



# 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.

**Keywords** Biosecurity · Exotic · Niche modelling · Quarantine pest · Pest risk analysis · Decision support · Predictive modelling · Quantitative ecology · Invasive · Native

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## 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 and Vietnam 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) (Dara et al. 2015; Barringer et al. 2015).

SLF feeds on plants using piercing-sucking mouthparts, which can result in wilting or the death of branches or whole plants under high pest population levels (Han et al. 2008; Barringer et al. 2015). 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 (Han et al. 2008; Barringer et al. 2015). 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). Beyond direct impacts to yield, there are also indirect or induced economic impacts associated with the pest (Harper et al. 2019). 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 does not currently occur (Wakie et al. 2020; Namgung 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 SLF occurrence followed areas with high human impact scores derived from population density, land transformation, accessibility, and electrical power infrastructure (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, isothermality, 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 univoltine within its known range – undergoing one generation per year. However, there is some uncertainty as to whether SLF may become multivoltine if it is able to establish in warmer climates (Lee et al., 2019). SLF is a hemimetabolous insect, passing through an egg stage, four immature instars (nymphs), and an adult stage. Eggs are typically laid during the autumn (Park et al. 2009; Lee et al. 2011; Dara et al. 2015) in masses of 30–50 eggs in an egg case (ootheca) (Park et al. 2009; Kim et al. 2011; Dara et al. 2015), 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 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 (Park et al. 2009; Kim et al. 2011; Lee et al. 2014; Dara et al. 2015). 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, 5.1–6.4 mm, 6.9–9.4 mm, and 10.9–14.8 mm for instars 1 to 4, respectively (Park et al. 2009; Dara et al. 2015). 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, a considerable amount of 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 (Park 2015) and 13.2 °C (Smyers et al. 2021). The reason(s) underpinning this variability between studies remain unclear, and could be due to regional/population differences, physiological preconditioning 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  $13.00 \pm 0.42$  °C,  $12.43 \pm 2.09$  °C,  $8.48 \pm 2.99$  °C, and  $6.29 \pm 2.12$  °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?

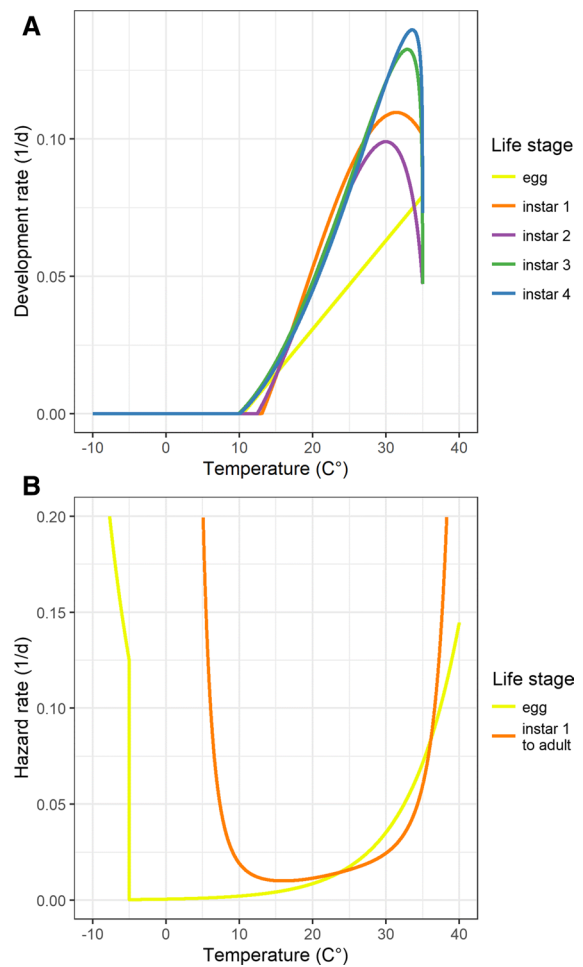
## Methods

The temperature responses for development and survival of SLF life stages were sourced from several recent studies (Park 2015; Kreitman et al. 2021; Smyers et al. 2021). While humidity, soil moisture and water availability are also important factors underpinning developmental responses and species distributions (Kearney and 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 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 ( $T$ ):

