sample unit is selected to reflect the local dispersal potential of larvae and adults for independent detection. Other covariates such as plot type, year, season, spatial stratification, and tree canopy could also play a role in its detection and abundance. As the preferred host, impact of milkweed to monarch butterfly abundance has to be considered as the most important covariate in model selection just like TOH in the current study. Utilization of N-mixture models in general insect survey could be endless if proper sample unit and associated covariates are identified to satisfy model assumptions. Interested parties are encouraged to plug in their own data into the associated R script (Supplemental Data 1) to test these models.

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Data Availability: All data described in this manuscript is provided as supplementary material.

## CRedit authorship contribution statement

**Houping Liu:** Conceptualization, Funding acquisition, Methodology, Investigation, Formal analysis, Validation, Writing – original draft.  
**James T. Julian:** Formal analysis, Validation, Writing – original draft.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

I have attached the data as supplemental material for online publication.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.cris.2024.100078](https://doi.org/10.1016/j.cris.2024.100078).

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