

Climate change can reduce the risk of biological invasion by reducing propagule size

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Abstract Climate change has been conclusively linked to species extinctions, and to expansion and contractions and shifts of species ranges. Climate change is exerting similarly profound pressures on the individual stages of biological invasion which can significantly impact the biodiversity and ecology of invaded areas. Propagule pressure is perhaps the single most important determinant of invasion success, but the effects of climate change on propagule pressure are still largely uncertain because we have few observations of introduction events (or their size) that can be analyzed together with climate records. The common surrogate variables for propagule pressure do not logically respond to climate. Here I use a process-based simulation model to examine the potential effects of climate change (specifically temperature) on propagule size of a common invading insect species by estimating in-transit survivorship rate of propagules using historical and future (projected) temperatures and two common trade routes between a donor and a recipient location (Yokohama, Japan and Sydney, Australia). Propagule size (=the number of individuals in an introduction event) was lower under climate change temperatures than under historical temperatures in both routes. The route had significant effects

on propagule size through its influence on the duration (and also the timing) of exposure to temperature conditions that are of time-sensitive importance to the development of the invasive species. Under historical temperatures propagule size was higher and less variable in the direct than the indirect route in 20 independent iterations. Under the future temperatures propagule size was also higher in the direct route but it was more variable than in the indirect route. Increased trade is increasing the opportunities for introductions, but the results reported here suggest that climate change will have inconsistent effects on biological invasion because of the complex relationship between temperature and insect ontogeny.

Keywords Climate change · Biological invasion · Introduction · Propagule pressure · Trade · Asian gypsy moth · Diapause · International trade

Introduction

The overwhelming majority of global trade is carried by sea (Hulme 2009, citing International Maritime Organization, 2008, International Shipping and World Trade: Facts and Figures), and the volume of seaborne cargo increased 35-fold between 1973 and 2007 (Hulme 2009, citing UN Conference on Trade and Development, 2007, Review of Maritime Transport). The distance between new trading partners also

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increased. A consequence of this trend to globalization has been a dramatic increase in the frequency of alien species introduction events (Meyerson and Mooney 2007; Capinha et al. 2015): the increase in transport networks has increased the number of potential sources and destinations for introduction. The annual rate of alien invertebrate introduction events has increased approx. 1200 % since 1900 (Hulme 2009). Propagule pressure [sensu Williamson (1996)] is a composite of the number of discrete introduction events (propagule number) and the number of individuals introduced in any event (propagule size). Establishment (i.e., the existence of a persistent, self-perpetuating population following an alien introduction) has been shown to be dependent on propagule pressure (Colautti et al. 2006b; Lockwood et al. 2009). As global trade continues to increase, the rate of introduction events is expected to continue to increase.

Biological invasion is described (with minor variation) as a multi-stage process: uptake in the native range; transport; introduction; colonization; establishment; spread (Colautti et al. 2006a; Theoharides and Dukes 2007; Hellmann et al. 2008). Climate change is expected to influence one or more of the stages of biological invasion, but the specifics of the changes remain uncertain (Hellmann et al. 2008; Hulme 2016). Many (or most?) authors have focussed on the establishment and spread stages of the process when considering the effects of climate change (Dukes and Mooney 1999; Walther et al. 2009; Hulme 2016). Fewer have attempted to investigate the potential effects of climate change on introduction, despite introduction being an obligatory first hurdle in the invasion process (Hulme 2016). This may be because direct observations of unintentional introductions usually do not exist. Trade volume often serves as a surrogate variable (Kobelt and Nentwig 2008; Bacon et al. 2014; Chapman et al. 2016, others), but trade volume does not logically respond to climate change.

Many of the world's most serious forest pests belong to the Order Lepidoptera in which diapause is a common developmental phase that enables the species to survive adverse environmental conditions such as temperature extremes, drought or the absence of suitable food. These characteristics render insects with diapause well suited to the long distance transport and introduction that occurs with global trade. Conversely, propagule pressure will be reduced in these species if future environmental conditions satisfy the

diapause requirements of a smaller proportion of the transported population (i.e., diapause is “broken” for fewer individuals, and fewer individuals eventually emerge to the larval (feeding) stage).