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

where  $a$ ,  $b$ ,  $T_{min}$ , and  $T_{max}$  are parameters (Briere et al. 1999). We also estimated a mortality response function for post-embryonic development using survival rates reported by Kreitman et al. (2021) for each life stage under the different temperature treatments. After exposure to temperature, mortality across each instar was assumed to follow an exponential survival



**Fig. 1** Temperature response of **a** development and **b** mortality across life stages of *Lycorma delicatula*, compiled and estimated from existing studies (Choi et al. 2012; Park 2015; Kreitman et al. 2021; Smyers et al. 2021)

model by taking the number of deaths ( $Y$ ) in a cohort as:

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

$$\log(E(Y|T)) = \log(N\varepsilon) + \theta'T$$

where  $\varepsilon$  is exposure (mean duration of each instar in days),  $N$  is the number of individuals measured in a cohort, and  $\theta$  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

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

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

<sup>a</sup> The parameters in the Briere function denote  $a$ ,  $b$ ,  $T_{min}$ , and  $T_{max}$  respectively as described in the main text

<sup>b</sup> The parameter for  $a$  was incorrectly reported by Kreitman et al. (2021)

other similar studies (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; 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). The piecewise linear model was used to minimise interpolation effects of higher order functions at intermediate temperatures with no available data (i.e.  $-5$  to  $10$  °C).

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) at  $20$  °C, we scaled the development rates estimated by Kreitman et al. (2021) by  $r_{lP}/r_{lK}$  where  $r_{lP}$  and  $r_{lK}$  is the development rate at  $20$  °C for instar  $l$  estimated by Park et al. (2009) and Kreitman et al. (2021), respectively. This resulted in adjustment factors of 1.17, 1.27, 2.13, 2.62 for first, second, third, and fourth instars, respectively, but simplistically assumes no changes to the functional form of the response curve. Further adjustment would require

re-estimation of four 4 parameters in the Briere temperature response equation for each instar for which there is insufficient data. This also brought predictions in line with other observational studies such as Park (2015) and Smyers et al. (2021). Additionally, we adjusted the hazard accumulation rate estimated from mortality data presented by Kreitman et al. (2021) by 50% to prevent the overestimation of mortality across the current distribution of SLF, which roughly corresponds to the reciprocal of adjustment factors to development rates. As discussed by Kreitman et al. (2021), the delay in development and high mortality was a result of suboptimal rearing conditions. The predictive performance from these “corrected” models were compared using the method described below.

To generate prediction maps we used gridded monthly climatic data available for the globe at the 1-km spatial resolution (Fick and Hijmans 2017) to map estimated development and mortality in the invaded ranges of China, eastern US and South Korea, as well as the uninvaded Australian and European regions. We compared the performance of monthly mean temperatures against hourly temperatures. Hourly temperatures were interpolated from the monthly mean minimum and maximum temperature using a cosine function for the diurnal cycle. 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). It is likely that some observations across winter represent adult cadavers that remain preserved in cold conditions for some time after mortality. However, as there was no systematic way to filter such observations, they are all included in the analysis. It is also worth highlighting that these predictions consider only broad-scale temperature effects on mortality and development, while other factors, such as microclimatic variability in temperature, moisture availability, and diet, may also be important considerations but lie outside the scope of the present study.

To compare the performance of alternate models described above, we calculated the mean predicted survival  $s$  weighted by the proportion of pre-adult development completed  $d$  across all observations  $i$  and months  $j$  as  $\frac{\sum_{ij} s_{ij} d_{ij}}{n}$  where  $n$  is the total number of observations. This metric has the advantage that it collapses both development and survival predictions into a simple score between 0 and 1 that reflects the observability of populations, which is assumed to scale in proportion with higher survival (i.e., larger populations) and development (i.e., larger and more conspicuous life stages). For example, the score will be 0 for populations of eggs and/or with complete mortality, while the score will be 1 for populations of adults with complete survival.

