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ARTICLE

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Intercontinental comparisons of invasive spotted lanternfly egg mass densities and mortality patterns

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Abstract

Spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), is an invasive species of planthopper native to China. Populations of this invasive insect have been detected in South Korea (2006), Japan (2009), and the United States (2014). Widespread economic damage to fruit crops has been reported from South Korea and the United States, primarily in grape vineyards. In Japan, no accounts of agricultural injury have been reported despite this species maintaining established populations in the country for over 15 years. To quantify intercontinental differences in egg mass demographics, egg mass densities and nymph hatching rates were compared in China, where *Ly. delicatula* is native and coexists with the associated egg parasitoid, *Anastatus orientalis* (Yang and Choi) (Hymenoptera: Eupelmidae), and South Korea, where *Ly. delicatula* is invasive and *An. orientalis* has been released for classical biological of *Ly. delicatula*. These data were compared to similarly collected data from Japan and the United States, countries where *Ly. delicatula* is invasive and *An. orientalis* is absent. The results indicated egg masses from field sites in Japan generally had the highest mean proportion of *Ly. delicatula* nymph hatch from individual eggs (0.82–0.95). Sites in South Korea generally had the highest mean proportion of parasitism on individual eggs (0.28–0.61) followed by sites in China (0.05–0.30). Field sites in the United States overall had the highest egg mass densities (326 ± 70 egg masses found per site in a 30-min time period in Year 1 and 739 ± 47 in Year 2 of surveys) (mean ± SE). In contrast, the overall lowest recorded egg mass densities were found from the sites in South Korea (31 ± 2 Year 1 and 33 ± 1 Year 2). Additionally, we assessed the roles that biotic (i.e., egg parasitism and host plant availability) and abiotic factors (i.e., climatic differences) play in observed *Ly. delicatula* egg densities and mortality rates. Overall, this study provides strong evidence that biotic and abiotic factors influence *Ly. delicatula* egg mass densities and hatch rates across regions where this species is native or invasive.

KEYWORDS
biological control, degree-days, egg mortality, invasive species, oviposition, parasitism

INTRODUCTION

Lycorma delicatula, native to China, is an invasive phloem-feeding planthopper, which has established populations in South Korea (in 2006), Japan (2009), and the United States (2014) (Barringer et al., 2015; Han et al., 2008; Liu, 1939; Tomisawa et al., 2013). This species is univoltine and overwinters as a wax covered oothecum (Dara et al., 2015; Park et al., 2009). Tree of heaven, *Ailanthus altissima* Mill. (Simaroubaceae), the main host plant for *Ly. delicatula* and also native to China, is classified as an invasive weed in South Korea, Japan, and the United States (Dara et al., 2015; Lee et al., 2019; Sladonja et al., 2015). In addition to its preferred host, *Ai. altissima*, *Ly. delicatula* can feed on over 100 different plants including several commercial crops (e.g., grapes, *Vitis vinifera* L. [Vitaceae]) (Barringer & Ciafré, 2020; Molfini et al., 2024; Murman et al., 2020). Feeding *Ly. delicatula* nymphs and adults form congregations on trunks or stems of host plants, and plant sap ingestion causes direct injury to crops (Han et al., 2008; Lee et al., 2019; Tomisawa et al., 2013). This pest also inflicts indirect damage by excreting a carbohydrate-rich waste product, honeydew, which stimulates sooty mold growth resulting in decreased photosynthesis (Dara et al., 2015; Urban & Leach, 2023).

Although *Ly. delicatula* is not considered a significant pest in its native range (i.e., China), studies have reported some economic damage to kiwifruit (*Actinidia chinensis* Planch. [Actinidiaceae]) and grape in China (Xin et al., 2021). In invaded regions, such as the United States and South Korea, *Ly. delicatula* is a serious economic pest, causing severe damage to vine, fruit, and nut crops, and to urban and forest trees (Park et al., 2009; Urban, 2020; Urban & Leach, 2023). Despite early quarantine efforts to restrict the spread of *Ly. delicatula* in the United States (Urban, 2020) and South Korea (Dara et al., 2015; Lee et al., 2019), founding populations underwent rapid range expansion. The highest levels of economic damage have been observed on grapes (Lee et al., 2009; Park et al., 2009), and in the eastern United States, *Ly. delicatula* infestations have resulted in as much as 90% yield losses and a threefold increase in insecticide applications in affected vineyards (Urban, 2020). Ecological niche models that use climate data have identified grape-producing regions in Japan, Europe, and the west coast of the United States (i.e., California) as areas vulnerable to invasion (Jung et al., 2017; Wakie et al., 2020).

In Japan, populations of *Ly. delicatula* have spread slowly relative to other invaded regions. The first detection of this species in Japan occurred in 2009 on *Ai. altissima* in Komatsu City, which is located in the Ishikawa Prefecture on Honshu Island in north-central Japan (Tomisawa et al., 2010). In 2013, specimens were found in the neighboring Prefecture, Fukui (Umemura et al., 2013). For eight years following the first detection of *Ly. delicatula* in Japan, reports of this insect were confined to Ishikawa and Fukui Prefectures. Currently, *Ly. delicatula* has been identified in 10 prefectures across Japan, and all detections have been reported from Honshu Island (Kamiyama & Konishi, 2022; Matsumoto, 2017; Okushima & Mizui, 2019; Suzuki & Shimada, 2023). Although Japan has sustained established populations of *Ly. delicatula* for over 15 years, incidents of economic damage to agricultural crops have yet to be reported, and *Ly. delicatula* is not designated nor regulated as a quarantine pest in Japan (Kamiyama et al., 2024).

One of the key natural enemies of *Ly. delicatula* in its native range, China, is the egg parasitoid *Anastatus* *orientalis* (Hymenoptera: Eupelmidae) (Choi et al., 2014; Manzoor et al., 2021; Xin et al., 2021). To reduce invasive *Ly. delicatula* populations to less damaging levels, *An. orientalis* was imported and released into South Korea in 2011 as part of a classical biological control program (Seo et al., 2019; Yang et al., 2015). Current *Ly. delicatula* population densities in South Korea appear to have been suppressed as a result of the introduction of *An. orientalis* (Wu et al., 2023). However, investigations into the host range specificity of *An. orientalis* against potential nontarget species conducted in the eastern and western United States determined that this parasitoid is oligophagous and not a suitable candidate for a classical biological control program targeting *Ly. delicatula* in the United States (Broadley et al., 2023; Gómez-Marco et al., 2023).

Previous research on *Ly. delicatula* has documented varying hatching rates of egg masses in the field. In Beijing, China, egg mass hatch rates are around 55% (Hou, 2013), in the eastern United States, rates range from 31.6% to 68.2% (Liu, 2019a, 2022), in northern and central South Korea, the range is 33.1% to 84.3% (Park, 2015), and in central Japan, hatch rates are 84.9% to 90% (Nakashita et al., 2022; Tomisawa et al., 2013). Variations in clutch size (i.e., number of eggs per egg mass) and egg mass densities have also been reported from native and invaded regions (Jung et al., 2022; Lee et al., 2014; Smyers et al., 2021). The high variance in reported hatch rates and egg clutch size across different regions may indicate the effects of different biotic (i.e., parasitism and host plant quality) and abiotic factors (i.e., temperature) affecting egg mass hatch and *Ly. delicatula* female fecundity.

Prevailing temperatures influence insect development. Accumulated degree-days (ADDs), the accumulation of heat units over time above a critical developmental base temperature, is one approach for determining the effect of this important abiotic factor on *Ly. delicatula* egg bionomics in different areas. Degree-day (DD) requirements for *Ly. delicatula* development have been determined from previous laboratory and field studies (Kreitman et al., 2021; Liu, 2020; Smyers et al., 2021). However, no prior work has been done relating ADD and egg mass metrics from *Ly. delicatula* populations across different regions. Insect species from different localized populations exhibit varying egg mass characteristics, including clutch size and hatch rate, based on exposure to specific climate conditions (Chanthy et al., 2015; Merrill et al., 2008). Thus, to better understand differences in geographically widespread populations of *Ly. delicatula*, it is necessary to determine the influence of ADD on *Ly. delicatula* egg mass sizes and deposition rates.

To the best of our knowledge, no coordinated, intercontinental studies comparing field egg mass hatch rates and related oviposition patterns between native and invaded ranges of *Ly. delicatula* had been conducted. This information is critical to understanding factors affecting establishment, survival, and population expansion rates of this invasive pest. An analysis and comparison of these parameters in invaded and non-invaded areas will help inform agencies regulating movement of this pest and researchers developing proactive control practices for *Ly. delicatula* prior to, and in the early phases of an invasion event. Therefore, the objectives of this multicountry study conducted in Japan, China, South Korea, and the United States were to (1) compare field *Ly. delicatula* egg mass clutch size, hatch rates, and egg mass densities between regions; and (2) determine the effects of regional biotic (i.e., egg parasitism and host plant availability) and abiotic (i.e., temperature and relative humidity) factors on egg mass hatch rates. The results of these studies are presented here.

MATERIALS AND METHODS

Study site selection

Egg mass data were collected from 12 field sites in four countries located in the native and invaded ranges of *Ly. delicatula*. Field sites were selected areas in each region with high densities of host plants and known populations of *Ly. delicatula*. The field sites were located as follows: Japan (invaded range, no known populations of *An. orientalis*): Hakusan, Ishikawa; Eiheiji, Fukui; Oji, Nara (Figure 1); China (native range, naturally occurring populations of *An. orientalis*): Haidian, Beijing; Tongzhou, Beijing; Daxing, Beijing (Figure 1); S. Korea (invaded range, introduced populations of *An. orientalis*): Hwaseong, Gyeonggi-do; Buyeo, Chungcheongnam-do; Gimje, Jeollabuk-do (Figure 1); and the United States (invaded range, no known populations of *An. orientalis*): Tullytown, Pennsylvania; Moorestown, New Jersey; Millville, New Jersey (Figure 1).

