

LETTER

Synchrony's double edge: transient dynamics and the Allee effect in stage structured populations

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Abstract

In populations subject to positive density dependence, individuals can increase their fitness by synchronizing the timing of key life history events. However, phenological synchrony represents a perturbation from a population's stable stage structure and the ensuing transient dynamics create troughs of low abundance that can promote extinction. Using an ecophysiological model of a mass-attacking pest insect, we show that the effect of synchrony on local population persistence depends on population size and adult lifespan. Results are consistent with a strong empirical pattern of increased extinction risk with decreasing initial population size. Mortality factors such as predation on adults can also affect transient dynamics. Throughout the species range, the seasonal niche for persistence increases with the asynchrony of oviposition. Exposure to the Allee effect after establishment may be most likely at northern range limits, where cold winters tend to synchronize spring colonization, suggesting a role for transient dynamics in the determination of species distributions.

Keywords

Conspecific attraction, *Dendroctonus frontalis*, ecophysiological model, insect pest, phenology, positive density dependence, seasonality, species range.

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INTRODUCTION

Recent interest in positive density dependence and the Allee effect has increased our appreciation of its ecological and evolutionary consequences, especially the potential for deterministic extinction in small populations (Courchamp *et al.* 1999; Stephens & Sutherland 1999). Decreasing survival or reproduction at low population density selects for life history traits that increase an individual's rate of interaction with conspecifics. Spatial aggregation, for instance, inflates local density (Reed & Dobson 1993). When success at particular life stages is positively density dependent, individuals can also improve their fitness via temporal aggregation (i.e. phenological synchrony). Mate-finding is a common example of a positively density dependent process (Allee 1931) that might occur only during a limited period of reproductive activity determined by an organism's behaviour, phenology, or physiology. Individuals improve their chance of finding a mate by entering reproductive activity at the same time as potential mates, inflating realized population density (Calabrese & Fagan 2004). Phenological synchrony (the focus of this study, not to be confused with the synchrony of population

dynamics across space) also increases individual fitness when Allee effects arise from other stage-specific mechanisms, such as predation risk (Stephens & Sutherland 1999; Peacor 2003) or cooperative host exploitation (Berryman *et al.* 1985; Clode 1993; Logan *et al.* 1998).

While phenological synchrony might improve a population's ability to overcome the challenge of an Allee effect, too much temporal aggregation can be maladaptive. For instance, a decline in individual fitness at high population density should select for some degree of asynchrony via negative frequency dependence (Iwasa & Levin 1995). Also, environmental stochasticity, such as detrimental weather events, can favour asynchrony as a bet-hedging strategy (Iwasa & Levin 1995; Simons & Johnston 1997; Post *et al.* 2001; Satake *et al.* 2001). The costs and benefits associated with synchrony suggest a model of stabilizing selection on phenology. However, phenology, even if highly heritable, may vary from year to year due to environmental effects (Post *et al.* 2001; Winterer & Weiss 2004), with demographic consequences. Hence, understanding the causes and consequences of synchrony are relevant to understanding short-term population dynamics and the ultimate causes of seasonal phenology.

A cost of phenological synchrony that has received little attention is its potential to induce large fluctuations in density, subjecting positively density dependent populations to the risk of extinction. Synchrony can be thought of as a disturbance away from the stable age or stage distribution, shifting the population into transient dynamics that are likely to include oscillations in density (Hastings 2001, 2004). Given positive density dependence, troughs of low abundance during transient dynamics will produce periods of reduced population growth or even yield deterministic extinction. Consider an insect population that completes several generations per year beginning with adult emergence in the spring. Assume that adult reproductive success is positively density dependent such that a threshold abundance of adults is necessary to achieve replacement (Courchamp *et al.* 1999). At sufficient adult mortality rates, a synchronous cohort will decline below critical threshold density before juveniles mature, thereby disrupting the continuity of sustainable population growth (Fig. 1, solid curves). In contrast, asynchronous emergence creates a temporal rescue effect (*sensu* Brown & Kodric-Brown 1977). Late-emerging adults replenish the declining population and maintain critical population density between cohorts (Fig. 1, dashed curves). In these circumstances, synchrony should only threaten population growth when two conditions are met; first that expected adult lifespan is shorter than the time required for development through juvenile stages and,