## Results

Comparison of candidate models in terms of the mean weighted survival scores across all observations is shown in Table 2. The model using default hazard and development rates estimated from data collected by Kreitman et al. (2021) and hourly temperatures performed the worst with a weighted survival score of 0.151, while the model with adjustments that increased the development rate and the reduced hazard accumulation rate using monthly mean temperatures performed the best with a score of 0.384. Hereafter, results are shown only for the model with the best fit.

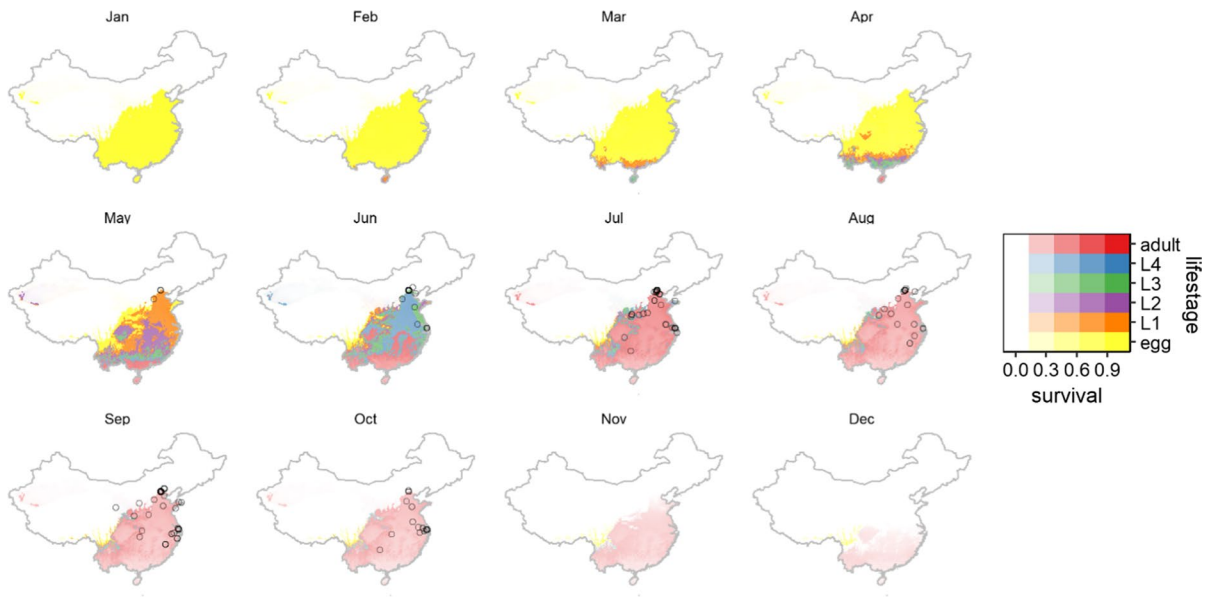
**Table 2** Comparison of model performance in terms of mean predicted survival of *Lycorma delicatula* across all observations (location and time) weighted by the proportion of development completed

Hazard rate	Development rate	Temperature profile	
		Hourly	Monthly mean
Default	Default	0.151	0.173
	Increased	0.271	0.297
Reduced	Default	0.181	0.183
	Increased	0.328	0.384

The fitted development rate functions indicate that optimal rates of development are estimated to occur between 30 and 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 (Fig. 1b). 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.

