

Mapping The Life-History, Development, And Survival of Spotted Lantern Fly In Occupied And Uninvaded Ranges

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Abstract

The Spotted Lantern Fly (SLF), *Lycorma delicatula* (Hemiptera: Fulgoridae), is a sap feeding pest native to southeast Asia that has become a global biosecurity threat following invasions into South Korea, Japan, and the United States in the last two decades. Environmental niche modelling has demonstrated considerable potential for further range expansions, including into Australia and Europe. Further analysis on the potential seasonal life-history and survival of this pest in its invasive range can inform monitoring programs and is a next step in biosecurity preparedness. Here, we incorporated eco-physiological information on the development and survival of SLF life stages across temperature regimes. Using gridded climatic data, we then mapped the developmental sequence of SLF across ranges already occupied in China, South Korea, and the United States, as well as uninvaded ranges in Australia and Europe. The model was able to capture global observations of the seasonal appearance of SLF and highlight regional and seasonal vulnerabilities in regions at risk of invasion. Policy makers can use these results to make science-based biosecurity decisions and target preparedness activities through improved life-history predictions in its invasive range.

Introduction

The spotted lanternfly, *Lycorma delicatula* (SLF, Hemiptera: Fulgoridae), is considered a significant ecological and economic threat to agricultural, environmental and amenity plant hosts (Dara et al., 2015). Recently, SLF has expanded its international distribution from its native range of China, Vietnam and India with invasive populations establishing in South Korea (Bourgoin, 2014; Han et al., 2008), Japan (Kim et al., 2013) and, most recently, the north-eastern part of the United States (US) (Barringer et al., 2015; Dara et al., 2015).

SLF feeds on plants using piercing-sucking mouthparts, which can result in wilting or the death of branches under high pest population levels (Barringer et al., 2015; Han et al., 2008). Large amounts of honeydew are excreted and deposited on host trees and the understories during feeding, promoting the growth of sooty mould that hinders plant photosynthesis and contaminates agricultural and forest crops (Barringer et al., 2015; Han et al., 2008). Significant damage has been recorded in vineyards in Korea (Han et al., 2008; Lee et al., 2009; Park et al., 2009), while in the US, a vineyard at the core of the original infestation, reported a 90% yield loss with a corresponding loss in fruit quality (Urban, 2020). Orchard trees have not, as yet, observed any significant damage (Urban, 2020). In countries like Australia, where SLF is not known to occur, it is expected to threaten nursery, fruit, landscape and hardwood industries. Impacts can also be expected on businesses and residents as it is a nuisance pest, congregating in large numbers on wood piles, garden furniture, fence posts and other inanimate objects (Liu, 2019).

Several studies modelling the environmental niche of SLF have estimated significant establishment potential in many regions where SLF is currently not known to occur (Namgung et al., 2020; Wakie et al., 2020). A south Korean study estimated that maximum temperatures in the warmest month of the year were an important predictor with some evidence that the occurrence followed areas of high human

impact (Namgung et al., 2020). A study on the global distribution potential of SLF identified highly suitable areas for SLF in Asia, Oceania, South America, North America, Africa, and Europe (Wakie et al., 2020). The authors found that the most important environmental variables for predicting the potential distribution of *L. delicatula* were mean temperature of the driest quarter, elevation, degree-days with a lower developmental threshold value of 11°C, iso-thermality, and precipitation in the coldest quarter. Further, contrary to other published predictions (e.g., Jung et al., 2017), Wakie et al. (2020) predicted that tropical habitats were not suitable for *L. delicatula* establishment. While researchers attempt to further refine predictions to incorporate important life-stage events, such as egg hatch following winter diapause (Smyers et al., 2021), modelling the timing of development throughout the entire life cycle of SLF across its global range remains unstudied.

In the northern hemisphere, SLF is generally considered univoltine – undergoing one generation per year – however there is some uncertainty surrounding whether it may become multivoltine if it is able to establish in warmer climates (D.-H. Lee et al., 2019). SLF is a hemimetabolous insect, passing through an egg stage, four immature instars (nymphs), and an adult stage. In the northern hemisphere, SLF eggs are typically laid during the autumn (Dara, Barringer, and Arthurs 2015; Lee et al. 2011; Park et al. 2009) in masses of 30–50 eggs in an egg case (ootheca) (Dara et al., 2015; J. G. Kim et al., 2011; J.-D. Park et al., 2009), with a large variation in the number of the masses found per tree. The eggs are approximately 2.6 mm in length and 1.4 mm in width, greyish and ovoid in shape with a distinctive ‘stem-like’ structure at the anterior end that runs back across the dorsal surface of the egg (Park et al., 2009). Embryonic development represents a crucial life stage as a significant duration is spent overwinter suspended in diapause under cold conditions not tolerable in other life stages (Dara et al., 2015; Park et al., 2009). First instars are black with white spots and emerge as early as the following mid-spring (Dara, Barringer, and Arthurs 2015; Kim et al. 2011; Lee et al. 2014; Park et al. 2009). The fourth instar is predominantly red, retaining the white spots of earlier stages but acquires a black longitudinal pattern. The average size of each instar is 3.6–4.4 mm, 5.1–6.4mm, 6.9–9.4 mm, and 10.9–14.8 mm for instars 1 to 4, respectively (Dara et al., 2015; J.-D. Park et al., 2009). Adult female *L. delicatula* are 24–27 mm in length; males are smaller at 21–22 mm (Dara et al., 2015). Adult males emerge first, followed by females, and may live up to four months (Liu 2019).

