



# Temperature affects phenological synchrony in a tree-killing bark beetle

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## Abstract

Phenological synchrony can promote population growth in species with positive density dependence. Variation among life stages in the thermal thresholds for development can foster phenological synchrony under thermal regimes that include frequent occurrence of temperatures between developmental thresholds. The southern pine beetle is an insect with positive density dependence that has recently undergone important shifts in population abundance at the northern extremes of their distribution. We evaluated the hypothesis that cooler winter temperatures in their northern range cause a convergence of the population life stage structure that leads to synchrony in spring flight phenology. We used a combination of approaches. First, in situ laboratory experiments demonstrated a threshold temperature for pupation that was greater than was required for larval development; rearing larvae at lower temperatures increased the pooling of individuals at the end stage of larval development and synchrony in adult emergence. Second, a development rate model showed a similar convergence of the majority of the population at the end stage of larval development when brood experienced the cooler temperatures of the northern region, but not with temperatures from the southern region, or as a null model. Finally, field trapping of wild beetles showed greater synchrony in the pine forests of New Jersey than in the warmer, historically occupied forests of Georgia and Mississippi. Given these results, pine-dominated forests in the northern edge of the southern pine beetle's range may experience more frequent occurrence of outbreaks, due to the positive feedbacks associated with a synchronous spring emergence of this insect.

**Keywords** Southern pine beetle · Stage structure · Synchrony · Climate change · Development model

## Introduction

For terrestrial ectotherms such as insects, extrinsic factors exhibit important influence on individual and population level processes. Temperature for instance, directly influences the rate of development, affecting both phenotype (size, fecundity) and phenology (timing of emergence) (Bale et al. 2002; Angilletta and Dunham 2003; Parmesan 2007).

But for some insects the influence of temperature differs by life stage, and this can have important ecological consequences. For example, pupation can be restricted to temperatures warmer than that at which larvae can feed and grow (Wagner et al. 1984; Ayres and Maclean 1987; Bentz et al. 1991; Ayres and Scriber 1994). The consequences of life-stage-specific thermal requirements become apparent when daily maximum temperatures are between these thermal thresholds for a prolonged period of time, as can occur during winter months. For insects that lack overwintering diapause, winter temperatures that permit larval development while inhibiting pupation can cause the life stage structure of a population to converge at the limiting stage (e.g., prepupae). Life stage convergence can subsequently produce landscape-scale synchrony of important phenological events, such as the timing of adult emergence the following spring (Bentz et al. 1991; Powell et al. 2000; Jenkins et al. 2001; Bentz et al. 2014). This temperature-driven mechanism for synchrony can affect population dynamics by influencing

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the overlap of adult insects in time and space. This is especially important for insects where there are positive feedbacks between abundance and per capita population growth (Liebhold and Tobin 2008; Tobin et al. 2009; Regniere et al. 2013).

In addition to thermal thresholds, life stage transitions may have additional physiological barriers. For example, larvae must attain a minimum size (critical weight) before pupation can proceed. The critical weight for pupation in holometabous insect larvae tends to be relatively insensitive to temperature (Davidowitz et al. 2003, but see De Moed et al. 1999). This means that larvae cannot generally compensate for slower growth rate by pupating at a smaller size, and cannot circumvent thermal restrictions on pupation by pupating earlier in the fall season before temperatures drop below the developmental threshold. Therefore, temperature may directly influence the transition between larval and pupal life stages.

In this study, we examined the consequences of different overwintering temperatures on population life stage structure of an important forest insect pest, the southern pine beetle (*Dendroctonus frontalis* Zimmermann, Scolytinae). This insect reproduces within the phloem of healthy pine trees through a coordinated pheromone-mediated mass-attack that overwhelms the tree's resin defense system. While historically a pest of southern pine forests, this insect has displayed increased abundance at the northern extremes of its geographic range over the past decade, coincident with increasing minimum winter temperatures in the eastern US (Weed et al. 2013). Because of this, a greater proportion of southern pine beetle populations are exposed to the colder winter temperature regimes of the north, versus their warmer southern habitat, where this insect has historically been an important forest pest. We hypothesized that the relatively colder temperatures during the fall and winter in the beetle's northern range would result in a pooling of those populations at late larval instars and pre-pupae due to more frequent and longer periods with temperatures between the thresholds for larval development and pupation. An expected result of this would be increased synchrony in the emergence of new adults the following spring, which could promote the occurrence of outbreaks via positive density-dependent effects associated with the beetle's mass-attack strategy of exploiting host trees. In addition, the pooling of individuals into the more cold-tolerant late larval and pre-pupal stages (Trân et al. 2007) could result in lower winter mortality, further increasing the number of emerging adults and success of spring mass attacks. Alternatively, warm spells during the winter months could disrupt this hypothesized mechanism for developmental synchrony, resulting in a mixed age structure. In this case, the spring flight phenology of northern populations may not be much different from those in their southern range.