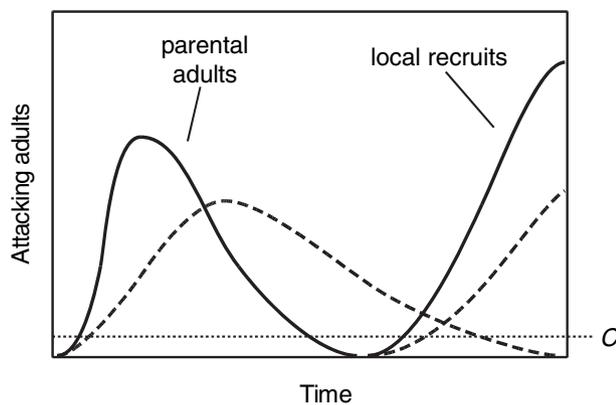


Figure 1 The concept of population continuity. An adult life history event, such as mating activity or the mass-attack of a host, occurs with some degree of synchrony, creating a distribution of adult density in time. After a period of juvenile development, local recruits emerge as adults. Due to parental mortality, adult population density decreases between cohorts. Under positively density dependence, the population faces extinction risk when adult density declines below a critical threshold, C (solid curve). While a less synchronous parent population (dashed curve) achieves a lower maximum density and takes longer to reach that maximum, adult density remains continuously above C between generations.

second, that the adult population is small enough to become rare. Hence, factors affecting adult survival, such as predation and host resistance, may induce a cost to synchrony in small populations. Likewise, population continuity may be disrupted if juvenile development is prolonged by stress (Winterer & Weiss 2004), such as competition or low nutrient supply, or (for ectotherms) by temperature.

The effects of temperature on poikilothermic populations suggests a strong influence of climate and climate change on species distributions (Logan *et al.* 2003). Recent studies have examined the role of temperature-dependent phenology alone (Chuine & Beaubien 2001; Logan & Powell 2001; Hicke *et al.* 2006) or phenology in combination with mortality (Ungerer *et al.* 1999; Crozier & Dwyer 2006; Tran *et al.* 2007) in determining current and future limits to species ranges. The complexity of applying ecophysiological models to biogeographic scales has encouraged studies to simplify population dynamics down to the core dichotomy of long-term persistence (fitness ≥ 1) vs. extinction (fitness < 1). This simplification can aid in understanding factors that influence the ecology and evolution of species at large temporal and spatial scales (Holt & Keitt 2005) at the expense of potentially important detail on short-term dynamics. Here, we investigate the role of climate, synchrony and mortality in determining the short-term transient dynamics of a stage structured population using an ecophysiological model for the mass-attacking southern pine beetle, *Denroctonus frontalis* Zimmermann (Coleoptera: Curculionidae). We focus on the persistence of an established infestation via threshold aggregation behaviour. We find that an increase in either cohort synchrony or adult mortality promotes discontinuity in adult population size between cohorts. We also find that population continuity is positively density dependent. Transient dynamics during the growth season are more sensitive to synchrony at the northern range limit than in the range interior. Our findings rely on common aspects of population biology and suggest a general expectation for geographic variation in the influence of transient dynamics on the persistence of populations subject to Allee effects, especially those relying on conspecific signals for habitat selection.

MODEL ORGANISM

Bark beetles are prime examples of seasonal organisms subject to positive density dependence. Populations can persist at low density through the use of weakened or susceptible hosts (Wallin & Raffa 2004), such as lightning-struck trees (Coulson 1980; Flamm *et al.* 1993). At higher densities, bark beetles can switch to an aggressive strategy for overwhelming healthy hosts (Wallin & Raffa 2004). The initiation of local infestations is a strongly positively density

dependent process; beetles must attack *en masse* to overcome a tree's chemical defenses (Raffa & Berryman 1983; Berryman *et al.* 1985, 1989). High attack densities are achieved by behavioural responses to aggregation pheromones (Gara *et al.* 1965; Payne 1980; Pureswaran *et al.* 2006). Models of bark beetle infestation dynamics suggest that the proportion of individuals locating a host increases with population density (Byers 1996) and with the synchrony of adult emergence (Logan *et al.* 1998). The synchrony of bark beetle populations is influenced by nonlinear temperature effects on juvenile development rate (Jenkins *et al.* 2001), and can vary annually depending on climatic events (e.g. Logan & Powell 2001). Synchrony is a good predictor of outbreaks in the univoltine mountain pine beetle, *Dendroctonus ponderosae* (Powell & Logan 2005). However, the consequences of synchronized spring emergence have not been examined in multivoltine bark beetles, or more generally for seasonal organisms that complete several generations per year.