Recently, significant temperature response data has accumulated from measurements of SLF development under different conditions. The reported lower temperature threshold for egg development varies between studies, including 8.1°C (Choi et al., 2012), 11.1°C (M. Park, 2015) and 13.2°C (Smyers et al., 2021). The reason(s) underpinning this variability between the studies remain unclear, and could be due to regional/population differences, physiological pre-conditioning and/or inconsistencies in the experimental methods. Egg duration is typically several months from autumn through to spring, while the first, second, third, and fourth instar durations are 18.8, 20.9, 20.8, and 22.2 d, respectively at approximately 20°C (Park et al., 2009). The lower developmental threshold was estimated at $13.00 \pm 0.42^\circ\text{C}$, $12.43 \pm 2.09^\circ\text{C}$, $8.48 \pm 2.99^\circ\text{C}$, and $6.29 \pm 2.12^\circ\text{C}$ for instars 1 to 4, respectively (Kreitman et al., 2021).

Here we build upon this recently acquired knowledge of the temperature response of SLF development to map the expected life-history and survival of SLF in both occupied and uninvaded ranges. Specifically, we address the following research questions: 1) Can compiled temperature response data on the development and survival of SLF life stages predict the seasonal observations of SLF occurrences in native and invaded ranges? 2) What is the predicted life-history and associated survival of different life-stages in the uninvaded ranges of Australia and Europe?

Methods

The temperature responses for development and survival of SLF life stages were sourced from several recent studies (Kreitman et al., 2021; M. Park, 2015; Smyers et al., 2021). While humidity, soil moisture and water availability are also important factors underpinning developmental responses and species distributions (Kearney & Maino, 2018; Maino et al., 2021), moisture limitation in SLF has been insufficiently investigated through ecophysiological studies to allow inclusion in the present study.

Kreitman et al. (2021) measured the development rate and survival of the pre-adult nymphs at constant temperatures of 5, 10, 15, 20, 25, 30, 35, and 40°C and estimated non-linear development rate functions for each instar (Fig. 1A, Table 1) using the Briere function of temperature (T)

$$f(x) = \begin{cases} a T (T - T_{min}) (T_{max} - T)^{\frac{1}{b}}, & T_{min} < T < T_{max} \\ 0, & \text{otherwise} \end{cases}$$

where a , b , T_{min} , and T_{max} are parameters (Briere, Jean-Francois; Pracros, Pascale; Le Roux, Alain-Yves; Pierre, 1999). We estimated a mortality response function for post-embryonic development using reported survival rates for each life stage under the different temperature treatments. After exposure to temperature, mortality was assumed to follow an exponential survival model by taking the number of deaths (Y) in a cohort as:

$$Y \sim \text{Poisson}(E(Y|x))$$

$$\log(E(Y|x)) = \log(N e) + \theta T$$

where e is exposure (mean instar duration in days), N is the number of individuals measured in a cohort, and θ is the vector of coefficients for up to fourth-degree polynomial terms for temperature T . This resulted in the fitted temperature responses of hazard rate accumulation shown in Fig. 1B and Table 1. These data generally correspond well with other similar studies (M. Park, 2015). Using an exponential survival model allowed the summation of hazards accumulated from exposures to different temperatures through time in the model simulations below.

For egg development, Smyers et al. (2021) compiled data from studies conducted in South Korea (Choi et al., 2012; M. Park, 2015), as well as new data using US populations, to estimate the response of egg hatch to accumulated temperature. Data collected by Park (2015) was used to estimate the hazard rate accumulation for temperatures where the effect of temperature was captured as two fitted linear functions splitting at -5°C (Table 1, Fig. 1B).

Initial simulations were run based on measurements from Kreitman et al. (2021), but incorrectly predicted that development could not be completed in regions known to support SLF, such as South Korea. Indeed, Kreitman et al. (2021) noted that the observed development rates of SLF were considerably shorter than observations made by Park et al. (2009). Thus, to match the development rates observed by Park et al. (2009), we scaled the development rate functions estimated by Kreitman et al. (2021) by a factor of 1.17, 1.27, 2.13, 2.62 for first, second, third, and fourth instars, respectively. This also brought predictions in line with other observational studies such as Park (2015) and Smyers et al. (2020). Similarly, we adjusted the hazard accumulation estimated from mortality data presented by Kreitman et al. (2021) by 50% to prevent the overestimation of mortality across SLF's current distribution. Given both the delay in development and high mortality estimated by Kreitman et al. (2021), it is likely that the rearing methodology used was suboptimal, however, the estimated shape of the developmental response to temperature was nonetheless useful in our study.

To generate prediction maps we used gridded monthly climatic data available for the globe at the 1-km spatial resolution (Fick & Hijmans, 2017). Following previous studies on the initiation of egg development (Smyers et al., 2021), we commenced simulations at January 1 for the northern hemisphere, and July 1 for the southern hemisphere, with eggs in each grid cell irrespective of whether temperatures would allow survival. Development and mortality hazard were then accumulated for a single generation for each grid cell and each month according to the fitted equations provided in Table 1. To assess monthly prediction maps, we overlaid time stamped occurrence data on SLF from the Global Biodiversity Information Facility (GBIF 2021).

Results

The fitted development rate functions indicate that optimal rates of development are estimated to occur at 30–33°C depending on the life stage (Fig. 1A). Overall, temperature responses of the four nymphal instars were similar, particularly during development at lower temperatures. However, the egg stage varied markedly in its developmental response and was less sensitive to warmer temperatures, which was unsurprising given the winter-adapted diapause strategy. Mortality at warmer temperatures appeared similar between the egg stage and post-embryonic stages and increased sharply after 30°C, coinciding with the optimal developmental threshold previously identified. In contrast, mortality with decreasing temperature differed markedly between the egg stage and post-embryonic stages. Mortality increased sharply under 10°C for post-embryonic stages while egg mortality remained low.

