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Developmental synchrony in multivoltine insects: generation separation versus smearing

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Abstract Many insect species undergo multiple generations each year. They are found across biomes that vary in their strength of seasonality and, depending on location and species, can display a wide range of population dynamics. Some species exhibit cycles with distinct generations (developmental synchrony/generation separation), some exhibit overlapping generations with multiple life stages present simultaneously (generation smearing), while others have intermediate dynamics with early season separation followed by late season smearing. There are two main hypotheses to explain these dynamics. The first is the 'seasonal disturbance' hypothesis where winter synchronizes the developmental clock among individuals, which causes transient generation separation early in the season that erodes through the summer. The second is the 'temperature destabilization' hypothesis where warm temperatures during the summer cause population dynamics to become unstable giving rise to single generation cycles. Both hypotheses are supported by detailed mathematical theory incorporating mechanisms that are likely to drive dynamics in nature. In this review, we synthesize the theory and propose a conceptual framework—where each mechanism may be seen as an independent axis shaping the developmental (a)synchrony—that allows us to predict dynamic patterns from insect life-history characteristics. High fecundity, short adult life-span and strong seasonality enhance synchrony, while developmental plasticity and environmental heterogeneity erode synchrony. We further review current mathematical and statistical tools to study multi-generational dynamics and illustrate using case studies of multivoltine tortrix moths. By integrating two disparate bodies of theory, we articulate a deep connection among temperature, stability, developmental synchrony and inter-generational dynamics of multivoltine insects that is missing in current literature.

Keywords *Adoxophyes honmai* · Insect outbreaks · *Paralobesia viteana* · Physiologically-structured models · Population cycles · Renewal equations

Introduction

A rich body of experimental and computational literature addresses the role of temperature on insect development and phenology to predict—with remarkable accuracy—the number of generations per year (voltinism) and the time of emergence of larvae, pupae and adult life stages (Logan et al. 1976; Lactin et al. 1995; Damos and Savopoulou-Soultani 2012; Régnière et al. 2012). This predictability stems from the fundamental role of temperature as a pacemaker for insect development, fecundity and mortality (Sharpe and DeMichele 1977; Wagner et al. 1984; Heinrich 1993; Gilbert and Raworth 1996). The body of knowledge

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on temperature-dependent phenology is of prime importance in insect pest management because it facilitates the matching of control tactics with the timing of vulnerable life stages. However, it does not explain the population-level phenomenon of generation separation versus generation smearing (Fig. 1): the phenomenon that certain populations—those exhibiting 'generation separation'—harbor individuals of the same stage and with very similar developmental index at any given time. In contrast, populations that exhibit generation smearing have most or all life stages present at the same time. While such diversity in inter-generational dynamics is curious in its own right, it also has important implications in pest management because they may require different management practices. Species exhibiting generational separation may be controlled with a single intervention per generation timed to a narrow period when all individuals are vulnerable. In contrast, species with overlapping generations may require more intensive management because of the developmental asynchrony among individuals. In this study we propose a mathematical framework to predict patterns of developmental synchrony from basic insect life-history characteristics including temperature-dependent vital rates and possibly distributed developmental delays.

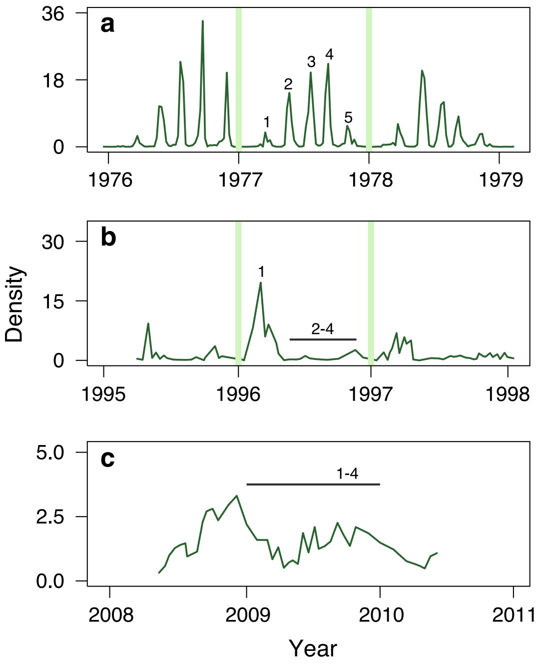

Fig. 1 Inter-generational dynamics in three tortrix species along the generation separation to smearing continuum. **a** The smaller tea tortrix display separate generations throughout the year. **b** The grape berry moth dynamics display transient generation separation with early distinct generation(s) and late smeared generations. **c** The light brown apple moth has overlapping generations throughout the season. The numbers enumerate the timing of adult flight for each generation through a year, and the vertical bars denote the midpoint of winter in the seasonal environments

There are two main bodies of theory that pertain directly to the phenomenon of generation separation versus smearing. As a short-hand we will refer to these as the 'seasonal disturbance' and 'temperature destabilization' hypotheses. The former has a longer history and is grounded in the developmental synchronization that often happens seasonally due to low winter temperatures. Synchronization can happen through three mechanisms. First, some species diapause (arrest their development) in the most cold tolerant stage towards the end of the growing season (Tauber and Tauber 1986; Denlinger 2002). Second, temperature-dependence in development alone can generate developmental synchrony in seasonal environments if stages have different base temperature thresholds for development (Powell et al. 2000). Finally, differences in stage-specific, temperature-dependent mortality rates can be a potent synchronizer. Gurney et al. (1992) developed a multi-seasonal model for the dynamics of stage-structured populations and showed that differential mortality can generate developmental synchrony in cases when some life stages does not survive the winter. Regardless of mechanism, winter may be thought of as a 'disturbance' that homogenizes population stage-structure by synchronizing the developmental index of individuals.

When development is synchronized by seasonal disturbance, the early season generation(s) will appear distinct. However, this distinctive pattern is generally a transient phenomenon giving way to increasingly overlapping generations as the season progresses. Intuitively, a number of factors will influence the transience towards developmental asynchrony. First, the level of initial synchrony at the beginning of the growing season will determine the variability in developmental indices in the first spring generation (Friedenberg et al. 2007). Second, a long adult life span will erode synchrony because the eggs from the first cohort will be laid and subsequently hatch across a wider time window. Third, individual variation in developmental rates, or variation in the timing of the initiation of development due to, for example, bet-hedging strategies, could likewise erode synchrony. Fourth, environmental heterogeneity will generally act to decrease synchrony because microhabitat differences in temperature will lead to a wider distribution of developmental periods within a cohort (Gilbert et al. 2004). For example, a mere temperature difference of 2 °C, in our tortrix case studies (below) causes an increase in the egg-to-adult developmental time of $\approx 20\%$ (at 20 °C), which in turn causes the variance in the distribution of developmental times to increase by a week or more for each generation. Finally, the ratio of developmental period to length of growing season is likely to be important: the more generations in a year, the greater the opportunity for all desynchronizing factors to compound and cause generation smearing. Acting to counter such erosion is various effects that penalize asynchronous development through Allee effects such as mate-finding problems (Calabrese and Fagan 2004; Yamanaka et al. 2012), predation (Gascoigne and Lipcius 2004) or asymmetric competition/cannibalism (e.g., Bjørnstad et al. 1998; Briggs et al. 2000). Furthermore, some evolutionary models show that natural selection could work to counteract these effects by maximizing synchronization of development with seasons (Gurney et al. 1992; Cobbold and Powell 2011).