Weather data

Daily minimum, maximum, and mean temperature data, along with mean daily relative humidity readings, were retrieved from weather stations nearest to each site for a 9-month period from September 2022 through May 2023. This period covers field conditions over the expected time between *Ly. delicatula* egg mass oviposition and nymph hatching. Weather stations ranged between 5 and 16 km from the egg mass collection

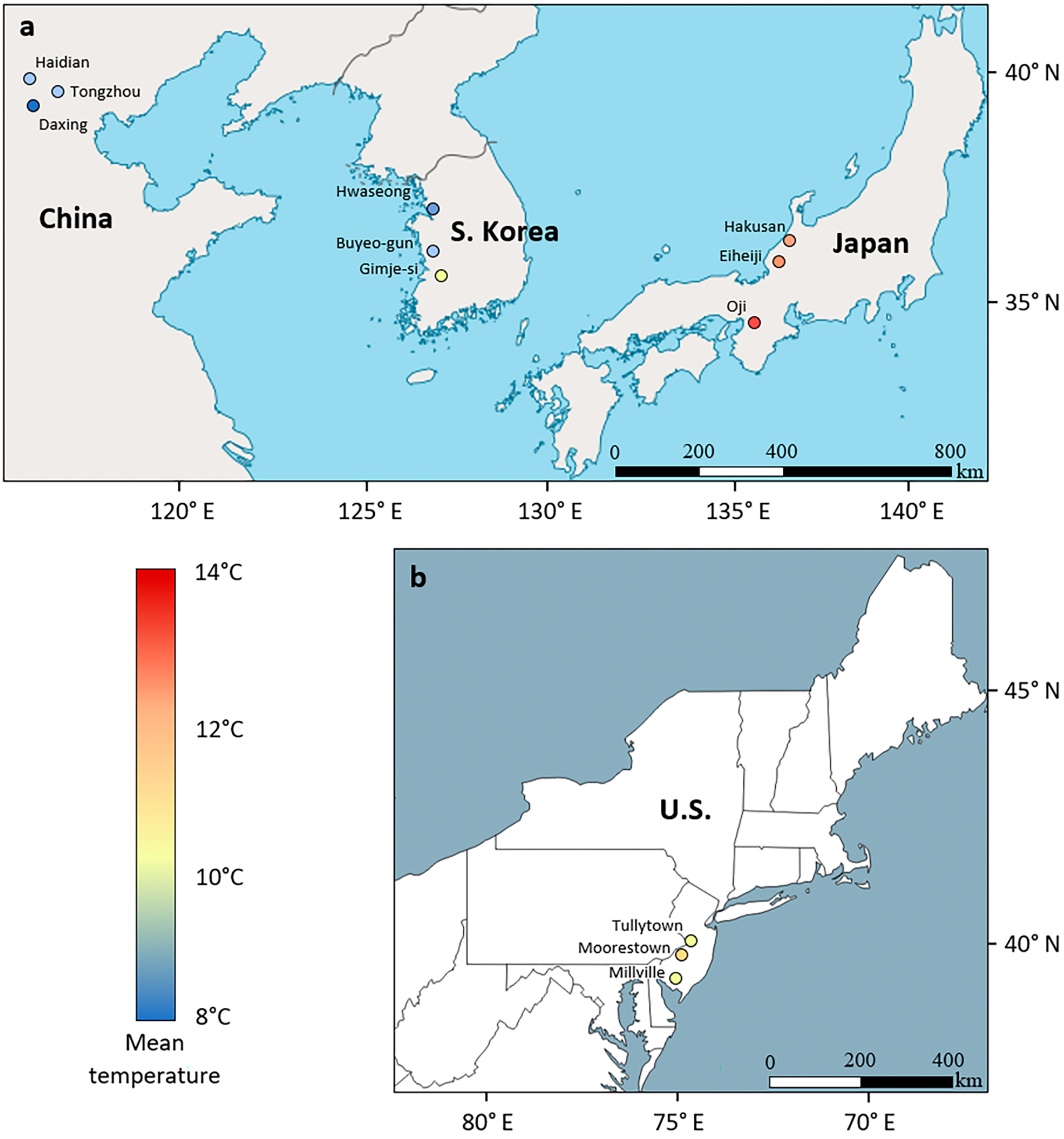

FIGURE 1 Latitudinal map of the *Lycorma delicatula* egg mass collection sites across the four countries used in this study: (a) China, South Korea, Japan; (b) United States. Mean temperature for the 9-month period from September 2022 through May 2023 for each site is indicated by the color gradient.

sites, except for one more distant station being 27.6 km from the collection site (Hwaseong, South Korea) (Appendix S1: Table S1).

Egg mass density surveys

Ly. delicatula egg mass density surveys were conducted at each site in each study region during late fall and winter 2022–2023 (Year 1) and 2023–2024 (Year 2) (Table 1), after all field egg masses were expected to have been laid for the respective years.

Egg mass density (number per square meter of tree)

Host trees with newly laid (unhatched, current year) *Ly. delicatula* egg masses were selected for surveys, and the total number of newly laid egg masses on the lower 2 m

TABLE 1 Location of *Lycorma delicatula* egg mass density surveys conducted during Years 1 (2022) and 2 (2023) of this study.

Country	State/Pref./Prov.	City/site	Coordinates	Date Year 1	Date Year 2
Japan	Ishikawa	Hakusan	36°29′22.3″ N, 136°35′57.4″ E	11/27/2022	11/20/2023
	Fukui	Eiheiji	36°05′46.7″ N, 136°17′58.8″ E	11/28/2022	11/24/2023
	Nara	Oji	34°35′10.3″ N, 135°41′07.4″ E	11/30/2022	12/4/2023
China	Beijing	Haidian	39°59′35.5″ N, 116°12′37.8″ E	10/16/2022	2/19/2024
	Beijing	Tongzhou	39°50′03.5″ N, 116°50′43.1″ E	10/13/2022	2/22/2024
	Beijing	Daxing	39°34′02.3″ N, 116°14′03.1″ E	10/25/2022	2/22/2024
South Korea	Gyeonggi	Hwaseong	37°13′04.1″ N, 126°41′00.4″ E	4/20/2023	12/8/2023
	Chungcheongnam	Buyeo	36°14′36.4″ N, 126°44′53.2″ E	12/9/2022	12/26/2023
	Jeollabuk-do	Gimje	35°46′24.6″ N, 127°02′18.0″ E	2/23/2023	12/28/2023
United States	Pennsylvania	Tullytown	40°08′35.5″ N, 74°44′08.6″ W	11/29/2022	12/14/2023
	New Jersey	Moorestown	39°56′52.6″ N, 74°57′41.9″ W	2/15/2023	12/14/2023
	New Jersey	Millville	39°24′49.1″ N, 75°02′02.9″ W	2/16/2023	12/12/2023

Abbreviations: Pref., prefecture; Prov., province.

of each tree was recorded. The lower 2 m of trees were selected because more *Ly. delicatula* egg masses were found on *Ai. altissima* trunks at 0–2 m above the ground surface than at 2–4 or 4–6 m from a study conducted in the Mid-Atlantic United States (Liu & Hartlieb, 2020). The trunk diameter (in meters) of each tree at 1 m above the ground surface was measured. Egg mass density was standardized to number of newly laid egg masses per square meter of tree. The total surface area up to 2 m in height from ground level for each tree used for oviposition was calculated in square meters as $A = (2\pi \times d/2 \times h)$ where d is the trunk diameter 1 m above the ground, and h is the height (2 m). The goal was to select 10 *Ai. altissima* with newly laid egg masses per site. However, in Japan, fewer than 10 *Ai. altissima* trees with new egg masses laid on them were reported from the Hakusan site during Year 1 (six trees total) and Year 2 (seven trees). In China, fewer than 10 *Ai. altissima* trees with new egg masses were reported from the sites in Haidian (two trees) and Tongzhou (one tree) during Year 1, and Haidian (four trees) during Year 2. Also, in South Korea, insufficient *Ai. altissima* was present at each site during both survey years. Consequently, newly laid egg masses were recorded from alternative hosts as follows: Hwaseong, *V. vinifera* (10 vines surveyed Years 1 and 2); Buyeo and Gimje, *Toona sinensis* de Jussieu (Meliaceae) (four trees Year 1 and three Year 2) and *Castanea crenata* Sieb. et Zucc. (Fagaceae) (six trees Year 1 and seven Year 2).

Timed 30-min egg mass counts

To determine the relative egg mass density per site (on all biotic [plants] and abiotic [rocks, tires, etc.]), a timed walk count was conducted, and newly laid egg masses were counted visually. Specifically, at each site, one researcher recorded the total number of newly laid *Ly. delicatula* egg masses found in 30 min at that site, including on plants (i.e., host plants and other plant material) and inert objects (e.g., rocks, dead logs, or metal structures). Oviposition substrate type was recorded for each recorded egg mass.

Egg mass clutch size and hatch

Egg mass metrics were determined from egg masses collected from each site. In winter 2022, 30 newly laid *Ly. delicatula* egg masses on hosts were located at each site and denoted by drawing a large circle around them. In South Korea, due to the limited number of *Ai. altissima* present at each site, alternative hosts were surveyed: Hwaseong, *V. vinifera* (30 egg masses were found satisfying the targeted goal of 30 egg masses [30/30]); Buyeo, *T. sinensis* (19/30) and *C. crenata* (11/30); Gimje, *Prunus serrulata* L. (Rosaceae) (9/30), *Populus tomentiglandulosa* T. B. Lee (Salicaceae) (8/30), *Zanthoxylum schinifolium* Sieb. et Zucc. (Rutaceae) (5/30), *Lindera glauca* Sieb. et Zucc. (Lauraceae) (3/30), *Robinia pseudoacacia* L. (Fabaceae) (3/30), *Ai. altissima* (1/30), and *Rhus javanica* L. (Anacardiaceae) (1/30).

In early summer 2023, after *Ly. delicatula* nymphs hatched from eggs, selected study sites were revisited and the marked 30 egg masses with the underlying bark were removed from host plants and returned to the laboratory. The total number of eggs per egg mass, hatched eggs, parasitized eggs, predated eggs, and unhatched eggs were recorded for each recovered egg mass from each study site. Eggs from which *Ly. delicatula* nymphs hatched were identified by an opened, elliptical operculum (Liu, 2022; Nakashita et al., 2022; Figure 2). Nymph hatch ratios for each egg mass were determined by dividing the total number of eggs with opened opercula by the total number of eggs per egg mass. Parasitized eggs were identified by the presence of round parasitoid emergence holes (apparent parasitism) (Yang et al., 2015). Parasitism ratios for each egg mass were determined by dividing the total number of eggs with circular parasitoid emergence holes and the number of dissected unhatched eggs containing undeveloped parasitoids by the total number of eggs per egg mass. Eggs displaying evidence of biting or chewing damage were classified as predated (Morrison et al., 2016). The predation ratios for each egg mass were determined by dividing the total number of predated eggs by the total number of eggs per egg mass. All unhatched eggs were dissected to determine if the dead egg contained a *Ly. delicatula* nymph or parasitoid that failed to develop or emerge, or if the contents were unknown/undetermined. The ratios of failure for nymph hatch and parasitoid emergence for each egg mass were determined by dividing the total number of unhatched/unemerged eggs by the total number of eggs per egg mass.

