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RESEARCH ARTICLE

Assessment of changes in thermal conditions for *Callipogon relictus* (Coleoptera, Cerambycidae) development under climate warming: a degree-day modelling approach

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Abstract

Temperature-based models can be used to assess how imposed warming scenarios alter the potential thermal contribution to insect development, although their outputs depend on the selected lower developmental threshold. We assessed the spatial sensitivity of a degree-day model for *Callipogon relictus* at four localities using daily air temperatures for 2010–2025 and five uniform temperature increments (+0.55 to +3.55 °C). A working threshold of 17.65 °C was derived from three published laboratory means; because this estimate is uncertain, the calculations were repeated using fixed thresholds of 10, 12 and 15 °C. Among the four localities, Chuguyevka exhibited the greatest relative reduction and Yeongwol the smallest at all four thresholds. Under the +3.55 °C scenario, the modelled reduction in thermal-time duration ranged from 29.0–32.8% at T0=10°C, 32.0–37.1% at 12 °C, 37.7–45.6% at 15 °C, and 44.9–56.0% at 17.65 °C. The ranking of localities was stable across the tested settings, whereas the magnitude of the response depended on T0. The uniform increments represent sensitivity scenarios rather than regional climate projections. Under the +3.55 °C scenario, normalised duration estimates ranged from 1.76 to 2.60 years, approaching the time scale of an approximately two-year semivoltine cycle. This result is conditional on the model assumptions and does not predict realised

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voltinism or calendar-time development, both of which also depend on wood microclimate, diapause, substrate conditions, larval instar plasticity and survival.

Keywords
Callipogon relictus, Cerambycidae, climate warming, degree-day model, larval development, phenological sensitivity, thermal threshold

Introduction

Temperature is one of the principal factors determining the rate of ontogeny, seasonal timing of activity, and potential generation time in insects. Under contemporary climate warming, changes in thermal conditions can shift phenological events, alter diapause and overwintering, and affect the potential number of generations (Altermatt 2010; Bale and Hayward 2010; Régnière et al. 2012; Forrest 2016; Pureswaran et al. 2018; IPCC 2021). However, the response of ectotherms is not limited to a linear acceleration of development: both the direction and magnitude of the response depend on the species and developmental stage, the seasonal timing of thermal exposure, resource availability, and proximity to sublethal or lethal limits (Altermatt 2010; Bale and Hayward 2010; Régnière et al. 2012; Moore and Remais 2014; Forrest 2016; Pureswaran et al. 2018). Therefore, the biological effect of an identical increase in mean temperature may differ among parts of a species' range even under the same direction of climatic change.

Interpreting thermal responses is especially difficult for saproxylic insects. Their larval development occurs inside wood, and ambient air temperature is only an external indicator of the thermal environment rather than a direct measure of it. Developmental rate may depend on host-tree condition, wood moisture and degree of decomposition, nutrient availability, and interactions with microorganisms. Accordingly, the temperature-dependent component of a multiyear life cycle must be separated from total field development, which is shaped by several interconnected abiotic and biotic factors.

Degree-day models make it possible to formalise one aspect of this relationship. In the classical linear formulation, the positive contribution of temperature to development is counted above the lower threshold T0, and completion of the stage requires accumulation of a defined thermal sum K. Such models are widely used to compare phenology among years and regions; however, their reliability depends on the quality of experimental estimates of the threshold and thermal constant, on the correspondence between the linear range and actual temperatures, and on the treatment of diapause, upper thermal limits, and stage-specific variation (Campbell et al. 1974; Danks 2000; Ikemoto and Takai 2000). For species with multiyear development, this approach is most informative as a tool for analysing relative thermal sensitivity; its transfer to an absolute field prediction requires independent biological validation.

The most detailed temperature–phenology models for Cerambycidae have been developed primarily for economically important and invasive species. In *Anoplophora glabripennis*, variable larval instar number has been incorporated into an individual-based climate model, and its individual components have been validated against field data (Trotter and Keena 2016; Schmitt et al. 2025a, 2025b). Laboratory studies of this species have also shown stage-specific heterogeneity in thermal response (Keena 2006; Keena and Moore 2010). For *Monochamus galloprovincialis*, threshold temperatures and degree-day requirements after dormancy have been determined (Naves and de Sousa 2009), whereas in *Psacothea hilaris*, the transition to diapause and subsequent metamorphosis depends not only on temperature and photoperiod, but also on the larva reaching a threshold body mass (Shintani et al. 1996; Munyiri et al. 2004). These studies show that additional heat can shorten developmental stages in longhorn beetles, but final generation time is also determined by instar structure, physiological condition, and seasonal constraints. Therefore, numerical parameters derived for model pests cannot be directly transferred to rare saproxylic species.