The multivoltine southern pine beetle, *D. frontalis* (hereafter, SPB) is an ideal system for examining the interplay of synchrony and population continuity. Most local SPB infestations begin in the spring (Thatcher & Pickard 1964; Coulson *et al.* 1999) and continue to grow through three to six generations of beetles (depending on climate, Thatcher & Pickard 1967; Ungerer *et al.* 1999) until the next spring. Individual host trees are overwhelmed by mass attacks involving hundreds to thousands of beetles (e.g. 62–128 attacks m^{-2} on the bark surface, Veysey *et al.* 2003; 100–1900 attacks m^{-2} , Coulson 1980). Local infestations are initiated and maintained over time by an aggregation pheromone released by attacking adults (Coulson 1980; Payne 1980). If the number of active attacking adults becomes low enough, the pheromone plume fails to enforce the philopatry of local recruits (Gara 1967) and the local infestation goes extinct. Although emigration likely incurs reduced survival and reproduction, our reference to extinction is restricted to the collapse of a local infestation; offspring may locate other growing infestations or weakened hosts. The beetles' threshold behavioural response to pheromone is considered essential to a common method for controlling infestations, called cut-and-leave, that removes or diminishes the pheromone plume by felling trees under active attack by adults (Billings 1980). The disruption of population continuity may also result from natural processes. As with other *Dendroctonus* species, SPB lack an overwintering diapause stage. Winter populations are dominated by eggs and larvae (Beal 1933), but will include later stages in warm climates (Thatcher & Pickard 1967). Recent observations at the northern range limit, in southern New Jersey, suggest a threshold for pupation at low temperature that causes overwintering populations to synchronize as mature larvae (Tran *et al.* 2007). Thus,

climate affects both the rate of development and the synchrony of adult emergence in the spring. The most common predator of SPB, the clerid beetle *Thanasimus dubius* Fabricius, responds to SPB aggregation pheromone and can cause up to 60% mortality among adults landing on hosts (Reeve 1997). Expected adult lifespan may therefore vary considerably with the abundance of predators.

The abundance of SPB and its impact on forests are closely monitored across the south-eastern USA. Regular aerial surveys detect local infestations as groups of four or more dying trees with red or fading crowns. The number of fading trees at the time of detection is a measure of the number of colonizing adults. Ground crews typically visit infestations within 30 days of aerial detection to count the number of still green trees that are presently experiencing attacks, mainly by the adult progeny of initial colonizers (Gara & Coster 1968; Hedden & Billings 1979; Cronin *et al.* 2000). In all but rare cases, the absence of new attacks indicates local extinction.

Analysis of survey data reveals that smaller initial infestation size is associated with a higher probability of local extinction (Fig. 2). We analysed operational data collected by the United States Forest Service (USFS) and collated within the Southern Pine Beetle Information System (SPBIS), which includes records from 1986 to present for 67 USFS Ranger Districts in 11 states (AL, AR, FL, GA, KY, LA, MS, NC, SC, TN and TX). Of the 26143 SPB infestations in the database having four or more trees and detected between 15 May and 31 August (when surveying activity is most intense), 90% started with four

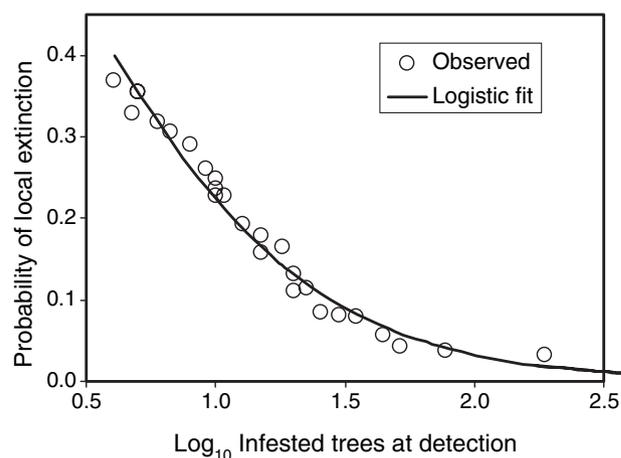


Figure 2 The probability of local extinction as a function of initial infestation size for southern pine beetles, *Dendroctonus frontalis*, across the south-eastern USA. Points are the proportion of infestations within each bin of 1000 observations that were found to be inactive within 30 days of aerial detection. Infestation sizes are bin medians. Curve is the fit of a logistic model to the data.

to 50 trees (median = 14 trees). By the time of ground surveys, 19% (5014 spots) had become inactive. The proportion of local extinctions in bins of 1000 infestations declined significantly with the median number of trees colonized in each bin (Fig. 2; $\chi^2 = 1618$, d.f. = 1, $P < 0.0001$ for logistic regression).