ADD calculations

ADDs by *Ly. delicatula* egg masses were calculated at each site from the daily minimum and maximum temperatures, incorporating a lower limit of 10.4°C (Smyers et al., 2021), a maximum limit of 35°C (Liu, 2019a). DDs were calculated using the following equation:

$$DD = [(T_{\min} + T_{\max})/2] - T_0,$$

where $T_{\min}$ is the daily minimum temperature at each site, $T_{\max}$ is the daily maximum temperature at each site, and T_0 is the lower developmental threshold of *Ly. delicatula* (Damos & Savopoulou-Soultani, 2012). Daily maximum temperatures did not reach 35°C at any site over the course of the temperature recordings. Daily DD totals were then summed for each site from September 2022 through May 2023.

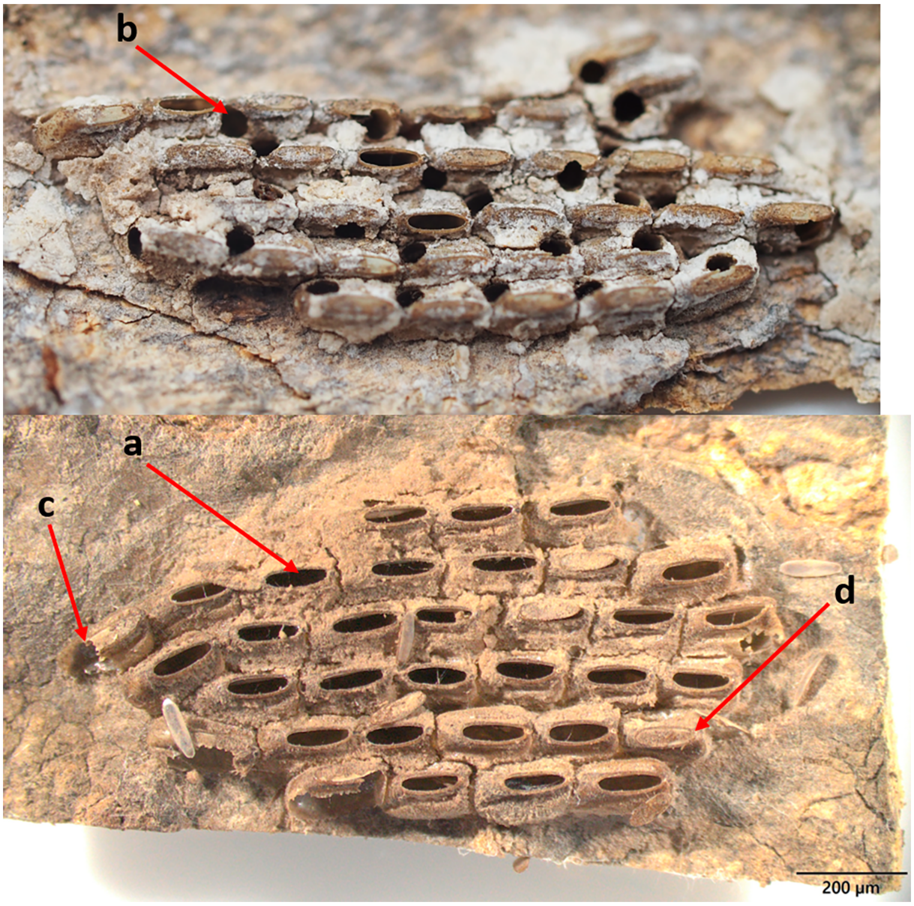

FIGURE 2 Field-collected *Lycorma delicatula* egg masses displaying examples of (a) successful *Ly. delicatula* nymphal hatch; (b) parasitoid exit hole; (c) egg predation; (d) unhatched egg. Photo credits: (top) Ke-Xin Bao; (bottom) Matthew Kamiyama.

Statistical analysis

All data were analyzed with the statistical software R (v.3.4.1, R Core Team, 2019). A two-way ANOVA including the effects of "region" and "site" was run to determine if there were differences in ADD between the different study locations. If differences between regions were detected, a Tukey's honestly significant difference (HSD) post hoc test was run to separate means at $p < 0.05$.

Generalized linear mixed models (GLMMs) implementing a *binomial* family and *logit* link using the *glmer* function from the *lme4* package were generated to determine the effect climate had on *Ly. delicatula* egg mass hatch rates in the different regions under assessment. A full model incorporated "minimum temperature," "maximum temperature," "mean temperature," and "relative humidity" as fixed effects, and "region," "site," and the "region × site" interaction as random effects. "Minimum temperature," "maximum temperature," and "mean temperature" refer to the total averaged daily minimum, maximum, and mean temperatures, respectively, of the entire 9-month period climate data were retrieved from each site. "Relative humidity" refers to the total averaged daily relative humidity of the entire 9-month period climate data were retrieved from each site. A reduced model was also generated including "mean temperature" and "relative humidity" as fixed effects, and removing the "region × site" interaction from the random effects. Model comparison assessments including an Akaike information criterion (AIC) and likelihood ratio test (LRT) were run to determine the best fitting model (full or reduced). The reduced model was selected as the more parsimonious model (full model AIC = 405.2; reduced model AIC = 399.4; LRT $p = 0.9894$). A lower AIC value suggests a better fitting model, and an insignificant LRT *p*-value indicates the null hypothesis (i.e., reduced model is correct) should not be rejected in favor of the alternative hypothesis (i.e., full model is correct) (Wood, 2006). One advantage of a GLMM is that it separates random and mixed effects, thereby producing a more interpretable model; however, this method limits model flexibility (Wood, 2006). Linear regression analyses were also conducted using the *lm* function from the *stats* package to analyze the relationship between hatch ratios and the 9-month mean temperature for all the study sites.

Egg mass density count data were overdispersed, so a negative binomial generalized linear model (nbGLM) with a *log* link using the *glm.nb* function from the *MASS* package was generated to determine the effect factors "region," "site," "year," and the "region × site" interaction had on number of egg masses per square meter of tree at each field site. A second nbGLM model was produced to determine the effect factors "region," "site," "oviposition substrate host," "year," and the "region × site" interaction had on number of egg masses found per site in 30 min of visual searching. If "year" was detected to have a significant effect at $p < 0.05$, data for each year were analyzed separately. If "site" was detected to have a significant effect at $p < 0.05$, data for each site were analyzed separately. If "region" and/or "site" was detected to have a significant effect at $p < 0.05$, a Kruskal–Wallis test was implemented to determine the regional effect of the number of egg masses per square meter of tree and number of egg masses found per region/site in 30 min. If significant effects were detected at $p < 0.05$, a pairwise Wilcoxon rank-sum test with a Benjamini–Hochberg *p*-value adjustment method was used to analyze differences between groups.

A two-way ANOVA including the effects of "region" and "site" was run to determine if there were differences in egg mass clutch size, and ratios of egg hatch, parasitism, predation, and unhatched eggs between *Ly. delicatula* populations surveyed across the different sites. If differences between sites were detected for a given metric, a Tukey's HSD post hoc test was run to separate means at $p < 0.05$. Linear regression analyses were also conducted to analyze the relationship between egg hatch ratios and parasitism ratios for all sites.

RESULTS

Effect of climate on egg hatch

The daily minimum, maximum, and mean temperatures for the study sites in each region varied for the 9-month period from September 2022 through May 2023 with sites in Japan and the United States generally having higher temperatures than sites in South Korea and China during the winter (i.e., December–February) (Figure 3). Sites in Japan overall had the highest mean relative humidities, and sites in China had the lowest, particularly during the winter. When analyzing the total mean ADD for *Ly. delicatula* egg masses from each location, the factor "site" did not have a significant effect on the mean ADD ($F_{8,1800} = 1.39$; $p = 0.20$), so ADDs for each region were pooled by site for each region. Total ADD from China were significantly higher than those from South Korea and the United States, and ADDs from Japan were significantly higher than those from the United States ($F_{3,1800} = 5.23$; $p < 0.01$) (Appendix S1: Table S2). ADDs from Japan, South Korea, and the United States were not statistically different from each other. The estimated required ADD (i.e., 164 ADD) for 5% of field *Ly. delicatula* egg mass hatch completion as determined by Smyers et al. (2021) using data from studies conducted in