Callipogon relictus Semenov, 1899 is a rare saproxylic longhorn beetle distributed in the southern Russian Far East, northeastern China, and the Korean Peninsula (Yi et al. 2018; Lee et al. 2018; Kang et al. 2021). Known populations are spatially fragmented, and the conservation of the species depends on the presence of old-growth broadleaf forests and large-diameter wood suitable for prolonged larval development (Yi et al. 2018; Lee et al. 2018; Kang et al. 2021; Lee et al. 2021). Recorded host plants include representatives of several genera of deciduous trees; accordingly, the availability of suitable larval substrate is determined not by a single tree species, but by a combination of host composition and wood characteristics (Yi et al. 2018; Lee et al. 2019; Lee et al. 2021). The combination of multiyear concealed development, fragmented distribution, and conservation status makes *C. relictus* a suitable model for examining how spatial heterogeneity in thermal conditions may be expressed in the life cycle of a rare wood-boring insect.

Field observations and semi-natural rearing data indicate that the larval stage of *C. relictus* usually lasts several years and varies across different parts of the range (Kuprin and Bezborodov 2012; Jingke et al. 2012, 2013; Kuprin et al. 2014; Yi et al. 2026). Moreover, rearing on artificial diets has demonstrated substantial developmental plasticity. At constant temperatures of 20, 25, and 30 °C, mean development time decreased sharply with increasing temperature, and at 30 °C trajectories with 8, 10, and 12 larval instars were recorded (Yi et al. 2019). The use of a fungal diet also substantially shortened the larval period relative to the presumed natural duration (Yi et al. 2017a). These data confirm the joint importance of temperature and substrate quality, but they were obtained under controlled conditions and do not by themselves determine developmental rates within wood under natural conditions.

For *C. relictus*, habitat suitability and its potential change under climate scenarios have already been assessed (Kuprin et al. 2024), but such models do not provide a quantitative estimate of the thermal phenology of the larval stage. The available ex-

perimental basis for a temperature model is limited to three published mean values (Yi et al. 2019), and local estimates of field duration differ in their degree of support (Jingke et al. 2012; Kuprin et al. 2014; Yi et al. 2026). None of the available biological data from natural conditions includes comparable measurements of wood microclimate. Therefore, the existing evidence is insufficient for an independent prediction of absolute developmental duration at a given site, and even more so for conclusions about future voltinism or population dynamics. However, these data allow a more specific question to be addressed: does the relative response of the temperature-dependent component of a multiyear cycle to an identical thermal increment depend on the local temperature distribution relative to the lower developmental threshold?

The aim of this study was to quantify threshold-mediated spatial variation in the sensitivity of the temperature-dependent component of larval development in *C. relictus* to imposed temperature increments. Working estimates of the lower thermal threshold and thermal constant were derived from three published laboratory means. Annual sums of effective temperatures were calculated from daily air temperatures for 2010–2025 at four localities with documented reference developmental durations, and model outputs were scaled to these reference values. The five uniform increments were used solely as a standardised framework for sensitivity analysis and not as regionally resolved climate projections.

Three interrelated hypotheses were tested: (i) at a fixed lower threshold, increasing temperature would monotonically increase annual sums of effective temperatures and reduce normalised model duration; (ii) the magnitude of the relative response would differ among localities because an identical increment alters the number of days exceeding the selected threshold; and (iii) the strongest relative response would occur where baseline daily temperatures are concentrated near or below that threshold. The results supported these expectations within the four modelled localities and the tested threshold settings.

Materials and methods

Study design and overview

This study comprised a deterministic sensitivity analysis of the temperature-dependent component of larval development in *Callipogon relictus*. The analytical framework comprised: (i) descriptive estimation of a linear temperature relationship from published laboratory means; (ii) daily air-temperature series for four locations within the species' range; (iii) calculation of annual sums of effective temperatures; (iv) scaling of model outputs to documented reference developmental durations; and (v) application of standardised temperature increments. This approach follows the general logic of degree-day models within an approximately linear range of thermal response (Campbell et al. 1974; Ikemoto and Takai 2000; Jarošík et al. 2004, 2014).

Climatic and biological input data

Daily maximum and minimum air temperatures at 2 m above ground level for 1 January 2010 to 31 December 2025 were obtained from the Open-Meteo Historical Weather API (Zippenfenig 2026) for the four model localities (Figure 1, Table 1). Each site-specific series comprised 5,844 calendar days, including leap years; 23,376 daily records were analysed in total.

Reference larval development durations were obtained from the published sources listed in Table 1. Where a source reported a range, its midpoint was used. Only localities with traceable reference-duration information were included in the normalised comparison; estimates based solely on unpublished observations, without an independent measure of uncertainty, were excluded. Reference durations were used only to scale model outputs, and their uncertainty was not modelled separately.