The seasonal disturbance hypothesis can explain how species with complete generation overlap in non-seasonal environments can have transient generation separation in more seasonal environments, and how late season populations with overlapping generations can be re-synchronized for the spring. However, this theory is incomplete because, in some species, generation separation appears to increase through the season (Fig. 1). The temperature destabilization hypothesis provides an alternative explanation for the maintenance of developmental synchrony and generation separation. This hypothesis is associated with a separate theoretical literature focusing on the relationship between temperature and stability of exothermic populations. In a general mathematical analysis of the consequences of climate change on consumer-resource systems, Vasseur and McCann (2005) predicted that “mathematical extinctions do not occur with warming; however, stable systems may transition into an unstable (cycling) state.” Similar results were found in more recent models of temperature-dependent, size-structured dynamics of fish, where the authors’ concluded that above “a critical temperature, the consumer population dynamics destabilize and shift from a stable equilibrium to competition-driven generation cycles” (Ohlberger et al. 2011). Temperature-dependent destabilization has been predicted in stage-structured models of mosquito (e.g., Beck-Johnson et al. 2013) and moth (Yamanaka et al. 2012; Nelson et al. 2013) dynamics. The latter of these examples is the smaller tea tortrix (*Adoxophyes honmai* Yasuda); this species is an interesting case study because it exhibits sustained generation separation across as many as 5 generations per year, and the generations become increasingly separate through the summer (Yamanaka et al. 2012). Our recent work in this system revealed that generation cycles are predicted to develop whenever the temperature is above 15 °C and that the population dynamics in the field show clear evidence of changes in stability each spring and fall in response to seasonal changes in temperature (Nelson et al. 2013).

Interestingly, the body of literature based on the seasonal disturbance hypothesis emphasizes developmental synchrony, whereas the body of literature based on temperature destabilization emphasizes population stability. Yet, both bodies of work actually make predictions about both developmental synchrony and population stability. Jansen et al. (1990) illustrate this point using models that are independent of the question of temperature and stability. They analyzed a number of models of generation cycles and found that some population models generate sustained population cycles where each cycle comprised essentially a single generation. Thus, they showed that developmental synchrony and population cycles can be emergent properties of a single model of unstable stage-structured dynamics. Along with the studies of temperature-driven destabilization, this conclusion suggests an alternative and general mechanism by which fluctuating temperatures and seasonality could influence developmental synchrony and generation cycles: namely, that high summer temperatures induce sustained generation cycles that prevent the smearing of summer and fall cohorts.

In this paper, we propose a conceptual framework that unifies the key features of the seasonal disturbance and the temperature destabilization hypotheses. We outline how renewal equations are a useful mathematical tool to study the impact of seasonality on inter-generational dynamics of multivoltine insects. We further suggest statistical methods that can be useful for quantifying the relative importance of the alternative mechanisms from time-series data. Finally, we illustrate the mathematical and statistical approaches using case studies of tortrix moths, a large cosmopolitan family that includes many economically important multivoltine species. By integrating the two disparate bodies of theory, we articulate a deep connection between temperature, stability, developmental synchrony and inter-generational dynamics of multivoltine insects that is missing in current literature.

Methods

Mathematical models

Temperature influences most aspects of an insects’ life cycle including ones that have an immediately apparent connection at the population scale, such as generation time and developmental synchrony. To understand the effect of temperature on population dynamics, such as predicting boundaries to stability and patterns of developmental (a)synchrony, we need a framework to scale the full suite of temperature-dependent vital rates up to the population scale. Physiologically-structured population models (De Roos et al. 2003) provide such a tool. These are a broad class of models that are based on an explicit representation of the organism’s life-history, and are used to predict the emergent population dynamics of a system based on stage-structured vital rates (birth, death and development rates) and how they are shaped by the abiotic environment (e.g., temperature). This class of models is formulated as a general age-structured model using renewal equations (e.g., Kermack and McKendrick 1927; Breda et al. 2012), which means that the composition of the population (the density of individuals of a certain age in the larval stage) is tracked explicitly. As a result, the models provide a tool to gain insight into both the predicted dynamics of the population and the changes in internal composition. Here we use this framework to study the relationship between insect life-history and developmental synchrony and develop statistical probes to quantify the patterns created by different processes.

The generic form of a physiologically-structured model can be written as a simple balance equation. In the Electronic Supplementary Material (ESM) S1, we provide detailed notes for the models presented here, including their derivation from PDE renewal equations. For the purpose of illustrating the structure of these models, we show just the balance equation for the larval stage of a four-stage insect life-cycle (eggs, larvae, pupae, adult; see ESM S1 for the full set of equations):

$$\frac{\mathrm{d}L(t)}{\mathrm{d}t} = R_E(t) - R_L(t) - \delta_L(t)L(t), \tag{1}$$

where $L(t)$ is the number of individuals in the larval stage at time t. Each term reflects how individuals move into and out of the larval stage. $R_E(t)$ is the number of individuals recruiting from the egg stage into the larval stage at time t, $R_L(t)$ is the number of individuals maturing out of the larval stage and $\delta_L(t)$ is the instantaneous per-capita larval mortality rate at time t.

Recruitment and maturation terms are calculated based on how individuals develop through a stage, their mortality rate and, for the egg stage, the birth rate. Since each of these rates can depend on temperature, the recruitment terms are calculated in a manner that allows for an external driver that itself can change through time. We begin by working with the development rate because it influences the overall mathematical structure of the model. Using the larval stage to illustrate, the development rate $h_L(a,t)$ is the instantaneous rate that larvae of age a mature from the larval stage to the pupal stage at time t, which is calculated directly from the probability distribution of through-stage development times $f_L(a,t)$ as

$$h_L(a,t) = \frac{f_L(a,t)}{1 - F_L(a,t)}, \tag{2}$$

where $F_L(a,t)$ is the cumulative probability density function of $f_L(a,t)$. The probability of maturing from a stage can take on wide range of shapes depending on the insect biology (Fig. 2). We assume that the development rate is both age- and time-dependent, but that the birth and death rates are only time-dependent, which allows us to write the recruitment and maturation terms more explicitly. Here are two examples for the maturation term from the larval stage (see ESM S1 for details):