We evaluated these hypotheses using the following approaches. (1) We experimentally examined the threshold temperature for larval development and pupation, and measured the synchrony of emerging adults by rearing larval southern pine beetle in situ at different temperatures. In addition, we assessed life stage structure before and after treatments to determine how the temperature treatments influenced development. (2) We constructed an individual-based modeling program, using an insect development rate model (Briere et al. 1999) to predict larval development as a function of temperature, and used this to explore the effect of late fall–spring thermal regimes on the stage structure of southern pine beetle populations. We compared the effect of larval development at temperatures from both the northern and southern extent of their range. (3) Finally, we analyzed empirical field trapping data to test for synchrony in the spring flight phenology of this insect in both northern and southern habitats.

## Methods

### Study system

Southern pine beetles reproduce within the phloem of living pine trees. Adult beetles enter the phloem by chewing through the outer bark and employ aggregation pheromones to attract conspecifics that sustain a mass attack on the tree. If sufficient numbers of beetles are available to respond to the pheromone, this mass attack can defeat the defenses of the host and permit successful reproduction by the beetles. Beetle pairs excavate galleries within which the female deposits eggs. Gallery construction by thousands of beetles rapidly girdles the tree, causing death. Some adults re-emerge from attacking their first tree to attack one or a few additional trees. Larvae feed within the phloem and then pupate in the outer bark. After completing development, the new adult beetles emerge and disperse in search of a new host. Multiple cohorts are produced in a season, helping to maintain high attack densities, and overlap of these cohorts means that all life stages are typically present in the population at any given time during most of their reproductive period. Toward the end of the season, as temperatures drop, larval development slows and effectively stops below approximately 10 °C. However, there is no diapause in this insect, and overwintering can potentially occur in any life stage. The number of generations per year has been estimated at 6 for the southern Gulf states, and 4 for the northern extremes of their distribution (Ungerer et al. 1999).

Southern pine beetle populations are characterized by alternate states of abundance: rare or outbreak (Martinson et al. 2013). Outbreak populations tend to be self-propagating because high abundance begets continued success

in attacking healthy trees. When rare, populations lack sufficient numbers of individuals to successfully overwhelm healthy trees. This confines rare populations to weakened or damaged host trees such as those that have been injured by lightning (Thatcher and Pickard 1964). As rare populations fluctuate in abundance, possibly due to density-independent effects such as host defenses and predation, they can sometimes exceed an escape threshold. Beyond this threshold their deterministic tendency is to increase to epidemic levels, where they typically remain for several years before dropping back below the escape threshold.

At the landscape scale, southern pine beetle outbreaks consist of numerous localized aggregations of colonized trees that are known as “spots” because of how they appear from an aerial view. New spots typically form during a dispersal period in spring, and grow via the accumulation of newly infested trees along their margin. Spots may cease to grow due to insufficient beetle recruitment or reproduction, or inadequate abundance of host trees (Gara 1967). However, successful spots may continue to expand throughout the summer and fall. Spot growth almost always declines in winter when cool temperatures suppress beetle metabolism, but in spring the spots that thrived the previous year produce dispersing adults that can form new aggregations. Once a spot has formed, dispersal of adult southern pine beetles becomes highly localized, with relatively little inter-spot migration (Gara 1967, but see Cronin et al. 2000). The within-spot behavior of adults is structured by the beetles’ aggregation pheromones (Sullivan 2011; Pureswaran and Sullivan 2012). In particular, aggregation pheromones produced by attacking beetles stimulate mass attacks on the same and adjacent trees; furthermore, they retain high concentrations of host-seeking beetles within the infestation and hinder dispersal of emergent brood. Continued spot growth is dependent upon the sustained recruitment of re-emergent and brood adult beetles from previously inhabited trees to the expanding edge of the spot, where healthy trees are currently under attack and releasing aggregation pheromone. An interruption of the attack progression, and consequent reduction or cessation of aggregation pheromone release is a frequent reason for spots to become inactive (Gara 1967).

## Experimental design

With a series of laboratory experiments we tested the influence of the thermal environment of developing brood on emergence synchrony of newly emerged adult southern pine beetle. Freshly attacked pitch pines (*Pinus rigida*) were selected from active southern pine beetle spots in their expanding northern population: two from a single spot in mid-November of 2011 (Wharton State Forest 39.6468°N, – 74.5537°E) and four from a different spot in November of 2013 (Peaslee Wildlife Mgmt. Area 39.3368°N,

– 74.8720°E). From each tree, four 30-cm length bolts were cut between branch whorls beginning at 2 m height. The cut ends of each bolt were sealed with wax to prevent desiccation. Bolts were held for 3 weeks within environmental chambers in darkness at one of four development temperature regimes (= treatments): fixed 12, 18, 21 °C, and alternating 15/21 °C (12/12 h). The rationale for the 15/21 °C was that this was predicted to have more rapid and less synchronous development than at a constant 18 °C if the minimum threshold for starting pupation was between 18 and 21 °C. The experimental design was a randomized complete block with tree as the blocking factor and with random assignment of treatments among bolts of each tree, with each tree represented once (i.e., one bolt) in each treatment. Phloem temperature was recorded hourly using a thermocouple placed beneath the bark. After the 3-week incubation period, bolts were transferred to emergence containers and maintained at a constant 25 °C. The number of adult southern pine beetle emerging from each bolt was counted daily until emergence ceased which required approximately 4–6 weeks. The appearance of larval feeding galleries within our study bolts and the size of adults that emerged from them were indistinguishable from those in nature.