The Asian gypsy moth (AGM) [*Lymantria dispar asiatica* Vnukovskij and *L. d. japonica* (Motschulsky)] is an example of an alien invasive species whose life cycle includes a diapause period. The AGM is a lepidopteran species that is alien to North America and Australasia. In mid to late summer, mated female AGM are attracted to the artificial lights around Asian ports (Schaefer and Strothkamp 2014) and they lay an egg mass of approx. 400 eggs (Leonard 1981) on the surfaces of vessels and containers, some of which are destined for North America or Australasia. The first detection of AGM in North America occurred in 1989 on a vessel in Victoria, British Columbia, Canada. There have been at least 20 separate introduction events in the United States (USDA APHIS-PPQ 2014a), and 28 vessels entering Canada's Pacific ports were found to have AGM egg masses in 2012.¹ Canada, the United States, New Zealand and Australia expend considerable effort to prevent the introduction of AGM. In North America the threat of introduction is addressed by predeparture inspection of maritime vessels in regulated Asian ports (i.e., where there is a known or suspected AGM population) and inspection of those same vessels upon arrival at a North American port.² Despite these preventive measures, onshore populations have been detected, requiring eradication programs.

Introduction of AGM occurs at the destination when larvae emerge from the egg masses while the ship is in port and they are carried by wind to the nearby shore, or when larvae emerge and disperse from the egg masses on offloaded and contaminated containers. Temperatures during transit and upon arrival must satisfy the alternating temperature preferences of the prediapause, diapause and postdiapause phases (high, low and high temperatures, respectively). Natural variability in developmental response to temperature exists within a population (i.e., faster

¹ L. Humble (Natural Resources Canada, Canadian Forest Service); pers. comm.

² If entering a U.S. port, inspection of these vessels is “mandatory” (USDA APHIS-PPQ 2014b). If entering a Canadian port, these vessels are “subject to inspection” (Canadian Food Inspection Agency 2013).

and slower developing individuals), and the size of the *introduced* population decreases as embryonic development is completed in a smaller proportion of the transported population.

Hellmann et al. (2008) listed several climate change-related hypotheses in biological invasion worthy of testing; among them is “[s]urvivorship of propagules during transport will be enhanced”. Bacon et al. (2014) stated that arthropods remain an understudied taxonomic group in invasion biology. I know of no direct investigation of how climate warming may alter the propagule pressure of a trade pathway by modifying the viability of the individuals transported by the pathway and thereby influencing the number of individuals introduced in each introduction event (propagule size). Here, I use the Asian gypsy moth as a model alien invasive arthropod, and a detailed simulation model of its temperature driven phenological development to examine how climate change (specifically temperature) may affect propagule size through its effects on in-transit survivorship of propagules. Further, I examine how the details of the introduction pathway (vector route from origin to destination) interact with climate to also influence propagule size.

Methods

The insect life cycle

Embryonic development within the oviposited egg begins with the relatively brief prediapause phase in which developmental rate is favored by high temperatures (Gray et al. 1991). Embryos must enter the freeze-tolerant diapause phase (Leonard 1968) before subzero temperatures occur. Developmental rate in the longer diapause phase is favored generally by cold temperatures (Pantyukhov 1964; Gray et al. 2001), but an age-dependent shift in temperature preference has been indirectly observed (Gray et al. 2001) whereby embryos gradually increase their response to warmer temperatures. This has been termed “sensibilization” by Zaslavski (1988). Larvae emerge after completion of a short postdiapause phase in which developmental rate is again favored by high temperatures (Gray 2009). An age-dependent shift in temperature preference has been indirectly observed in this phase also (Gray 2009). The entire embryonic stage lasts approx.

8–9 months under natural conditions. Developmental rates in the larval and pupal stages are favored by high temperatures and adults survive only a few days (Fig. 1).

The phenology model

The viability of a poikilothermic population can be examined by a phenology model: a model that simulates developmental progress through the life cycle in response to temperature. The Gray–Logan–Sheehan Gypsy Moth Life Stage (*GLS*) phenology model has been completely described in Gray (2004), but a brief description is given here. The *GLS* model is a composite model assembled from the published literature; it encompasses the complete gypsy moth life cycle: embryonic development (including separate prediapause, diapause and postdiapause phases) leading to egg hatch; larval and pupal development; and adult oviposition of the next generation. The natural variability in a population is represented in *GLS* in two ways by necessity. Developmental rate in the embryonic stage has been determined to be nonlinearly temperature- and age-dependent; i.e., the nonlinear rate functions undergo change during the diapause and postdiapause phases as phenological development progresses (Gray et al. 2001; Gray 2009). Developmental variability in the population during the embryonic stage is, therefore, represented by rate classes (500 classes from slowest to fastest developers) so that the age of each rate class is known at each time-step of the model simulation; developmental response of each rate class to a given temperature is then influenced by the temperature and the age of the rate class. The relative abundance of each rate class in the model corresponds to empirical observations of the frequencies of prediapause, diapause, and postdiapause durations (Gray et al. 2001; Gray 2009). Developmental rate in the post-hatch life stages is strictly nonlinearly temperature-dependent. Therefore, developmental variability in the post-hatch life stages is simulated by the more computationally efficient “distribution model” (Sharpe et al. 1977) which uses a mathematical function to approximate the empirically observed frequency distribution of each life-stage duration. The *GLS* model has been used to estimate risk of establishment, given an introduction, based on climatic suitability: the probability that the inter-annual climatic variability satisfies the life cycle requirements. Simulations in *GLS*