Mapping the estimated life-history and survival of SLF in its native Chinese range (Fig. 2) demonstrated that, despite their high cold-tolerance, eggs had low estimated persistence in northern and western steppes, alpine, and desert regions due to extreme cold temperatures. In south-eastern regions of China, predicted hatching corresponds with the first observations in the season, with adult development completed by July. As temperatures begin to cool from October, mortality accelerates as diapausing eggs are laid, corresponding with the lack of observations of nymphs and adults in November and December.

For the invaded ranges of the US (Fig. 3) and South Korea (Fig. 4), seasonal observations largely correspond with model predictions, however there are some occurrence records in areas that predicted eggs to remain unhatched or where cumulative survival was predicted to be low. Nevertheless, the seasonal observations of SLF generally aligned with model predictions across wide spatial ranges. Across all observations, there were few locations where SLF is known to occur in the warmer and wetter southern regions of China, South Korea and the US, despite high predicted suitability based on development and survival. Despite the simple focus on temperature at the exclusion of other potentially important abiotic and biotic factors, correspondence with observations was high providing greater confidence when extending predictions to novel ranges not yet invaded.

In Australia, in contrast to South Korea, there was larger latitudinal variation in the estimated life history and survival of SLF. In the north, development to the adult stage was estimated to be completed by October (assuming eggs could be laid in these regions). In southern Australia, hatching was predicted to occur from November with adult development complete in most regions by March. By April, survival was estimated to be highest in southern coastal regions in line with previous studies modelling the environmental niche of SLF (Namgung et al., 2020; Wakie et al., 2020). Development was predicted to be delayed in the alpine regions in Australia's southeast, with hatching not occurring until after January in some of the highest altitude regions, while in Tasmania (Australia's southernmost region), hatching was not predicted to occur in many western areas where temperatures remain too cool. In contrast to eastern Asia and North America, Australia rarely sees freezing temperatures, so cold mortality was predicted to be low except for alpine regions along Australian Great Dividing Range and Tasmania.

In Europe (Fig. 6), development proceeded most quickly for southern countries such as Portugal, Spain and Italy, with hatching predicted to occur across May to June in these regions. In much of northern Europe, such as parts of Norway or Sweden, temperatures remained too cold for hatching to occur at all. Further south where hatching was possible, development to the adult stage was frequently unable to be completed before temperatures became too cold (such as the United Kingdom, and Germany). As predicted in China, South Korea and the United States, following the completion of adult development, conditions gradually became less favourable from October until low predicted survival in December.

Discussion

By mapping the potential seasonal life-history and survival of SLF across continents, our study builds on previous environmental niche modelling (Namgung et al., 2020; Wakie et al., 2020), which has demonstrated significant potential for further range expansions. Estimations of the development and survival of SLF life stages across temperature regimes from recently published eco-physiological studies provided enhanced granularity and biological interpretation of suitability predictions (compared with the simple metrics between 0 and 1 of previous studies). The modelled developmental sequence of SLF was able to accurately predict the procession of seasonal observations across ranges already occupied in China, South Korea, and the United States, providing confidence that this biological model can be applied to novel ranges (Maino et al., 2016).

In this study, we synthesised existing regionally specific studies on the developmental response to temperature of embryonic and post-embryonic life stages (Choi et al., 2012; Kreitman et al., 2021; M. Park, 2015; Smyers et al., 2021). The validation of our approach relied on over 2000 time-stamped and geo-referenced observations of SLF occurrence records across its native and exotic range, utilised here for the first time to explore seasonal activity patterns. Of course, such data was opportunistically compiled, and stronger validation would be achieved through a field study across diverse locations. However, to span a similar range as our compiled dataset, such a field study is impractical and, consequently, such data is unlikely to be available in the future. Nevertheless, some limited observations have been made on the relative abundance of different life-stages at two field sites in South Korea as part of a larger study on the overwintering ecology of SLF (M. Park, 2015) and more recently in the eastern United States (Liu, 2020). Park (2015) monitored SLF across the spring and summer period at Cheonan in 2010–2012 and Suwon, Gyeonggido in 2012 in the northwest range of SLF. While there was some variation across years, SLF generally hatched in June, completed development by August, with observations of adults decreasing to zero in October. In eastern Pennsylvania the United States, Liu (2020) observed that SLF generally hatched in June, with adult development completing towards the end of September. Adult abundance decreased in October until complete absence by early November. These observations align with predictions for both the United States (Fig. 3) and South Korea (Fig. 4) providing some additional model validation.

While the high correspondence between observations and predictions based solely on environmental temperature is remarkable (though not uncommon (Wilson et al., 1983)), there remain some key uncertainties that will likely be influenced by other biotic and abiotic factors not considered in the present study. Some occurrence records in areas that predicted eggs to remain unhatched or where cumulative survival was predicted to be low likely reflects microclimatic variation not captured in atmospheric temperature data, particularly in protected environments that buffer cold temperatures and promote development and survival. In addition, the higher sampling effort in invaded ranges due to biosecurity concerns has likely resulted in the occasional detection of marginal populations. In addition, humidity, soil moisture and water availability are important factors underpinning species distributions (Kearney & Maino, 2018) and seasonal activity of populations (Maino et al., 2021) that were unable to be considered here. Our model predicted that at sub-tropical latitudes, temperatures generally appeared suitable for SLF development despite few SLF occurrence records in these regions. Rainfall is a key environmental variable that increases at lower latitudes, which was not considered and could potentially be limiting factor to the range of SLF either directly (e.g. exposure to rainfall) or indirectly (e.g. through affecting the prevalence of predators, parasitoids or pathogens).