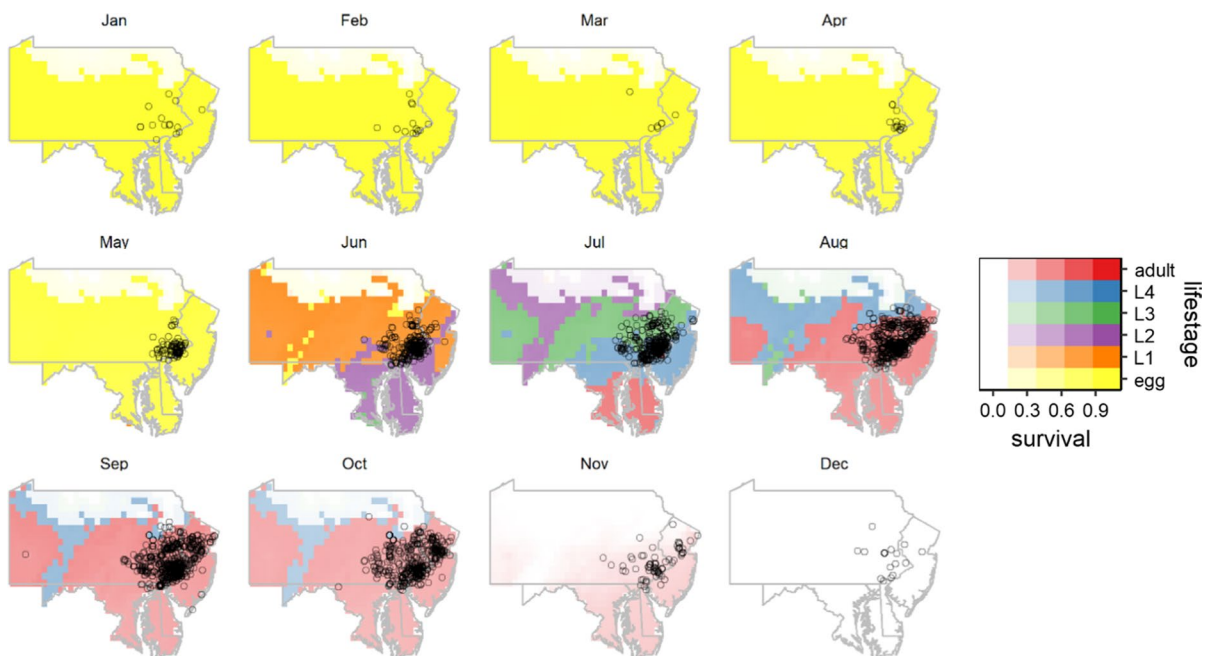
Mapping the estimated life-history and survival of SLF in its native Chinese range (Fig. 2) demonstrated that eggs had low estimated persistence in northern and western steppes, alpine, and desert regions due to extreme cold temperatures. In south-eastern regions of China, predicted hatching corresponds with the first observations in the season, with adult development completed by July. From October, mortality was predicted to accelerate, 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