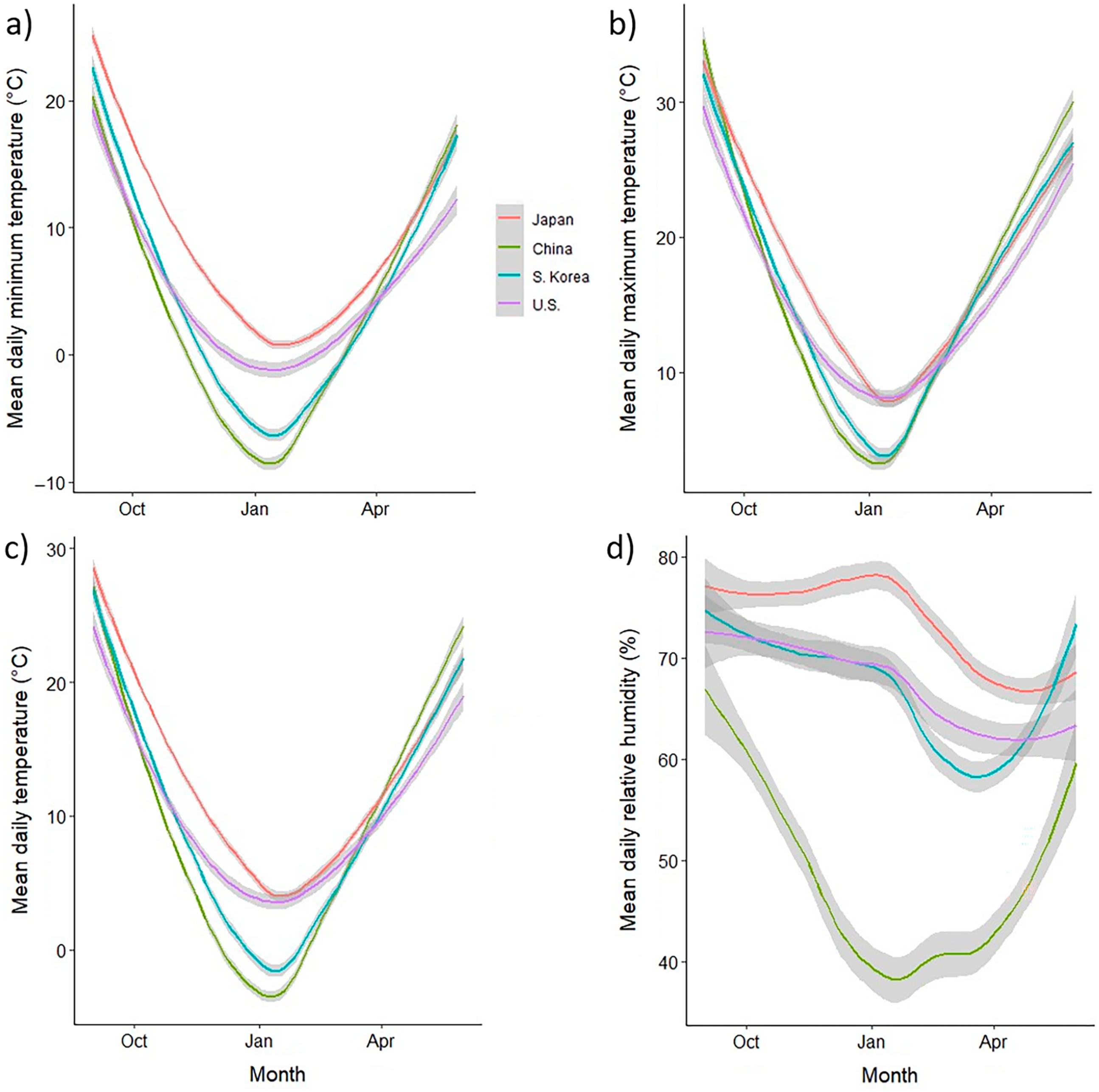

FIGURE 3 Mean (a) daily minimum temperatures, (b) daily maximum temperatures, (c) daily temperatures, and (d) daily relative humidity for each region pooled by site from September 2022 through May 2023. Gray bands for each region represent the 95% CI.

South Korea and Pennsylvania (United States) was first met in the field sites from Japan and China, then South Korea, and then the United States (Appendix S1: Figure S1). The estimated required ADD for 50% (242) and 95% (320) of field egg mass hatch completion (Smyers et al., 2021) were sequentially reached first in China, followed by Japan, South Korea, and then the United States.

The GLMM analysis determined that the coefficient estimate for the effect of 9-month mean temperature on *Ly. delicatula* hatch rate was 0.80 ($z = 2.98$; $p < 0.01$). At a significance level of $p < 0.05$, mean temperature had a significant positive effect on egg mass hatch. The effect of mean relative humidity on egg mass hatch was not significant (coefficient estimate $= -0.0074$; $z = -0.22$; $p = 0.83$).

The linear regression analyses relating *Ly. delicatula* egg mass hatch with mean temperature for each site also indicate egg mass hatch increases with increasing mean temperature ($F_{1,357} = 64.31$; $p < 0.001$; $r^2 = 0.13$) (Figure 4).

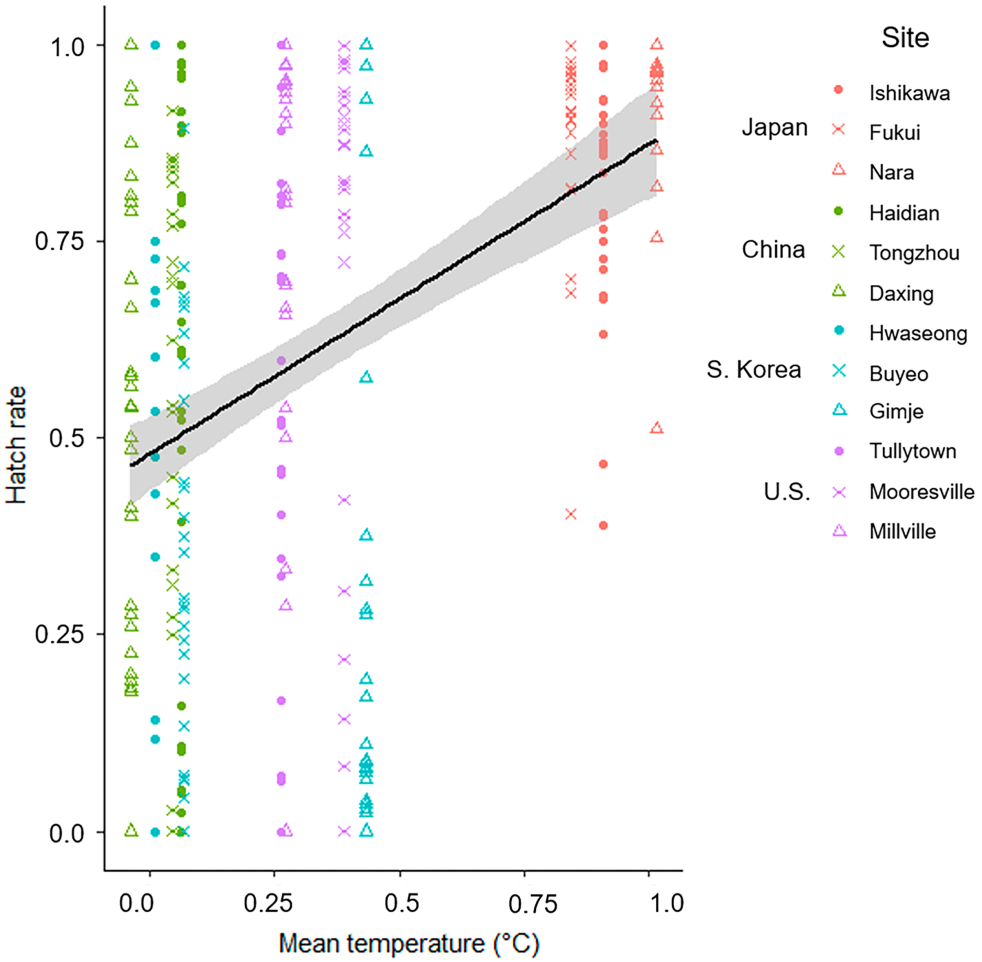

FIGURE 4 Relationship between *Lycorma delicatula* egg mass hatch and 9-month mean temperature from the study sites.

Egg mass density surveys

Egg masses per square meter of surveyed host plants

Analyses of newly laid *Ly. delicatula* egg mass densities per host plant area indicated that the factor "year" had a significant effect on the mean number of egg masses per square meter of tree ($\chi^2_{1,225} = 4.12$; $p = 0.04$). Consequently, data from each year were analyzed separately. Additionally, the factor "site" had a significant effect on the mean number of egg masses per square meter of tree ($\chi^2_{8,226} = 36.98$; $p < 0.001$). Therefore, egg mass densities were analyzed between sites. During the first year of sampling, egg mass densities per square meter of host plant at the Tullytown site (United States) were significantly higher than those observed from the Eiheiji site (Japan), Daxing site (South Korea), and Millville site (United States) ($\chi^2_{11,107} = 33.30$; $p < 0.001$) (Table 2; Figure 5). Egg mass densities per square meter of tree were significantly lower at the Daxing site (China) than those observed from the Hwaseong site (South Korea) and Tullytown site (United States). During the second year of sampling, site had a significant effect on egg mass densities per square meter of tree ($\chi^2_{11,123} = 22.04$; $p = 0.02$). However, no significant pairwise differences were detected between sites as determined by the Wilcoxon rank-sum test at a significance level of $p < 0.05$ (Figure 5).

Timed 30-min egg mass counts and host plant associations

Analyses of *Ly. delicatula* egg mass density measures from 30-min count visual surveys indicated that the factor "year" had a significant effect on the mean number of egg masses found during the 30-min search interval ($\chi^2_{1,11} = 15.07$; $p < 0.001$). Consequently, data from each year were analyzed separately. Additionally, the factor "site" did not have a significant effect on the number of egg masses found per 30 min ($\chi^2_{8,12} = 13.07$; $p = 0.11$),

TABLE 2 Site comparisons within countries of *Lycorma delicatula* egg mass density metrics.

		Tree transect		30-min count	
		Year 1 (2022)	Year 2 (2023)	Year 1 (2022)	Year 2 (2023)
Country	Site	Mean no. egg masses per square meter of tree	Mean no. egg masses per square meter of tree	Total mean no. egg masses per country	Total mean no. egg masses per country
Japan	Hakusan	13.20 ± 11.29 AB	11.49 ± 5.69	85.67 ± 8.22 AB	31.33 ± 2.04 B
	Eiheiji	6.49 ± 1.87 BC	6.81 ± 1.41		
	Oji	9.82 ± 3.59 AC	13.76 ± 3.45		
China	Haidian	3.24 ± 0.66 AC	5.88 ± 3.53	102.00 ± 13.61 B	32.67 ± 1.26 C
	Tongzhou	2.28 ± 0	7.07 ± 1.55		
	Daxing	4.39 ± 0.73 C	7.95 ± 4.23		
South Korea	Hwaseong	9.23 ± 1.20 AB	7.91 ± 0.70	40.00 ± 4.67 B	326.00 ± 70.28 A
	Buyeo	7.53 ± 1.41 AC	6.79 ± 1.27		
	Gimje	7.58 ± 1.23 AC	11.91 ± 2.51		
United States	Tullytown	19.86 ± 5.15 A	24.89 ± 7.56	71.00 ± 7.51 C	739.33 ± 46.72 A
	Moorestown	7.30 ± 3.23 AC	4.89 ± 1.28		
	Millville	3.98 ± 0.82 BC	17.49 ± 4.63		

Note: Different uppercase letters within a column designate significant differences in counts between sites/countries (pairwise Wilcoxon rank-sum test with Benjamini–Hochberg adjustment, $p < 0.05$). No significant differences were detected between sites during Year 2 of the tree transect survey.