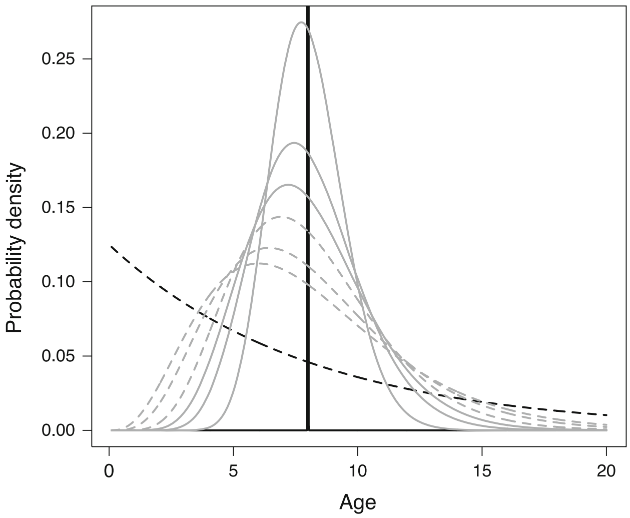

Fig. 2 Different developmental distributions that illustrate a range of maturation rules. If all individuals have identical maturation requirements the development time distribution is a Dirac delta function (*vertical line*); if all individuals have identical rates of maturation that are independent of age, then the developmental distribution is exponential (*dashed black line*). With individual variation in development, the distribution will be in between. It is mathematically convenient to model this using the Erlang distribution (*grey lines*). Six examples are shown with increasing amounts of developmental variability (*solid grey lines* CV = {0.05, 0.15, 0.25}, *dashed grey lines* CV = {0.4, 0.7, 0.99})

Exponential maturation times If every individual is assumed to have an equal probability of maturing from the stage at any age, then the distribution of maturation times will follow an exponential distribution. With exponentially distributed maturation times, the model simplifies to a set of coupled ordinary differential equations with larval maturation given by

$$R_L(t) = h_L(t)L(t). \tag{3}$$

Dirac delta maturation times Assuming all individuals mature at exactly the same age (although that age can vary through time depending on temperature), then the distribution of maturation times is a Dirac delta function. With Dirac delta maturation times, the model simplifies to a set of coupled delay differential equations (e.g., Nisbet 1997) with larval maturation given by

$$R_L(t) = \frac{h_L(t)}{h_L(t - \tau_L(t))} R_E(t - \tau_L(t)) S_L(t), \tag{4}$$

where $\tau_L(t)$ is the larval stage duration that can change through time from changing temperature, $R_E(t - \tau_L(t))$ is the number of individuals that recruited from the egg stage at time $t - \tau_L(t)$, and $S_L(t)$ is the through-stage survival. Since mortality rates can vary through time, the survivorship expression will be

$$S_L(t) = \exp\left(-\int_{t-\tau_L}^{t} \delta_L(\xi)\mathrm{d}\xi\right). \tag{5}$$

These two examples represent the extremes for how individuals mature through the stages. Given genetic and environmental variation expected in nature, the realized distribution of maturation times is more likely to be somewhere between these two extremes (Fig. 2). If the distribution is assumed to be an Erlang distribution (i.e., a gamma distribution with integer 'shape' parameter), then the set of integro-differential equations can be solved using a 'gamma-chain' model of coupled ordinary differential equations (e.g., Blythe et al. 1984; de Valpine et al. 2014) referred to as 'linear chain trickery' by Metz and Diekmann (1991). We refer to this as a distributed delay model.

The final step in developing the model is to define temperature-dependence in the vital rates. Here we assume that temperature-dependence in the birth, death, and development rates follow an exponential relationship under typical seasonal variation in temperature (see ESM S2 for details). Since development rates vary with temperature, some of the models can be rather tedious to simulate numerically. To simplify the analysis, we transform the model to a physiological time scale where the developments rates are constant. The transformation is analytical, which allows the simulated dynamics to be readily back transformed to the time scale. The scale transformation has analogies to approaches using growing degree-days.

Statistical methods

From a functional point of view, we categorize individuals according to their life stage: egg, larva, pupa or adult. However, in the study of inter-generational dynamics, it is useful to order individuals according to a developmental index that in the parlance of Powell and Logan (2005) "captures the essential circularity of life history, in which egg [begets] egg through the intermediaries of adults and the other developmental phases". This continuous circular (Gurney et al. 1992; Powell and Logan 2005) representation of nonlinear temperature-dependent development provides a more resolved way of conceptualizing developmental (a)synchrony.

The development index is the clock that measures how far each individual is along the path to senescence and death. Individuals in the egg stage will have a low developmental index, and individuals in the adult stage will be close to their terminal developmental index. Populations with generation separation, and developmental synchrony, will exhibit a distribution of development indices among individuals that are concentrated within a narrow developmental range. When development is asynchronous and generations overlap, the distribution of development indices will be less concentrated through time the developmental index distribution will eventually become uniform.

The two theories for generation separation versus generation overlap predict different patterns of population dynamics and different patterns of the developmental index distribution over time. The seasonal disturbance hypothesis predicts a concentration of individuals into a narrow range of developmental indices early in the growing season with the population showing transient generation cycles. As the generation separation decays through time, the initially narrow distribution of development indices becomes increasingly widened. In contrast, the temperature destabilization hypothesis predicts sustained population cycles with a developmental index distribution that remains narrow over time. Indeed, whenever the inter-generational dynamics are caused by crossing a critical temperature threshold for stability in the spring, cycle amplitudes should increase with temperature (Nelson et al. 2013). Since the two alternative mechanisms predict qualitatively different patterns in dynamics and developmental (a)synchrony, they should be distinguishable by evaluating the seasonal change in (1) cycle amplitude, and (2) the distribution of developmental indices. We propose that wavelet analysis can quantify the former and circular dispersion can quantify the latter.

Wavelet analysis is a spectral decomposition method that estimates the amplitude of population cycles at different frequencies (Torrence and Compo 1998). The significance of wavelets in our context is that they allow estimates of changes in cycle amplitude from ecological time series (e.g., Grenfell et al. 2001; Cazelles et al. 2008; Nelson et al. 2013). In our previous paper (Nelson et al. 2013) we detailed the use of the Morlet wavelet as a mid-pass filter to estimate the amplitude at the time-scale corresponding to the length of the life cycle. Changes in cycle amplitude can then be tested for trends through time and as a function of environmental covariates such as temperature. This requires time series regression methods that incorporate the serial-dependence in the amplitudes (e.g., Pinheiro and Bates 2000) such as using year as a random effect and a 1st-order moving average model for within-year serial dependence (Nelson et al. 2013). In the case of transient developmental synchrony, wavelet amplitudes should decrease through the spring and summer months. In the case of sustained developmental synchrony caused by temperature-induced destabilization, the amplitudes should be an increasing function of temperature. We used such a relationship as evidence to support the temperature destabilization hypothesis for the generation separation in the dynamics of the smaller tea tortrix (Nelson et al. 2013). We use the Rwave-package (Carmona et al. 1998) for R (R Development Core Team 2015) for the wavelet analysis. An example R script is provided in ESM S3.