Another key consideration is the occurrence of suitable host plants, which will play an important role in further modulating the potential global distribution and seasonal activity of SLF. While SLF is reported to feed on over 100 host plants (Barringer & Ciafré, 2020), a preferred host plant, *Ailanthus altissima* (Tree of heaven), is found in all invaded countries and is also present and widespread in Australia (Kowarik & Sämel, 2007). SLF can complete its development and reproduce without access to *A. altissima* without affecting survival, although development time is increased and the number of egg masses produced is

reduced (Uyi et al., 2020). Furthermore, it remains unclear if SLF offspring from parents that do not have access to *A. altissima* can complete their development and successfully produce a second generation without themselves having access to *A. altissima* (Uyi et al., 2020). This has important implications for the potential survival and spread of SLF in areas where *A. altissima* is absent. Indeed, the absence of *A. altissima* in tropical ranges (Kowarik & Säumel, 2007) may explain the fewer observations of SLF in such climates. Future research aiming to improve the establishment, spread, and seasonal activity potential of SLF should explore how interactions with climate, host availability and quality affect population development capacity.

Similarly, future studies aiming to enhance biosecurity preparedness for SLF through the identification and mitigation of spread pathway risk will need to consider dispersal processes. Adult SLF typically travel 10 to 50 metres in a single flight (Baker et al., 2019; Myrick & Baker, 2019; Wolfin et al., 2019, 2020), although there have been reports of up to 80 m (Parra et al., 2017) or 65 m after 10 d from release (Keller et al., 2020). Adults of both sexes typically launch themselves in level or gradually descending straight-line flight trajectories into the wind from an elevated position in a tree, or from human made structures such as posts (Baker et al., 2019; Domingue & Baker, 2019; Wolfin et al., 2019). Longer distance dispersal capacity and movement patterns at spatial scales larger than single host plants are largely unknown (Dara et al., 2015). Nonetheless, as SLF is not a strong flyer, human-mediated dispersal (e.g. through hitch-hiking), particularly during the egg stage, is likely to play a greater role in spread across large spatial scales compared with natural dispersal, as is common in many insect quarantine pests (Burne, 2019; Maino et al., 2020).

The application of the model to the uninvaded ranges, highlighted regional and seasonal vulnerabilities, and should assist with biosecurity planning and preparedness activities aimed at reducing incursion risks, and accelerating the transition to management in the case that SLF successfully establishes (Maino et al., 2020). While modern surveillance technologies continue to advance, such as the use of terrestrial eDNA surveys able detect SLF presence ahead of visual surveys (Valentin et al., 2020), improvements to the sensitivity and cost-effectiveness of surveillance will also be achieved through predictive modelling that can incorporate important biological processes and spatial datasets. Our study, which identifies likely periods of seasonal activity for different life-stages, will help to better target regional monitoring programs to more efficiently direct resources for specific surveillance goals. Building on previous SLF studies highlighting the environmental suitability of currently uninvaded regions, our predictions of development and survival suggest that the periods of pest activity will also overlap with key periods across susceptible plant production industries. For example, significant table grape production in southern Australia is highest from January to March (HIA, 2019), which corresponds with SLF entering its later life stages with higher feeding activity and damage potential. Our model is freely available to be used to investigate the development of SLF for other regions concerned with SLF incursion (with source code available at <https://github.com/cesaraustralia/SpottedLanternFly>). Thus, in regions not considered in this study, policy makers can use these results to make science-based biosecurity decisions and target biosecurity preparedness activities through improved life-history predictions in novel ranges. The global scope of requisite input data (i.e., climatic layers) will allow such

applications with minimal modification. More broadly, this research can be used by national plant protection organisations to assist development of phytosanitary measures and the monitoring of accidental introductions (e.g., when and where conditions are most conducive to development and survival). In post-border activities, the maps can be used in pest control efforts, such as the design of sampling strategies in currently infested areas or, at the farm management scale, to guide targeted pest risk assessments.

Declarations

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Conflicts of interest/Competing interests The authors declare no conflict of interest.

Availability of data and material All data utilised in the study is published or publicly available with sources provided in text.

Code availability Source code required to reproduce the analysis is available at <https://github.com/cesaraustralia/SpottedLanternFly>

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Tables

Table 1. Estimated functions for developmental and mortality functions across SLF life stages using existing studies (Choi et al., 2012; Kreitman et al., 2021; M. Park, 2015; Smyers et al., 2021)

Life stage	Development	Mortality
Egg	$f = \begin{cases} -0.03 + 0.003T, & T < 10.4 \\ 0, & \text{otherwise} \end{cases}$	$\log\left(\frac{E(Y)}{Ne}\right) = \begin{cases} -3.0 - 0.17T, & T < -5 \\ -7.5 + 0.14T, & \text{otherwise} \end{cases}$
Instar 1	$f = \text{Briere}^a(1.28 \times 10^{-5}, 0.93, 13.1, 43.81)$	$\log\left(\frac{E(Y)}{Ne}\right) = 4.0 - 1.6T + 0.1T^2 - 2.8 \times 10^{-3}T^3 + 3.0 \times 10^{-5}T^4$
Instar 2	$f = \text{Briere}(7.88 \times 10^{-5}, 1.98, 12.4, 35.58)$	
Instar 3	$f = \text{Briere}(1.56 \times 10^{-4}, 6.47, 9.87, 35.00)$	
Instar 4	$f = \text{Briere}(1.70 \times 10^{-4}, 9.69, 10.0, 35.0)^b$	
Adult	<i>Not applicable</i>	

^a The parameters in the Briere function denote a , b , T_{min} , T_{max} and respectively as described in the main text.