The data consisted of the number of days post-treatment until each individual adult beetle emerged from the bolt. For each bolt, a mean and standard deviation of emergence time was calculated. Synchrony in adult emergence was estimated as the standard deviation of emergence times. A more synchronous population has a smaller standard deviation in emergence time compared to a less synchronous population. Analysis of the data, therefore, consisted of a randomized complete block ANOVA on the standard deviation of emergence times from each bolt. The response variable, standard deviation of emergence times, was approximately normally distributed. We followed this analysis with a Tukey–Kramer HSD post hoc multiple comparisons test to determine differences in the mean of the standard deviation among treatments. The 2011 and 2013 experiments were combined for this analysis.

For the 2013 experiment, additional bolt(s) were cut from three of the sampled trees and these were used to estimate the within-tree population stage structure (egg, larva, pupa, adult) pre- and post-treatment. These additional bolts were cut in half length-wise using a log splitter. One half of each bolt was immediately sampled for population stage distribution, and the other was waxed and then placed into the incubators at one of the four temperature treatments and sampled after the 3-week treatment period. Given the limited number of additional bolts available, each temperature treatment was sampled only once, and every tree was not represented in every treatment. Sampling consisted of carefully removing the bark, locating each individual beetle and noting its life stage. In the case of larvae, individuals were further

classified by instar (early or late), by examining the size of the head capsule. Data were expressed as the proportion of the population in each life stage prior to and following treatment for each bolt.

### Development rate model

We used the following four-parameter insect development rate model described by Briere et al. (1999) to predict the effect of temperature on the development of southern pine beetle larvae in cooler northern climates to that of warmer, southern climates. This was used to test the hypothesis of the temperature-driven mechanism for synchrony.

$$R(T) = aT(T - T_0) \cdot (T - T_L)^{1/m},$$

where  $R$  is the rate of development (%/day) of an individual,  $T$  temperature at time  $t$ ,  $T_0$  lower developmental temperature threshold,  $T_L$  upper development temperature threshold,  $m$  a parameter determining the non-linear shape of the line as the temperature approaches the upper threshold ( $T_L$ ), and  $a$  determines the non-linear shape as temperature approaches the lower development threshold ( $T_0$ ). For the southern pine beetle, parameters were estimated using non-linear model fitting to empirical data from Wagner et al. (1984). These parameter estimates are shown in Table 1. The shape of this temperature-dependent development curve is generally linear, with a slight non-linear region at the lower development temperature threshold, and a pronounced non-linearity at the upper development temperature threshold, similar to that of the other development rate models (Logan et al. 1976; Sharpe and Demichele 1977).

We ran the parameterized model to project the progression of larval development over time using temperatures from fall to spring in our study area. Model output was summarized as the number of days required for beetles to finish larval development as a function of the initial percent of larval development completed at the beginning of the model simulation. The model was run using three separate sets of hourly temperature data. The first set represented temperatures in their expanding northern region (Millville, New Jersey USA), and temperature data spanned the time period October 1, 2010–May 31, 2011. The years of 2010 and 2011 corresponded to a period of rapid population growth and

sustained outbreaks in northern populations of this insect. The second data set represented temperatures within their historic southern range (Natchez, Mississippi USA). Here the temperature data spanned the period November 1, 2010–May 31, 2011 to account for the later onset of cooler weather. Both data sets were acquired from the NOAA National Climate Data Center (<http://www.ncdc.noaa.gov>) and were adjusted to phloem temperatures to account for the buffering effect of tree bark using the Newtonian heat transfer model as outlined in Tr an et al. (2007).

$$T_{t+\Delta t} = T_t + K(A_{t+\Delta t} - T_t)\Delta T,$$

where  $T_{t+\Delta t}$  is the phloem temperature at time  $t + \Delta t$ ,  $A_{t+\Delta t}$  is the air temperature at time  $t + \Delta t$ ,  $T_t$  is the phloem temperature at time  $t$ , and  $K$  is the cooling constant. The adjustment was initiated with a 2 °C temperature reduction and used the equation to predict phloem temperature in each subsequent time step using the measured air temperature data and the predicted phloem temperature from the previous time step. We used a value of 0.28 for the parameter  $K$  in the equation. This value was the average  $K$  obtained by direct, simultaneous measurements of air and bark temperatures from six loblolly pine trees (~25 cm diameter at breast height) at two locations in the Homochitto National forest in 2013 (Lombardo et al., in prep). Finally, the third set of temperatures was drawn at random from a normal distribution with a mean of 25 °C and a standard deviation of 10 °C. This represented a null set with no seasonal pattern in the temperatures. For each of the three temperature data sets we ran the model 100 times with each simulation representing the development of a single individual. To account for initial variation in the point of larval development of each individual on October 1, we started each individual (model run) at a random point of larval development with a mean of 50 percent development completed, and a standard deviation of 10 percent.