Circular dispersion is a measure of the variance of circular distributions (Jammalamadaka and SenGupta 2001). Conceptually, if we define birth as developmental index of zero degrees and adult senescence as 360°, then individuals in a population can be represented along this circular distribution at any point in time (Gurney et al. 1992; Powell and Logan 2005). The amount of synchrony can then be estimated by the dispersion among individuals. Circular variance (V) is calculated as $V = 1 - R$ (Fisher 1993), where R is the order parameter:

$$R = \frac{1}{n}\sqrt{\left(\sum_{i=1}^{n}\cos\theta_i\right)^2 + \left(\sum_{i=1}^{n}\sin\theta_i\right)^2}, \qquad (6)$$

where θ_i is the development index in radians for individual i and n is the total number of individuals. A dispersion of 0 indicates that all individuals in the population are at exactly the same development index while a value of 1 indicates that individuals are spread evenly across all development indices.

In practice, we often only know the number of individuals in a developmental stage (e.g., number of larvae), even though the actual developmental stages span a far wider range of development indices. We can modify the equation for circular dispersion for this type of stage-based data. To calculate circular variance based on the densities at each development index rather than the number of individuals:

$$R = \frac{1}{\sum_{j=1}^{k} y_j}\sqrt{\left(\sum_{j=1}^{k} y_j\cos\theta_j\right)^2 + \left(\sum_{j=1}^{k} y_j\sin\theta_j\right)^2}, \qquad (7)$$

where y_j is the population density of stage j, θ_j is the midpoint (in radians) of the developmental index of stage j and k is the total number of stages. We have found that this stage-based analysis works relatively well even for a limited number of stages. As with wavelet analyses, testing for a trend in circular variance can be treated as a time-series regression problem. R functions for circular dispersion are provided in ESM S3.

Biology and model development

To study the theory and statistical methodology pertaining to developmental synchrony and generation cycles, we focus on two agricultural pest species that we have previously studied in some detail: The smaller tea tortrix, *A. honmai*, and the grape berry moth, *Paralobesia viteana* (Clemens). Both species are temperate tortricid moths that undergo 3–5 generations per year, but exhibit distinct intergenerational dynamics, from sustained generation separation to relatively rapid generation smearing. The smaller tea tortrix exhibits a very high degree of development synchrony and complete generation separation (Yamanaka et al. 2012; Nelson et al. 2013) (Fig. 1a). It is native to Korea and Japan and is one of the most common pest of tea plantations (Tamaki 1991). The larvae feed preferentially on young leaves of cultivars of tea (*Camellia sinensis*). There is no diapause stage although late season larvae will overwinter until environmental conditions become favorable to continue development. Adult females oviposit around 200 eggs at optimal temperatures (Nabeta et al. 2005). The grape berry moth, native to eastern North America, typically exhibits one initial separate generation early in the season followed by decreasingly distinct generations thereafter (Tobin et al. 2003) (Fig. 1b). Larvae primarily attack wild and cultivated grape (*Vitis* spp.) and feed within the fruit. Unlike the tea tortrix, *P. viteana* undergoes an obligate diapause (Tobin et al. 2008); Depending on the photoperiod at which an egg is oviposited, it will either develop into a reproducing adult or a diapausing pupa that can overwinter (Nagarkatti et al. 2001). Females oviposit an average of 30–40 eggs (Luciani 1987). The temperature dependence in development and birth rate is very similar for the two species (ESM S1). A third species of interest is the light brown apple moth, *Epiphyas postvittana* (Walker), which at least in part of its range exhibit almost completely asynchronous developmental and overlapping generations (Wearing et al. 1991; Brown et al. 2010) (Fig. 1c). We will consider this third case study, for which we only have preliminary results, in the discussion. For each tortrix moth, we use a common distributed-delay model with parameters fit to species-specific data on the temperature dependence of the development and birth rates (see ESM S1 for details).

Results

We used laboratory data on temperature dependence in fecundity, survival and development to parameterize our mathematical model for the grape berry moth and smaller tea tortrix the separately. The resultant models suggest that the grape berry moth remains in the asymptotically stable regime irrespective of temperature, while—as we reported previously (Nelson et al. 2013)—the smaller tea tortrix crosses into a cyclic regime for most parts of each summer. The qualitative difference in dynamics is likely caused by the lower fecundity of the former species. As a consequence, the former species' developmental dynamics may be seen to adhere to patterns predicted by the 'seasonal disturbance' hypothesis, while the latter species is more in line with the ‘temperature destabilization’ hypothesis. When assuming fixed species-specific developmental periods, we can drive the models with historical daily temperatures from the locations from which the time series in Fig. 1 were derived (tea tortix: Chiran, Japan; grape berry moth: Erie, Pennsylvania). The models capture the distinctive inter-generational dynamics of each species; the tea tortrix model predicts sustained developmental synchrony that increases with temperature among the 4–5 generations each year (Fig. 3a). There is evidence of widening of the last generation, as temperatures falls below 15 °C. In contrast, the grape berry moth is predicted to have a relatively distinct 1st generation, but the 2nd and partial 3rd generations (Chen et al. 2011) are smeared because of increasing developmental asynchrony there after (Fig. 3b).

Conceptually, the two hypotheses are not mutually exclusive and we posit that they should be seen as two continuous axes that both need to be considered to understand inter-generational dynamics of multivoltine insects. One axis reflects the strength of seasonality, while the other axis reflects population stability and the propensity to decorrelate development. The latter is also a continuous axis in the sense that while it is true that dynamics go into sustained oscillations when the stability boundary is crossed, transients (‘return times’) become continuously longer as a system approaches this boundary (e.g., Yodzis 1989). A schematic of the two-dimensional space defined by the two mechanisms with representative simulations overlaid is presented in Fig. 4. Simulations are shown for systems with asymptotically stable dynamics (grape berry moth model) dynamics and highly unstable dynamics (tea tortrix model) dynamics. To provide an example of intermediate stability, we created an artificial life-history based on the tea tortrix model but with reduced fecundity. All three systems were simulated under low, medium and high seasonal regimes. The regimes assume sinusoidal variation in temperature with amplitudes of 1, 6 and 12 °C respectively. Distinct generations can be discerned in all unstable regimes, but only in the presence of significant seasonality in the stable regime. For lower seasonality, overall abundances are predicted to track temperature but generations are completely overlapping. This happens even in the absence of any developmental heterogeneity, because each adult will lay eggs over their adult lifespan, which means the next generation will be started over a wider range of days than a particular cohort of adults