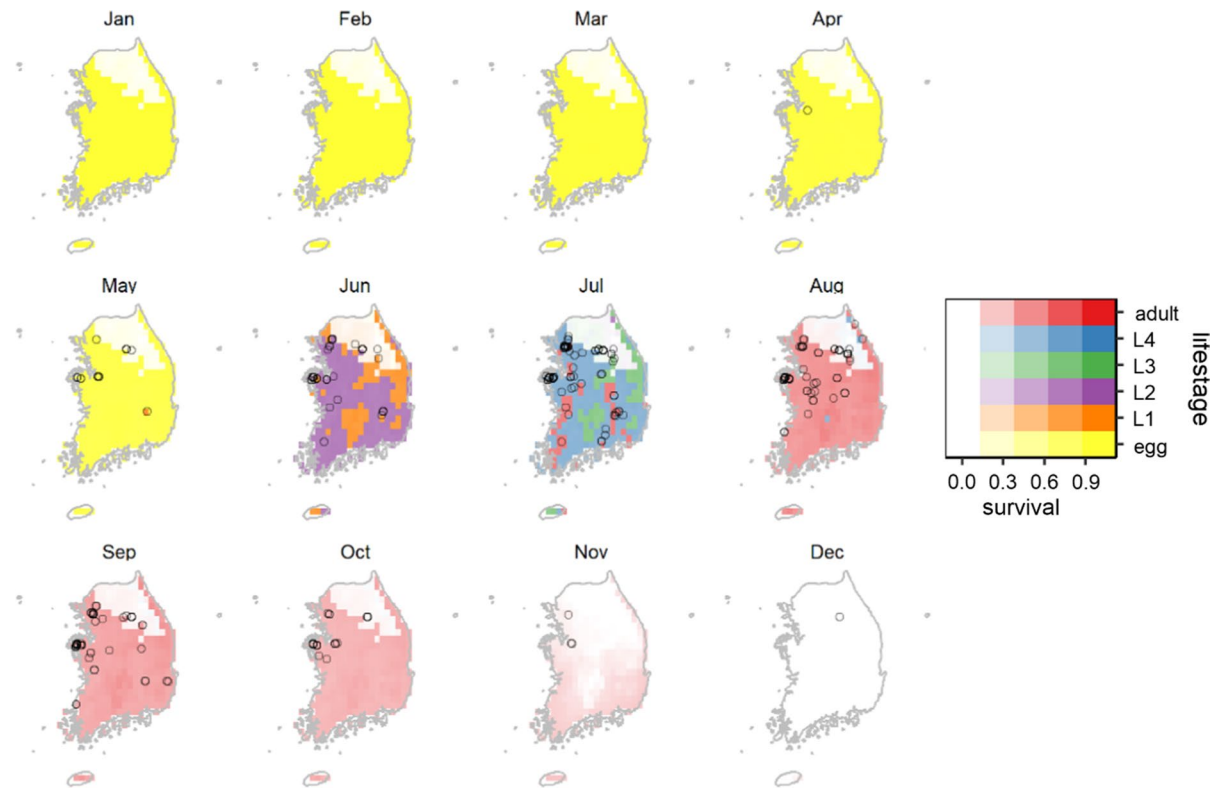
**Fig. 2** Monthly predicted development and cumulative mortality of *Lycorma delicatula* in China (northern hemisphere) where unique colors represent unique life stages and transparency denotes the predicted survival at the end of each

month based on the total hazard accumulated from 1 January. Monthly occurrence records of nymphs and/or adults are shown as open circles



**Fig. 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 the predicted survival at the end of each

month based on the total hazard accumulated from 1 January. Monthly occurrence records of nymphs and/or adults are shown as open circles. See Figure S1 for expanded view of the United States



**Fig. 4** Monthly development and mortality of *Lycorma delicatula* in South Korea (northern hemisphere) where unique colours represent unique life stages and transparency denotes