The increase in extinction rate with decreasing numbers of colonists is evidence for strong positive density dependence in growing infestations. The results of our 20-year, 11-state analysis agree qualitatively with those of a more localized 3-year study in east Texas (Hedden & Billings 1979). The Texas study, however, showed a more striking pattern of 100% extinction in infestations involving fewer than 10 trees, suggesting that sensitivity to initial population size may vary annually or geographically.

ECOPHYSIOLOGICAL MODEL

Predicting the rate of population growth for poikilotherms is challenging due to variance both in environmental temperature and individual responses to such variation. A model of great enough sophistication to accurately describe phenology in light of this complexity will necessarily suffer for lack of generality and difficulty of exposition. Our approach in this paper is to use a detailed model parameterized for a specific organism in specific environments to characterize the general conditions under which transient dynamics may affect local persistence in a broad array of species.

For the purposes of this study, we will describe our modelling approach in terms of the natural history of SPB. Ecophysiological models typically have high dimensionality; a more detailed exploration of parameters and model behaviour will be published separately. We model population dynamics in a stage structured population with fixed survival probabilities per stage (Fig. 3). The rate at which

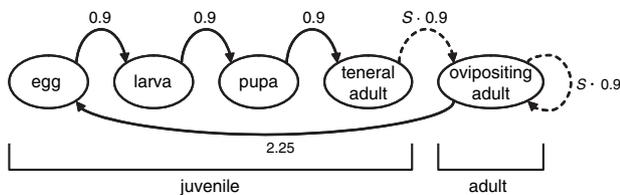


Figure 3 The life cycle of simulated southern pine beetles. Survival and fecundity per stage is constant, whereas development rates are temperature dependent. Adults re-emerge (with probability 0.9) from their first host to lay a second brood. Between-tree survival, S , of adults was set to 0.5 unless otherwise noted, affecting emerging teneral adults and re-emerging adults during host-finding. The average number of female eggs per female per brood is 2.25. The life cycle can be divided into a juvenile stage developing in the brood tree and an adult stage ovipositing in new hosts.

individuals pass through each stage is determined by development curves fit to data obtained by Gagne *et al.* (1982) and Wagner *et al.* (1984) from populations reared at fixed temperatures in the laboratory. The curves follow the form summarized by Ungerer *et al.* (1999), with the exception that pupae only develop between 7 and 33 °C. These thresholds are suggested by the original developmental data of Wagner *et al.* (1984), but were previously excluded from population dynamics models by the uniform application of a biophysical model without absolute thresholds (Sharpe & DeMichele 1977; Schoolfield *et al.* 1981). The existence of upper and lower limits on the thermal niche for pupal development implies a significant nonlinear influence of temperature on fitness (Huey & Berrigan 2001) and population structure (Powell *et al.* 2000) in both warm and cold climates.

We address the problem of individual variation and variable temperatures using the extended McKendrick-von Foerster (EvF) method described by Gilbert *et al.* (2004), which assumes that individual variance in developmental rate is constant with respect to temperature. The probability density function of reaching the end of developmental stage j (physiological age $a_j = 1$) in time t depends jointly on the distribution of emergence from the previous stage, p_{j-1} ($a = 1, t$), and the mean, r_j , and variance, v_j , of developmental rates, such that

$$p(a = 1, t) = \int_0^t P_{j-1}(a = 1, \tau) \frac{1}{\sqrt{4\pi v_j(t - \tau)^3}} \exp \left\{ - \frac{[1 - \int_{\tau}^t r_j(T(s)) ds]^2}{4v_j(t - \tau)} \right\} d\tau, t > 0. \quad (1)$$

The r_j must be calculated by relating a developmental rate function $T(s)$ to temperature at each point in time, while individual variability around mean rates is estimated from developmental data. The integrand in (1) can be viewed as the emergence distribution of a cohort of individuals all starting life stage j at time τ ; the integration then sums cohorts across their times of initiation. Sequentially integrating numerically from one life stage to the next, these operations project an initial population of ovipositing adults, assumed to be normally distributed about a mean date of colonization, forward into a distribution of emerging adults in the next generation. Per-stage mortality (Fig. 3) is assessed against the entire distribution of emerging brood, as is between-tree mortality and net fecundity (2.25 surviving female eggs per ovipositing female). The estimates of individual variance in daily rates of development used in our model were 0.00134, 0.000573, 0.000155, 0.0448 and 0.0208 for oviposition, eggs, larvae, pupae and teneral adults, respectively.

