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Is seasonal reversal a significant barrier to interhemispheric invasion?

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Abstract

Diapausing life stages are a particular biosecurity concern because they are environmentally robust and can be transported inadvertently on non-host materials. Three invasive species of major concern to New Zealand, the brown marmorated stink bug (*Halyomorpha halys*), spotted lanternfly (*Lycorma delicatula*), and spongy moth (*Lymantria dispar*), undergo winter diapause and have spread widely across the Northern Hemisphere, yet remain largely absent from the Southern Hemisphere. We hypothesised that interhemispheric transport may constrain establishment by disrupting seasonal temperature and daylength cues. Individuals arriving in diapause from the Northern Hemisphere must terminate diapause, complete development, and re-enter diapause before the onset of winter conditions, effectively reducing the time available for population establishment. We modelled diapause and phenology for all three species to assess whether arrival in New Zealand during diapause would permit successful completion of their life cycles. Simulations were run backwards from winter to estimate the latest arrival dates that allowed sufficient developmental time. Predicted establishment potential varied among species and locations. Spongy moth was least constrained by a shortened growing season, whereas spotted lanternfly was most constrained. For all three species Auckland and Northland provided the greatest opportunities for establishment, permitting completion of a generation within approximately half a season. Climate change substantially increased the predicted establishment window for all species. Our results suggest that the reversal of seasonality associated with interhemispheric transport can significantly limit establishment success for some diapausing invasive species. This mechanism may contribute to the relative absence of some Northern Hemisphere pests from the Southern Hemisphere.

Introduction

The growing volume of global trade and travel places increasing pressure on biosecurity systems (Hulme 2009). Pest invasions multiply as more organisms are accidentally moved across biogeographic and seasonal boundaries, impacting on human health, native biodiversity and primary production (Hulme et al. 2023). For many insect species, successful invasion depends not only on surviving transportation but also on the physiological state and seasonal timing of arrival. Insects transported while active may face starvation, desiccation, or unsuitable temperatures during transit, while those with a diapausing life stage may be better able to persist through transportation and then resume development or reproduction after arrival (Hahn & Denlinger 2011).

Diapause is a physiological stage of restrained development and reduced metabolic activity (Gordh & Headrick 2011) by which populations can regulate the timing of growth to match favourable environmental conditions (Mansingh 1971, Tauber & Tauber 1976, Denlinger 2002). Diapause may be obligatory, occurring at a fixed stage in each generation, or facultative, with entry regulated by environmental cues such as photoperiod, temperature, or resource availability (Denlinger 2008, Hand et al. 2016). Although diapause is often associated with harsh or unfavourable conditions, it differs from quiescence because development is not simply halted by immediate environmental limitation. Instead,

diapause is induced by cue-based physiological programming, and development may not resume immediately even when favourable conditions return (Hance et al. 2007, Hodek 2013).

Diapause has important implications for invasion dynamics because it can alter survival during transport, the timing of post-arrival development, and the likelihood that an introduced population completes its life cycle before seasonal conditions deteriorate. Invasive insects could already be in diapause on the transported consignment (e.g. from harvest), or the conditions on the pathway could induce diapause or quiescence (e.g. chilled freight). Many of the invasive exotic invertebrates of global concern have a winter diapausing life stage; well-known examples include *Halyomorpha halys* (McDougall et al. 2021) and *Lycorma delicatula* (Keena & Nielsen 2021) (Hemiptera), *Rhagoletis cerasi* (Moraiti et al. 2020) (Diptera), *Tetranychus kanzawai* (Mochizuki & Takafuji 1996) (Acari), *Lymantria dispar* (Gray et al. 2001) (Lepidoptera), and *Harmonia axyridis* (Reznik & Vaghina 2013) (Coleoptera).

The timing of entry into and exit from diapause directly affects population dynamics and, therefore, establishment potential of insect pests in temperate climates. For example, diapausing pests arriving at sub-optimal times may encounter a temporal mismatch between their life cycle requirements and suitable environmental windows to be able to complete their development and reproduction before the onset of winter. This is particularly relevant to those species attempting to establish at new latitudes, such as those crossing the equator. Reversed seasonality may create a strong phenological mismatch for insect species moving between hemispheres (Grevstad et al. 2022, Ma et al. 2024). Individuals arriving from a winter or post-harvest pathway may emerge into a recipient environment with only part of the growing season remaining. Establishment will therefore depend on how arrival date, diapause status, developmental thresholds, and local temperature regimes interact to determine whether individuals can mature, reproduce, and generate an overwintering stage before winter (Jarošík et al. 2015, Grevstad et al. 2022). Species that terminate diapause too late may fail to complete development, whereas species with lower thermal requirements or more flexible diapause responses may recover from seasonal displacement. These processes can create geographic variation in establishment risk, even among locations connected by similar trade pathways.

Here we investigate how winter diapause timing and post-arrival development affect the invasion potential to New Zealand of three high-profile diapausing insect pests originating from the Northern Hemisphere: brown marmorated stink bug (BMSB, *Halyomorpha halys* Stål, Hemiptera: Pentatomidae), spotted lanternfly (*Lycorma delicatula* (White), Hemiptera: Fulgoridae) and spongy moth (*Lymantria dispar* (L.), Lepidoptera: Erebidae). These represent species with increasingly complex diapause biology, from a simple daylength response in BMSB (McDougall et al. 2021, Reznik et al. 2022) to complex interactions between warming and chilling in spotted lanternfly (Park 2015, Shim & Lee 2015) and spongy moth (Gray 2004, Gray & Keena 2019). We used the models to investigate where and when an arrival of a winter diapausing life stage might have sufficient seasonal temperatures to develop, reproduce and reach their diapausing life stage in time for the following winter. Interactions between diapause timing and developmental requirements may determine whether crossing the equator poses a significant barrier to pest invasions.