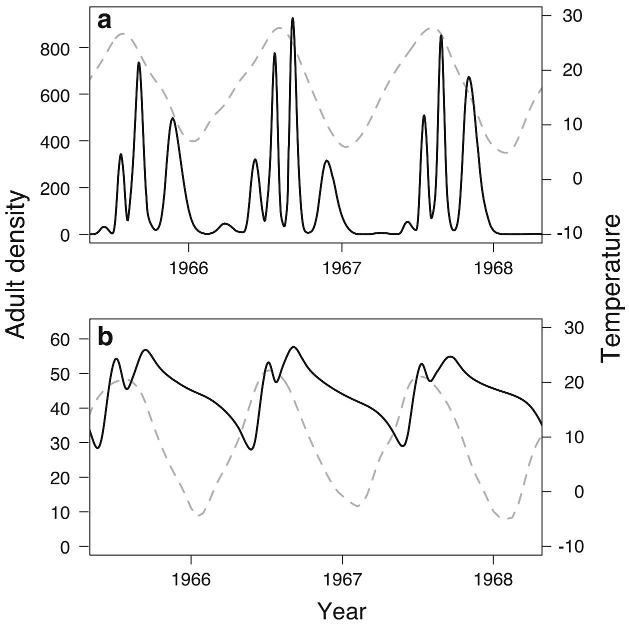

Fig. 3 The effect of stability and seasonality. Simulated dynamics for **a** the smaller tea tortrix, which has life-history traits that result in generation cycles at warm temperatures, and **b** the grape berry moth, which has life-history traits that result in asymptotically stable dynamics. For illustrative purposes, the seasonal drivers used in the simulations are the observed mean daily temperatures from regions where each species is common (tea tortrix: Chiran, Japan; grape berry moth: Erie, USA). *Solid lines* represent predicted adult abundance, *dotted lines* represent temperature. The model structure is the same for both species—the difference in dynamics is the result of different life-history parameters and different temperature drivers (see ESM S2)

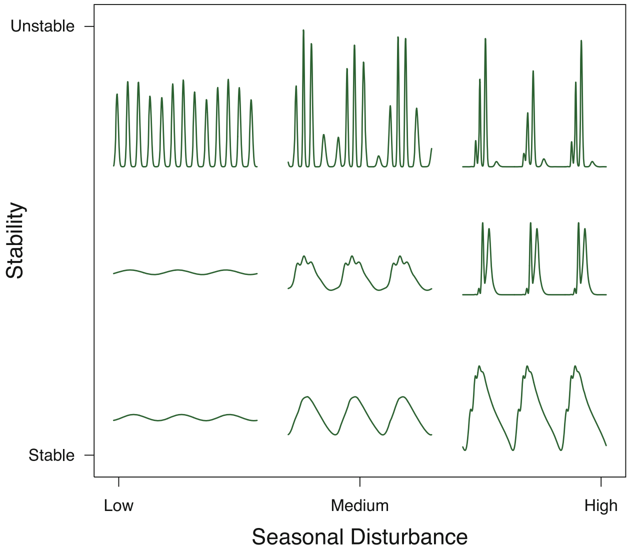

Fig. 4 A conceptual framework for the combined influence of stability and seasonality on inter-generational dynamics. The *horizontal* axis depicts different strengths of seasonality. The *vertical* axis depicts the stability of a species population dynamics (measured by the real part of the dominant eigenvalue of the model). Simulated dynamics are based on the smaller tea tortrix (*top row*), smaller tea tortrix with fecundity reduced by 85% (*middle row*), and the grape berry moth (*bottom row*) under three amplitudes of sinusoidal temperature variation (low: amplitude of 1 °C; medium: amplitude of 6 °C; high: amplitude of 12 °C

originally emerged (Yamanaka et al. 2012; Nelson et al. 2013).

The space defined by the two axes makes specific predictions about intergenerational patterns. Asymptotically stable populations (viz. the seasonal disturbance hypothesis) in a low-seasonal environment should exhibit developmental asynchrony and complete smearing of cohorts. Asymptotically stable populations in a seasonal environment should exhibit transient developmental synchrony that increasingly overlaps as the season progresses in accordance with the seasonal theory. The timing of life stages early in the season will be determined by emergence and accumulation of heat units above the minimum base temperature threshold (Logan et al. 1976; Lactin et al. 1995; Damos and Savopoulou-Soultani 2012). In contrast, for asymptotically unstable populations (viz. the temperature destabilization hypothesis) in a low-seasonal environment, we expect sustained developmental synchrony with weak seasonal phase-locking. Finally, asymptotically unstable populations in a seasonal environment will have sustained generation cycles that are phase-locked with season with no erosion of developmental synchrony with time—indeed, if temperature is responsible for destabilizing the dynamics, we should, if anything, expect developmental synchrony to increase into the peak of the summer. Thus, the seasonal disturbance hypothesis predicts a concentration of individuals into a narrow range of developmental indices early in the growing season with transient/dampened generation cycles in abundance. As the generation separation decay through time, the initially narrow distribution of development indices should become increasingly widened. In contrast, the temperature destabilization hypothesis predicts sustained population cycles with a developmental index distribution that remains narrow over time and the amplitude of the cycle in abundance should increase with temperature.

Since the two alternative mechanisms predict qualitatively different patterns in dynamics and developmental (a)synchrony, they should be distinguishable by evaluating the seasonal change in (1) cycle amplitude, and (2) the distribution of developmental indices. As outlined in the ‘statistical methods’ we propose that wavelet analysis may be useful in quantifying the former and circular dispersion the latter. We test the methods on simulated data from the unstable (Fig. 5a) and asymptotically stable (Fig. 5b) models. We assume constant temperatures but initial developmental synchrony. In the simulations we keep track of the developmental index of all individuals in addition to overall adult and larval abundance.

Using the wavelet analysis we quantify the amplitude of fluctuations corresponding to the time scale corresponding to egg to senescence. In the stable regime the amplitude decays to zero after an initial period of transient generation separation (Fig. 5d). In the unstable regime, in contrast, the corresponding amplitudes increase to a plateau as the dynamics locks on to the generation cycle (Fig. 5c). The circular variances show how the changes in wavelet amplitude are mirrored by the changes in circular variance. In the stable regime the circular variance grows with asynchrony as the stage-distribution becomes uniform (Fig. 5d). In the unstable regime, the circular variance remains low because developmental synchrony is maintained by the generation cycle. A comprehensive evaluation of the utility of these statistical tools is beyond the scope of this study. However, we believe this preliminary application supports our contention that they are worthy of future attention.