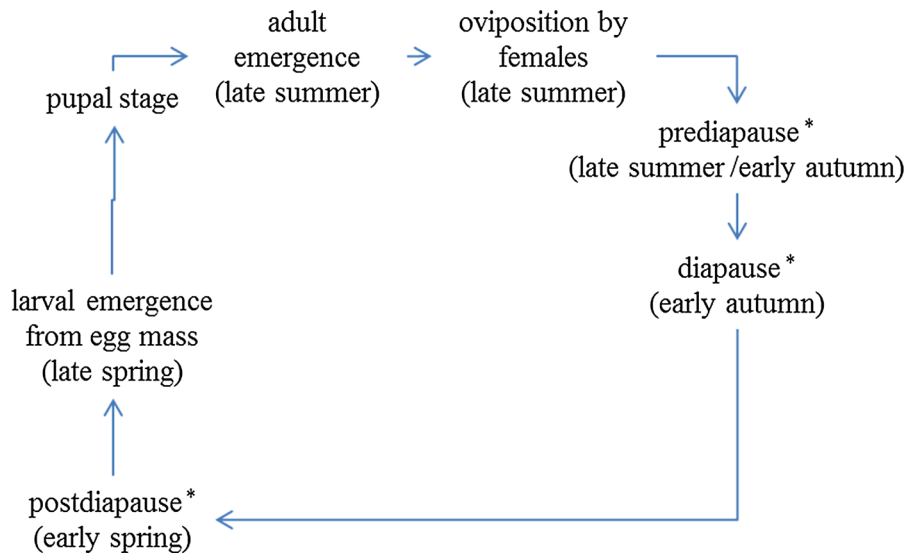


Fig. 1 Life cycle of the Asian gypsy moth with approx. time periods for the different life stages under natural conditions (i.e., when individuals do not experience an unnatural temperature regime as they might with long-range transport). *Embryonic stage

are done at individual point locations—thousands, if desired—and establishment risk is mapped based on the estimated climatic suitability from the individual points. *GLS* has been used to estimate establishment risk based on climatic suitability of the locations in British Columbia, Canada (Régnière and Nealis 2002), Utah, USA (Logan et al. 2007), New Zealand (Pitt et al. 2007, but see Gray 2014), and Canada (Gray 2004; Régnière et al. 2009). *GLS-2d* is a simple extension in which the location of a modelled population moves according to the schedule of the ship that carries it, and the population, therefore, experiences a series of 1 day exposures to the temperatures of the daily locations (Gray 2015).

The objective of the simulations described here was to determine the potential effect of future climate on survivorship of propagules, specifically during transit. Therefore, each iteration was initiated by simulating the oviposition pattern in Yokohama, Japan using a temperature regime from the historical port database (see below for a description of all databases). *GLS-2d* then “placed” one cohort of eggs on a ship on each day of a 7d (30 June–6 July) port visit to Yokohama. The relative sizes of the seven cohorts reflect that 7d portion of the simulated oviposition pattern (rising then falling oviposition frequency) that occurred during the port visit. Cohort sizes were altered by a uniform factor to sum to 1.4 million eggs oviposited on the ship. The actual number is not important; but

1.4 million allows easy division into the seven cohorts (1 per day), and division of each cohort into the multiple, slow to fast, developmental rate classes (Gray 2004). Cohorts vary in size, but each cohort has the same relative proportion of slower and faster developing individuals. The ship with its egg cohorts was replicated (four replicates) and the replicate ships departed 7 July, two on each of two routes to Sydney, Australia (described below). After departure from Yokohama the cohorts on one ship of each route experienced temperatures from the historical database and cohorts on the other experienced temperatures from the future (projected) database. Twenty independent iteration were simulated. Each iteration used a different temperature regime from the 20-y database of historical Yokohama temperatures to produce a unique oviposition pattern, and a different en route temperature regime from the 20-y database of historical or future temperatures.