^b The parameter for a was incorrectly reported by Kreitman et al. (2021).

Figures

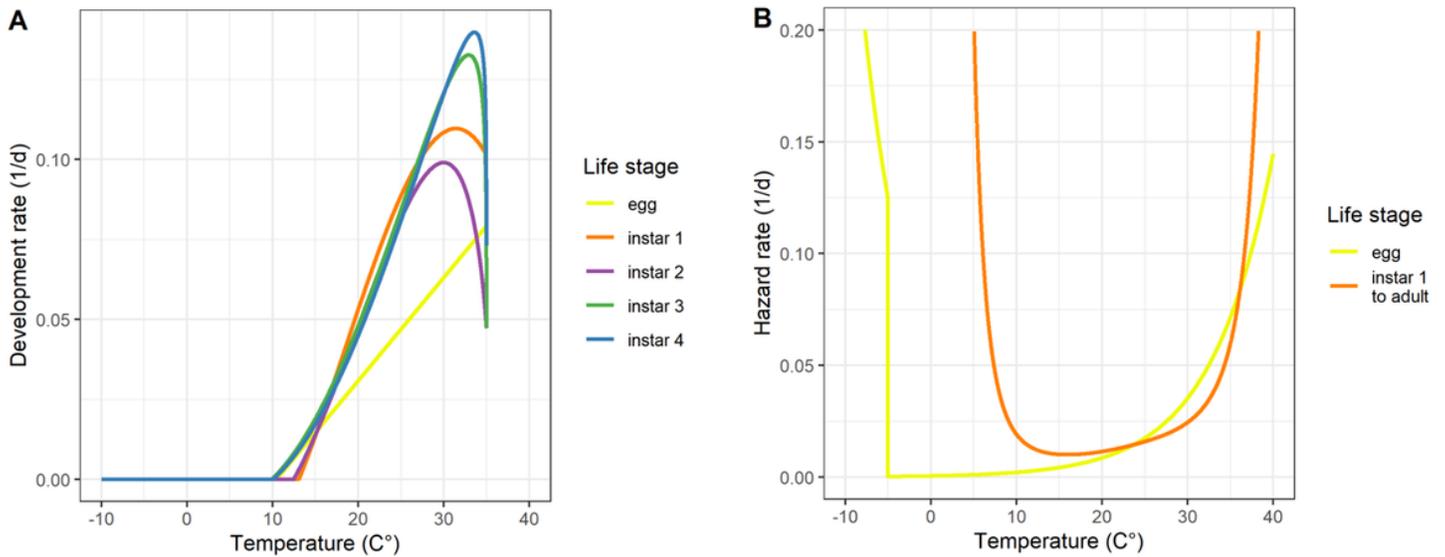


Figure 1

Temperature response of (A) development and (B) mortality across life stages of the spotted lanternfly, *Lycorma delicatula*, compiled and estimated from existing studies (Choi et al., 2012; Kreitman et al., 2021; M. Park, 2015; Smyers et al., 2021).