By focusing on winter diapause as a driver of post-arrival population dynamics, this study provides an approach for assessing invasion risk under seasonal displacement. Although motivated by biosecurity pathways into New Zealand, the findings are broadly relevant to invasions in which transported insects experience a seasonal mismatch between origin and destination by moving between hemispheres.

Methods

Population models

We modelled the diapause and life cycles of BMSB, spotted lanternfly and spongy moth using object-oriented programming in R version 4.5.3 (2026-03-11 ucrt) (R Core Team 2024) with principles and libraries of the TidyVerse (Wickham et al. 2019).

Each insect life stage was represented as an object with specific developmental requirements, each tracking integer-based sets of equal-age cohorts. The proportion of development achieved by each cohort was incremented to simulate development based on the day-degree relationships specific to each species and life stage (Table 1). The brown marmorated stink bug model relied primarily on developmental relationships documented by Nielsen et al. (2008) and Baek et al. (2017), with diapause induced in adults by declining daylength below 14.5 h and terminated by increasing daylength above 13.5 h (McDougall et al. 2021). Since diapause is facultative in this species, it may achieve more than one generation per year in suitably warm climates. A new model for obligate diapause of spotted lanternfly eggs was developed to fit the data reported by Keena & Nielsen (2021) and assumes that temperature-based development rate is initially low but increases with exposure to chilling (M. Keena, pers. comm.). Development of subsequent spotted lanternfly life stages follows published data (Liu 2020, Dechaine et al. 2021, Kreitman et al. 2021, Laveaga et al. 2023, Barker & Coop 2024). For spongy moth, we reproduced the ‘GLS’ model of Gray (2004) with the post-diapause eggs stage updated according to Gray (2009). This features relatively complex relationships for obligate pre-diapause, diapausing and post-diapause egg stages dependent on interactions between warming, chilling and age. Specific details for each species are given as Supplementary information.

Table 1
Summary of life stages and key model features for the three study species. Diapausing life stages are asterisked.

Life stage	Developmental drivers	Key references
Brown marmorated stink bug (BMSB), *Halyomorpha halys*		
Eggs	Temperature	Nielsen et al. (2008); Baek et al. (2017)
Nymphs (5 instars grouped)	Temperature	Nielsen et al. (2008); Baek et al. (2017)
Diapausing adults*	Photoperiod	McDougall et al. (2021); Musolin et al. (2022)
Pre-reproductive adults	Temperature	Medal et al. (2013); Baek et al. (2017)
Reproductive adults	Calendar age	Baek et al. (2017)
Spotted lanternfly, Lycorma delicatula		
Eggs*	Temperature + chilling	Keena & Nielsen (2021)
Nymphs (4 separate instars)	Temperature	Kreitman et al. (2021); Barker & Coop (2024)
Pre-reproductive adults	Temperature	Laveaga et al. (2023)
Unmated adults	Photoperiod	M. Keena (pers. comm.)
Reproductive adults (male/female)	Calendar age	Jung et al. (2022)
Spongy moth, Lymantria dispar		
Pre-diapause eggs	Temperature	Gray et al. (1991)
Diapausing eggs*	Temperature + chilling	Gray et al. (2001)
Post-diapause eggs	Temperature + age	Gray (2009)
Larvae (5–6 instars grouped)	Temperature	Sheehan (1992)
Pupae	Temperature	Sheehan (1992)
Adults (male/female)	Calendar age	Koshio (1996)

Variability in the duration of life stages was implemented by modelling the probability of each individual moving to the next life stage by a logistic equation centred around the mean developmental requirement:

$$P_{mat} = \frac{1}{1 + exp\left(-\left(4.6/w\right)\left(D - m\right)\right)}$$

where P_{mat} is the probability of maturation to the next life stage, D is the proportion of the developmental requirement that has been accumulated to date, m is the mean of the curve (default = 1), and w is the width of the curve. The value 4.6 in the denominator scales w to be equivalent to 3 times the standard deviation so that when $D = m - w$, $P_{mat} = 0.01$ and when $D = m + w$, $P_{mat} = 0.99$.

The probability of maturation was then integerised to the actual number maturing N_{mat} from a cohort of N_{cohort} equal-staged and equal-aged insects using binomial rounding:

$$N_{mat} \sim Bin\left(N_{cohort},\ P_{mat}\right)$$

This introduces realistic demographic stochasticity into simulations (Gustafsson & Sternad 2007), which is important for modelling rare events and/or small populations. Since we are only interested in the timing of life stages, we did not explicitly model survival and reproduction. Instead, adult females were assumed to die at their age of median reproductive output, and oviposition replaced an equivalent number of new eggs to maintain the same total population size.

Temperature data

Daily meteorological data were compiled for six key New Zealand locations representing a broad latitudinal gradient and proximity to important ports of entry: Kerikeri Research Station (-35.17862 °N, 173.93021 °E); Mt Albert Research Station, Auckland (-36.89035 °N, 174.72752 °E); Te Puke Research Station, Tauranga (-37.82284 °N, 176.32065 °E); Richmond, Nelson (-41.2706 °N, 173.2840 °E); Lincoln Research Station (-43.64613 °N, 172.45668 °E); and West Cromwell (-45.05657 °N, 169.15179 °E). For each location, daily minimum, maximum, and mean air temperature data from 2015–2024 were used, and daylength was calculated from latitude and date.

For a country-wide analysis, we drew on time-averaged data for a further c. 11,450 sites from Earth Science New Zealand's Virtual Climate Station Network (VCSN) (Cichota et al. 2008). These data have been down-scaled from calibrated ground-based climate stations to a grid of locations with a resolution of 0.05° arc, which is equivalent to approximately 5 km north-south by ~ 4 km east-west (this varies slightly with latitude).