### Empirical field data

The spring emergence of southern pine beetle in both southern and northern populations was measured with pheromone-baited traps in 2010 and 2011. Throughout the historic range of southern pine beetle, a trap-based monitoring program has been in effect for decades, from which beetle population levels in national and state forests across the region are assessed each spring (Billings and Upton 2010; Peacher 2011). We replicated this trapping procedure and established networks of twelve Lindgren funnel traps distributed over 167 km within two National Forests in the historic southern distribution of southern pine beetle and one in the expanding northern regions. Study locations were Homochitto National Forest in Mississippi (MS), Oconee National Forest in Georgia (GA), and Wharton State Forest in New Jersey (NJ). Traps were situated within or adjacent

**Table 1** Equation 1 model parameters for southern pine beetle

Stage	$T_{\min}$	$T_{\max}$	$a$ ( $10^{-3}$ )	$m$
Larvae	10	33	0.6039	12.22
Pupae	15	33	1.1366	2.22

Model fit to data by Wagner et al. (1984).  $T_{\max}$  and  $T_{\min}$  reported as degrees celsius

to pine stands but separated from the nearest pine tree by at least 10 m. The traps were baited with a combination of the aggregation pheromone component frontalin (racemic) plus a blend of alpha- and beta-pinene, two monoterpenes that are typically abundant in pine resin, which strongly synergizes the attractiveness of the pheromone (elution rates of 5 and 170 mg/days, respectively). The traps were deployed to coincide with the approximate beginning of southern pine beetle emergence: mid-February at both southern sites, and mid-March in the North. The traps were emptied weekly and the contents were sorted and identified. Trapping occurred for 8 weeks each spring in each forest, with exception of the northern site in 2010, which had to be terminated while spring captures were still occurring after 7 weeks (for this reason these data were omitted from portions of the analyses).

Trap data were analyzed for synchrony of captures for all six forest-years (3 sites  $\times$  two or three spring trapping seasons per site). This was done by pooling the data from the 12 traps in each forest, estimating the standard deviation of capture date of individual southern pine beetles, and using the reciprocal of the standard deviation as a measure of synchrony. This produced a single estimate of adult emergence synchrony for each forest-year. We compared the influence of fall–winter temperature on adult emergence synchrony by examining the relationship between synchrony and the occurrence of synchronizing temperatures for the six forest-years. Daily maximum and minimum temperatures for both locations in the historic southern range (Oconee and Homochitto) and for the three trapping years (2010, 2011, 2013) were acquired from the National Climate Data Center (NCDC). These were downscaled to hourly air temperatures following Cesaraccio et al. (2001), and the hourly air temperatures were adjusted as before to estimate hourly phloem temperatures. For northern sites, hourly temperature data for both trapping years was available from NCDC. The temperatures for each forest-year were plotted as a frequency distribution, and the proportion of fall and winter temperatures below the 15 °C pupation threshold in each forest-year was calculated by integrating under the density function fit to the data. We then used a linear regression analysis to examine the relationship between the proportion of temperatures below 15 °C in each forest-year, and adult emergence synchrony ( $1/\text{sd}$  of capture date). We used the reciprocal of the standard deviation to make interpretation of the figure more intuitive.