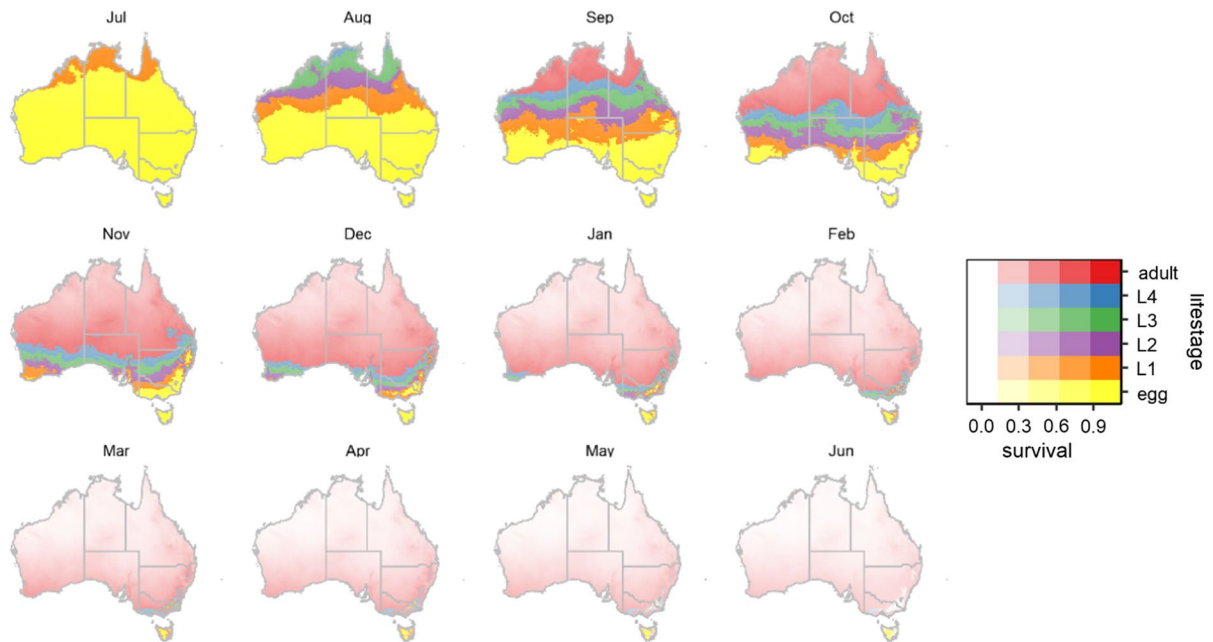
the predicted survival at the end of each month based on the total hazard accumulated from January 1. Monthly occurrence records of nymphs and/or adults are shown as open circles

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 contrast to South Korea, which spans ~500 km north to south, there was larger latitudinal variation in the estimated life history and survival of SLF in Australia, which spans ~3200 km (Fig. 5). 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 (Wakie et al. 2020; Namgung 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 the US, Australia rarely sees freezing temperatures, so cold mortality was predicted to be low except for alpine regions along the Australian Great Dividing Range and Tasmania.

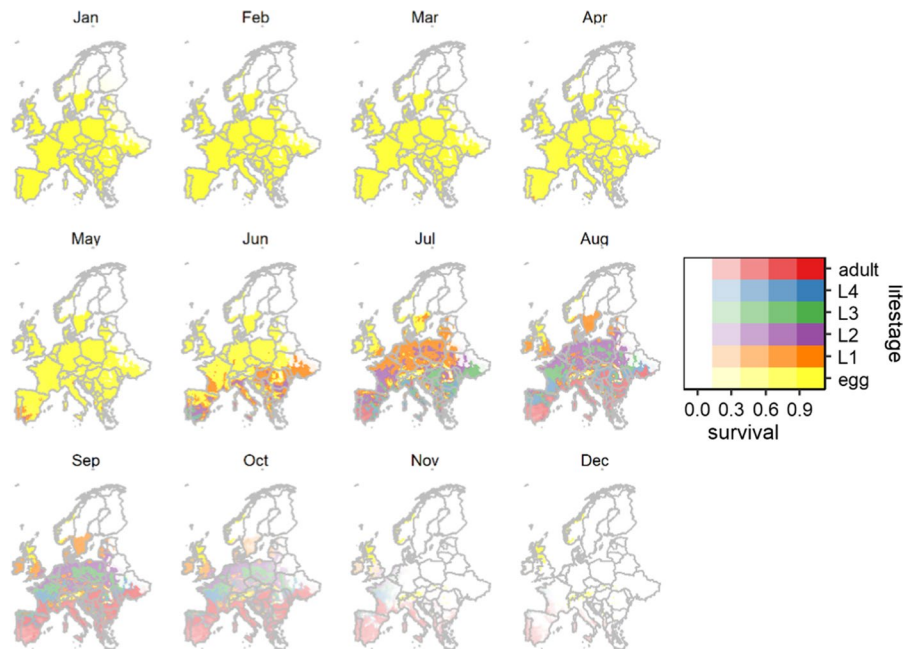
In Europe (Fig. 6), development proceeded most quickly for southern countries such as Portugal, Spain and Italy, with hatching predicted to occur across May to June in these regions. In much of northern Europe, such as parts of Norway or Sweden, temperatures remained too cold for hatching to occur at all. Further south where hatching