In all cases the daily mean temperature was estimated as the mean of daily minimum and maximum temperatures. Temperature fluctuations within a day were modelled as 6 h each of the daily minimum, mean, maximum and mean (again) temperatures. This is consistent with the "trapezoidal" method that has been shown to work well for predicting insect phenology in New Zealand (Kean 2013).

Critical arrival dates

On entry to New Zealand, it was assumed that an invasive species must have sufficient time to advance through its lifestages to reach the diapausing (overwintering) stage before temperatures become too cold and kill off any remaining non-diapausing stages. For each life stage and arrival location, therefore, we hypothesise there is a critical arrival date after which establishment is unlikely due to insufficient development time remaining in the season. We assumed that non-diapausing life stages would not be able to survive through the winter, noting that this restriction may not necessarily apply in some warmer northern areas. Since July is the coldest month of the year in New Zealand, we assumed 1 July as the winter date beyond which non-diapausing stages would not survive. By reversing the temporal order of temperature data and life stages, we ran the phenology models backwards from this date to estimate critical arrival dates. This time reversal was possible because almost all non-diapausing life stages were dependent only on temperature, calendar age or photoperiod (Table 1). The more complex life stages (spotted lanternfly eggs, and spongy moth diapausing and post-diapause eggs) could not be run backwards in this way, but this wasn't necessary since propagules of those species are most likely to arrive already in those diapausing stages. Results were generated in this way for each of the six key locations.

Daily temperature data were not available to generate these results at high spatial resolution across the whole country, so a simplified approach was used for country-wide mapping of critical dates. Here, the thermal requirement for development across non-diapausing stages was approximated as a linear day-degree relationship fitted to available data. A common base temperature threshold was assumed as the mean base temperature across all life stages and the day degree requirements above this threshold were adjusted using the method of Morris & Fulton (1970):

$$q_2 = q_1 \frac{(p - b_1)}{(p - b_2)}$$

where q is the day degree requirement, b is the base temperature below which development ceases, subscripts 1 and 2 refer to the original and adjusted values respectively, and p is the pivot temperature (assumed to be 20°C). Once adjusted to a common base temperature, the day degree requirements for each stage could be summed to estimate the requirement across the relevant life stages. We sourced values for b_1 and q_1 from the published literature and estimated parameters for each species as shown in Table 2.

Table 2
Approximated day-degree requirements for development from the end of one generation's diapausing life stage to the start of that of the next.

Species	Base temperature (°C)	Degree-day requirement (°d)	Data sources
Brown marmorated stink bug	13	749	Nielsen et al. (2008); Govindan & Hutchison (2020); Baek et al. (2017)
Spotted lanternfly	10.4	1684	Liu (2020); Keena & Nielsen (2021); Kreitman et al. (2021); Laveaga et al. (2023); Barker & Coop (2024)
Spongy moth	7.4	1127	Gray et al. (1991); Sheehan (1992)

We estimated the day degree accumulation for each location and day of the year, then summed backwards from 1 July to estimate and map critical arrival dates. Since this method relied on approximated developmental requirements (Table 2) the predictions were validated against the more robust results generated from running the models backwards at the six key locations. We repeated the analysis for a climate change scenario, using temperatures projected for the 20 years centred on 2090 under the RCP6.0 scenario (Ministry for the Environment 2020).

Actual arrival dates of live and dead brown marmorated stink bugs to New Zealand could be inferred from border and post-border interception records from 2022 to 2026 obtained from the Ministry for Primary Industries, New Zealand (Michael Ormsby, pers. comm.). These were compared to the critical dates suggested by the model to identify what proportion of live arrivals might produce a new generation with sufficient time to successfully overwinter. No similar data were available for the other two species.

Results

Figure 1 shows model outputs for all three taxa differed across the six key locations, demonstrating the effect of local climatic conditions on predicted seasonal population dynamics. Overwintering adult brown marmorated stink bugs are predicted to break diapause in mid to late October, in response to daylength reaching the threshold of 13.5 h. Earlier emergence from diapause in southern locations is counteracted by a longer preoviposition period, with the result that adults are predicted to become reproductive during December at all sites. Nymphs are predicted to appear in early January, but only those in the North Island (Kerikeri, Auckland and Tauranga) are expected to experience sufficient thermal accumulation in autumn to reach the diapausing adult stage by winter. Cooler southern locations (Lincoln and Cromwell) are predicted to be marginal for BMSB persistence, since few modelled individuals were able to complete a full generation there.

Similar results were predicted for spotted lanternfly, with southern locations also expected to be too cool for completion of a full generation. Unlike BMSB, spotted lanternfly life stages would appear at different

times along the country, with southern sites lagging behind those in the north by four to six weeks. The model suggests that spotted lanternfly would be unlikely to persist in the South Island because of insufficient time to complete a full generation.

Unlike the other two species, spongy moth might establish and persist in the South Island (Fig. 1). Its life stages are also predicted to appear slightly later in the season in the North than in the South, because of protracted exit from diapause under warmer northern conditions. The model suggests that eggs would hatch in October (through to almost January in the far north), with adults appearing in January to February.

Running the BMSB model backwards from mid winter suggested that adults arriving in the north (Kerikeri and Auckland) would need to emerge from diapause before January in order for the next generation of adults to reach diapause before winter (Fig. 2). Given that daylengths exceed the threshold of 13.5 hours for adults to leave diapause, this would not impose a significant constraint on such arrivals. Further south, however, diapausing adult BMSB arrivals would be more constrained. At Tauranga they would need to arrive before mid December, but South Island arrivals would need to be earlier to experience sufficient thermal accumulation to complete the necessary development. Given that daylengths only become suitable for diapause cessation in mid to late October relatively few diapausing adults arriving in the South Island even early in the springtime would be likely to establish and survive the following winter. For reference, Northern Hemisphere populations of BMSB tend to enter diapause in mid September through October, and leave diapause in mid April though May (Reznik et al. 2022).