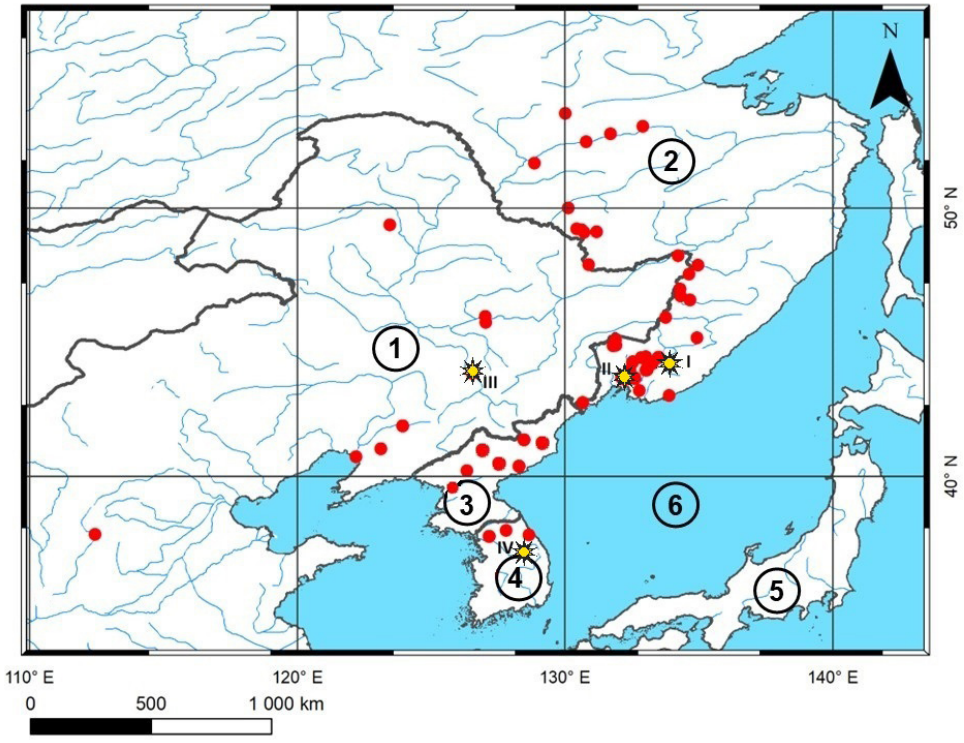


Figure 1. Known geographical distribution of *Callipogon relictus* in northeast Asia (Kuprin et al. 2024). Numbers indicate: 1 – China; 2 – Russia; 3 – North Korea; 4 – South Korea; 5 – Japan; 6 – Japanese (Eastern) Sea. The model sites are designated by Roman numerals: I – Chuguyevka (CHU); II – Ussuriysk (USS); III – Jilin (JIL); IV – Yeongwol (YEO).

Table 1. Characteristics of the four model localities included in the analysis

Location	Code	Lat.	Lon.	Elev. (m)	Reference field duration (years) / source
Chuguyevka, Primorye Territory, Russia	CHU	44.1828°N	133.9024°E	260	4.0 / Kuprin et al. (2014)
Ussuriysk, Primorye Territory, Russia	USS	43.6907°N	132.2172°E	79	4.0 / Kuprin et al. (2014)
Jilin, Jilin Province, China	JIL	43.9016°N	126.5455°E	203	5.0 / Jingke et al. (2012)
Yeongwol, Gangwon Province, Korea	YEO	37.1836°N	128.4617°E	223	3.5 / Yi et al. (2026)

Laboratory parameters of temperature-dependent development

The published mean durations of larval development at constant temperatures of 20, 25, and 30 °C on an artificial diet were used as the biological basis of the analysis (Yi et al. 2019). The numbers of individuals that completed development were 5, 11, and 9, respectively; the mean larval development durations were 1360.20 ± 1.72, 338.50 ± 2.30, and 226.89 ± 66.93 days, respectively (Table 2).

Table 2. Mean duration of larval development in *C. relictus* and derived development rate at three constant temperatures according to Yi et al. (2019)

Temperature (°C)	Observed larval duration D (days)	Developmental rate (day^{-1})	n	Duration ± SD (days)
20	1360.20	0.0007352	5	1360.20 ± 1.72
25	338.50	0.0029542	11	338.50 ± 2.30
30	226.89	0.0044074	9	226.89 ± 66.93