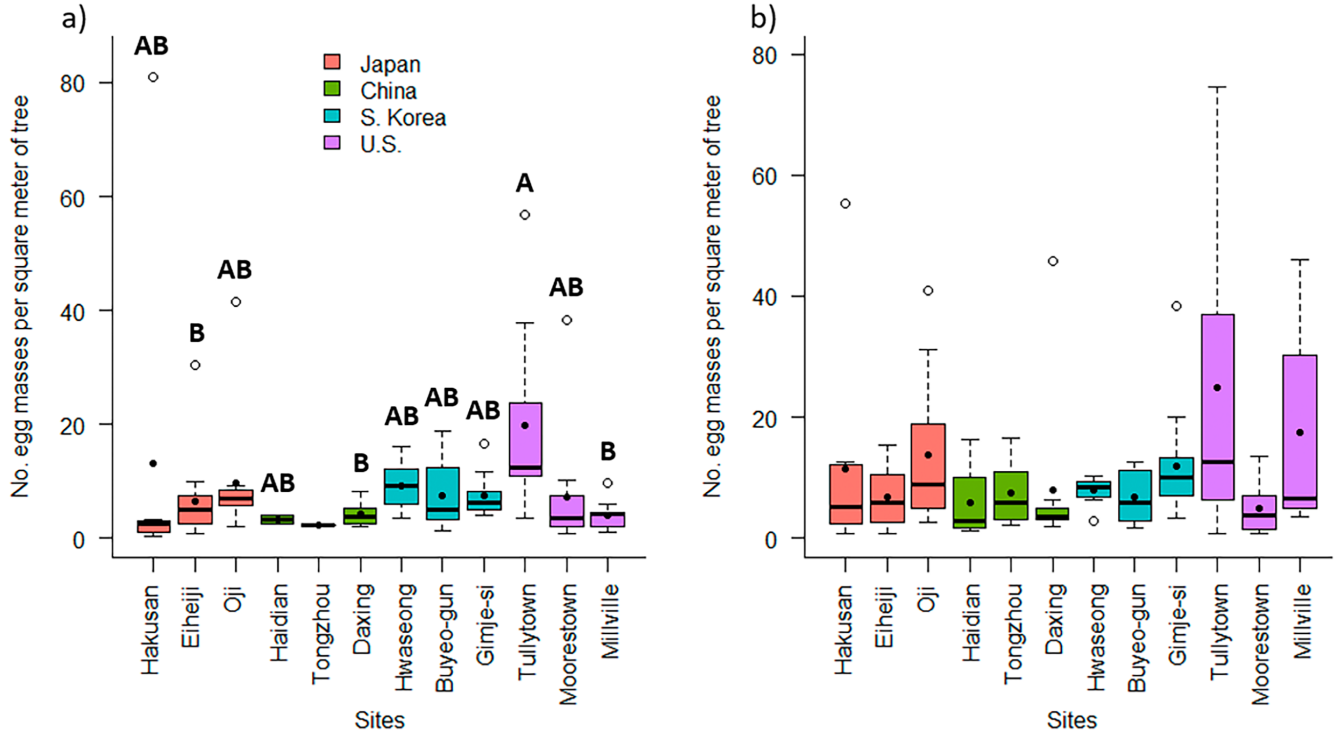

FIGURE 5 Number of *Lycorma delicatula* egg masses per square meter of tree for each site during (a) Year 1 and (b) Year 2. Black dots represent mean values, middle lines represent median values, box limits are the interquartile range (IQR), whiskers show 1.5 × IQR, and white dots represent outliers. Different uppercase letters designate significant differences between sites (pairwise Wilcoxon rank-sum test with Benjamini–Hochberg adjustment, $p < 0.05$). There were significant differences across sites in Year 1 (as indicated on the figure) but there were no significant differences detected in Year 2.

and egg mass densities for each region were pooled across sites. During the first year of sampling, the number of egg masses found per site in 30 min in Japan, China, and South Korea were not significantly different from each other, but the number of egg masses found per site in the United States were significantly higher than those in China and South Korea and similar to those in Japan ($\chi^2_{3,11} = 16.26$; $p < 0.01$) (Table 2; Figure 6). Numerically, the highest mean number of egg masses found per site was in the United States (326.00 ± 70.28) (mean ± SE) and the lowest was found in South Korea (31.33 ± 2.04). During the second year of sampling, the number of egg masses found per site in 30 min in the United States were significantly higher than those in Japan, China, and South Korea, and the number of egg masses found per site in Japan were significantly higher than those in China and South Korea ($\chi^2_{3,11} = 19.16$; $p < 0.001$) (Table 2; Figure 6). Numerically, the highest mean number of egg masses per site was found in the United States (739.33 ± 46.72) and the lowest was found in South Korea (32.67 ± 1.26).

Oviposition substrate (rocks, logs, host plants, etc.), on which new *Ly. delicatula* egg masses were laid had a significant effect on number of egg masses found in 30 min in each region ($\chi^2 = 301.26$; df = 29; $p < 0.001$). Japan had three different types of oviposition substrates, with the majority being *Ai. altissima* (92% of new egg masses from Japan were found on *Ai. altissima*) (Table 3; Figure 7). China had nine different oviposition substrates, with the majority being *Ai. altissima* (45%). South Korea had 12 different oviposition substrates, with the majority being *C. crenata* (40%). The United States had 12 different oviposition substrates, with the majority being *Ai. altissima* (76%). *Ai. altissima* was the only egg mass substrate all surveyed regions had in common, and Japan had the highest frequency of egg masses found on *Ai. altissima*, followed by the United States, and China had the lowest ($\chi^2_{2,13} = 10.43$; $p < 0.01$). Egg masses found on *Ai. altissima* from South Korea were only reported from one field site (Gimje).

Egg mass clutch size and hatch

The mean number of eggs per *Ly. delicatula* egg mass was significantly higher from the Tullytown site (United States) than from all other sites except for the Hakusan site (Japan), which displayed a similar mean number of eggs per egg mass ($F_{11,347} = 8.01$; $p < 0.001$) (Table 4; Figure 8). The mean number of eggs per egg mass from the Daxing site (China) were significantly lower than those from all other sites except for the Tongzhou site (China), the Hwaseong and Gimje sites (South Korea), and the Mooresville site (United States). The highest regional mean number of eggs per egg mass

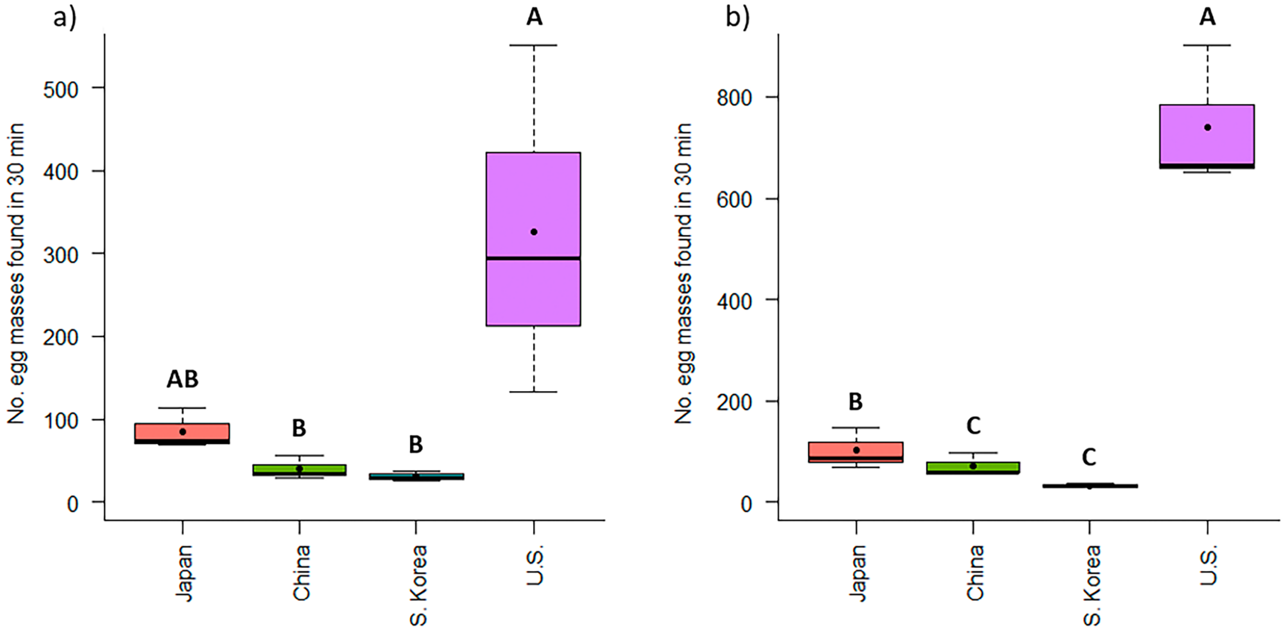

FIGURE 6 Number of *Lycorma delicatula* egg masses found during 30-min counts in each country pooled by study site for (a) Year 1 and (b) Year 2. Black dots represent mean values, middle lines represent median values, box limits are the interquartile range (IQR), whiskers represent 1.5 × IQR, and white dots represent outliers. Different uppercase letters designate significant differences between regions (pairwise Wilcoxon rank-sum test with Benjamini–Hochberg adjustment, $p < 0.05$).

TABLE 3 Number of *Lycorma delicatula* egg masses found on different host plant and nonliving substrates from timed 30-min counts in each country during Years 1 (2022) and 2 (2023) combined.

		Country			
Host plant substrate	**Common name**	**Japan**	**China**	**South Korea**	**United States**
Acer sp.	Maple				135
Ailanthus altissima	Tree of heaven	519	133	1	2346
Bambuseae	Bamboo	1			
Betula nigra	River birch				1
Castanea crenata	Japanese chestnut			76	
Cedrus deodara	Deodar cedar		6		
Celtis occidentalis	Hackberry				17
Elaeagnus angustifolia	Russian olive				126
Juglans ailantifolia	Japanese walnut	43			
Juniperus chinensis	Chinese juniper		3		
Lindera glauca	Asian spicebush			2	
Lonicera maackii	Amur honeysuckle		3		
Malus sp.	Crabapple				102
Populus sp.	Poplar				48
Populus tomentiglandulosa	Korean poplar			7	
Prunus davidiana	David's peach		62		
Prunus serrulata	Japanese cherry			17	
Prunus sibirica	Siberian apricot		40		
Prunus sp.	Stone fruit				114
Rhus chinensis	Chinese sumac			12	
Robinia pseudoacacia	Black locust			2	68
Salix matsudana	Chinese willow		5		
Toona sinensis	Chinese mahogany			29	
Vitis vinifera	Grape vine			30	
Wisteria floribunda	Japanese wisteria			5	
Zanthoxylum schinifolium	Mastic-leaf prickly ash			5	
Unknown				5	
Nonliving substrates					
Dead log					118
Rock			21		15
Stone wall			60		
Tire					13

was found from sites in the United States (40.37 ± 2.42), and the lowest was from China (29.00 ± 1.05).