**Fig. 5** Monthly development and mortality of *Lycorma delicatula* in Australia (southern hemisphere) where unique colors represent unique life stages and transparency denotes the pre-

dicted survival at the end of each month based on the total hazard accumulated from 1 July

**Fig. 6** Monthly development and mortality of *Lycorma delicatula* in Australia (southern hemisphere) where unique colors represent unique life stages and transparency denotes the predicted survival at the end of each month based on the total hazard accumulated from 1 January



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 US, 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 (Wakie et al. 2020; Namgung 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). For example, our model outputs provide additional information on the likely life stages that would be observed through time across different regions. 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 US, 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; Park 2015; Kreitman et al. 2021; 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 field surveys across diverse locations. However, to span a similar range as our compiled dataset, such a 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 (Park 2015) and more recently in the eastern US (Liu 2020). Park (2015) monitored SLF across the spring and summer period at Cheonan between 2010 and 2012, and in Suwon 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 (US), 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 our predictions for both the US (Fig. 3) and South Korea (Fig. 4) providing some additional model validation.

Our mechanistic modelling approach contrasted to species distribution models (SDMs) based on statistical inference using occurrence records (e.g. Elith & Leathwick, 2009; Phillips et al., 2006). Species distribution models are useful for identifying complex, and often latent and interacting, ecological processes, so long as appropriate environmental covariates that sufficiently characterise the species' niche can be selected (Phillips et al. 2006; Guillera-Aroita et al. 2015). However, such approaches are challenged by the inherent risk of extrapolating statistical inference to novel conditions, such as spatial ranges not yet invaded (Dormann et al. 2012). In contrast, the underlying biological processes restricting species ranges, such as the temperature responses included in our model, are more likely to remain relevant in novel ranges (Maino et al. 2016). Standard SDM approaches also lack methods to account for dynamic population level traits such as life stage (to take an example addressed in the present study). In our approach, we were able to utilise rich information on the ecophysiology of this species to develop robust predictions of the effect of environmental temperature on life history responses, at the cost of a more specialised modelling approach.

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 and 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 occurrence records in these regions. Rainfall is a key environmental variable that increases at lower latitudes, which was not considered and could potentially be a 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) (Clifton et al. 2020).

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 and Ciafré 2020), a preferred host plant, *Ailanthus altissima* (tree of heaven), is found in all invaded countries and is also present and widespread throughout parts of Australia (Kowarik and Säumel 2007). Indeed, the lack of *A. altissima* in the northern and interior regions of Australia may play an important role in reducing the predicted suitable range (Figure S2). However, 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 and Säumel 2007) may explain the fewer observations of SLF in such climates in the US and China (Figure S2). Future research aiming to improve the establishment, spread, and seasonal activity potential of SLF should explore how interactions with climate, host availability and host 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 m in a single flight (Myrick and Baker 2019; Wolfin et al. 2019, 2020; Baker et al. 2019), 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 (Domingue and Baker 2019; Wolfin et al. 2019; Baker 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 for incursions. This information should assist with biosecurity planning and preparedness activities aimed at reducing incursion risks, and accelerate the transition to management in the case that SLF successfully establishes (Maino 2020). For example, the North American range of SLF remains in an early stage and will likely continue to expand into new regions. Surveillance priorities may be informed by our predictions of novel ranges not yet invaded (Figure S1), while future observations in new ranges will serve as a validation of predictions. Where observations misalign with predictions, insight will be provided into other important processes for future inclusion into similar models or the inappropriateness of simplifying assumptions.

While modern surveillance technologies continue to advance, such as the use of terrestrial environmental DNA surveys to detect small traces of target species DNA (Pirtle et al. 2021), 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 pressure 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 SLF development and survival). In post-border activities, the maps generated here 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.

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**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>

**Declaration**

**Conflict of interest** The authors declare no conflict of interest.

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