The routes between Yokohama and Sydney

Two maritime routes were examined for their potential to introduce AGM populations from Japan to Australia (Fig. 2) under historic climate conditions and under a future climate scenario (see below for a description of the temperature scenarios). The “direct route” is a 14-d transit from Yokohama to Sydney (7 July–21 July). The “indirect route” is an 11-d transit to

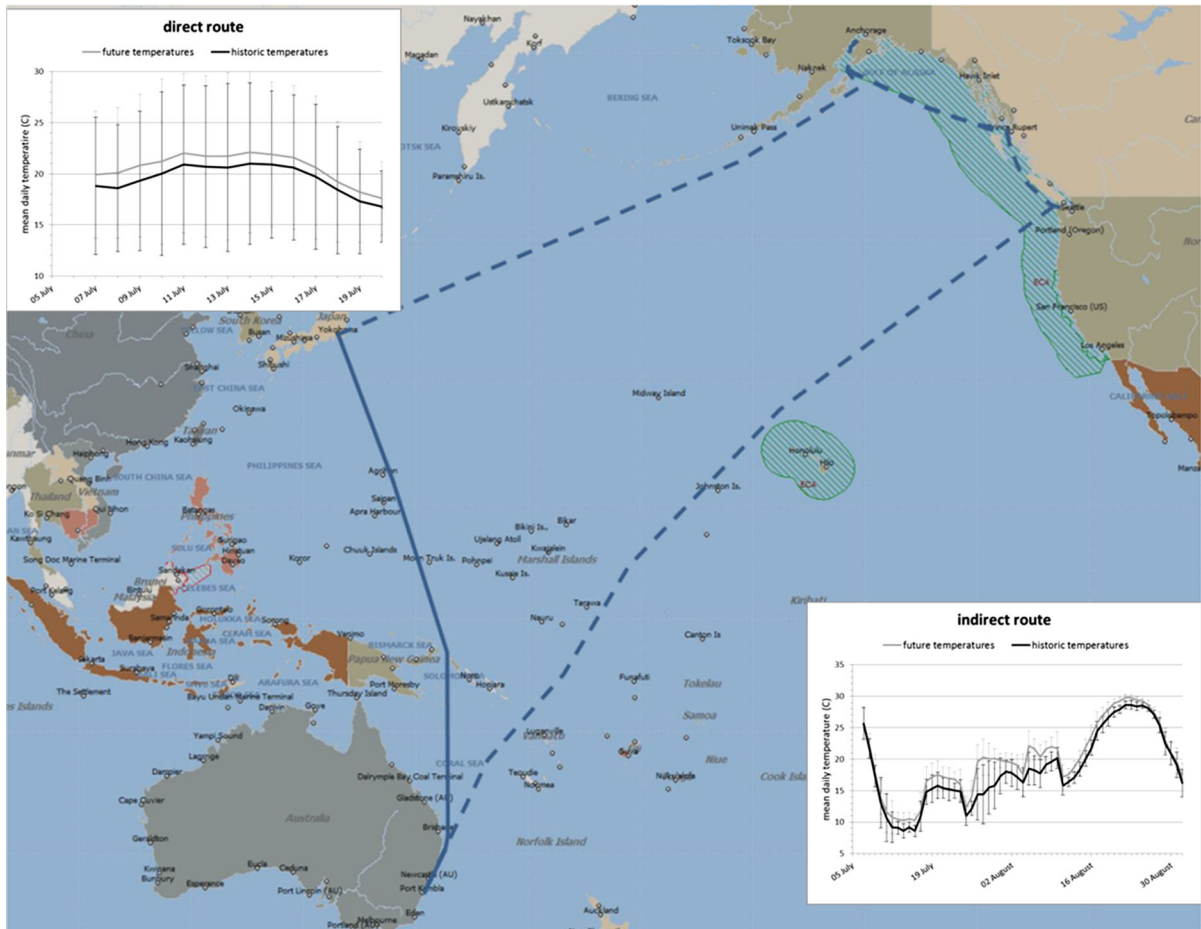


Fig. 2 A direct and an indirect maritime trade route between Yokohama, Japan and Sydney, Australia. *Insets* show the mean \pm S.E. ($n = 20$) of the average daily temperatures ($(T_{\max} + T_{\min})/2$) for each Yokohama-Sydney route

Anchorage, USA (with a 6-d port stay), then a 3-d transit to Kitimat, Canada (with a 6-d port stay), then a 2-d transit to Vancouver, Canada (with a 5-d port stay), then a 22-d transit to Sydney (7 July–1 September).