RESULTS AND DISCUSSION

Effect of population synchrony

In typical years in the south eastern USA, most SPB infestations begin with colonization between March and May following a period of adult dispersal (Thatcher & Pickard 1964; Payne 1980; Coulson *et al.* 1999). We modelled an infestation with a mean colonization date of Julian day 90 (late March) and manipulated variance around that mean to examine the effect of asynchrony (increasing standard deviation, σ , of colonization dates) on population continuity. Developmental rates were computed using daily minimum and maximum temperature normals for Hattiesburg, Mississippi, a location within the interior of the SPB range in the USA. We conservatively estimated an attack density of 3000 SPB per host tree and investigated infestation sizes ranging from 10 to 30 trees.

As expected, asynchrony increased the minimum adult attack rate attained between generations of beetles (Fig. 4). Minimum attack rate increased linearly with total founding population size for a given degree of synchrony (Fig. 4). However, even a large population ($n = 90\,000$) failed to maintain a critical density of attacking adults between

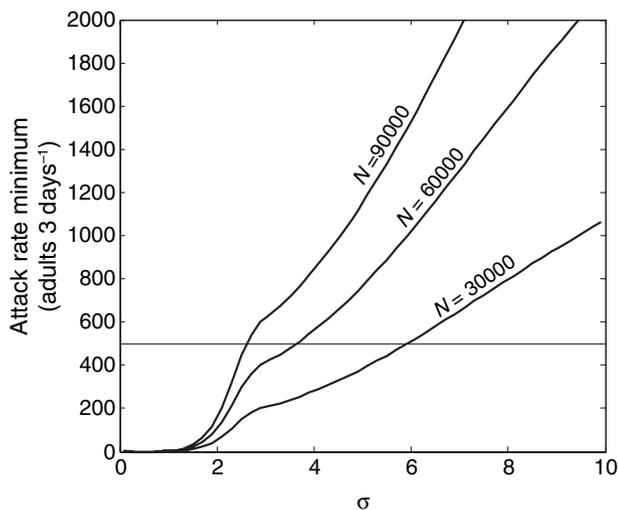


Figure 4 The effect of synchrony on population continuity. The standard deviation of colonization date is plotted on the horizontal axis (synchrony decreases from left to right). The vertical axis shows the minimum number of adults attacking in a three day period. Curves are for three population sizes, n , as labelled. The horizontal line represents a hypothetical threshold below which emerging offspring will emigrate due to insufficient parental production of aggregation pheromone. Simulations employed 1971–2000 temperature norms from Hattiesburg, Mississippi with a mean oviposition date of Julian day 90. Other parameters as in Fig. 3.

cohorts if colonization was too synchronous. The spring dispersal flight of SPB, though occurring within a 3 month window on average, typically peaks over a shorter period of 3–6 weeks. Given a population of 60 000 individuals, the colonization period is roughly 2, 4, and 6 weeks for $\sigma = 2, 5,$ and 8, respectively. Let us assume 500 attacking adults per 3 day period are required to maintain pheromone-mediated aggregation (production of anti-aggregation pheromone begins 3–4 days after attack, Coulson 1980). Our model suggests an infestation initiated in the spring by 60 000 adults requires a colonization period of about 1 month ($\sigma = 5$) to ensure the philopatry of local recruits (Fig. 4). The number of attacking beetles required to maintain aggregation behaviour might be higher or lower and may vary with factors such as the local density of hosts and the number of hosts under attack. Over a large range of threshold values, however, the model suggests that infestations can fail due to an insufficient colonization period, even when the number of colonists is large.

If we assume that synchrony of colonization increases the probability of establishing an infestation, as suggested by Logan *et al.* (1998), then establishment and persistence appear to be in opposition. A population of 30 000 SPB might be able to overwhelm a small number of host trees if it colonizes over a short period, but the infestation will not grow to include more hosts. Conversely, a slow, prolonged colonization might fail to overwhelm the first host. The tension between establishment and persistence becomes moot for populations large enough to overcome the Allee effect at both phases, but for populations of intermediate size there is a finite range of synchrony sufficient for both overwhelming hosts and maintaining pheromone production through offspring emergence.