## Results

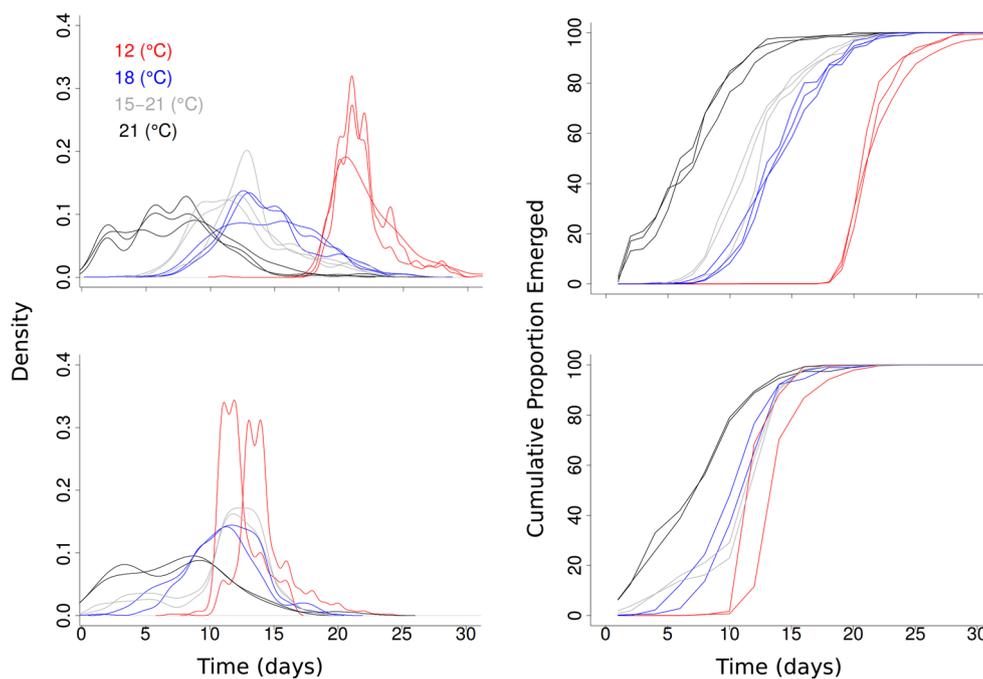
### Emergence synchrony lab experiments

There was a strong effect of larval thermal environment on emergence synchrony of new adult beetles for both experiment years combined, with colder temperatures resulting in greater synchrony even though development time was longer ( $F_{3,12} = 26.21$ ,  $p < 0.001$ ). Post hoc Tukey–Cramer multiple comparisons indicated that synchrony in the 12 °C treatment was significantly greater than all other treatments, and synchrony at 18 °C was greater than at 21 °C. This was evident in the distributions of emergence times (Fig. 1). The mean ( $\pm$  SD) synchrony values (SD of emergence time) for the 12, 18, 15/21 and 21 °C treatments were  $1.9 \pm 0.4$ ,  $3.0 \pm 0.5$ ,  $3.6 \pm 0.1$ , and  $4.2 \pm 0.3$  d, respectively, for the 2011 experiments, and  $2.5 \pm 0.6$ ,  $3.5 \pm 0.3$ ,  $3.5 \pm 0.3$ , and  $3.9 \pm 0.3$  d, respectively, for 2013. There was little or no variation in treatment effects among study trees ( $F_{4,12} = 2.71$ ,  $p = 0.08$ ).

Temperature treatment effects on population stage structure were also evident in the destructively sampled bolts of the 2013 experiment. Prior to the treatments, all larval instars were present in all trees, and there were no pre-pupae or pupae (pre-pupa are those that have completed feeding and migrated to the outer bark for pupation; Tr an et al. 2007) (Table 2). The life stage structure varied somewhat amongst trees, but all were skewed toward late instar larvae (Table 2). Following 3 weeks of treatment, all temperatures except for the 12 °C treatment included individuals that had developed into pupae. Thus, the threshold temperature for pupation was above 12 °C and below 18 °C (lower than our a priori hypothesis of 15–20 °C). The stage structure of the 12 °C treatment was almost all late larvae, as expected if the minimum temperature for molting into pupae is greater than 12 °C. Across the three warmer temperature treatments, the percentage of individuals that pupated during the 3-week exposure period increased as a function of temperature.

### Development model results

Using hourly temperature records from the northern distribution of this insect (Fig. 2) the model predicted a bifurcation of the population following the onset of cold temperatures in the fall (beginning October 1, 2010) (Fig. 3). Simulated individuals that had completed approximately 48% or more of total larval development by October 1 completed larval development that fall, approximately 4–8 weeks later. However, by the time most of these individuals completed larval development, temperatures were consistently cool and possibly below the minimum needed for pupation. This is clearly evident in Fig. 2. Because of this, these individuals were expected to overwinter as pre-pupa. Therefore, the



**Fig. 1** Density plots of emergence time (left), and cumulative emergence (right) for the 2013 (top) and 2011 (bottom) temperature–synchrony experiments. Each accumulation curve represents data from a single bolt.  $N=712$ , 546, 342, and 756 southern pine beetles for

the 12, 18, 21, and 15–21 °C temperatures, respectively, in the 2011 experiment, and  $N=1496$ , 1698, 1467, and 1166, respectively, for the 2013 experiment

**Table 2** Beetle life stage distribution in bolts pre- and post-3-week temperature treatments

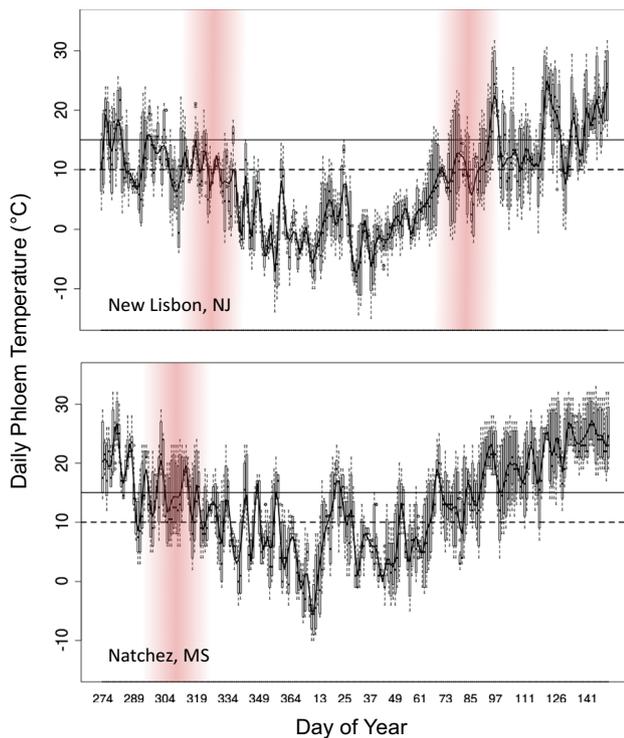
Treatment (°C)	Larval instar				<i>N</i>
	Early	Late	Pupae	Teneral adults	
12					
Pre	11	89	0	0	392
Post	2	98	0	0	101
18					
Pre	39	61	0	0	155
Post	0	60	41	0	89
15–21					
Pre	32	68	0	0	255
Post	0	53	48	0	254
21					
Pre	36	65	0	0	146
Post	0	0	59	41	76

Values indicate percentage of total number in each life stage. Early and late instar classifications were approximated by head capsule size. Late instars included pre-pupae

variation in larval development that existed in individuals in this portion of the population was essentially removed, and all of these simulated individuals overwintered at the same end-point of larval development (pre-pupae). This convergence of the life stage structure facilitates a synchronous

emergence of adults the following spring. The remaining individuals in the simulated population overwintered at various stages of larval development, and were predicted to complete larval development approximately 6 months later, once temperatures warmed (Figs. 2, 3). Because individual variation in larval development was preserved through the winter, we would expect this portion of the population to have a less synchronous spring adult emergence.