Temperature databases and simulation protocol

GLS-2d (and *GLS*) can produce real-time predictions of phenological development (i.e., up to the day of the simulation run) if up-to-the-day temperatures are available. However, maintaining such a database on the global scale necessary for *GLS-2d* simulations is not practical. Therefore, instead, *GLS-2d* uses a built-in database of the most recent 20 years of daily minimum and maximum temperatures for a collection of Asian, North American and Australasian ports

(users can add to the port database), and of estimated daily minimum and maximum near-surface atmospheric temperatures of 6143 maritime locations (2.81° latitude \times 2.81° longitude grid). The maritime database was obtained from the third-generation coupled global climate model (CGCM3) of the Canadian Centre for Climate Modelling and Analysis³ running a IPCC SRES A1B1 scenario. A 20-y database of future (projected 2046–2065) minimum and maximum daily temperatures was downloaded from the SRES A1B1 scenario of the CGCM3. Future port temperatures were estimated by calculating the average monthly changes between the 2046–2065 and the 2001–2020 estimated minimum and maximum

³ <http://www.cccma.ec.gc.ca/data/data.shtml>;

accessed December 13, 2013.

temperatures of the nearest CGCM3 simulation point, and adding the monthly changes to the historic daily minimum and maximum temperatures of the port.

Phenological development of each onboard cohort begins in *GLS-2d* on the day that the cohort is “placed” on the ship. Phenological development is advanced hourly by a sine wave approximation (Allen 1976) of temperatures from the daily minimum and maximum temperatures of the port database (the days the ship is in a port) and the maritime database (the days the ship is between ports). Between ports, the daily positions of the ship are calculated by interpolating a great-circle path between each of the port-to-port waypoints retrieved from the web-based database of NetPas Distance,⁴ and the temperatures of the nearest location in the maritime database are used. Netpas Distance has more than 12,000 ports worldwide and more than 72 million waypoints describing the routes and transit times between the ports. Phenological development is advanced by the temperatures of the destination port (Sydney) from the date of arrival until larval emergence is completed.

GLS-2d outputs the embryonic survival rate of the onboard population and the temporal pattern of larval emergence at the destination port from each iteration of each climate \times route combination. Each iteration is considered an equally likely outcome ($p = 0.05$). In order to illustrate the range and variability in survival rate from the 20 iterations of each combination, and to compare survival rates among the four combinations, survival rate within each combination is presented as a cumulative frequency distribution [$p(\text{survival rate} \leq x \%)$]. The earliest predicted emergence pattern from the 20 iterations of each climate \times route combination is also presented to compare with the scheduled ship arrival in Sydney (21 July or 1 September) via the two routes.

Results

For the transit days of the direct route, future daily minimum and maximum temperatures were an average 1.064 and 1.061 °C warmer, respectively than historical daily minimum and maximum temperatures.

For the transit days of the indirect route (via Anchorage), future daily minimum and maximum temperatures were an average 1.179 and 2.156 °C warmer, respectively than historical daily minimum and maximum temperatures (Fig. 2).

Under historic temperatures there was a $p = 0.8$ of an onboard embryonic survival rate of $>80 \%$, and a $p = 0.5$ of a survival rate $>95 \%$ in the direct route simulations. In the indirect route simulations (under historic temperatures) there was a $p = 0.95$ of a survival rate $\leq 80 \%$, and survival rate was never $>87 \%$. Under future temperatures there was a $p = 0.35$ of $>40 \%$ and $p = 0.95$ of $>30 \%$ embryonic survival in the direct route simulations. In the indirect route simulations (under future temperatures) there was a $p = 1.0$ of a survival rate $\leq 40 \%$, and a $p = 0.95$ of $\leq 30 \%$ survival. Embryonic survival rate was higher under historic temperatures than future temperatures with both routes (Fig. 3).