Effect of adult mortality

Synchrony can only affect abundance between cohorts if adults are short-lived enough to dissipate in the time required for juvenile development. In essence, this is a statement about the overlap of generations. The effect of overlapping generations on a population's approach to stable stage distribution is well understood from stage-based population models, in which transient dynamics following a perturbation are characterized by the damping ratio (quotient of the first and second eigenvalues of the transition matrix, λ_1 and λ_2). Consider a simple case for a population with two life stages. If we scale time to juvenile development and there is no juvenile mortality, then all juveniles become adults after one time step. If the long-term growth rate of the population is 1, such that the adult reproductive rate, b , is equal to the proportion of adults dying before offspring mature (a metric of generational overlap), $0 \leq d \leq 1$, then the damping ratio is

$$\left| \frac{\lambda_1}{\lambda_2} \right| = \frac{1}{d}. \quad (2)$$

The damping ratio increases as adult lifespan increases (decreasing d) relative to juvenile development time, meaning the population will experience fewer and less severe oscillations on its approach to the stable stage distribution after a perturbation such as seasonal synchrony.

In our ecophysiological model of SPB development, the expected adult lifespan is determined by four factors: temperature, the maximum number of broods an adult might produce in sequence, the probability that adults re-emerge to produce each new brood, and between-host survival. With realistic parameter sets, the number of hosts attacked has the greatest effect on generational overlap by setting the upper limit on adult lifespan. Field observations suggest that attacks by re-emerged adults are integral to sustaining infestation growth (Coulson *et al.* 1978; Coulson 1980), but Thatcher & Pickard (1964) noted that SPB do not produce more than two broods in nature. We allowed model adults to lay a maximum of two sequential broods and manipulated the probability of re-emergence and between-host survival to test the effect of adult mortality on population continuity. Our focus on a single mean colonization date in a single environment isolated the effect of mortality from that of temperature.

Population continuity increased linearly with between-tree survival (Fig. 5). This effect was due not only to adult lifespan, as in (2), but also to an increasing number of offspring (Fig. 5a). By reducing expected adult lifespan relative to juvenile development time, between-tree mortality caused a small population to drop below critical levels between cohorts even when per capita reproduction exceeded replacement (Fig. 5). Thus, continuity in the first generation is necessary but not sufficient for long-term infestation growth. Changes to the probability of attacking a second host had identical effects on continuity.

Our model results suggest that predators could play a key role in promoting infestation failure even when predation does not directly reduce adult survival and reproduction below replacement. During infestation growth, between-tree mortality of adult SPB may be driven in large part by the abundance of clerid beetle predators, but per capita predation risk decreases with the abundance of SPB relative to clerids (Reeve 1997). On annual time scales, predator abundance appears to track that of SPB in a delayed fashion characteristic of predator-prey cycles (Turchin *et al.* 1999). The impact of predation may also vary with season and between years due to climatic effects not only on the synchrony of colonization, but on the importance of synchrony to population continuity.

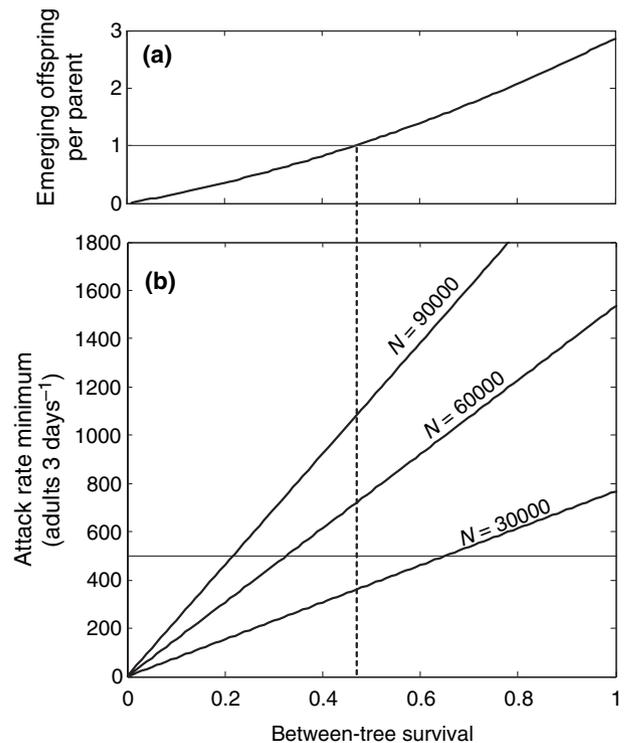


Figure 5 The effect of between-tree survival of adults on (a) emerging offspring per parent and (b) the density of the parent population at first offspring emergence for $\sigma = 5$. The midpoint probability of survival (0.5) represents the same set of parameter values as the midpoint of Fig. 4. Details and labels as in Fig. 4.