In contrast, the same model run with hourly temperature records from the historic southern range of the southern pine beetle (Natchez, MS 2010) did not show the same pattern of convergence in the life stage structure of the simulated individuals. Rather, we saw a continuous, almost linear decline in the number of days required to complete larval development as a function of an individual's initial percent of development completed (Fig. 3). Most importantly, as individuals completed larval development, temperatures remained above the pupation threshold for an extended period of time (Fig. 2). Therefore, simulated individuals under these warmer conditions would likely have overwintered at various stages as pupae or teneral adults and, therefore, were expected to have relatively low synchrony of adult emergence in the spring. Finally, results from the null model run with temperatures lacking seasonality ( $25 \pm 5$  °C) resulted in a linear decline in the number of days required to complete larval development. As was the case with southern temperatures, individuals in this simulation would likely



**Fig. 2** Temperature data from northern [New Lisbon, New Jersey USA (top)] and southern [Natchez, Mississippi USA (bottom)] regions of southern pine beetle habitat in 2010. Dotted line indicates lower development threshold for southern pine beetle larvae (10 °C, see Wagner et al. 1984). Solid line indicates estimated lower threshold for pupation (15 °C). Red shaded area indicates the approximate mean and standard deviation of the date when larval development was completed. Separate estimates were calculated for the two modes in the NJ model of development data

have overwintered as pupae or teneral adults and, therefore, would be expected to have low synchrony the following spring (Figs. 2, 3).

### Field trapping results

Results from the three seasons of field trapping data generally supported the hypothesis that cooler winter temperatures promote synchrony in spring adult emergence. There was a significant positive relationship ( $t=4.39$ ,  $p=0.007$ ) between the occurrence of synchronizing temperatures the previous fall–winter period ( $<15$  °C), and synchrony in the following spring of adult beetles for the most complete data sets (Fig. 4). The exception was the 2010 trap catches from the northern sites, which had low synchrony (1/sd of capture date) compared with the southern forests (Table 3). However, this was likely an artifact of our northern trapping program having begun too late in 2010, missing the critical start of the spring adult emergence. Because of this, the 2010 northern trapping data were excluded from subsequent analysis. In the following season (2011), northern

beetle captures were clearly more synchronous than either of the two southern forests.

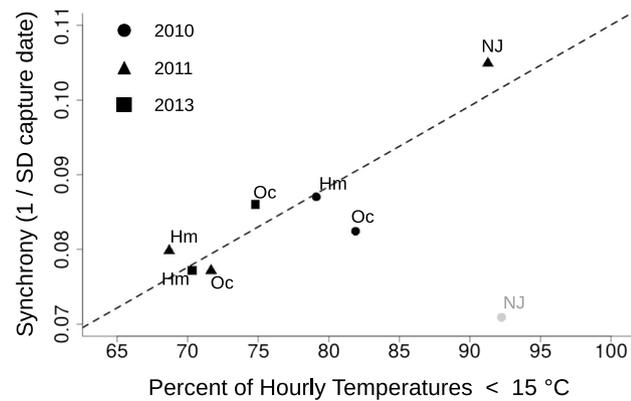
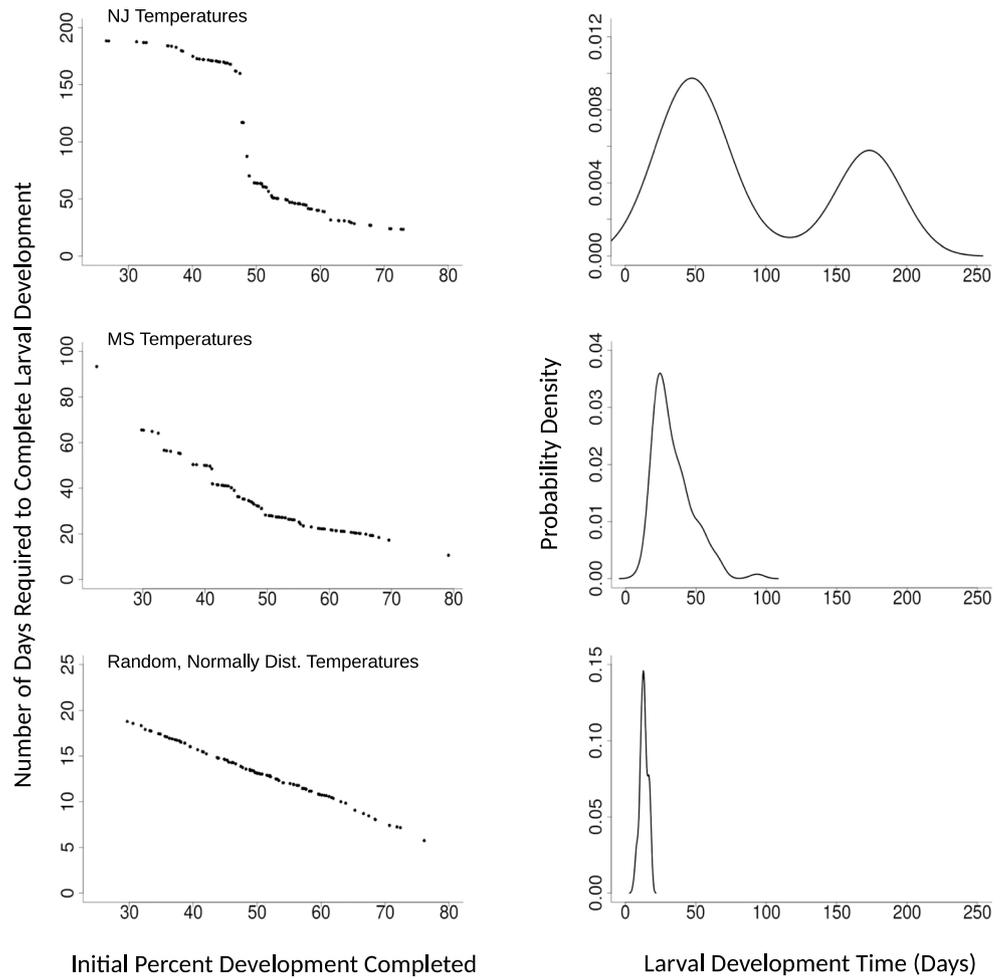
### Discussion