Even in the most stylized mathematical model, which assumes developmental periods to be fixed, the maintenance of developmental synchrony in perpetuity through temperature-induced destabilization is puzzling. This is because even with fixed development the time from egg to offspring-egg will be distributed because of the distribution of oviposition dates through the life of each adult. For the more realistic scenario of distributed developmental delays (Fig. 2; see preliminary analysis of the light-brown apple moth in discussion), this may be more puzzling still. It is natural to wonder if the population instability erases this variability. To investigate this, we track the distribution of offspring, grand-offspring, great-grand-offspring, etc., of a single cohort of eggs, laid at a singular time point in the stable or unstable regime. As is evident from Fig. 6, simply having reproduction over the lifespan of an adult leads to a wider and wider offspring distribution with time (Fig. 6c). In the unstable regime this erosion happens much more slowly because the reproductive success of ‘outliers’ is close to zero (Fig. 6d). Interestingly, though, destabilization maintains developmental synchrony without erasing developmental variability, as is evidenced from the simulation by how the 10th generation offspring contributes a small fraction of the adults in the 9th cycle. Even after 90 generations, there is little difference between the variance of the developmental distribution under stable versus cyclic dynamics (ESM S4). Under cyclic population dynamics, the distribution has distinct peaks reflecting that animals of the same generation can be found in multiple cycles. Under stable dynamics the distribution is a unimodal distribution as a consequence of continuous reproduction over the adult lifespan.

Discussion

It is a puzzling phenomenon that even closely related taxa (such as Tortricid moths) with relatively similar life histories (with respect to development, voltinism, etc.) exhibit

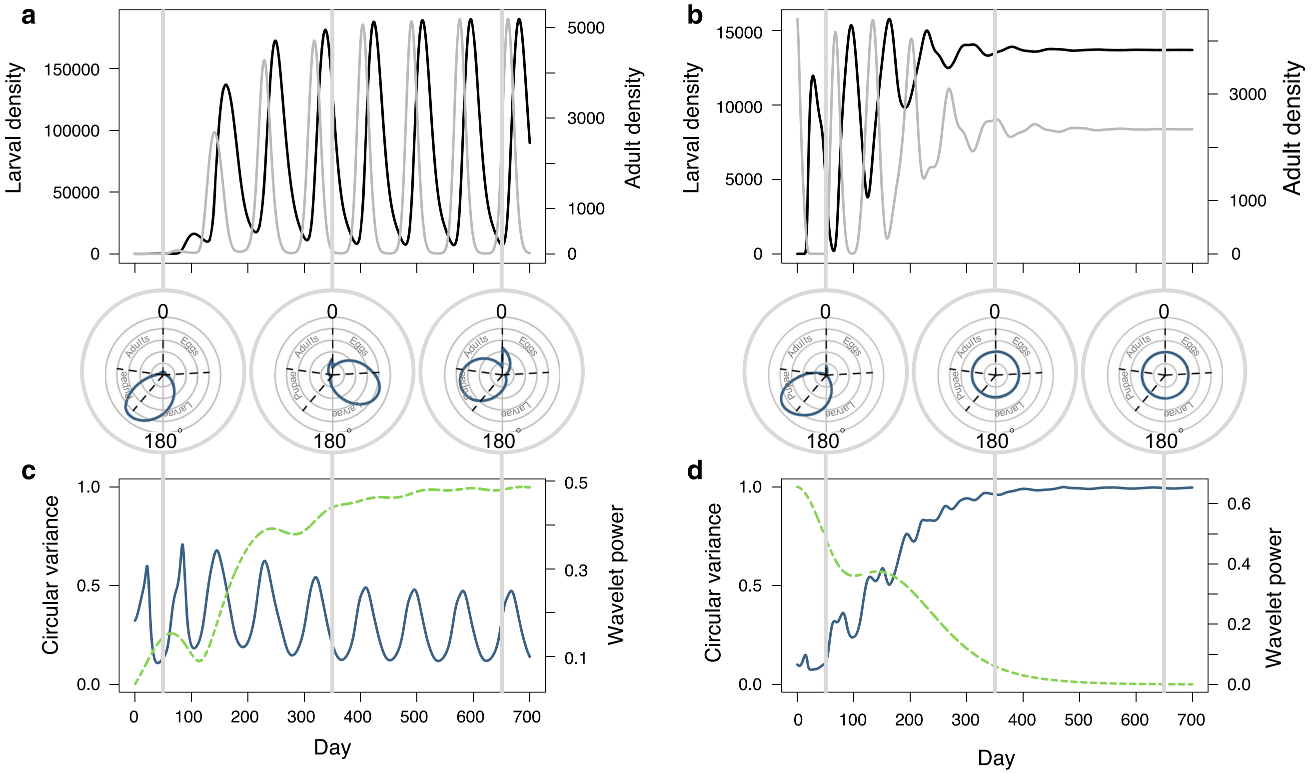

Fig. 5 Wavelet amplitudes and circular variances to quantify generation separation/smearing and developmental (a)synchrony. **a** Simulations of larval (*gray*) and adult (*black*) abundance in the unstable regime. **b** Simulations of larval and adult abundance in the asymptotically stable regime. *Inset* radar *plots* show the developmental index distribution at three time points for each simulation. **c** Circular variance (*solid line*) remains low through time, and the wavelet amplitude (*dotted line*) remains high in the cyclic regime. **d** Circular variance increases through time, and the cycle amplitude decreases through time as the population development desynchronizes in the stable regime. Simulations are based on the models of **a** the smaller tea tortix and **b** the grape berry moth

vastly different patterns of developmental (a)synchrony. The broad literature on developmental (a)synchrony has developed in two largely isolated fields of work that approach the problem from different perspectives. One field emphasizes seasonal disturbance as a mechanism for synchronizing developmental stages, and the other emphasizes population instability. Our study is an attempt to lay out a mathematical theory to understand this phenomenon within a single framework. The framework we propose is based on renewal equations (e.g., Breda et al. 2012), which is a purposefully general formulation of physiologically structured population models that aims to emphasize the match between the biology of any particular insect and the assumptions of the mathematical model (ESM S1). For example, for an insect with a large amount of variation in development rates, it might be most appropriate to assume an exponential distribution of development times, which leads to a set of coupled ordinary differential equations. In contrast, for an insect with small amounts of variation in development, in might be most convenient to assume Dirac delta distribution of development times, which leads to a set of coupled delay differential equations. Intermediate cases may require distributed delay models (that sometimes can be solved using the gamma-chain trick). The renewal equations allow for a transparent mapping between insect life-histories and mathematical models.

Our modeling framework explicitly incorporates both the seasonal disturbance and population instability hypotheses because vital rates can depend on density and environmental variables. As a result, the models can be driven by any relevant environmental variables using values that are directly measured in the field. When a number of vital rates are impacted by the same environmental variable (e.g., temperature), we show that a transformation-of-scales method can help simplify the resulting mathematical models (ESM S1). We further propose some statistical tools—wavelet analysis and circular variances—that we believe will be useful for quantifying patterns in data that can distinguish the contribution of the alternative mechanisms. We provide broad-brush outlines of the mathematical and statistical approaches in the methods. All technical details are provided in ESM S1–S4.