Our model results offer a testable hypothesis for the observed pattern of increased local extinction rates in small infestations (Fig. 2). The persistence of smaller populations is more sensitive to both synchrony and adult survival. If all infestations are colonized at the same rate, then small infestations are the result of a short duration of colonization and are therefore more prone to extinction. Alternatively, if the synchrony of colonization is independent of initial population size, then all infestations are equally likely to be highly synchronous, but the probability of persistence will still decrease with decreasing population size. It is also possible that the pattern in Fig. 2 is explained by processes other than phenology and predation. For instance, initial infestation size might reflect aspects of habitat quality, such as the availability of susceptible hosts, that would in turn affect the probability of continued growth. However, Hedden & Billings (1979) found that infestations initially involving fewer than 20 trees were likely to fail regardless of the basal area of the surrounding forest stand (a measure of host density). Furthermore, there was no relationship (among failed infestations) between basal area and initial infestation size.

Effect of climate

Thus far, we have only considered population dynamics for a single mean colonization date in a single location. The transient dynamics of an ectothermic population following colonization may vary both seasonally and geographically. For instance, differential responses among juvenile and adult stages to low temperatures may reduce the temporal overlap of parental and offspring generations during the fall and winter. In such a case, the amplitude of seasonal variation will affect the temporal window over which population growth is likely to occur. Seasonal variation in temperature increases with latitude (Taylor 1981). Hence, the study of transient dynamics may augment our understanding of geographic range limits or challenges to range expansion not captured by traditional analyses of voltinism and thermal tolerance. We compared the influence of seasonal variation in temperature on population continuity in the interior of the species range, Hattiesburg, MS, to that in the location of the northernmost known current population of SPB, Cape May, NJ, USA. In both the interior and northern environments, declining temperatures during fall caused a sharp increase in the predicted time for peak offspring emergence relative to the limit of adult

lifespan (Fig. 6a,b). The modal duration of the juvenile and adult stages then decreased in approximate parallel through winter and spring before stabilizing in summer (Fig. 6a,b). For any colonization date, juveniles required more time to develop than an average adult was likely to survive. The overlap of generations depends on variance in colonization date and the variance among individuals in their developmental rates.

Annual temperature cycles led to seasonal changes in the sensitivity of transient dynamics to cohort synchrony. Regardless of synchrony, the overlap of parental and offspring cohorts decreased in the fall, coincident with the increased disparity between juvenile and adult developmental rates (Fig. 6). Continuity then increased in the spring or early summer as developmental rates stabilized (Fig. 6). The amplitude and duration of the intervening period of high continuity during summer increased with decreasing synchrony (Fig. 6c,d).

Seasonal changes in the severity of transient dynamics may explain why SPB tend to disperse and establish new infestations in the spring. The end of the summer period of high continuity was marked approximately by the last date on which a cohort could reach peak emergence in the same year it was oviposited (T in Figs 6c,d). For cohorts