Southern pine beetles can be added to the list of insects in which life stages are known to differ in their thermal sensitivity (Bentz et al. 1991; Kingsolver et al. 2011; Briscoe et al. 2012; Radchuk et al. 2012; Pincebourde and Casas 2015). In our experiments, larval growth proceeded at 12 °C but, unlike the warmer treatments, pupation did not occur and larvae pooled up as pre-pupae (Table 2). Accordingly, when our experimental bolts were then warmed so that development could proceed, the adults emerged abruptly from the 12 °C, but were distributed over time in the warmer treatments (Fig. 1). This indicates that temperatures during fall and winter can promote or limit the synchrony of southern pine beetle activity in spring. The same could be true for any insects that have variable thermal responses among life stages, lack diapause, and experience cool winters. The absence of diapause is more common in insects native to tropical, subtropical, or temperate regions and becomes less common poleward (Tauber et al. 1986). The absence of diapause may become more common as species such as the southern pine beetle expand their distributions poleward in response to warming climates (Lesk et al. 2017).

Results from the variable 15–21 °C temperature treatment were remarkably similar to the constant 18 °C treatment, in both the timing of adult emergence and in emergence synchrony. This demonstrated that the lower developmental threshold for pupation was not within the range of 16–20 °C. If there had been a developmental threshold in this range, the corresponding nonlinearity in development rate as a function of temperature would have caused development time at variable temperatures (15–21 °C) to diverge, via Jensen's inequality, from those of animals experiencing a constant temperature with the same average (18 °C) (Ruel and Ayres 1999).

Our results and the apparent mechanism match those of Bentz et al. (1991), who studied the effects of temperature on phenological synchrony of the closely related mountain pine beetle, *Dendroctonus ponderosae*. Mountain pine beetles have but one generation per year, versus several in southern pine beetles, but both progress similarly through developmental stages and both lack overwintering diapause. Subsequent work with mountain pine beetle has proven that even modest discrepancies in the developmental thresholds of different life stages can create synchrony as long the threshold for at least one life stage was significantly greater than the others (Logan and Bentz 1999; Powell et al. 2000; Jenkins et al. 2001).

**Fig. 3** A model of southern pine beetle larval development showing the influence of temperature on population stage structure. The population is split into a high- and a low-synchrony portion when the model is run with 2010 temperature data from the northern region of their distribution [New Jersey (top)], but not when using temperatures from Mississippi (middle), nor in a null model (bottom) with temperature drawn from a normal distribution (mean = 25, SD = 10). Each point represents one individual. Temperatures were taken from October 1–May 31 (Fig. 2). Each individual started from a random development point (normal distribution, mean = 50%, SD = 10%). Note differences in scales of y-axes



**Fig. 4** Occurrence of temperatures in the synchronizing range (< 15 °C) and synchrony of the spring dispersal flight of adult southern pine beetle ( $t=4.390$ ,  $p=0.007$ ,  $Adj\ r^2=0.75$ ). Data are from three trapping seasons at two sites in the species southern range [Homochitto Natl. Forest (Hm), Oconee Natl. Forest (Oc)], and one season in the northern range (Pinelands region of New Jersey). The northern 2010 trapping was incomplete and, therefore, the data point (shown in grey) was not included in the regression model

**Table 3** Data from two seasons of spring emergence field trapping of new adult southern pine beetles from two forests in its historic southern range (Homochitto and Oconee National Forests) and one in the northern range of its distribution (New Jersey)

Forest	Year	$N_{SPB}$	Trap installation (day of year)	$N_{weeks}$	1/SD of capture date
New Jersey	2010	13,124	107	7	0.071
Homochitto	2010	898	70	8	0.087
Oconee	2010	5325	95	8	0.082
New Jersey	2011	8613	106	8	0.105
Homochitto	2011	11,862	69	8	0.080
Oconee	2011	2825	76	8	0.077
Homochitto	2013	7298	58	8	0.077
Oconee	2013	6803	66	8	0.086