The mean proportion of eggs in each surveyed egg mass that *Ly. delicatula* nymphs hatched from was significantly higher from the Oji site (Japan) than from all other sites except the Eiheiji and Hakusan sites (Japan) and the Mooresville site (United States), which displayed a similar mean proportion of hatched eggs per egg mass ($F_{11,347} = 17.44$; $p < 0.001$) (Table 4; Figure 9). The mean proportion of hatched eggs per egg mass was significantly lower from the Gimje site (South Korea) than from all other sites except the Buyeo site (South Korea) and Tongzhou site (China). The highest regional mean proportion of hatched eggs was found from the sites in Japan (0.89 ± 0.01), and the lowest was from South Korea (0.41 ± 0.04). The mean proportion of parasitized eggs per egg mass was highest from the Gimje site (South Korea), followed by the Hwaseong and Buyeo

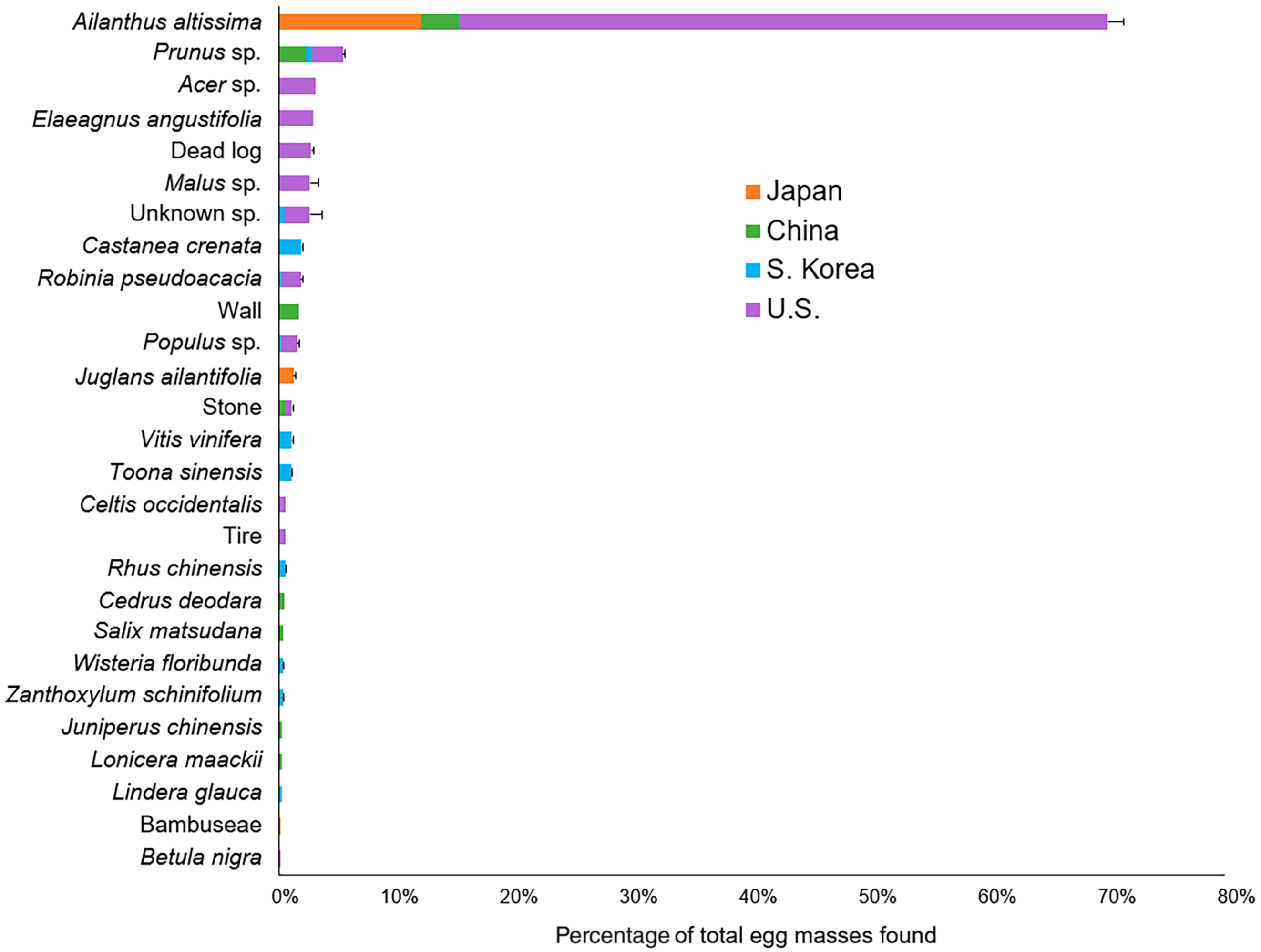

FIGURE 7 Percentage of *Lycorma delicatula* egg masses found laid on different host substrates for all egg masses found in each country during 30-min counts for Years 1 (2022) and 2 (2023) combined. Error bars represent SE.

TABLE 4 Comparison of mean *Lycorma delicatula* egg mass hatch metrics from each study site.

Country	Site	Clutch size	Hatch rate	Parasitism rate	Predation rate	Unhatched rate
Japan	Hakusan	39.63 ± 2.03 AB	0.82 ± 0.03 ABC	0	0.001 ± 0.001	0.18 ± 0.03 CD
	Eiheiji	37.43 ± 1.51 B	0.91 ± 0.02 AB	0	0.004 ± 0.004	0.09 ± 0.02 D
	Oji	36.10 ± 1.14 B	0.95 ± 0.02 A	0	0.003 ± 0.002 B	0.05 ± 0.02 D
China	Haidian	35.67 ± 1.50 B	0.59 ± 0.07 CDEF	0.30 ± 0.07 B	0.02 ± 0.01 B	0.13 ± 0.02 CD
	Tongzhou	28.03 ± 1.80 BC	0.44 ± 0.06 EFG	0.05 ± 0.02 C	0.007 ± 0.005 B	0.52 ± 0.07 A
	Daxing	23.30 ± 1.42 C	0.54 ± 0.05 DEF	0.23 ± 0.05 BC	0.05 ± 0.02 AB	0.32 ± 0.05 BCD
South Korea	Hwaseong	26.97 ± 2.49 BC	0.67 ± 0.07 BCDE	0.28 ± 0.06 B	0	0.06 ± 0.03 D
	Buyeo	39.13 ± 2.32 B	0.34 ± 0.05 FG	0.38 ± 0.05 B	0	0.29 ± 0.05 BCD
	Gimje	34.13 ± 1.53 BC	0.23 ± 0.06 G	0.61 ± 0.06 A	0	0.17 ± 0.03 CD
United States	Tullytown	51.45 ± 5.46 A	0.52 ± 0.06 DEF	0.004 ± 0.004	0.10 ± 0.04 A	0.37 ± 0.07 AB
	Moorestown	34.33 ± 2.72 BC	0.76 ± 0.06 ABCD	0.004 ± 0.004	0.03 ± 0.01 AB	0.21 ± 0.05 B
	Millville	35.70 ± 3.45 B	0.68 ± 0.07 BCDE	0	0.02 ± 0.01 B	0.30 ± 0.06 BC

Note: Different uppercase letters within a column designate significant differences in means between sites (Tukey's honestly significant difference test, $p < 0.05$).

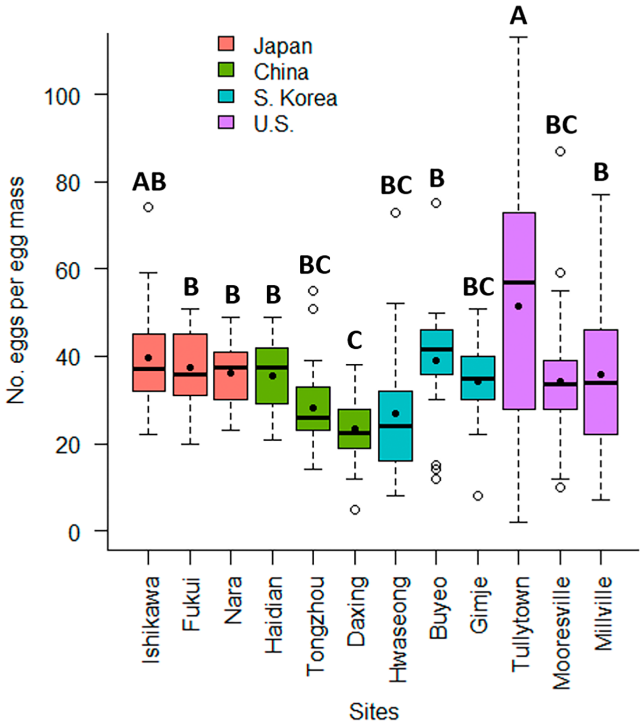

FIGURE 8 Number of eggs per egg mass for field-collected *Lycorma delicatula* egg masses from each site and region. Black dots represent mean values, middle lines represent median values, box limits are the interquartile range (IQR), whiskers represent 1.5 × IQR, and white dots represent outliers. Different uppercase letters designate significant differences in means between sites (Tukey's honestly significant difference test, $p < 0.05$).

sites (South Korea) and the Haidian site (China) ($F_{7,231} = 20.27$; $p < 0.001$). The mean proportion of parasitized eggs per egg mass from the US sites were all below 0.005. The highest regional mean proportion of parasitism of total eggs was found from sites in South Korea (0.42 ± 0.04), and no egg parasitism was found from sites in Japan. The mean proportion of eggs per egg mass fed upon by unidentified predators was significantly higher from the Tullytown site (United States) than from all other sites except the Mooresville site (United States) and the Daxing site (China) ($F_{8,260} = 3.40$; $p < 0.001$). The highest regional mean proportion of predation was found from the sites in the United States (0.05 ± 0.01), and there was no evidence of eggs fed upon by predators from sites in South Korea. The mean proportion of unhatched eggs per egg mass was significantly higher from the Tongzhou site (China) than from all other sites except the Tullytown site (United States) ($F_{11,347} = 6.84$; $p < 0.001$). The mean proportion of unhatched eggs per egg mass was significantly lower from the Eiheiji and Oji sites (Japan) and the Hwaseong site (South Korea) than from all other sites except the Hakusan site (Japan), the Haidian and Daxing sites (China), and the Buyeo and Gimje sites (South Korea). The highest regional mean proportion of unhatched eggs was found from the sites in China (0.32 ± 0.03) and the lowest was from Japan (0.10 ± 0.01).