For each temperature level j, the development rate (rj) was calculated as the inverse of development duration (Dj) (Campbell et al. 1974; Ikemoto and Takai 2000; Ikemoto 2005):

$$r_j = \frac{1}{D_j} \tag{1}$$

Because individual observations and their variances were not incorporated into the primary model, each published mean was treated as a point estimate. Linear regression was used as a descriptive approximation of the temperature dependence within the studied range:

$$r(T) = a + bT \tag{2}$$

where a is the intercept, b is the slope, and T is the constant rearing temperature (°C). This yielded the equation $rT=-0.00648165+0.00036722T$, with a descriptive $R^2=0.9857$. The lower developmental threshold (T_0) and thermal constant (K) were calculated as:

$$T_0 = -\frac{a}{b} \tag{3}$$

$$K = \frac{1}{b} \tag{4}$$

The point estimates were $T_0=17.6504$ °C and $K=2723.14$ degree-days (hereafter, 17.65 °C and 2723.1 degree-days). The high R^2 reflects the fit to the three published means and does not represent independent validation of the parameters; T_0 and K were not interpreted as final physiological constants of the species (Campbell et al. 1974; Ikemoto and Takai 2000; Yi et al. 2019). Biologically, T_0 represents the estimated lower boundary below which the temperature contribution to larval development is assumed to be zero, whereas K denotes the cumulative amount of effective heat required to complete larval development under conditions comparable to the laboratory experiment.

The linear fit is descriptive: with three temperature means, it has one residual degree of freedom and does not provide a reliable test of model form or a precise estimate of the physiological threshold. Because the reported dispersion differed substantially among temperature treatments, an exploratory weighted least-squares model was also fitted using the weights:

$$w_j = SE(r_j)^{-2} \tag{5}$$

where the delta-method approximation was

$$SE(r_j) \approx \frac{SD(D_j)}{\sqrt{n_j} D_j^2} \tag{6}$$

This weighted fit was treated only as a diagnostic because it was based on three aggregate values and an approximate variance transformation (Oehlert 1992; Ikemoto 2005).

Calculation of daily and annual degreeday sums

For each day i and locality l, mean daily temperature was calculated as the average of daily maximum and minimum temperatures:

$$T_{mean,\,i,\,l} = \frac{T_{max,\,i,\,l} + T_{min,\,i,\,l}}{2} \tag{7}$$

The daily contribution to degree-day accumulation was defined relative to T_0=17.65 °C, with negative values set to zero:

$$GDD_{i,\,l} = max[0;\ T_{mean,\,i,\,l} - T_0] \tag{8}$$

The annual sum of effective temperatures for year y was calculated by summing daily contributions over 365 or 366 days:

$$AGDD_{y,\,l} = \sum GDD_{i,\,l} \tag{9}$$

In addition, the number of days per year with mean temperature exceeding T_0 was determined. For the 16 annual values obtained at each locality, the mean, standard deviation (SD), standard error (SE), coefficient of variation (CV = 100 × SD/mean), and a descriptive 95% t-interval (mean ± $t_{0.975;15}$ × SE) were calculated. The intervals were computed under the assumption of independence of annual values; temporal autocorrelation was not assessed separately.

This calculation based on mean daily temperature does not account for threshold crossing within a day. In addition, the linear parameters were derived at 20–30 °C, whereas the GDD (growing degree-days) calculation formally extrapolates the relationship beyond this range and does not define an upper thermal threshold. Therefore, daily contributions outside the experimental range were treated as part of the computational approximation rather than as a direct physiological measurement (Campbell et al. 1974; Ikemoto and Takai 2000; Jarošík et al. 2014).

Normalisation to reference development duration

First, for each locality, a direct temperature-based estimate of larval development duration (Ldirect) was calculated as the ratio of the laboratory thermal constant to the mean annual sum of effective temperatures for the baseline period:

$$L_{direct,\,l} = \frac{K}{AGDD_{baseline,\,l}} \tag{10}$$

This value was used only as an intermediate calculation and was not treated as field development duration, because it does not account for diapause, winter arrest, temperature and moisture conditions of the wood, or substrate quality. To convert the result to the scale of reference duration, a scaling coefficient was introduced:

$$q_l = \frac{L_{direct,\,l}}{L_{ref,\,l}} = \frac{K}{AGDD_{baseline,\,l} \cdot L_{ref,\,l}} \tag{11}$$

The scaling coefficient was introduced solely to express the model output on the scale of the selected reference duration. It is not an independently estimated biological parameter and does not validate the absolute duration obtained from the degree-day calculation. After normalisation, the thermal constant Kcancels algebraically from the relative scenario comparison; the relative reduction is determined by the ratio of baseline to scenario AGDD. Absolute normalised durations therefore depend on the reference duration, whereas relative reductions do not.

Standardised temperature increments

Model sensitivity was evaluated for five uniform temperature increments: +0.55, +0.95, +1.85, +2.75, and +3.55 °C (Table 3). The numerical range was chosen with reference to central global warming estimates presented by the IPCC (2021); however, each increment was uniformly added to all daily temperatures at all studied localities. Therefore, these levels were treated exclusively as standardised sensitivity scenarios, without attribution to specific emission scenarios or regional climate projections.