The spotted lanternfly model gave similar results, with the prediction that eggs would need to arrive and leave diapause before December in the North Island in order to complete a life cycle. In North America, eggs are observed from late September to mid November (Calvin et al. 2023) so this seems feasible. Late-instar nymphs might be able to establish if arriving as late as mid March, but these tend to occur in July and August in North America (ibid.) and would be more conspicuous and less robust on introduction pathways, so the main risk of entry and establishment is likely to be eggs.

Outside of the diapausing stage, spongy moth development is relatively rapid compared to BMSB and spotted lanternfly, and the model suggests that arriving eggs might successfully complete a full life cycle before winter if the eggs eclose before mid-February in the north and late December in the south. In the Northern Hemisphere, eggs are typically present from late August to mid-May (Boukouvala et al. 2022).

Actual arrival dates of BMSB in New Zealand across all pathways of entry are indicated by Fig. 3. These data indicate that BMSB arrivals to New Zealand occur predominantly between October and April, with a peak in interceptions during the summer months (December–February), corresponding to the Northern Hemisphere diapause period. Relatively few intercepted individuals are detected alive, virtually all from October to January. Simulation results (Fig. 2) suggest that, if arriving in adult diapause in Auckland or Kerikeri, most of these would have sufficient time to mature and lay eggs that could develop to diapausing adults before winter. However far fewer would have a chance in southern locales.

Across the whole country, using the VCSN data, the analysis suggests that the ability of diapausing invaders from the Northern Hemisphere to establish may vary considerably. Brown marmorated stink bug might find sufficient developmental resources to complete its first life cycle in a shorter season in Northland, Auckland and coastal North Island, plus a few seasonally warm valleys in the South Island (Fig. 4). The latest arrival times allowing establishment are January in the far north and November-December south of Tauranga. This suggests that BMSB intercepted from February on (Fig. 3) are unlikely to pose as great a risk of permanent establishment as those earlier arrivals.

For spotted lanternfly, establishment is expected only in the northernmost third of the North Island, and diapausing invaders would need to arrive before December, which is quite early in the season. In contrast, spongy moth is predicted to have sufficient time to develop before winter even when arriving in February in northern or coastal North Island. These results aligned well with the detailed assessments at six key locations (Fig. 2).

Under climate change, the seasonal window and geographic range for establishment widens considerably for brown marmorated stink bug and spotted lanternfly (Fig. 5). Brown marmorated stink bug arrival dates as late as February might experience enough thermal accumulation to establish, while those arriving in November (start of the diapause season in the Northern Hemisphere) might develop sufficiently in Canterbury and other South Island areas with relatively warm summers. The risk pattern for spotted lanternfly is considerably expanded under climate change and is similar to that for brown marmorated stink bug under current climates (Fig. 4). Less change is predicted for spongy moth because it already had extensive opportunities for establishment.

Discussion

Survival during transport is only one of several barriers that an introduced insect must overcome before establishment can occur. Introduced insects must pass through multiple sequential filters, including transportation, introduction, survival, reproduction, population persistence, and spread (Levine 2008, Davis 2009). For insects with diapause, these filters are strongly shaped by phenology. Diapause may increase survival during transport or adverse seasonal conditions, but establishment also requires that individuals arrive in a physiological state compatible with post-arrival development, reproduction, and production of an overwintering stage before conditions become unsuitable (Davis 2009).

Our results highlight the importance of this post-arrival timing filter. We assumed that arriving individuals were in diapause and examined whether, after arrival in New Zealand, they could reproduce and generate offspring capable of entering diapause before winter. Under some combinations of arrival date and location, diapausing life stages that arrived alive were able to resume activity, reproduce, and produce offspring that reached the next overwintering (diapausing) stage before conditions precluded further development. Under other combinations, populations failed because development and reproduction were not completed before the onset of unsuitable seasonal conditions. This suggests that establishment risk is not determined by climatic suitability alone, but by the interaction between arrival

time, diapause status, developmental requirements, and the seasonal environment in the recipient region. For species with short-lived adult stages, like spongy moth (Boukouvala et al. 2022), asynchrony in adult emergence as is predicted for northern North Island (Fig. 1) could also hamper establishment in small founding populations.

For species with a winter diapause, these results highlight a limitation of invasion risk models that are based only on climatic suitability or growing-season temperature (e.g., Paini et al. 2018). Climate matching approaches like CLIMEX (Kriticos et al. 2015), MaxEnt (Phillips et al. 2006) and range bagging (Drake 2015) are useful for identifying broad areas of potential suitability but may not fully capture diapause-mediated constraints on establishment for these insects, especially in the early stages of invasion. Incorporating diapause biology can improve predictions by accounting for whether seasonal timing permits completion of the life cycle, rather than only whether temperatures are suitable for development. The importance of diapause in biosecurity risk assessment is likely to increase under changing trade and climate conditions as increases in trade volume and faster transport pathways may alter the number and physiological condition of individuals arriving alive. Climate change may further modify establishment risk because temperature, but not photoperiod at a given latitude, will change, potentially altering the environmental cues that regulate diapause expression and seasonal development (Bale & Hayward 2010, Tougeron et al. 2017, Tougeron 2019). Warmer conditions may extend the period available for development in some recipient regions, increasing the probability that offspring complete development before winter. However, warm conditions can also disrupt diapause requirements or increase energetic costs during dormant periods, reducing post-arrival viability (Gray 2017, Nielsen et al. 2022).