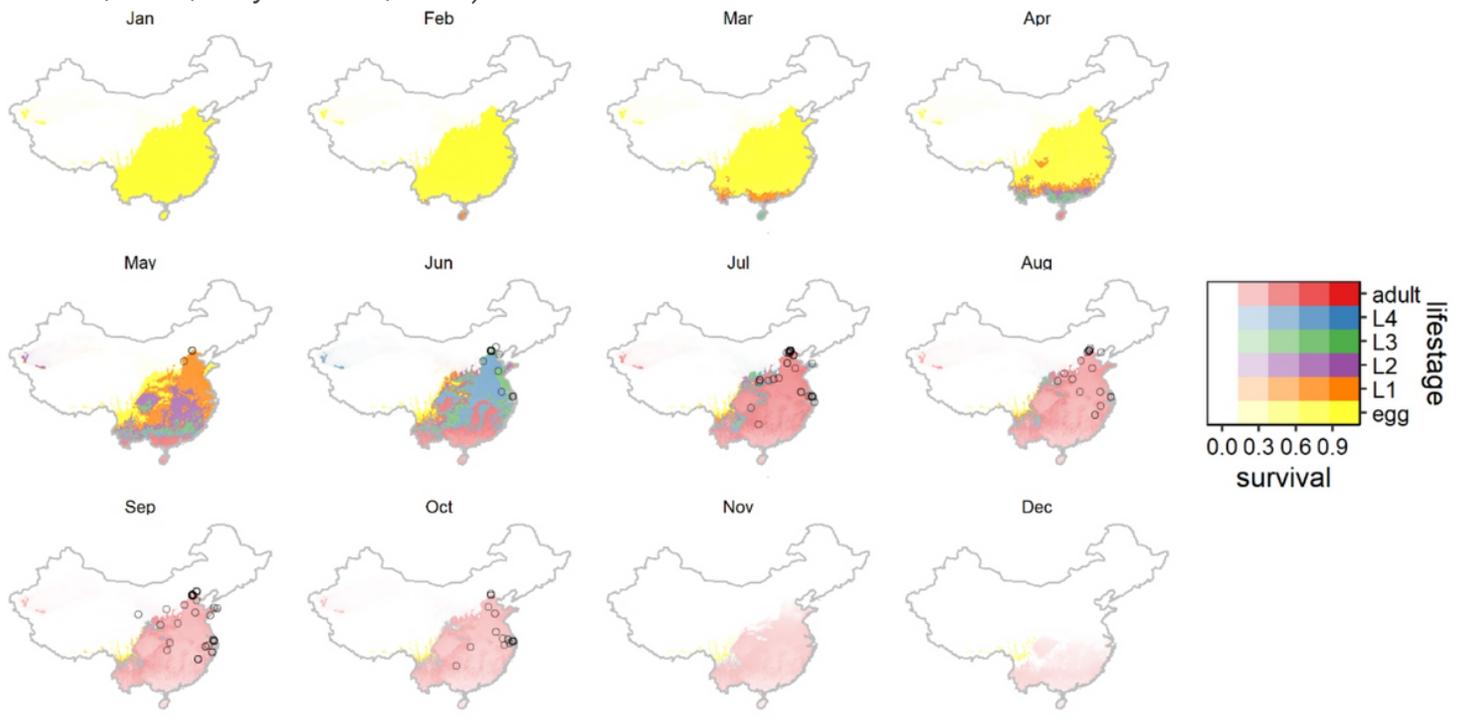


Figure 2

Monthly predicted development and cumulative mortality of *Lycorma delicatula* in China (northern hemisphere) where unique colors represent unique life stages and transparency denotes survival. Monthly occurrence records of nymphs and/or adults are shown as open circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion

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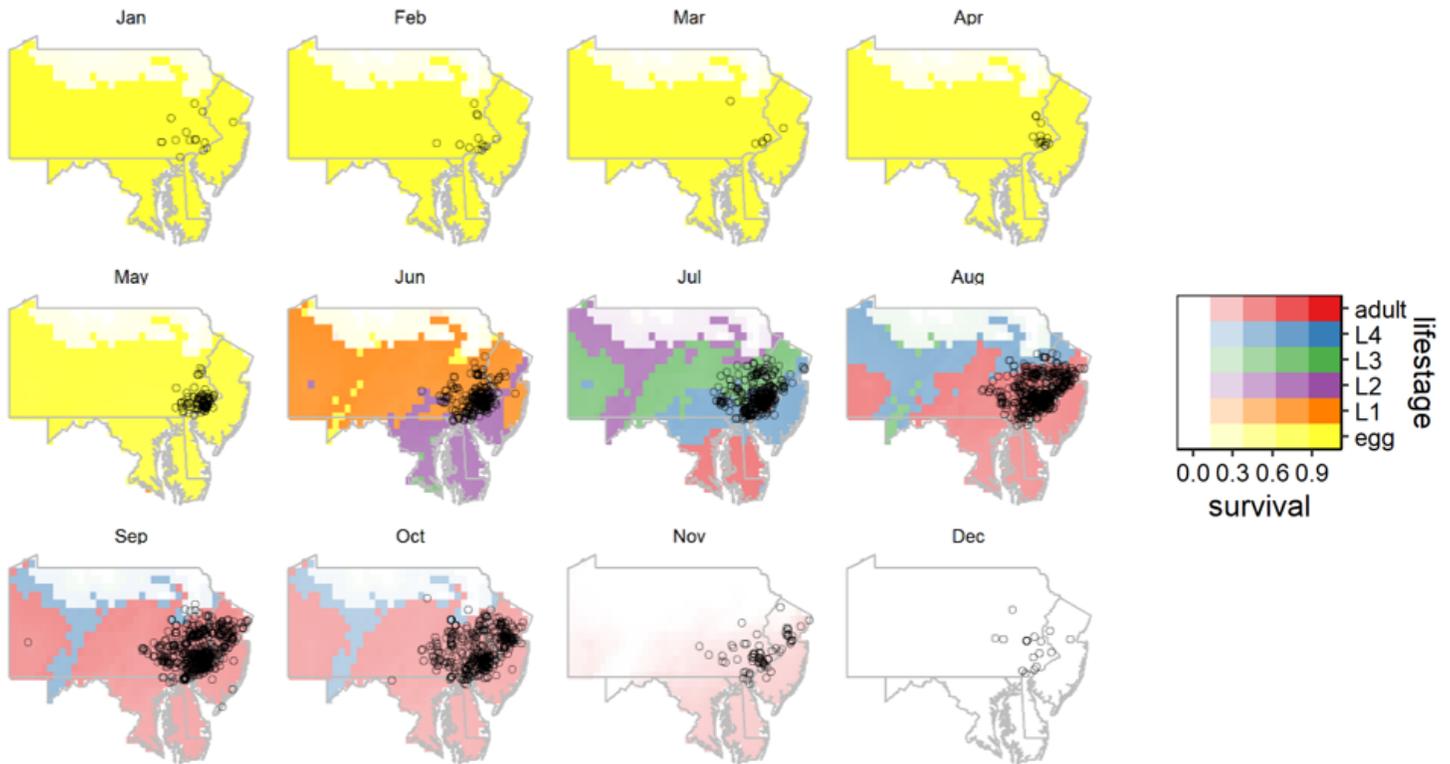


Figure 3

Monthly development and mortality of *Lycorma delicatula* in the eastern United States (northern hemisphere), for the states of Delaware, Maryland, New Jersey, and Pennsylvania where unique colors represent unique life stages and transparency denotes survival. Monthly occurrence records of nymphs and/or adults are shown as open circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