Table 3. Standardised temperature increments used in the sensitivity analysis (IPCC 2021)

Analysis level	ΔT (°C)	Calculated difference (°C)	Role in analysis
Baseline period	0.00	2010–2025 series	Reference level
Increment 1	+0.55	1.40 – 0.85	Sensitivity level
Increment 2	+0.95	1.80 – 0.85	Sensitivity level
Increment 3	+1.85	2.70 – 0.85	Sensitivity level
Increment 4	+2.75	3.60 – 0.85	Sensitivity level
Increment 5	+3.55	4.40 – 0.85	Sensitivity level

Note: Estimates of 1.40–4.40 °C refer to 2081–2100 relative to 1850–1900; 0.85 °C corresponds to 1995–2014 relative to 1850–1900 (IPCC 2021).

Calculation of indicators under standardised temperature increments

Each increment ΔT_s was added to all daily values of T_{max} and T_{min}; equivalently, the mean daily temperature was modified as:

$$T_{mean,\,i,\,l,\,s} = T_{mean,\,i,\,l} + \Delta T_s \tag{12}$$

Daily and annual sums of effective temperatures were then recalculated relative to the unchanged T_0:

$$GDD_{i,l,s} = max[0;\ T_{mean,i,l} + \Delta T_s - T_0] \tag{13}$$

For each level, the mean AGDD (accumulated growing degree-days) over 16 years was used. The estimated duration on the scale of reference values was determined as:

$$L_{scenario,l,s} = \frac{K / AGDD_{l,s}}{q_l} \tag{14}$$

After substitution of expression (9), the formula simplifies to:

$$L_{scenario,l,s} = \frac{L_{ref,l} \cdot AGDD_{baseline,l}}{AGDD_{l,s}} \tag{15}$$

Accordingly, after normalisation, K cancels out algebraically. The influence of the laboratory-derived data on the relative scenario estimates is retained through T_0, which determines the baseline and recalculated AGDD values. Absolute and relative reductions in duration were calculated as:

$$\Delta L_{l,s} = L_{ref,l} - L_{scenario,l,s} \tag{16}$$

$$S_{l,s} = 100\ (1 - \frac{L_{scenario,l,s}}{L_{ref,l}}) \tag{17}$$

Precipitation, relative humidity, soil temperature and moisture, the condition of the host wood, and demographic parameters under different ΔT levels were not measured and were not included in the development rate calculations.

Sensitivity analysis using alternative lower thresholds

Because the lower developmental threshold was estimated from only three laboratory means, we assessed the extent to which the spatial response depended on the selected threshold. Daily calculations were repeated using fixed thresholds (T_0) of 10, 12 and 15 °C, in addition to the primary working value of 17.65 °C. These alternatives represent sensitivity settings rather than experimentally established thresholds for *C. relictus*. For each setting, daily effective temperature sums were recalculated for the baseline period and each uniform increment. The relative reduction in modelled thermal-time duration was calculated as:

$$1 - \frac{AGDD_{baseline}}{AGDD_{scenario}} \tag{18}$$

This ratio is independent of the site-specific reference duration and thermal constant K. The analysis therefore assesses the sensitivity of relative scenario responses to T_0, rather than the accuracy of absolute duration estimates.

Reproducibility and Model limitations

Site metadata (Data S1), the daily climate matrix (Data S2) and derived tables (Data S3–S7) are provided in the Supplementary Materials. Calculations were performed in R (R Core Team 2025) using base R. The workflow imported the climate matrix for the four sites, estimated the laboratory model parameters, calculated daily and annual degree-day sums, applied the temperature increments, normalised the outputs and exported the final tables.

The primary linear parameterisation is based on three published mean values and does not incorporate individual-level variability. The weighted fit and alternative-threshold calculations provide diagnostics of statistical and structural sensitivity; they do not identify a physiological optimum or upper thermal limit. Air temperature was used as a proxy for temperature within wood, and humidity, shading, trunk diameter, substrate quality, fungal colonisation and diapause were not modelled. Reference durations were held constant, and the uniform increments were not treated as regional climate projections. The results therefore describe the comparative sensitivity of the temperature-dependent component of development, rather than providing direct estimates of voltinism, survival or population dynamics in *C. relictus*.

Results

Thermal parameters of larval development

The larval development rate reported for *Callipogon relictus* increased across the three constant temperatures examined (Yi et al. 2019). The unweighted descriptive regression yielded T_0=17.65°C and K=2723.1 degree-days (R^2=0.9857; p=0.076; residual df=1). An exploratory weighted fit, using inverse squared delta-method standard errors, yielded T_0=18.34°C and K=2253.5 degree-days. These estimates are exploratory diagnostics derived from three published means; neither fit establishes a physiological threshold, and the weighted result additionally depends on an approximate variance transformation.

For the baseline period, the unscaled degree-day calculation yielded estimates ranging from 4.24 years at Yeongwol to 9.61 years at Chuguyevka. The documented

reference durations for the four localities ranged from 3.5 to 5.0 years. Accordingly, the scaling coefficient ranged from 1.171 to 2.401. These values reflect the normalisation procedure and were not interpreted as independent biological differences among local populations.