From a biosecurity perspective, diapause-based establishment models can help identify which pathways, source regions, commodities, and arrival periods represent the greatest risk. Such information could refine inspection and surveillance timing, distinguish survival in transit from biologically plausible establishment, and support more targeted pathway management. For example, New Zealand's Ministry for Primary Industries (MPI) defines a high-risk season for brown marmorated stink bug introductions from September to April (Kim et al. 2025), corresponding to the months when BMSB adults are in diapause in the Northern Hemisphere (Reznik et al. 2022). During this time MPI increases BMSB surveillance and auditing activities at the border to detect and manage BMSB in containers and on goods. Our results suggest that this high risk window might be shortened as diapausing adults arriving after January would likely not have sufficient time to complete their life cycle before the onset of winter (Fig. 2). The fact that BMSB is frequently found on introduction pathways (Fig. 3) but has not yet established in New Zealand (Kim et al. 2025) might be partly explained by the seasonal reversal experienced by invaders. Importantly, BMSB has now established south of the equator, in Chile (Faúndez & Rider 2017), and these populations may present an elevated risk to other Southern Hemisphere countries because invaders would not experience the seasonal reversal that might have constrained establishment previously. The predictions generated in this research could also be used to inform a high-risk season for spotted lanternfly and spongy moth, where resources could be allocated at the highest-risk periods for establishment.

Few previous studies have modelled invasion risk as an interaction between insect diapause, transportation pathways and climatic conditions on arrival. Paini et al. (2018) focused on the suitability of receiving ports for spongy moth eggs originating in Asia but did not consider seasonality nor the implications of its reversal on crossing the equator. Gray (2010) modelled spongy moth egg development during and after a simulated voyage from Kobe, Japan to Auckland, New Zealand, and noted that the reversal of the seasons disrupted phenological development and approximately halved the probability of establishment on arrival. We have expanded on these studies to consider a wider range of invasive species, the potential for arrival beyond a major seaport, and potential implications of climate change. We have uniquely focused on the seasonal reversal associated with crossing the equator and how it might affect establishment risk. However, several model limitations should be considered. First, we assumed that individuals arrived in a diapause state and did not explicitly model diapause progression during transport. In reality, pathway temperatures may maintain diapause, terminate diapause, or induce activity before arrival, with consequences for survival, energy reserves, and reproductive capacity. Second, the model assumed that non-diapausing stages cannot survive winter. This is a simplification since winter survival is likely to vary among species, life stages, microhabitats and regions. For example, brown marmorated stink bug has invaded Florida, where gravid females have been observed in mid-February (late winter) (Penca & Hodges 2018) suggesting either that they overwintered in a non-diapausing reproductive state or that the daylength cues directing diapause are less rigid than previously thought. Third, the model did not include senescence or mortality associated with prolonged developmental delay following phenological mismatch. Individuals delayed in diapause or development may die before conditions become suitable, even if a model allows them to persist (Lewkiewicz et al. 2022) and a range of sub-lethal effects of chilling length have been observed in BMSB (Song et al. 2025). Finally, the model did not represent finer-scale thermal variability, microclimate, host availability, mate limitation, or stochastic mortality, all of which may influence establishment probability in small founding populations.

A key next step is to model and experimentally evaluate diapause progression during transport. Previous work has shown that pathway temperatures can influence the mobility and survival of diapausing BMSB during simulated shipping, with warmer conditions causing some individuals to become active when food and moisture are absent or suboptimal (Nixon et al. 2019). However, little research has tested how interhemispheric transport affects diapause completion, post-arrival viability, and subsequent establishment probability. Many authors have described, from laboratory trials, how diapause allows insects to survive unfavourable conditions or seasons and determine insect persistence during transport, thereby in both cases increasing establishment potential (e.g., Cira et al. 2018, Koštál 2006, Gray 2017, Poitou et al. 2020). Like Gray (2010), future work should combine pathway temperature data, diapause physiology, and post-arrival population models to ask what condition insects are likely to arrive in, whether diapause is maintained or broken during transit, and how this affects the probability of reproduction and population persistence after arrival. Experimental shipping simulations, including assessment of diapause status and reproductive condition on arrival, would provide an important validation step for these models.

Declarations

Competing interests

The authors have no relevant financial or non-financial interests to disclose

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Author contributions

All authors contributed to the study conception and design. Data collation, modelling and analysis were performed by John Kean, Rachael Horner and Sulav Paudel. The first draft of the manuscript was written by John Kean and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