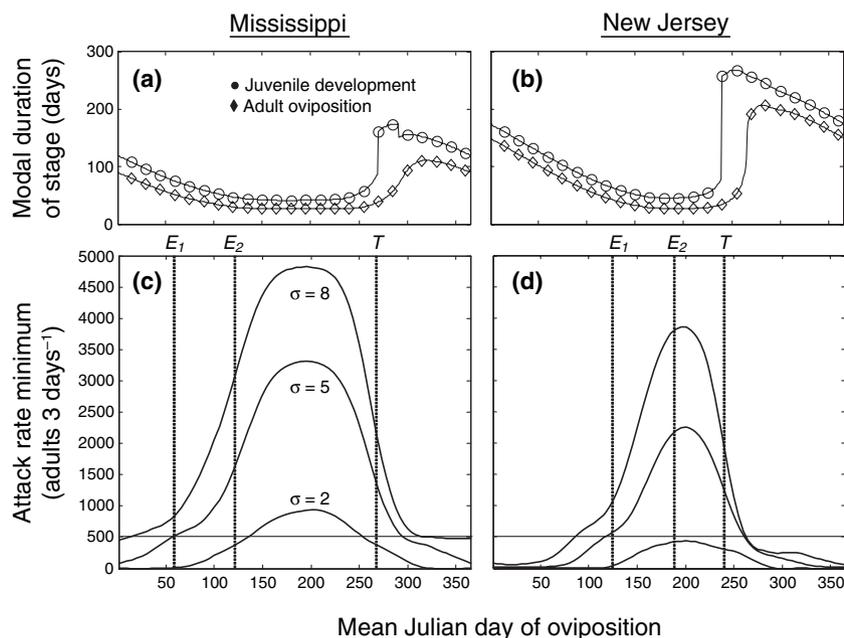


Figure 6 Cohort development time and attack rate minimum as functions of mean oviposition date and geographic location. Temperature norms (1971–2000) were used to calculate developmental rates in Hattiesburg, MS (a, c) and Cape May, NJ (b, d). The top row of panels (a, b) compares the time required for peak juvenile emergence to the lifespan of adults. The bottom row of panels (c, d) shows the effect of decreasing colonization synchrony ($\sigma = 2, 5, 10$, as labelled) on the overlap of generations for $n = 60\,000$. Horizontal lines mark a hypothetical threshold below which emerging offspring will emigrate due to insufficient parental production of aggregation pheromone. Vertical lines: T indicates the threshold mean oviposition date for a cohort to reach peak emergence in the same year. Cohorts centered on dates between T and E_1 have peak emergence dates in the interval from E_1 to E_2 .

oviposited after T , the mode of the emergence distribution shifted to a date in the spring of the following year, the interval from E_1 to E_2 in Figs 6c,d, an interval that corresponds well to the observed dispersal periods in both Mississippi and New Jersey. The minimum adult attack rate between generations decreased substantially for cohorts oviposited late in the season. Discontinuity of pheromone production due to differential life stage responses to cold temperature may therefore explain the timing of the spring dispersal flight.

It appears that northern populations of SPB face a phenological paradox. Excessively synchronous colonization reduced population continuity in both interior and northern climate (Fig. 6c,d). However, winter stage structure in the New Jersey population is dominated by final instar larvae that have completed feeding (Tran *et al.* 2007), consistent with the hypothesis of synchronization by low temperature (Jenkins *et al.* 2001). If strong seasonal effects on stage structure lead to increased colonization synchrony, then a larger population of colonists will be required for persistence. Thus, the interaction of physiology, transient dynamics, and a behavioural threshold for aggregation should increase the strength of Allee effects at northern range limits.

CONCLUSIONS

Our ecophysiological model formalizes previous predictions that local infestations of SPB fail due to an insufficient period of colonization (e.g. Gara 1967; Hedden & Billings 1979). Synchronous colonization of hosts induces transient dynamics that lead to periods of low adult population density and increased extinction risk. The absolute severity of transient dynamics decreases with increasing population size, leading to an Allee effect on persistence after establishment. These model results agree with an empirical pattern of increasing extinction rates with decreasing infestation size in SPB. Our model also indicates that the typical spring dispersal period of SPB results from the discontinuity of chemical communication in overwintering populations.

The interplay of transient dynamics and the Allee effect could be a common constraint on population growth, especially at species distribution limits. For many species, geographic range expansion is not directly limited by dispersal (e.g. Crozier & Dwyer 2006) and some species demonstrably fill their fundamental ecophysiological niche (Chaine & Beaubien 2001). However, populations subject to strong positive density dependence, including many pest species, are likely to occupy only a fraction of suitable habitat or geographic range due to the attrition of peripheral or isolated populations (Hanski 1994; Korniss & Caraco 1995; Amarasekare 1998; Keitt *et al.* 2001; Harding & McNamara 2002). Moreover, habitat selection behaviours

that lead to aggregation should generally slow the expansion of species ranges or the colonization of empty habitat (Fretwell & Lucas 1970; Ray *et al.* 1991; Reed & Dobson 1993; Stephens & Sutherland 1999; Greene & Stamps 2001; Donahue 2006). Cues from conspecifics regarding habitat quality appear to be a common and important aspect of animal behaviour (Stamps 1988; Danchin *et al.* 2001; Valone & Templeton 2002; Aragón *et al.* 2006), suggesting that Allee effects may often arise from reduced communication in small populations. It is precisely the dependence of habitat selection behaviour on sustained chemical communication across generations in SPB (Gara 1967) that makes infestation growth vulnerable to excess phenological synchrony. Finally, our model suggests that population discontinuity arises from strong seasonal effects on stage structure. Reduced seasonal temperature variation could increase the probability of persistence in small infestations, especially at northern latitudes. Hence, transient dynamics may play a central role in the rate of species range expansion following climate change.

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