Sensitivity of scenario responses to the lower developmental threshold

The relative response depended on the selected lower threshold, although the ranking of the four localities remained unchanged across the tested values. Under the +3.55 °C scenario, the reduction in modelled thermal-time duration ranged from 29.0% to 32.8% at T_0=10°C, from 32.0% to 37.1% at 12 °C, from 37.7% to 45.6% at 15 °C, and from 44.9% to 56.0% at 17.65 °C. Chuguyevka exhibited the greatest reduction and Yeongwol the smallest at each threshold. Thus, the tested thresholds preserved the same ranking of localities but produced different magnitudes of response.

Baseline climatic heterogeneity and annual GDD accumulation

During 2010–2025, mean annual AGDD across the four study localities ranged from 283.5 to 642.7 degree-days (Table 4). The highest mean value was recorded at Yeongwol (642.7 ± 74.5 degree-days), whereas the lowest was recorded at Chuguyevka (283.5 ± 45.4 degree-days). The mean number of days per year with a mean daily temperature exceeding T_0 ranged from 81.5 to 128.9.

Jilin occupied an intermediate position in thermal accumulation (465.1 ± 49.7 degree-days). Among the two Russian localities, mean AGDD at Ussuriysk (367.0 ± 69.4 degree-days) exceeded that at Chuguyevka (283.5 ± 45.4 degree-days). The coefficient of variation ranged from 10.7% to 18.9% and reflected interannual variability during the baseline period; CV was not used as a measure of warming sensitivity.

Table 4. Baseline climatic conditions and calculated AGDD indicators for the four study localities during 2010–2025

Location	Mean AGDD (T_0=17.65 °C)	SD	SE	95% descriptive interval	CV (%)	Days exceeding T_0	L_{ref} (years)
CHU	283.5	45.4	11.3	259.3–307.7	16.0	81.5	4.0
USS	367.0	69.4	17.3	330.1–404.0	18.9	93.2	4.0
JIL	465.1	49.7	12.4	438.6–491.6	10.7	105.4	5.0
YEO	642.7	74.5	18.6	603.0–682.4	11.6	128.9	3.5

Note: SD, SE, CV, and the 95% descriptive interval were calculated from 16 annual values; temporal autocorrelation was not assessed.

Changes in AGDD and estimated development duration under standardised temperature increments

Increasing the imposed temperature increment resulted in a monotonic increase in AGDD at all four localities (Table 5). The normalised duration values are conditional model outputs scaled to the selected reference durations and do not constitute validated estimates of calendar-time development. Across the four localities, the mean relative reduction in normalised duration was 12.1%, 19.5%, 33.0%, 43.2% and 50.4% under the successive increments. Mean AGDD across the four localities increased from 439.6 degree-days under baseline conditions to 497.7, 542.1, 648.0, 761.9 and 869.7 degree-days under the five increments.

Table 5. AGDD and normalised developmental-duration outputs for *C. relictus* under uniform temperature increments at the four study localities

Site	Δ*T* (°C)	Mean AGDD (T_0=17.65 °C)	SD	SE	CV (%)	Days > T_0	Duration (years)	Reduction (%)
CHU	+0.55	330.4	48.7	12.2	14.7	88.0	3.43	14.2
	+0.95	366.6	51.1	12.8	13.9	92.9	3.09	22.7
	+1.85	455.0	55.5	13.9	12.2	103.3	2.49	37.7
	+2.75	552.1	59.5	14.9	10.8	111.7	2.05	48.7
	+3.55	644.8	63.1	15.8	9.8	119.1	1.76	56.0
USS	+0.55	420.4	73.6	18.4	17.5	99.7	3.49	12.7
	+0.95	461.5	76.8	19.2	16.7	105.3	3.18	20.5
	+1.85	560.8	82.7	20.7	14.7	115.1	2.62	34.6
	+2.75	668.7	87.5	21.9	13.1	123.9	2.20	45.1
	+3.55	771.9	90.9	22.7	11.8	133.1	1.90	52.4
JIL	+0.55	524.5	51.7	12.9	9.8	110.3	4.43	11.3
	+0.95	569.5	53.1	13.3	9.3	114.3	4.08	18.3
	+1.85	675.8	56.1	14.0	8.3	121.6	3.44	31.2
	+2.75	789.1	58.6	14.6	7.4	129.6	2.95	41.1
	+3.55	896.0	60.8	15.2	6.8	136.9	2.60	48.1
YEO	+0.55	715.6	76.4	19.1	10.7	135.1	3.14	10.2
	+0.95	770.7	77.5	19.4	10.1	139.6	2.92	16.6
	+1.85	900.3	79.4	19.9	8.8	148.0	2.50	28.6
	+2.75	1037.6	82.1	20.5	7.9	156.8	2.17	38.1
	+3.55	1166.3	85.1	21.3	7.3	164.6	1.93	44.9

Note: Normalised durations are conditional outputs scaled to reference values, not validated estimates of calendar-time development. They do not establish the number of generations per year or a change in voltinism. Relative reductions do not depend on the reference duration or *K*.