Embryonic survival rates of the onboard populations from the 20 iterations of each climate \times route combination were not normally distributed. Therefore estimated means and standard deviations are not strictly appropriate descriptors. Nonetheless, they illustrate gross differences among the combinations. Embryonic survival was higher with the direct route than the indirect route under both historic (means: 90.8 vs. 62.5 %, respectively) and future temperatures (means: 43.2 vs. 17.5 %, respectively). Variability in survival rate among the 20 iterations was higher with the indirect route (s.d. = 13.0 %) than the direct route (s.d. = 8.1 %) under historic temperatures, but higher with the direct route (s.d. = 11.8 %) than the indirect route (s.d. = 9.1 %) under future temperatures (Fig. 3).

The differences between embryonic survival rates (direct route $>$ indirect route; and historic climate $>$ future climate) are mostly attributable to differences in diapause completion in the two routes and two temperature regimes. Under historic temperatures diapause was successfully completed by 91 and 63 % of individuals in direct route and indirect route simulations, respectively (Fig. 4). Under future temperatures a combination of higher diapause and postdiapause completion rates in the simulations of the direct route than of the indirect route (diapause: 43 vs. 18 %; postdiapause: 99 vs. 90 %) contributed to a higher embryonic survival rate (Fig. 4).

⁴ Netpas Webservice 3.0. http://netpas.net/products/product_detail_DE_EN.php.

Fig. 3 Cumulative probability of percent embryonic survival rate [$p(\text{survival rate} \leq x\%)$] of the onboard population from the 20 iterations of each combination of a Yokohama to Sydney route (direct and indirect) and climate regime (historic and projected future). For example, the dotted line illustrates that $p(\text{survival rate} \leq 60\%) = 0.6$ in the historic climate/indirect route combination

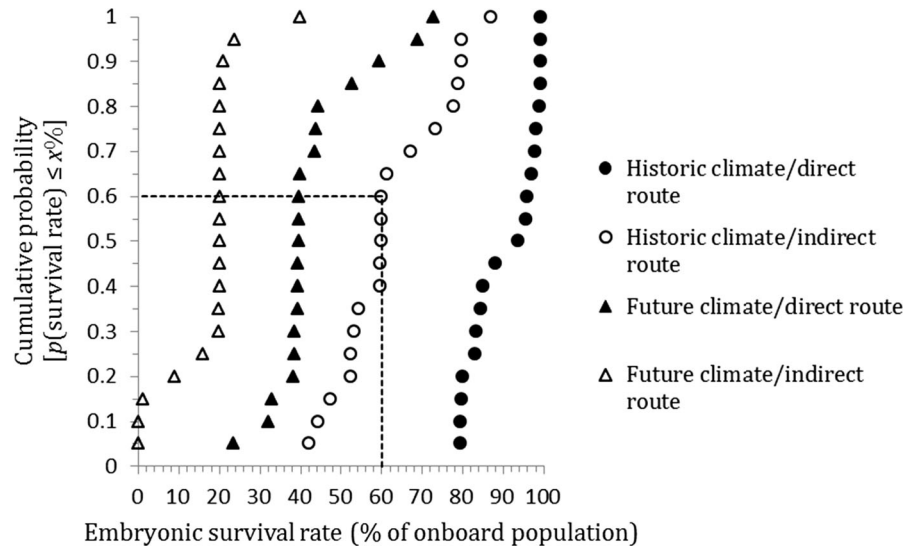
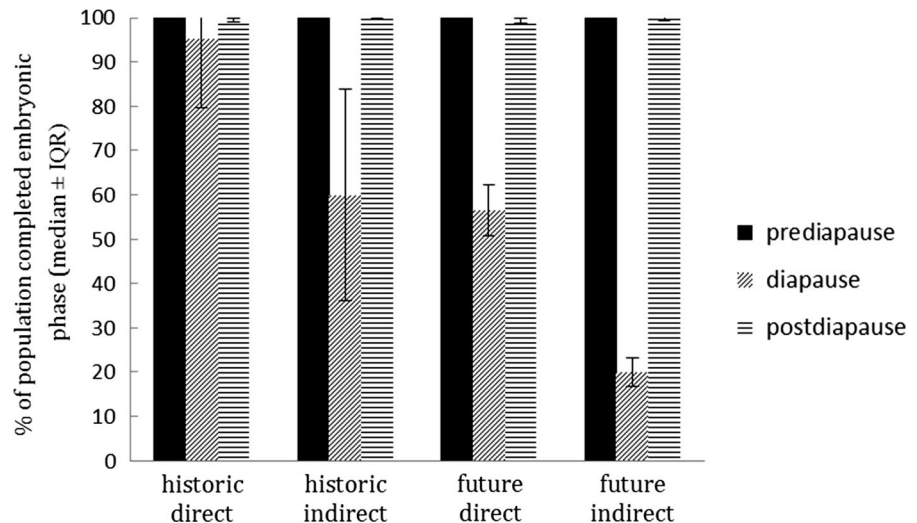