Dissections of unhatched eggs from egg masses collected from the sites in Japan revealed a high proportion of undeveloped *Ly. delicatula* nymphs (0.94–1.00 of dissected unhatched eggs), and no undeveloped parasitoids were found (Table 5). The majority of unhatched eggs from the sites in China revealed unknown contents (0.66–0.96), while undeveloped parasitoids were also found (0.04–0.34). The majority of unhatched eggs from the Buyeo and Gimje sites in South Korea revealed unknown contents (0.85 and 0.91, respectively), while a large proportion of undeveloped *Ly. delicatula* nymphs (0.71) was found from the Hwaseong site. The majority of unhatched eggs from the US sites revealed unknown contents (0.71–0.83), and no undeveloped parasitoids were found.

Effect of parasitism on egg hatch

Linear regression analyses relating *Ly. delicatula* egg mass hatch with parasitism indicate that nymph hatch decreases with increasing parasitism for all sites surveyed ($F_{1,357} = 229.90$; $p < 0.001$; $r^2 = 0.39$) (Figure 10).

DISCUSSION

Results presented here suggest that egg parasitism has a strong impact in suppressing the hatch of *Ly. delicatula* egg masses in the field. Nymph hatch was high from the study sites in Japan (0.82–0.95 hatch ratio of total eggs sampled) and the United States (0.52–0.76 hatch ratio), where *Ly. delicatula* is invasive and experiences negligible egg parasitism (sites from both regions had a proportion of parasitized eggs below 0.005 of total eggs). Conversely, egg mass hatch was lower from the surveyed sites in China (0.44–0.59 hatch ratio) and South Korea (0.23–0.67 hatch ratio), regions with the highest measured egg parasitism proportions (0.05–0.30 of total eggs in China and 0.28–0.61 in South Korea). The inverse relationship of these effects is supported by linear regression analyses, which illustrate a significant negative correlation of egg mass hatch with egg parasitism. Higher overall nymph hatch in Japan and the United States may be explained, in part, by the enemy release hypothesis, which states that invading species experience population growth and expansion because they have "escaped" their natural enemies which results in decreased population regulation, and this in turn causes unnaturally high population densities (Keane & Crawley, 2002).

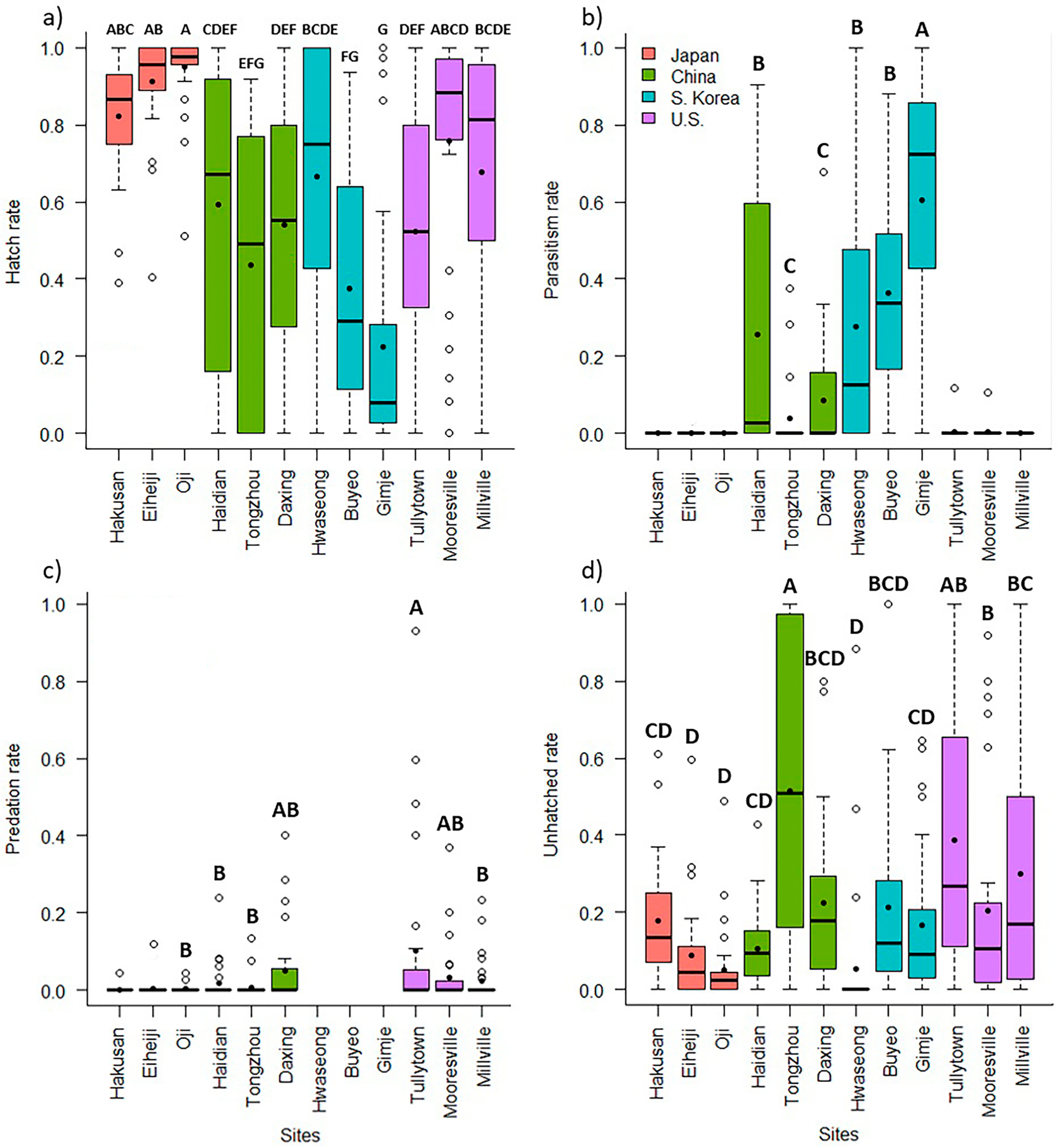

FIGURE 9 Field-collected *Lycorma delicatula* egg mass (a) hatch rates; (b) parasitism rates; (c) predation rates; (d) unhatched egg rates from each site and country. Black dots represent mean values, middle lines represent median values, box limits are the interquartile range (IQR), whiskers represent 1.5 × IQR, and white dots represent outliers. Different uppercase letters designate significant differences in means between sites (Tukey's honestly significant difference test, $p < 0.05$).

Although the identity of the egg parasitoids from this study could not be confirmed since egg parasitism ratios were determined from the presence of emergence holes, *An. orientalis* is the only parasitoid that has been reported parasitizing *Ly. delicatula* eggs in China and South Korea (Choi et al., 2014; Xin et al., 2021). *An. orientalis* has not been detected in the United States and will likely not be released as part of a classical biological control program because host specificity testing revealed potential nontarget impacts (Broadley et al., 2023; Gómez-Marco

TABLE 5 Results of the dissections of unhatched *Lycorma delicatula* eggs from the egg mass hatch study.

Country	Site	Proportion of unhatched *Ly. delicatula* nymphs	Proportion of unemerged parasitoids	Proportion of unknown egg contents
Japan	Hakusan	0.94 ± 0.04	0	0.06 ± 0.04
	Eiheiji	0.95 ± 0.05	0	0.05 ± 0.05
	Oji	1.00 ± 0.00	0	0
China	Haidian	0	0.24 ± 0.06	0.76 ± 0.04
	Tongzhou	0	0.04 ± 0.03	0.96 ± 0.03
	Daxing	0	0.34 ± 0.07	0.66 ± 0.07
South Korea	Hwaseong	0.71 ± 0.24	0.29 ± 0.24	0
	Buyeo	0.09 ± 0.04	0.06 ± 0.03	0.85 ± 0.05
	Gimje	0.04 ± 0.04	0.05 ± 0.04	0.91 ± 0.05
United States	Tullytown	0.17 ± 0.04	0	0.83 ± 0.04
	Moorestown	0.19 ± 0.06	0	0.81 ± 0.06
	Millville	0.29 ± 0.08	0	0.71 ± 0.08

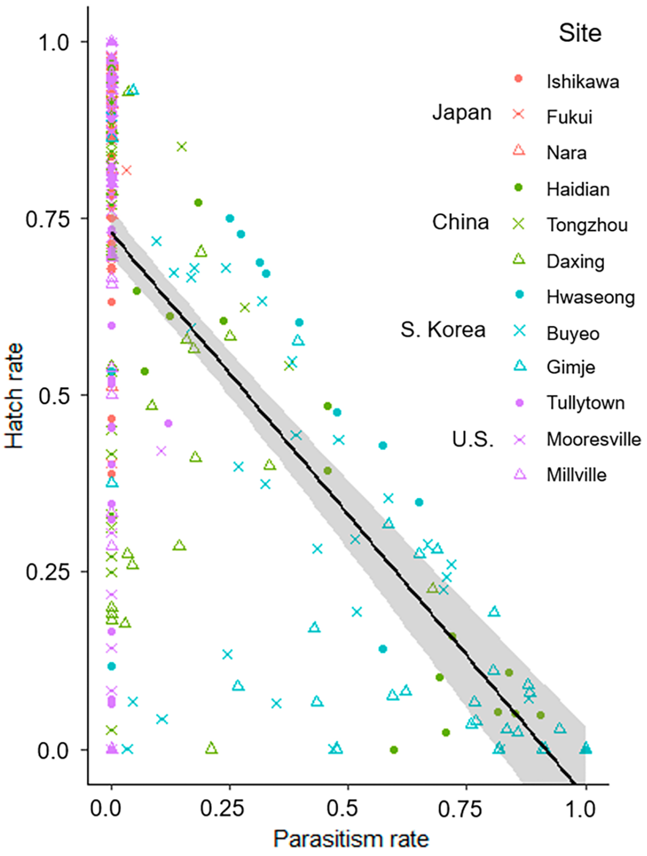

FIGURE 10 Relationship between *Lycorma delicatula* egg mass hatch and parasitism from the study sites. Gray bands for each region represent the 95% CI.

et al., 2023). However, another classical biological agent candidate, a nymphal parasitoid *Dryinus sinicus* (Hymenoptera: Dryinidae) is under evaluation for possible future release targeting *Ly. delicatula* (Xin et al., 2021). Parasitism of *Ly. delicatula* eggs by native and previously introduced egg parasitoids is rare in the United States. *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae), an egg parasitoid formerly imported to the United States to control *Lymantria dispar* (L.) (Lepidoptera: Erebidae), has been detected parasitizing *Ly. delicatula* egg masses in the field in the eastern United States, though at very low rates (<1.5% of total eggs) (Liu, 2019b). Another *Anastatus* species, *Anastatus reduvii*, has been recorded parasitizing field *Ly. delicatula* egg masses in the United States, but also at low rates (0.04%–0.17% of eggs) (Broadley et al., 2022; West et al., 2025; Williams, 2024). To date, no egg parasitoids of *Ly. delicatula* have been reported from Japan. A proactive assessment of resident natural enemies, either native or introduced, needs consideration for potential future use against *Ly. delicatula* in areas at risk of future invasion (Gómez-Marco et al., 2023; Molfini et al., 2025; West et al., 2025).