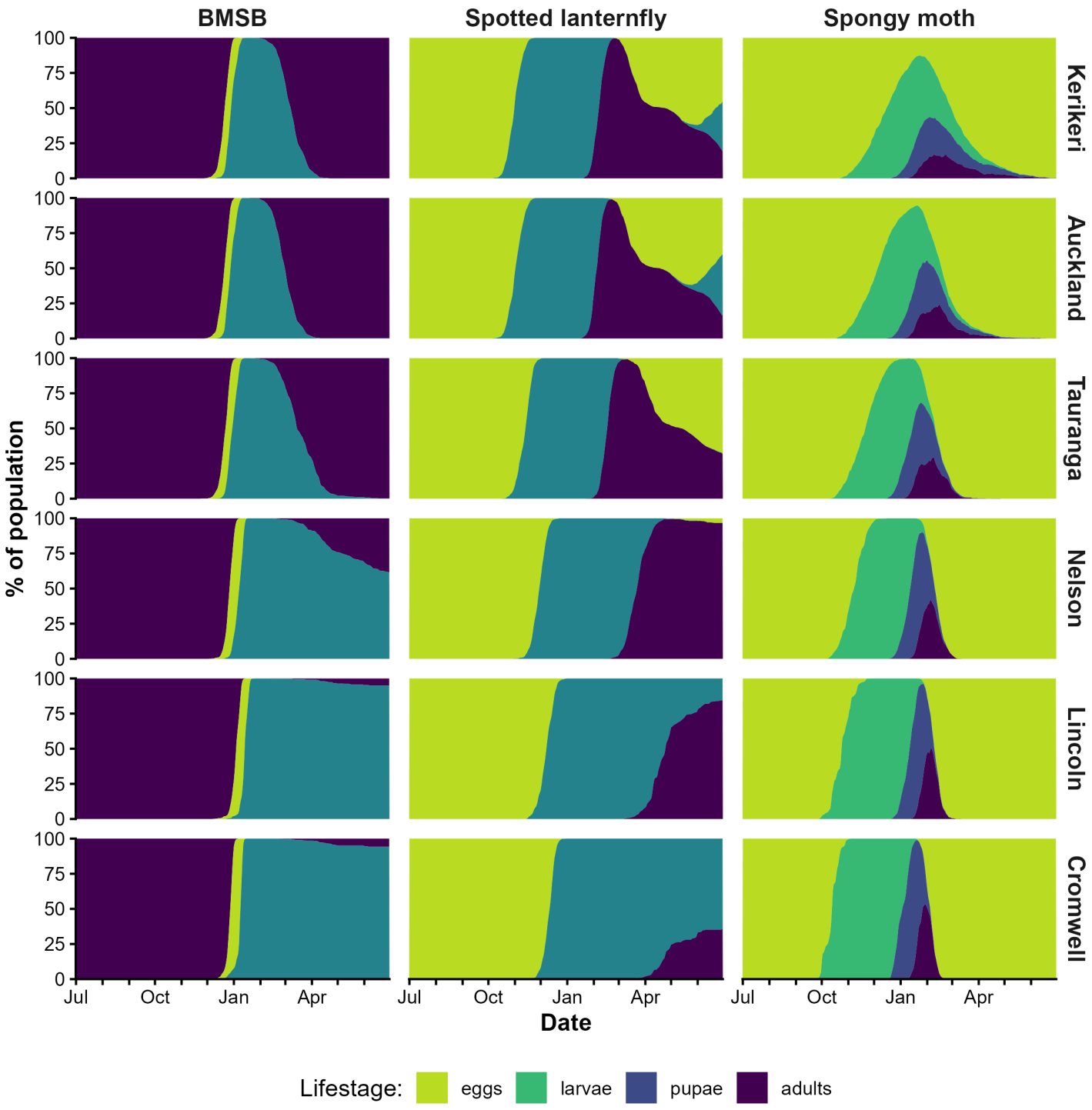


Figure 1

Predicted phenology of each of the three case study species at six New Zealand locations, July 2023 to June 2024. Simulations were initialised as 1000 new diapausing life stages on 1 July (winter).

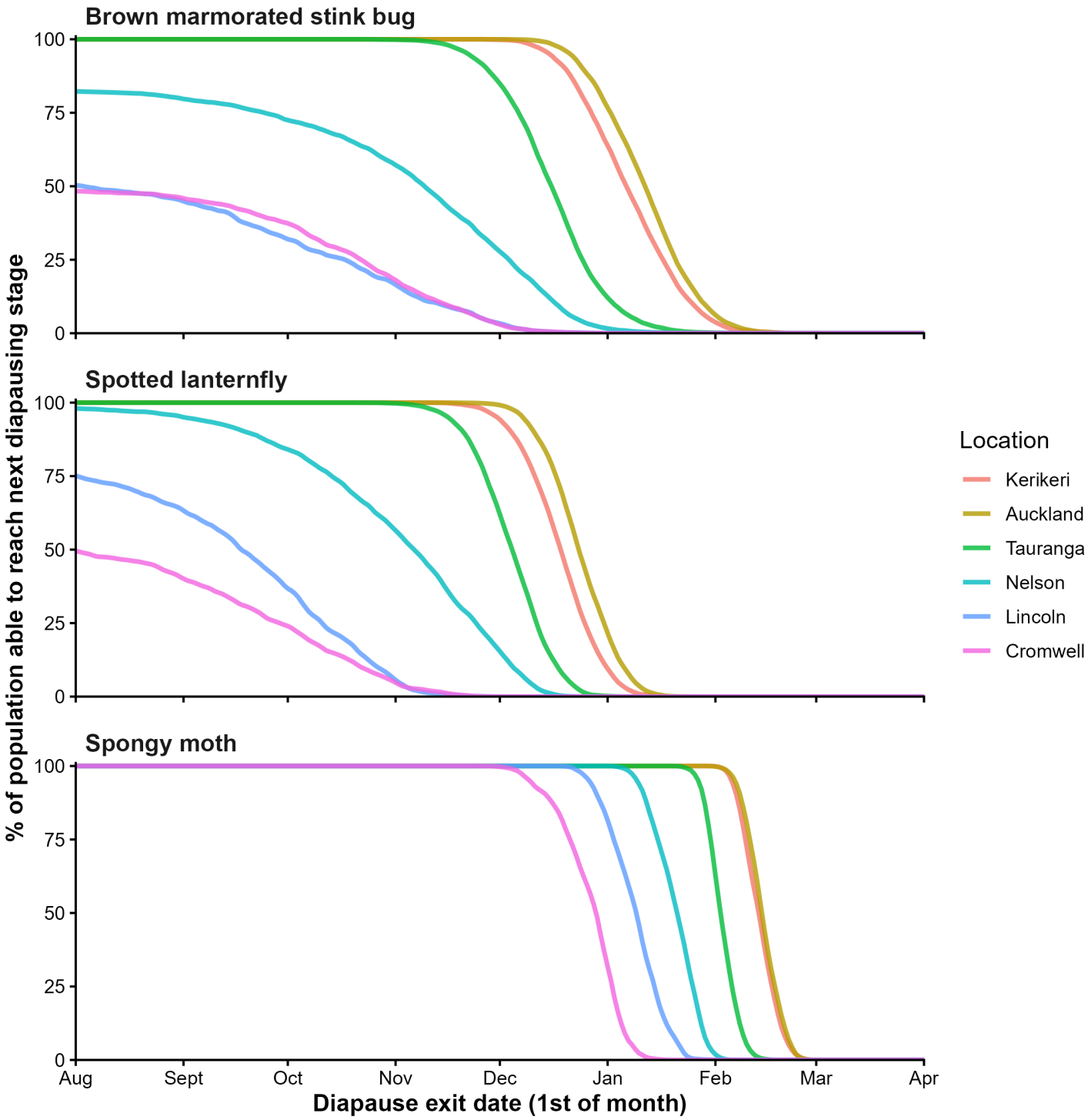


Figure 2

The percentage (y-axis) of each case study species able to reach the next diapausing stage before winter in key locations. Results were obtained from running the phenology model backwards from 1 July and averaged over nine seasons from 2015 to 2024.