We focused on two tortricid pest species, the smaller tea tortrix and the grape berry moth, to illustrate key concepts, theory and methodology. We showed that the models can

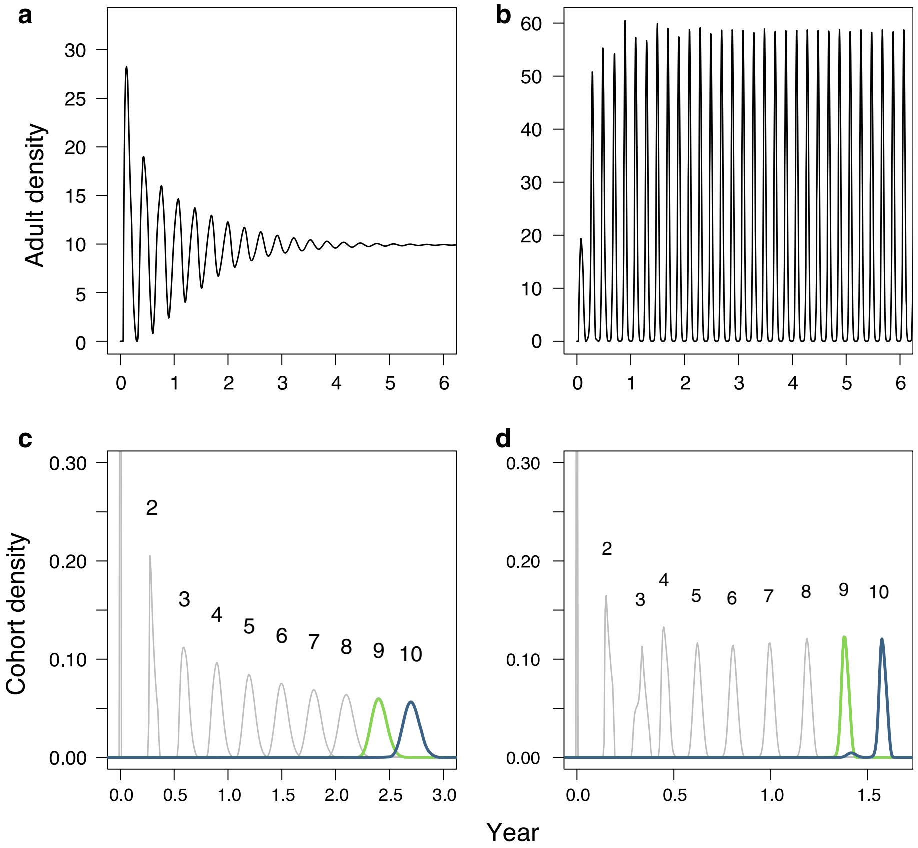

Fig. 6 Cohort dynamics illustrating that developmental synchrony depends on stability as well as developmental variation. **a** stable dynamics (at 12 °C) and **b** generation cycles (20 °C). Simulations are based on a model parameterized for the smaller tea tortix. **c** Cohort dynamics through time for stable dynamics (12 °C) and **d** generation cycles (20 °C). For each temperature, a single cohort is initiated at time $t = 0$, and followed for multiple generations (*grey lines*). The *numbers* indicate the peak abundance of each generation. Generation nine (*light thick line*) and ten (*dark thick line*) are highlighted to illustrate that developmental heterogeneity occurs under both stable and cyclic dynamics

accurately predict both voltinism and dynamics of developmental synchronization (generation separation versus smearing) because of subtle differences in their temperature dependences and life history traits. In the absence of such a mathematical framework it would be hard to predict that one species, the smaller tea tortrix—from two species with otherwise similar life-span, degree-day requirements, adult longevity, etc.—should exhibit sustained developmental synchrony and recurrent generation-specific outbreak, while the other, the grape berry moth, should exhibit developmental asynchrony and relatively smooth patterns of attack to host plants through each season.

The light brown apple moth is a third species with very similar biology that provides an interesting additional case study. We present some results in the discussion because our model is preliminary. The moth is native to Australia but has been accidentally introduced into New Zealand and California. It has several generations a year (Suckling and Brockerhoff 2010), with up to 4.5 generations predicted for California (Buergi et al. 2011). Available monitoring data suggest a high degree of developmental asynchrony and generation smearing (Fig. 1c) with multiple life stages present concurrently (Wearing et al. 1991; Brown et al. 2010). Similarly to the smaller tea tortrix, there is no diapause stage but late season larvae will arrest development when temperatures are too low. Females can oviposit up to 500 eggs at optimal temperatures (Danthanarayana 1975; Danthanarayana et al. 1995). Intriguingly, if we parameterize a model using average light-brown apple moth data and assume no developmental variability, we predict that—like the tea tortrix—this species should exhibit cycles and sustained synchrony during warm weather. However, unlike the tea tortrix, this species is highly polyphagous, attacking hundreds of host plant species (Suckling and Brockerhoff 2010). Moreover, host species has been shown to greatly influence both development and fecundity (Danthanarayana et al. 1995) possibly leading to significant variability in development within any one cohort.

Thus, an emerging hypothesis is that we may need to consider a 3rd axis when modeling developmental synchrony: the coefficient-of-variation in development rates. Is there a threshold for how much variability in life-cycle length that the generation cycles can sustain before they collapse? In a preliminary analysis, we have addressed this question using the general renewal-equation framework to address how such variability influences dynamics. A bifurcation plot of predicted light brown apple moth dynamics at 20 °C as a function of coefficient-of-variation in developmental period is shown in Fig. 7. With average parameters for light brown apple moth, cycles are predicted to collapse and synchrony give way asynchrony when the CV increases beyond about 30%. Below this threshold—