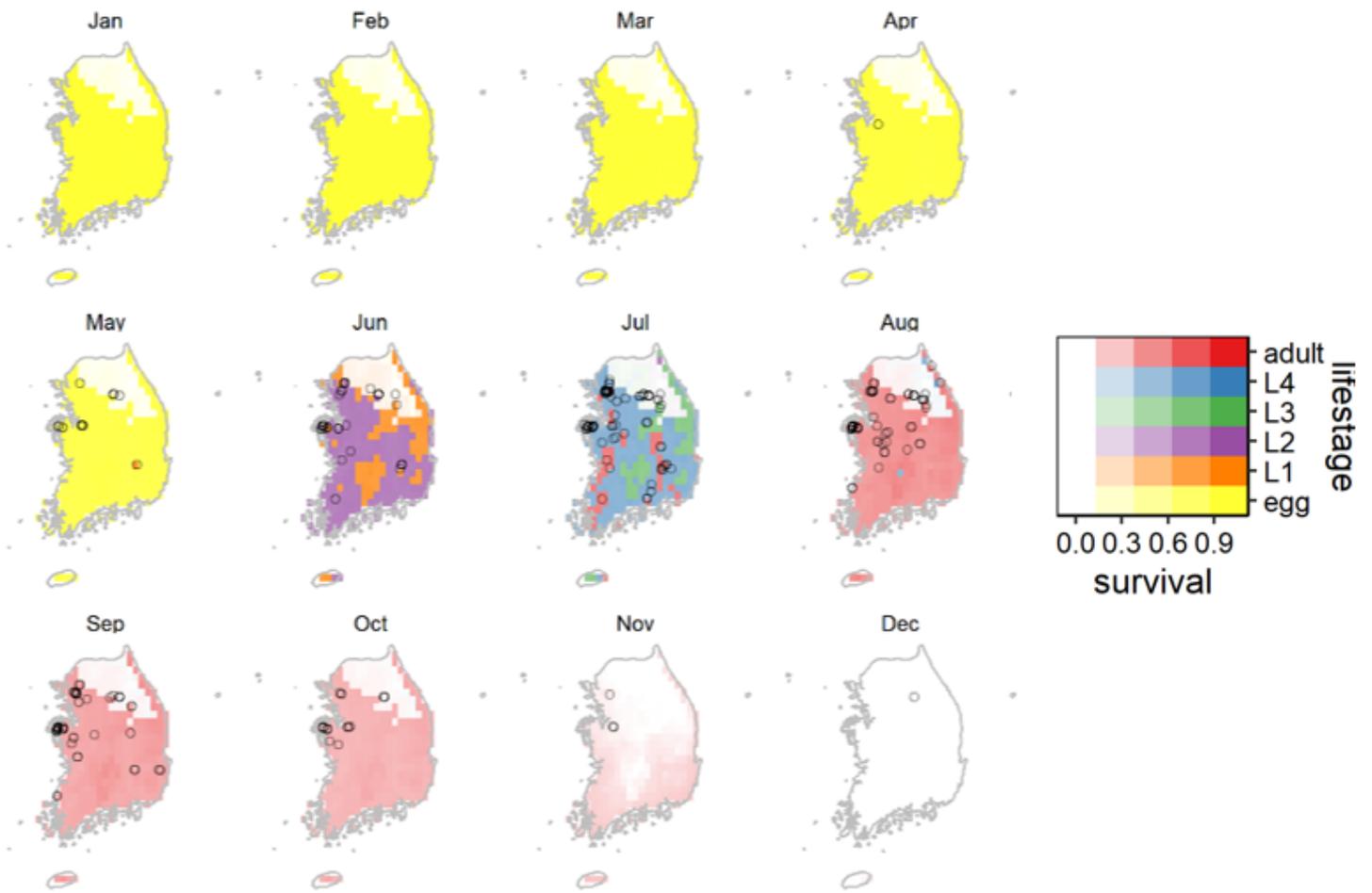


Figure 4

Monthly development and mortality of *Lycorma delicatula* in South Korea (northern hemisphere) where unique colors represent unique life stages and transparency denotes survival. Monthly occurrence records of nymphs and/or adults are shown as open circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