Spatial variation among the four study localities

The spatial pattern in relative response did not correspond to the gradient in absolute heat accumulation. Yeongwol had the highest baseline AGDD but the smallest relative reduction under the tested increments, whereas Chuguyevka exhibited the largest reduction. This ranking was consistent across all tested thresholds. Within this threshold-based model, the pattern arises from the distribution of daily temperatures relative to T0and does not constitute independent evidence of a species-specific physiological response. It describes conditional model sensitivity and does not establish site-specific calendar-time developmental durations.

Under the largest increment, normalised duration values became more similar among the four localities, although this apparent convergence depends on the reference durations used for scaling. The relative response to an identical imposed increment provides the more direct comparison and retained the same ranking across the four tested thresholds. Neither pattern indicates climatic homogenisation nor provides a validated prediction of development within wood.

All examined increments increased modelled heat accumulation, but the relative response varied among the four localities and depended on the selected lower threshold. Alternative thresholds preserved the same ranking of localities while altering the estimated magnitude of the response. Under the largest increment (+3.55 °C), normalised duration estimates ranged from 1.76 to 2.60 years among the four localities (Table 5). Some estimates therefore approach an approximately two-year semivoltine time scale. Because these values are conditional model outputs scaled to reference durations, they indicate a potential shortening towards this time scale but do not establish that the same developmental cycle occurs under field conditions or that realised voltinism would change.

Discussion

Interpretation of thermal sensitivity in *C. relictus*

Laboratory observations have shown that the larval development rate of *C. relictus* varies with temperature under controlled conditions (Yi et al. 2019). In the present study, these data were used within a degree-day framework for four localities. Under the stated model assumptions, imposed warming increased heat accumulation and reduced the normalised thermal-time output; the magnitude of this response depended on local temperature distributions and the selected threshold.

The working threshold of 17.65 °C was derived by fitting a linear relationship to three published mean development times, leaving one residual degree of freedom. It should therefore be treated as a model parameter rather than an experimentally established physiological threshold. Under the +3.55 °C scenario, the reduction in modelled thermal-time duration across the four localities ranged from 29.0% to

32.8% at T_0=10°C and from 44.9% to 56.0% at T_0=17.65°C. The ranking of localities remained unchanged across the tested thresholds, with the greatest reduction at Chuguyevka and the smallest at Yeongwol. This pattern is conditional on the tested scenarios, and its magnitude remains uncertain. Thresholds reported for other cerambycid species provide context but cannot be transferred directly to *C. relictus*.

Semifield observations in north-eastern China reported larval development lasting 1,800–1,825 days under the rearing conditions used by Jingke et al. (2012), with egg and pupal stages each lasting 30–35 days. Larvae were associated with the roots of large dead trees and maintained substrate moisture. These observations document multiyear development under the described conditions; however, they do not calibrate the present air-temperature model or determine how voltinism might respond to future warming.

Within the degree-day framework, a temperature increment increases daily heat accumulation both by increasing the thermal excess above the selected threshold and by shifting some days from below to above it. Consequently, local relative responses depend on the baseline distribution of daily temperatures around T_0. This is an expected mathematical property of threshold-based degree-day calculations rather than a species-specific physiological response. The ranking observed here is conditional on the four temperature series and on the use of air temperature as a proxy; it does not quantify development within wood.

The semifield rearing described by Jingke et al. (2012) produced 34 larvae from approximately 120 eggs and only two adult males; therefore, survival estimates from that study cannot be quantitatively extrapolated to natural populations. Greater modelled heat accumulation should not be equated with biological success or with a shorter calendar-time life cycle. Completion of ontogeny may also depend on wood temperature and moisture, substrate quality, the availability of large dead trees and stage-specific mortality. The present calculations do not establish emergence timing, survival or population dynamics.

Comparison with the thermal phenology of other Cerambycidae

Temperature-dependent development in large longhorn beetles often combines changes in growth rate with plasticity in the number of larval instars and seasonal constraints. In *C. relictus*, developmental trajectories with 8, 10, and 12 larval instars have been described at 30 °C (Yi et al. 2019). In *Anoplophora glabripennis*, the number of instars is also variable, and phenological models account for age structure and thermal history (Trotter and Keena 2016; Schmitt et al. 2025a, 2025b). For *A. glabripennis*, experimentally derived and stage-specific lower developmental thresholds are lower and differ among stages, at approximately 10 °C for early instars and pupae and about 12 °C for later instars; at temperatures above 30 °C, development of most instars was suppressed, and at 40 °C it did not complete (Keena 2006; Keena and Moore 2010). In contrast to these experimentally differentiated estimates, the value of 17.65 °C for *C. relictus* is a parameter of a linear model based on

three mean laboratory temperatures. Therefore, the difference in thresholds should be regarded as a hypothesis about interspecific differences rather than as a proven physiological characteristic of the species.