Fig. 4 Mean percent completion rate (\pm s.d.) of embryonic developmental phases (prediapause, diapause and postdiapause) of onboard populations on two Yokohama to Sydney routes (direct and indirect) under two climate regime (historic and projected future); $n = 20$

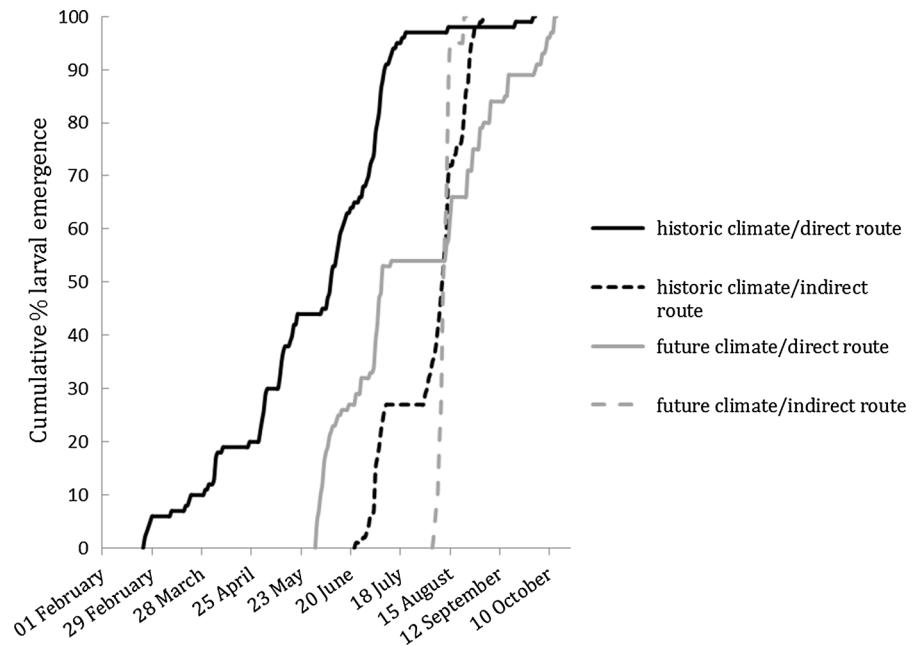


None of the combinations of temperature regime \times route described here poses a threat of AGM introduction via ballooning of emerging larvae while the vessel is in Sydney. Vessel arrival in Sydney on 21 July (and a likely departure approx. 1 week later) precedes the earliest predicted larval emergence in any of the simulations by 211d (Fig. 5). However, embryonic survival rate in egg masses on offloaded containers is >0 in 80 % of the indirect route simulations under future temperatures, and is >23 in 100 % of the simulations of the three other route \times temperature combinations.

Discussion

Propagule pressure is defined as the absolute number of individuals introduced *and* the number of separate introduction events. Williamson (1996) may have been the first to stress the importance of propagule pressure as a predictor of invasion success. In a later meta-analysis Colautti et al. (2006b) found that propagule pressure was positively associated with the establishment of successful invaders in 13 of 15 cases; and importantly, that no other characteristic was consistently associated with successful invaders.

Fig. 5 Earliest predicted cumulative (%) larval emergence of an onboard population from the 20 iterations of each combination of a Yokohama to Sydney route (direct and indirect) and climate regime (historic and projected future)



Increased global trade has been linked to increases in biological invasions (Meyerson and Mooney 2007; Ricciardi 2007; Hulme 2009) principally through increases in introduction frequency (i.e., the number of separate introduction events). Further increases in trade will likely increase the frequency of alien introduction events still more (Levine and D'Antonio 2003). But we know little about how future climates may affect future introductions (Hulme et al. 2008; Chapman et al. 2016) through its effect on propagule size (the number of individuals introduced *per introduction event*).