12 traps were monitored at each site in both years. Trap captures were pooled for each forest-year to calculate SD

We tested the hypothesis of geographically structured, climatically enforced, patterns in emergence synchrony of southern pine beetles by applying an individual-based model

of larval development rate to compare simulated populations experiencing temperatures of northern (New Jersey) vs. southern (Mississippi) locations. With northern temperatures, but not with southern temperatures, populations tended to bifurcate during fall and winter into high- and low-synchrony fractions, with the percent of larval development completed leading into the late fall cold periods as the determining factor. The high-synchrony portion of the northern population was comprised of simulated individuals that completed larval development in mid-winter, by which time the onset of cold temperatures prevents pupation (Fig. 2). The remainder of the population was quiescent at various stages of larval development through the winter until temperatures warmed the following spring. Temperatures from the historical southern range of the population failed to produce the same patterns of synchrony in the modeled population (Fig. 3). Although temperature in the historical southern range consistently fell within the 10–15 °C synchronizing zone, it also frequently crossed the threshold for pupation (Fig. 2), which would likely disrupt the synchrony mechanism. These results are consistent with previous reports that pre-pupae are an ephemeral life stage in southern populations, even during winter months (Thatcher 1967; Ayres et al. 2011), but can become a dominant fraction of the population in more northern areas (Lombardero et al. 2000; Trân et al. 2007). Pre-pupae are also the most cold-tolerant life stage of southern pine beetles (Trân et al. 2007). Thus, individuals that enter the winter as life stages other than pre-pupae (the low-synchrony group in population simulations) are more likely to die from cold during the winter. This mortality pattern could further increase the tendency for synchrony of southern pine beetle activity in spring, by eliminating the out-of-sync individuals.

Our spring trapping data of wild beetle populations indicated that geography, which was correlated with fall and winter temperatures, was related to synchrony, with a tendency for greater synchrony in the region that had more temperatures lower than the threshold for pre-pupae to molt (ca. 12–15 °C). The northern trapping results from 2010 were an exception. We think this was partly because we started out trapping too late that year, but we would expect that geographic patterns in synchrony would vary depending on particulars of fall and winter temperatures in each year.

It is conceivable that geographic patterns in the size threshold for pupation, as have been reported in some insects (Shelomi 2012), could influence geographic patterns in flight synchrony. To our knowledge, geographic patterns in the size of *D. frontalis* adults have not been specifically studied. However, we sorted and counted many *D. frontalis* from MS, GA, and NJ as part of the present study and perceived no geographic patterns in body size.

Our modeling results and interpretation of the trapping data assume little or no genetic variation among populations

of *D. frontalis* in the traits that influence adult emergence time. This is consistent with existing evidence for limited genetic isolation by distance in *D. frontalis* across our study regions and a lack—at least thus far—of any unique genetic signatures in *D. frontalis* from New Jersey (Schrey et al. 2011). However, it is logical that natural selection would act on such traits and there is a need for further study of regional patterns in the developmental biology and emergence phenology of *D. frontalis*.

Our results inform understanding of southern pine beetle population dynamics. Southern pine beetles have been regarded as having cyclical dynamics (Reeve 1997; Cronin et al. 2000; Reeve and Turchin 2002), but the evidence now indicates that rather than cycles there are alternative, approximately stable, equilibria, one at low abundance and one at outbreak abundance (Mawby et al. 1989; Martinson et al. 2013; Weed et al. 2016). The stability of low and high equilibria depends upon negative density dependence at both high and low densities, and the transitions between them occur due to a region of positive density dependence (from increasing reproductive success when there are more beetles to join in the attacks of host trees) (May 1977; Boucher 1985 pg. 257–258). While at low abundance, populations are restricted to attacking trees that have been previously weakened—typically lightning struck trees (Hodges and Pickard 1971; Coulson et al. 1986), which are rare on the landscape. Stochastic fluctuations in abundance can permit populations to escape bounds of the lower equilibrium and increase to outbreak abundances. Interannual variations in fall and winter temperatures that sometimes produce high synchrony of spring activity are one mechanism that could promote the start of outbreaks. Predictors of spring flight synchrony could be candidates to enhance the reliability of southern pine beetle population predictions based on spring trap captures (Billings and Upton 2010; Aoki 2017).

Despite the benefits to southern pine beetle populations of synchronous spring flights, there are demographic costs of synchrony beyond the initial spring cohort. Southern pine beetles rely on continuous attacks of trees, with continuing release of aggregation pheromones, to sustain the growth of individual infestations; synchrony in the initial colonization of host trees aids in the attack phase but promotes the risk of a subsequent demographic gap in the appearance of new adults to sustain attacks (Friedenberg et al. 2007). There is need for further work to understand how temperature influences southern pine beetle life stage structure throughout the annual cycle, but for most multivoltine insects, synchrony accrued during the overwintering period has a tendency to break down through the course of the growing season (Bjørnstad et al. 2016). Improved understanding of controls on synchrony can be useful for management of southern pine beetles and perhaps for other populations that are similarly structured by thermal effects on life stage structure.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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