The present degree-day calculation does not represent variation in the number of larval instars. *C. relictus* has been reported to complete development with different numbers of instars under laboratory conditions, but the available data do not quantify how this plasticity affects development under natural temperature regimes. Because the model holds the thermal constant and developmental trajectory constant, it cannot determine whether warming would alter instar number, calendar-time duration or voltinism. The results are therefore interpreted as changes in potential heat accumulation under the stated assumptions.

Under the +3.55 °C scenario, the normalised outputs for the four localities (1.76–2.60 years; Table 5) approach the time scale of an approximately two-year semivoltine cycle. This result supports further investigation of a possible shortening towards a semivoltine interval a plausible hypothesis for further investigation. However, the model does not represent wood microclimate, diapause duration, stage-specific survival or temperature-related changes in instar number, and therefore cannot determine whether the modelled time scale would correspond to a change in the realised generation interval or voltinism in natural populations.

Field studies of *A. glabripennis* in South Carolina reported synchronous univoltine development, whereas two- and three-year cycles are typical of more northern populations (Schmitt et al. 2025a, 2025b). These findings demonstrate that generation time can vary geographically in another cerambycid species; they do not provide evidence for a corresponding change in *C. relictus*.

The ecological consequences of warming cannot be inferred from degree-day outputs alone. For *C. relictus*, a higher modelled heat sum does not establish a greater probability of completing development, a shorter field life cycle or a greater number of generations per year. Such outcomes also depend on the availability of suitable dead wood, substrate moisture, diapause, instar number and stage-specific survival. The present analysis therefore identifies a conditional thermal pattern relevant to monitoring, rather than providing a demographic forecast.

Why accelerated thermal development does not necessarily imply population increase

In insects, increasing temperature can affect not only development rate but also survival, morphology, reproductive potential and synchronisation with seasonal cues (Angilletta et al. 2004). The present model does not estimate these outcomes. In *C. relictus*, morphological abnormalities have been described during laboratory ontogeny, with the highest frequency recorded at the pupal stage; the authors cautiously suggested moisture and temperature as possible contributing factors (Yi et al. 2017b). Rapid development under controlled laboratory conditions at 30 °C (Yi et al. 2019) does not establish a corresponding response in natural wood substrates.

A similar distinction between accelerated development and biological success has been shown in other Cerambycidae species. In *A. glabripennis*, larvae and pupae respond strongly to temperature, but development of most larval instars is suppressed at constant temperatures above 30 °C and completely stops at 40 °C (Keena 2006; Keena and Moore 2010). Adults of this species also have a pronounced thermal optimum: lifespan and fecundity decline when temperature deviates from the optimum, oviposition ceases at high temperatures, and larval hatching from eggs decreases near the upper thermal limits (Keena 2006). In *Monochamus galloprovincialis*, post-diapause development is also described by degree-day accumulation, but development rate decreases above 30 °C, and the upper lethal threshold lies approximately between 32 and 35 °C (Naves and de Sousa 2009). For *A. chinensis*, it has been shown that development slows down or ceases at low temperatures and is also disrupted at temperatures above 35 °C, while larval mass and pupation may depend not only on temperature but also on wood moisture (Keena and Richards 2022).

The modelled reduction in normalised thermal-time duration should be interpreted as a conditional scenario of heat accumulation, not as a prediction of actual larval duration, voltinism or population response. Future models would require measurements of wood temperature and moisture, together with biological data on diapause, instar number, pupation success, adult body size and fecundity.

Conclusion

This analysis indicates that the relative response of degree-day accumulation to identical imposed temperature increments varied among the four modelled localities. Across the tested lower thresholds (10, 12, 15 and 17.65 °C), Chuguyevka consistently exhibited the greatest relative reduction in normalised thermal-time duration, whereas Yeongwol exhibited the smallest. Because the magnitude of the response depended on threshold choice, the estimate derived from three laboratory means should not be interpreted as a precise physiological prediction.

The principal result is a threshold-dependent pattern of spatial sensitivity that preserved the same ranking of localities across the tested settings, while the magnitude of the response changed with threshold choice. Under the largest increment (+3.55 °C), normalised duration estimates of 1.76–2.60 years approached the time scale of an approximately two-year semivoltine cycle. This scenario-based possibility warrants empirical investigation but does not establish a corresponding change in field development duration or realised voltinism. The analysis identifies candidate locations for monitoring and underscores the need for additional biological and microclimatic data before predictive models for *C. relictus* can be developed.

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