Authors have relied on a surrogate variable in place of propagule pressure when investigating the effects of climate change on invasion biology (Cassey et al. 2004; Bacon et al. 2014; Brockerhoff et al. 2014), probably because direct observations are seldom made of accidental introductions. However, introduction is the obligatory first step in the invasion process (Hulme 2016), and propagule pressure is arguably the most critical factor in invasion success. Chapman et al. (2014) argue persuasively that process-based models are a critical addition to the study of invasion biology under climate change because such models include estimates of the ecological processes that will determine future invasion success. *GLS* (and the *GLS-2d* extension) is such a process-based model. The temperature-dependent duration of the embryonic

stage of *Lymantria dispar* confounded researchers since at least 1913 (Sanderson and Peairs 1913). The duration of the embryonic stage (and, therefore, the time of larval emergence from the egg) is probably the most critical life cycle event in establishing appropriate synchrony with the environment (Gray 2004). Gray et al. (1991, 1995, 2001) used the respiration rates of many thousands of individual embryonic larvae to separate the embryonic phases and estimate temperature- and age-dependent relationships for phenological developmental rates. Unfortunately, the age-dependence of the relationships (i.e., the developmental response to temperature shifts as phenology progresses) makes a general statement about the effect of high or low temperatures on embryonic development impossible—the response to any given temperature depends on the age of the individual which is itself dependent on all the preceding temperatures to which the individual has been exposed. This complexity also make it impossible to generalize the effects of climate change on propagule size when the propagules are transported vast distances and experience a temperature regime unlike any that occurs naturally in one location. A process-based model, such as *GLS-2d*, is required to simulate the interacting effects of climate change and vector route (with its specific temperature regime) on survival rate of transported propagules. The routes presented in this

study were chosen without any pre-existing information of how propagule size would be affected under the two climate regimes. They indicate that propagule size (and therefore invasion success) will be adversely affected by climate change in these trade routes (Fig. 3). They also indicate that future increases in introduction events (from increased trade) may be partially offset by a reduction in propagule size (the number of individuals introduced per event) for some species under future climates. However, they should not be used to make statements regarding how climate change will affect propagule size on trade routes generally.

Climate change will likely have a effect also on establishment of successfully introduced propagules. The climatic suitability (=the geometric mean of intergenerational survival that is due solely to phenological considerations) of Sydney for gypsy moth will diminish from 0.997 under historic temperatures to 0.775 under the future temperatures used here (data not presented).

The mechanism by which climate change may negatively affect survival is not necessarily the same for all diapausing species. For example, Régnière et al. (2012) suggest that a northward expansion of *Choristoneura fumiferana* (Clemens) will be limited under climate change because the warmer winter temperatures will prolong the non-feeding diapause period (by slowing developmental progress) while simultaneously increasing the metabolic rate, resulting in mortality from an exhaustion of overwintering energy reserves before diapause is broken. Regardless of the specifics of the mechanisms, species with diapause are generally well suited to the long distance transport and introduction that occurs with global trade. And it seems clear that detailed process-based phenology models such as *GLS*, that encompass the entire life cycle of a species are useful tools when we wish to predict the potential effect(s) of climate change on the introduction rate and establishment success of invasive species (diapausing or non-diapausing). Contrary to Sutherst's assertion that "climate change *per se* is likely to have limited direct effects on movement of invasive species along trade routes" (Sutherst 2000: 219), this study illustrates that climate change will directly affect the survival rate of transported alien species populations: propagule pressure is affected.

Conclusions

Invasions of alien species can significantly impact the biodiversity, ecology and economy of invaded areas (Liebhold and Tobin 2008), and human-mediated movement of species is an increasingly important factor in defining species distribution (Capinha et al. 2015). Walther et al. (2009, Fig. 1) hypothesized that a future (warmer) climate "facilitates transport through... higher intensity and/or frequency of extreme events". The results presented here support only a portion of that hypothesis: a future climate (with its extreme events) will produce greater variability in embryonic survivorship of transported populations, but only in the case of the direct route (Fig. 3). In the case of the indirect route, the future climate reduces the variability in embryonic survival. And in both the direct and indirect routes, average survivorship is lower in a future climate. Walther et al. (2009, Fig. 1) also hypothesized that the warmer climate "enables successful reproduction and establishment". But the evidence reported here, and elsewhere (Gray 2004; Régnière et al. 2012), suggests that in areas with warm winter temperatures, higher winter temperatures will reduce intergenerational survival of a diapausing insect: likelihood of establishment will be lower. These results indicate that we may be unable to make general conclusions regarding the effect(s) of climate change on biological invasion. A fuller, more detailed understanding of the effects of climate change, trade and trade routes is an important addition to efforts to minimize the negative impacts of biological invasion.

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