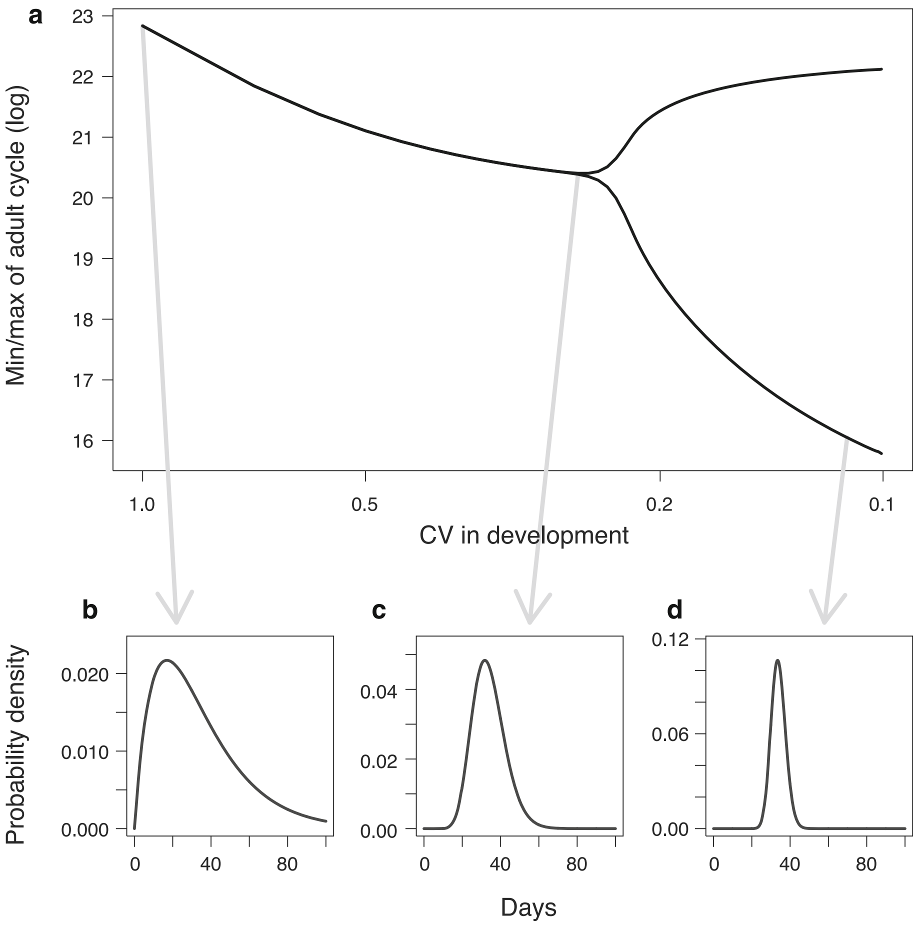

Fig. 7 Destabilization of population dynamics with decreasing developmental heterogenity in simulated dynamics for the light brown apple moth. **a** Bifurcation diagram showing the maximum and minimum amplitude of adult density as a function of the coefficient of variation in the development-time distribution (on a log-scale). Developmental distributions with CV >0.3 result in stable dynamics (cf. *dashed lines* in Fig. 2), and distributions with CV <0.3 result in generation cycles and developmental synchrony (cf. *solid lines* in Fig. 2). **b–d** Development-time distributions for three levels of developmental variation along the bifurcation axis

which may still harbor substantial developmental variability—developmental synchrony is predicted to be maintained (Fig. 7). As an illustration, the distributions in Fig. 2 are additionally encoded with solid curves represents distributions that would lead to synchrony if used in the light brown apple moth model and dotted lines to asynchrony. When synchrony is maintained it is despite the fact that the variability will over time make grand-offspring of any given cohort contribute to multiple outbreak cycles much more quickly than in Fig. 6 (see Fig. S3 in ESM). Thus, destabilization result in population cycles and developmental synchrony, but it does not lead to long-term generation separation in the presence of developmental variability. This conclusion parallels that of Jansen et al. (1990) with respect to the over-compensation (2-generation) cycle of Nicholson's blowflies.

We proposed two sets of statistical tools to quantify synchrony and cyclicity: wavelet amplitudes and circular variance. These seem to do well in highlighting dynamical features when applied to the simulated data. Sometimes concurrent time-series may be available for multiple life stage (e.g., larval and adult abundance; Figs. 3, 4). In preliminary analyses, we hoped that wavelet phase coherence (e.g., Cazelles et al. 2008) would be an additional tool to study developmental synchrony. However, in explorations using simulated data from across the full range of scenarios along a continuum from separated to smeared generational cycles, we found that the phase coherences associated with the developmental-period time-scale were strongly confounded by the cycle amplitude and therefore not helpful (O.N. Bjornstad, unpublished data).

Many tortricid pest species are controlled using integrated pest management programs, which involve multiple methods including biological, mechanical, and semiochemical control. However, the application of chemical pesticides remains the cornerstone control method (e.g., Van der Geest and Evenhuis 1991). As with any management strategy, the application of chemical pesticides needs to be carefully timed with the phenological window of vulnerable life stages, which for most species are early instars. Due to concerns about non-target effects and environmental persistence of pesticides, there is an ongoing desire to minimize the amount of chemicals used, which further narrows the management window because of the reduced time interval over which lethal chemical concentrations remain on the plant resource. The application of pesticides is even more challenging when larvae feed inside a fruit or nut, as is the case for many tortricid pests.

In these cases, pesticides have to be applied prior to egg hatch but sufficiently synchronized with hatch so that larvae have the opportunity to come into contact with the pesticide before they burrow into the relatively protective interior of a fruit or nut.

The applied challenge has motivated the development of detailed phenological models to predict the time of emergence of vulnerable stages for many high impact tortricid pests (e.g., Van der Geest and Evenhuis 1991). In species with highly synchronized development (indicated by distinct 'flight periods' of the adults), the temporal windows in which insects are vulnerable can be narrow but predicable. In such cases, costs can be reduced by timing interventions using well-calibrated phenology models. In contrast, if development is asynchronous so that many, and in some cases all, stages are present at all times, control may be more expensive because it requires frequent interventions. Previous research has characterized many of the key factors, such as photoperiod, temperature, and host plant quality, which influence the number of generations per year in multivoltine tortricids (Tauber and Tauber 1986; Hunter and McNeil 1997; Tobin et al. 2003). However, predicting voltinism alone may be insufficient for a complete theory of management because it does not indicate the degree of synchrony or asynchrony among the insect stages, which directly determines the frequency of applications to sufficiently cover susceptible life stages. We thus believe our renewal equation framework may provide an additional tool for management.

Conclusion

Developmental synchrony is of fundamental importance in stage-structured populations. In the context of basic ecology, it influences the extent to which interactions within a population will be largely intra-stage—among individuals of the same cohort—or inter-stage and inter-cohort. This, in turn, may have very important consequences, as the relative and absolute magnitude of intra- and inter-stage interactions can drive population dynamics from stable to cyclic and even chaotic dynamics (Nisbet and Onyiah 1994; Costantino et al. 1997). In applied ecology, the degree of developmental synchrony is a critical factor in determining the frequency of management interventions required to control a pest species. In the case of pesticides, this frequency can directly equate to total pesticide load, which consequently influences the likelihood of non-target effects, environmental contamination and monetary cost. Herein we have reviewed and synthesized two separate bodies of theory pertaining to developmental synchrony in insect populations and show that there are two key underlying mechanisms: seasonality and stage-specific mortality/development versus temperature-dependent destabilization. Using three tortrix moth case studies, we further outlined the relevant mathematical formalism to study the phenomena, and highlight possible statistical methods to confront theory with data and test alternative hypotheses. Our more comprehensive model adds to ecological theory by showing how temperature not only determines the developmental rate of insects, but also molds their developmental synchrony through emergent population dynamical patterns.

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