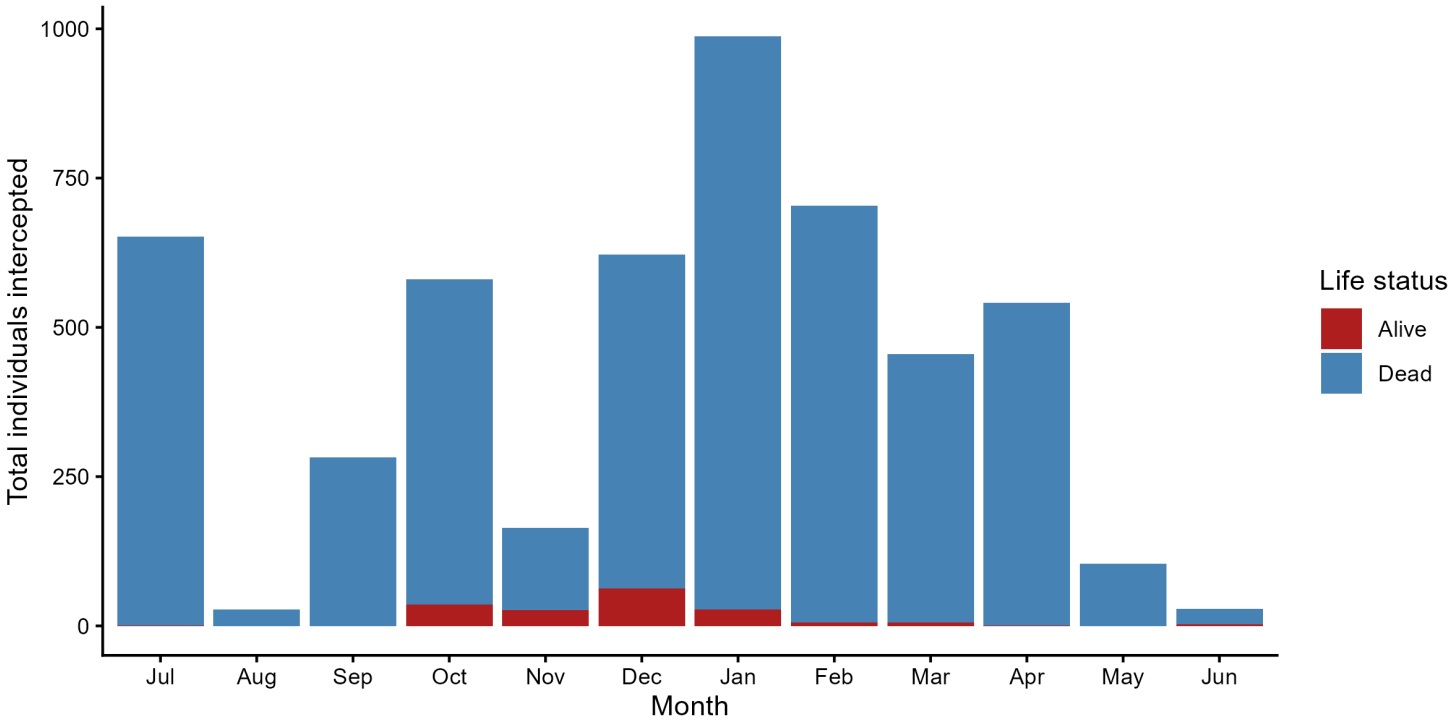


Figure 3

Histogram of recorded border and post-border interceptions of brown marmorated stink bugs in New Zealand from 2022 to 2026.