Climate plays an important role in affecting the hatch, development, and survival of phytophagous insect pests (Godfrey & Holtzer, 1991; Graf et al., 2006; Kreitman et al., 2021). ADD analyses from this study indicate egg masses in the native region of *Ly. delicatula* (i.e., China) accumulate more DDs through spring than in invaded regions (i.e., Japan, South Korea, and the United States). It is important to note that the study sites within each country were relatively close to one another, and do not represent *Ly. delicatula* populations from each individual country as a whole. Egg masses from sites in China reached critical DD points of 50% and 95% of total estimated field egg mass hatch (Smyers et al., 2021) earlier than those from Japan, South Korea, and the United States. Egg masses from sites in the United States accumulated DDs particularly late in the season, as the United States was the only region to not reach the estimated 95% hatch critical point by the end of May. This timing aligns with previous *Ly. delicatula* phenology studies conducted in the eastern United States which report peak activity of first instar nymphs from late May to early June (Dechaine et al., 2021; Leach & Leach, 2020). Study sites in the United States also had significantly lower 9-month ADD totals than sites in Japan and China, regions where *Ly. delicatula* is not considered an economic pest, indicating high early season ADD may not be an important driver of invasion success. Invasive populations of *Ly. delicatula* in the United States, which hatch and develop later in the season, may have access to its main host, *Ai. altissima*, at critical growth windows when the plant is most suitable for feeding, providing a high-quality food resource resulting in enhanced population growth (Jones, 2001; Rand & Louda, 2006). Further studies in the nutritional differences of *Ai. altissima* throughout the season would help elucidate *Ly. delicatula* population feeding and growth behavior.

Previous laboratory studies indicate that the highest egg hatch rates were produced from newly laid egg masses collected from the field and held a constant temperature of 15°C (58.4%) or chilled at 10°C for 84 days then held at 25°C (52.7%) (Keena & Nielsen, 2021). In the current study, sites from Japan had the highest hatch rates and the highest 9-month mean temperatures (12.2–13.1°C) from September 2022 through May 2023. A past study from South Korea reported the estimated minimum threshold for *Ly. delicatula* egg survival as −12.72°C on the basis of mean daily minimum temperatures over a month (31-day period) (Lee et al., 2011). This finding suggests that egg masses in some surveyed regions (e.g., China and South Korea) from this study may have experienced lower nymph hatch due to egg mortality resulting from excessive exposure to extreme cold. For example, the survey site Daxing (China) had the lowest mean monthly temperature across all regions at −9.9 ± 0.5°C in December, with the lowest minimum daily temperature recorded at −19.5°C in January. The site Hwaseong (South Korea) had the second lowest mean monthly and minimum daily temperature at −8.4 ± 0.7°C in December and −16.7°C in January, respectively. In comparison, the lowest mean monthly and minimum daily temperatures were −3.3 ± 1.1°C and −14.3°C in December, respectively, from the Millville site (United States), and 0.6 ± 0.4°C in February and −4.4°C in January, respectively, from the Eiheiji site (Japan). In the laboratory, *An. orientalis* was able to successfully parasitize *Ly. delicatula* egg masses that have been killed via cold treatments (i.e., exposure to −40°C for 24 h), with parasitism rates up to 89% (Gómez-Marco & Hoddle, 2022). This result suggests that in the field, *An. orientalis* may able to successfully parasitize winter-killed eggs that do not deteriorate after being killed by lethal cold temperatures. The effects of prolonged low temperature exposure on *Ly. delicatula* nymph hatch and survival of unemerged parasitoids in the field are largely unknown and warrant future investigation.

Overall, *Ly. delicatula* eggs in Japan and the United States had the highest hatch ratios, had the largest mean clutch size, and were present in high densities. Specifically, study sites in Japan had the highest mean proportion of *Ly. delicatula* nymph hatch (specifically from the Eiheiji and Oji sites, with a proportion of 0.90 of individual eggs hatching). Sites in the United States also exhibited high hatch ratios, with proportions ranging from 0.52 to 0.76. The site with the largest mean egg mass clutch size was from Tullytown, United States (51.45 ± 5.46 eggs per egg mass), followed by Hakusan, Japan (39.63 ± 2.03). This pattern of large clutch size with high hatch rates was also documented in previous field studies conducted in north-central Japan, which reported a nymph hatch proportion of 0.90 and a mean of 40.4 ± 5.3 eggs per egg mass (Nakashita et al., 2022). In the eastern United States, a 0.68 nymph hatch proportion has been reported (Liu, 2019a), where mean egg mass sizes range from 33.5 to 45.4 eggs (Gómez-Marco & Hoddle, 2022; Smyers et al., 2021). Conversely, egg masses collected from sites in China and South Korea generally had lower *Ly. delicatula* hatch proportions (0.44–0.59 and 0.23–0.67, respectively) and a smaller clutch size (23.30–35.67 and 26.97–39.13 eggs per egg mass, respectively) in this study. These findings are comparable to past fieldwork from eastern China which reported a *Ly. delicatula* nymph hatch proportion of 0.55 (Hou, 2013), and from north-central South Korea which reported a clutch size of 34.1 ± 1.9 eggs per egg mass (Jung et al., 2022). Additionally, significantly more *Ly. delicatula* egg masses were found during the 30-min timed counts from the US sites than from the China and South Korea sites during the first year of observations, and from the Japan, China, and South Korea sites during the second year. Mean egg mass counts from the US sites (739.33 ± 46.72 egg masses found) were over seven times higher than those from the next highest region, Japan (102 ± 13.61), during the second year of field observations. However, these results should be viewed with caution due to differences in human sampling effort and the species of available host plants surveyed, as well as the limited diversity of climates at the sites examined within the respective native and invaded ranges.

Ovipostion patterns have significant effects on egg hatch rates, and subsequently, overall survival rates for immature insect life stages (Parker & Courtney, 1984). Ovipositional behavior is especially difficult to understand in polyphagous insects such as *Ly. delicatula*, which has been documented ovipositing on more than 20 different host plant species and numerous inert nonhost substrates (Liu, 2019a). Abundant egg masses with large clutch sizes in the United States and Japan may be the result of *Ly. delicatula* not experiencing fitness costs related to a lack of preferred host plants. Intercontinental differences in egg mass oviposition-host substrate preference were detected. During 30-min timed counts in Japan and the United States, more egg masses were found laid on *Ai. altissima* (92% and 73% of total egg masses found per region, respectively), than in China and South Korea (33% and 0.5%, respectively). Insect egg mass clutch size is related to host search time (Skinner, 1985), meaning female *Ly. delicatula* are likely able to produce more eggs in regions where *Ai. altissima* is abundant as there is only a small fitness investment in host foraging. High nymph hatch rates and egg masses with large clutch sizes, along with high egg mass densities and the absence of significant natural enemies, indicate how *Ly. delicatula* can quickly reach high population densities. Consequently, this scenario may have amplified the pestiferousness of *Ly. delicatula* which has resulted in economic damage to agricultural crops and rapid spread in the United States (Urban, 2020; Urban & Leach, 2023). Curiously, similar egg mass characteristics and environmental conditions were quantified in Japan; however, *Ly. delicatula* is not currently considered as an agricultural pest species in Japan (Kamiyama et al., 2024). One potential reason for this discrepancy may be that *Ly. delicatula* is not yet present in important Japanese agricultural areas due to adverse climate and natural geographic barriers (Kamiyama et al., 2024).

Substrate selection for oviposition can also be influenced by parasitoid presence, as phytophagous insects have been observed laying fewer eggs or utilizing suboptimal substrates for nymphal development, but which offer reduced parasitism risk (Fatouros et al., 2020). For example, a low-quality host plant may be used for oviposition as it may not release volatiles attractive to egg parasitoids; hence, vulnerable eggs experience a reduced risk of parasitism, but at the cost of lowered nymph survivorship and development rates (Michereff et al., 2024; Peñaflor et al., 2011). Therefore, *Ly. delicatula* populations in China and South Korea, where parasitism is relatively high, may be less likely to use *Ai. altissima* as an oviposition substrate to minimize egg mass detection rates by *An. orientalis*. However, this phenomenon may also be a reflection of the relative abundances of different host plant species available for egg laying in the different regional study sites. Additional laboratory and field experiments should be performed to confirm this host-avoidance-oviposition-substrate hypothesis.

The findings provided here indicate there is strong evidence that biotic (i.e., egg parasitism) and abiotic (i.e., temperature) factors influencing *Ly. delicatula* egg mass densities and hatch vary across different countries where it is considered a native (China) or invasive (Japan, South Korea, and United States) species. Specifically, in field sites from China and South Korea where rates of parasitism are relatively high and average minimum temperatures are cooler, lower egg mass hatch ratios, clutch sizes, and egg mass densities were generally observed, whereas in sites from Japan and the United States where parasitism is inconsequential and mean temperatures are warmer, higher egg hatch rates, clutch sizes, and egg mass densities were measured. Parasitism of *Ly. delicatula* eggs may explain, in part, why observed population densities in China and South Korea are lower than those observed in Japan and the United States, where *An. orientalis* is absent (Choi et al., 2014; Wu et al., 2023). Future research extending these surveys to a broader range of sites in China and South Korea, and covering the enlarging invasive range in the United States, would help in confirming and expanding on the finding of these results.

In conclusion, results from this work provide important data on *Ly. delicatula* egg masses (i.e., clutch sizes, densities, nymph hatch, and parasitism rates) and associated effects of host plants and temperature across four different countries where this pest is native and invasive and where egg parasitism is prevalent or not. This information makes significant contributions to improving understanding of how biotic (i.e., natural enemies) and abiotic (i.e., climate) factors affect the demography of *Ly. delicatula* egg masses and the interactive effects these variables are likely to have on the invasion dynamics of this pest.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kamiyama, 2025) are available from Figshare: https://doi.org/10.6084/m9.figshare.29421584.v1.

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SUPPORTING INFORMATION

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