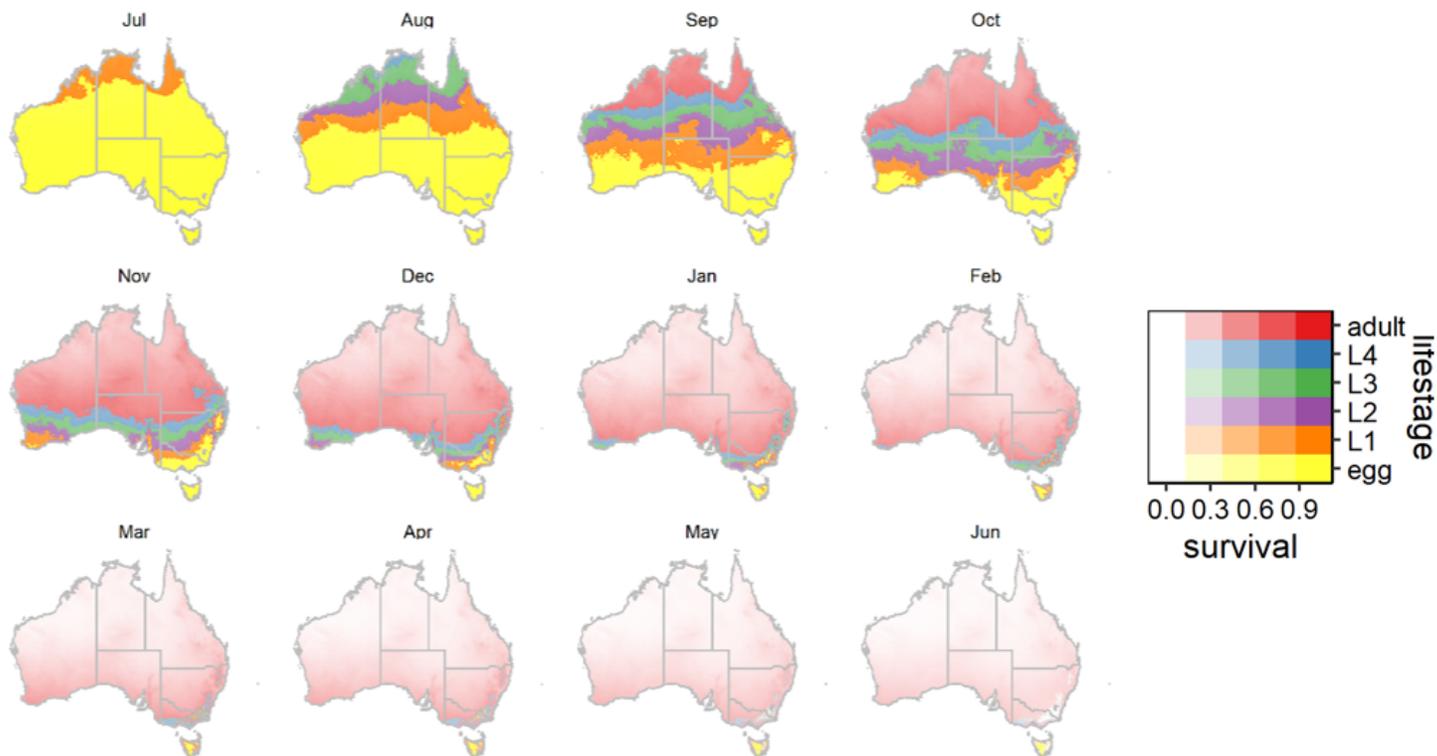


Figure 5

Monthly development and mortality of *Lycorma delicatula* in Australia (southern hemisphere) where unique colors represent unique life stages and transparency denotes survival. Monthly occurrence records of nymphs and/or adults are shown as open circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

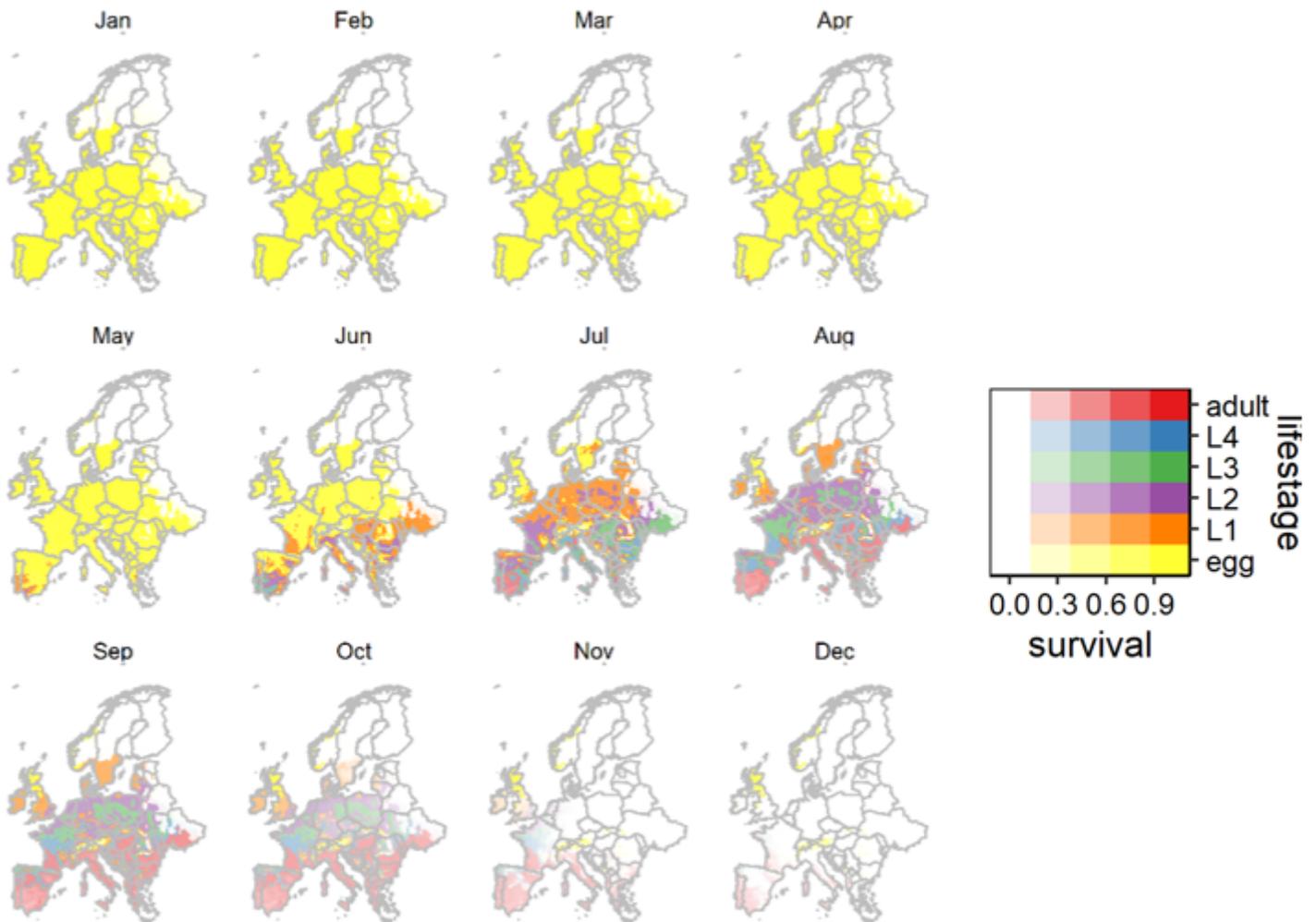


Figure 6

Monthly development and mortality of *Lycorma delicatula* in Australia (southern hemisphere) where unique colors represent unique life stages and transparency denotes survival. Monthly occurrence records of nymphs and/or adults are shown as open circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.