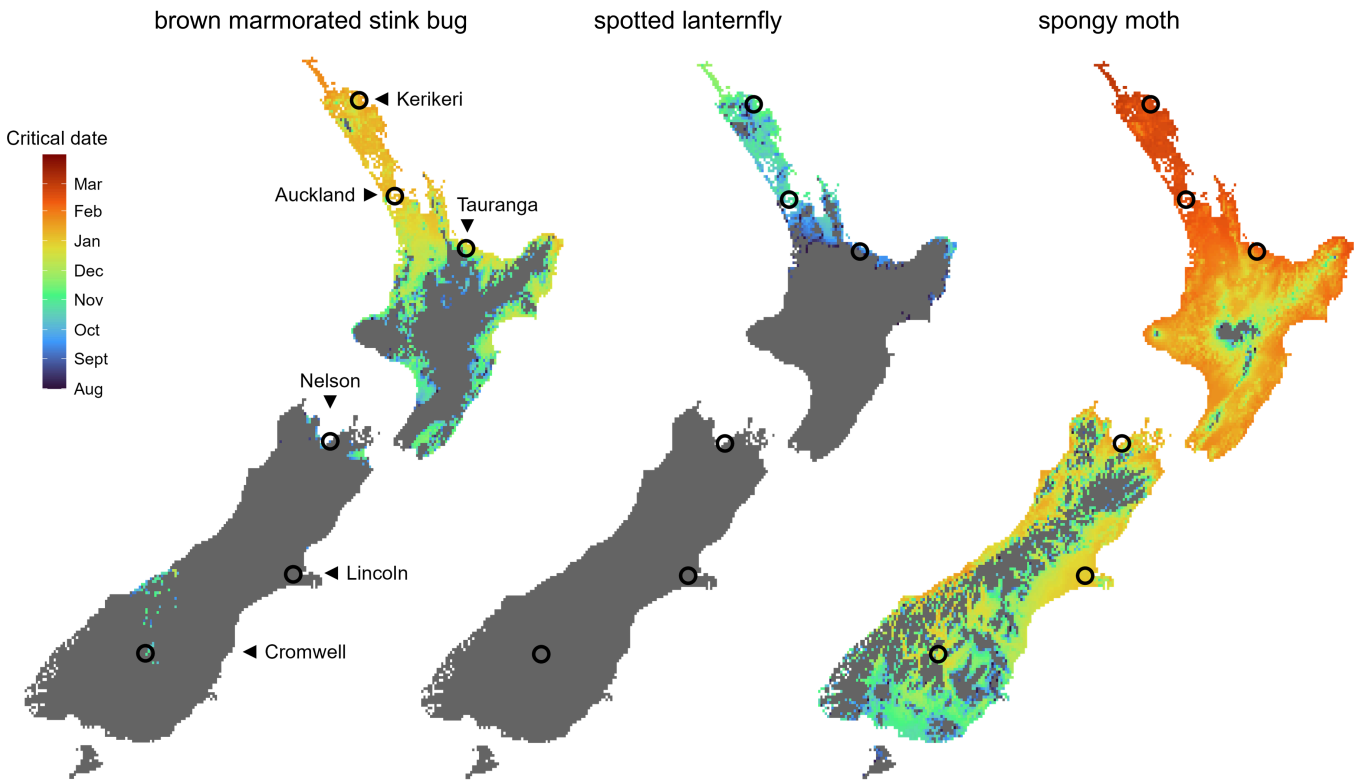


Figure 4

Critical dates for the introduction of each case study species as life stages exiting diapause, being the latest day after which there remains sufficient time to reach the next diapausing stage before mid winter.

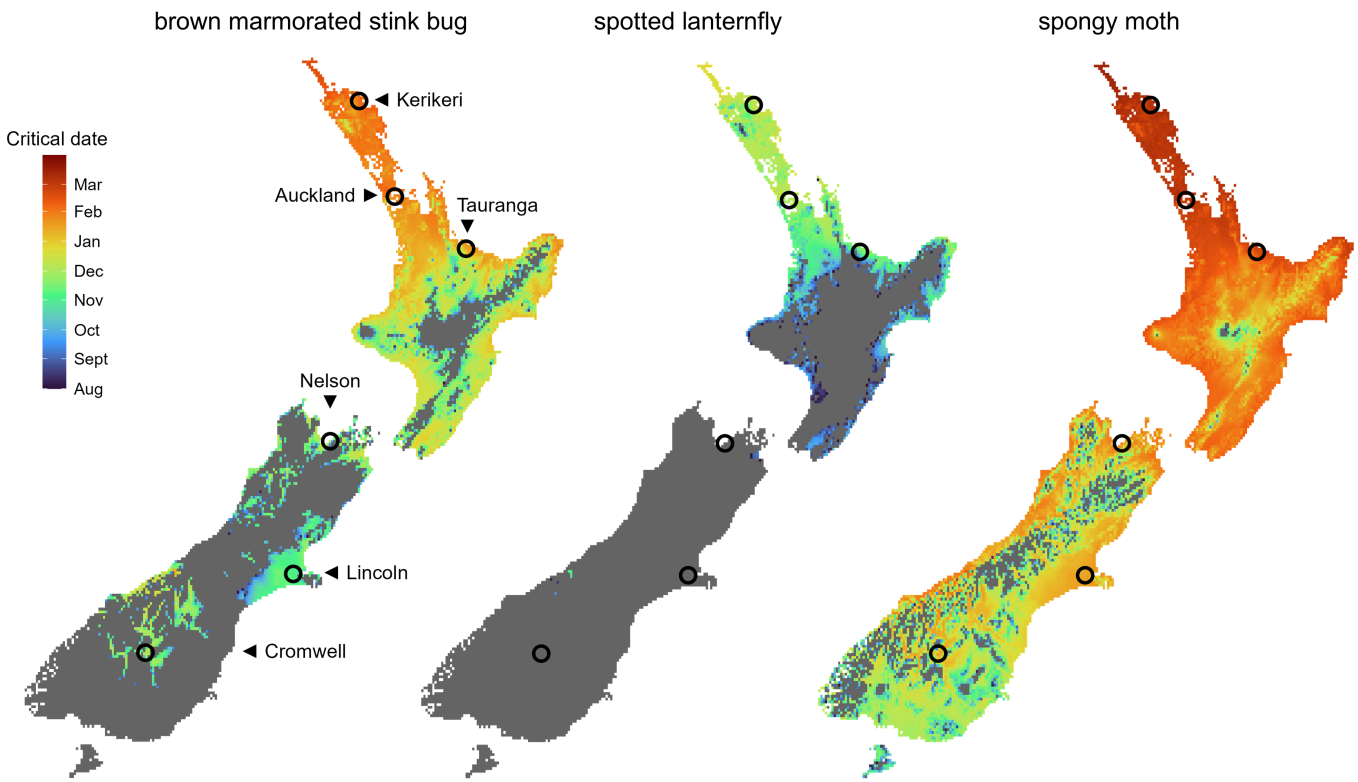


Figure 5

Critical dates under climate change (RCP6.0 in 2090) for the introduction of each case study species as life stages exiting diapause, being the latest day after which there remains sufficient time to reach the next diapausing stage before mid winter.

Supplementary Files

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