



Diurnal temperature fluctuations improve predictions of developmental rates in the spruce bark beetle *Ips typographus*

Sven Hofmann^{1,2} · Martin Schebeck² · Markus Kautz¹

Received: 17 October 2023 / Revised: 24 January 2024 / Accepted: 24 January 2024
© The Author(s) 2024

Abstract

The European spruce bark beetle *Ips typographus* is a widespread pest in Norway spruce-dominated forests in Eurasia. Predicting its phenology and voltinism is crucial to plan forest management measures and to mitigate mass outbreaks. Current phenology models are based on constant temperatures inferred from laboratory experiments; however, insect life cycles under natural conditions are rather driven by diurnal and seasonal temperature fluctuations. Therefore, phenology models based on fluctuating temperatures would reflect field conditions more realistically and might thus improve model predictions. In a laboratory experiment, we investigated the development of *I. typographus*, applying mean temperatures between 3 and 35 °C and diurnal temperature oscillations of up to ± 15 °C. Subsequently, we calibrated developmental rate models and applied them to climate data, in order to assess the effect of temperature fluctuations on voltinism under field conditions. Our results showed that diurnal temperature oscillations significantly affected developmental rates. Compared to constant temperatures, development was faster at temperature oscillations falling below the lower developmental threshold, and slower at temperature oscillations exceeding the developmental optimum. Furthermore, short exposures to suboptimal temperatures affected *I. typographus* less than expected from constant conditions. Natural temperature fluctuations thus accelerate development under cool, shaded conditions, whilst slowing it under hot, sun-exposed conditions, thereby ultimately affecting voltinism. Our findings highlight the importance to account for diurnal temperature fluctuations for more accurate predictions of developmental rates of *I. typographus* in natural thermal environments, and provide the fundament for improving current phenology models to support effective bark beetle management in a warming climate.

Keywords Bark beetle · Climate change · Developmental rate models · Phenology · *Ips typographus* · Temperature fluctuations

Key messages

- Diurnal temperature fluctuations affect insects but their influence on *Ips typographus* is unknown.
- In a laboratory experiment, temperature fluctuations significantly influenced developmental rates.
- Fluctuations accelerated development at low temperatures and decelerated it at high temperatures.
- These results have substantial impact on phenology and voltinism under natural conditions.
- Precise developmental rates improve phenology models and coordination of management measures.

Communicated by Jon Sweeney.

Martin Schebeck and Markus Kautz have contributed equally to this work.

✉ Sven Hofmann
sven.hofmann@forst.bwl.de

Martin Schebeck
martin.schebeck@boku.ac.at

Markus Kautz
markus.kautz@forst.bwl.de

¹ Department of Forest Health Protection, Forest Research Institute Baden-Württemberg, FVA, Freiburg, Germany

² Department of Forest and Soil Sciences, Institute of Forest Entomology, Forest Pathology and Forest Protection, University of Natural Resources and Life Sciences, BOKU, Vienna, Austria

Introduction

Insect life histories are strongly affected by ambient temperature, which influences geographic range and abundance (Stange and Ayres 2010), morphology (Hogue and Hawkins 1991) and reproduction (Kingsolver et al. 2011). Temperature is also a crucial factor in developmental processes, as shown in laboratory experiments conducted on numerous insect species under constant temperatures (Rebaudo and Rabhi 2018). Understanding the effects of temperature on development and performance is particularly interesting for ecologically and economically relevant insects, such as forest pests. Phenology models that incorporate temperature-dependent development can help to effectively manage population outbreaks, which are predicted to increase due to climate change (Seidl et al. 2017; Johnson and Haynes 2023).

The European spruce bark beetle (*Ips typographus*) is one of the most important species affecting forest ecosystems across Eurasia by causing widespread mortality of its primary host tree, Norway spruce (*Picea abies*) (Raffa et al. 2015; Patacca et al. 2023). *I. typographus* is a potentially multivoltine bark beetle that can currently complete up to three generations per year. Most of the beetle's life cycle occurs under the bark, where it reproduces and develops in galleries that are excavated in the phloem. The reproductive season starts when warm spring temperatures end hibernation and lasts until short day lengths and low temperatures in late summer induce reproductive diapause (Baier et al. 2007; Doležal and Sehnal 2007; Schebeck et al. 2022). Its species-specific life-history traits that facilitate mass outbreaks include the ability to successfully colonise even hardly stressed trees (via intraspecific communication using aggregation pheromones), high fecundity, and phenological plasticity (Wermelinger 2004; Schebeck et al. 2023). Major triggers of the expected increasing frequency and magnitude of population outbreaks under future climate comprise a drought-induced higher predisposition of forest stands, and a temperature-driven increase in developmental rates resulting in additional annual beetle generations (Marini et al. 2017; Jakoby et al. 2019).

Temperature-dependent development is commonly described using developmental rates (DR), which are the inverse of mean developmental durations (D) (Damos and Savopoulou-Soultani 2012). DR in numerous species is represented by an optimum curve with a lower developmental threshold (DT_L), and an almost linear increment towards the optimum temperature (T_O), where they plateau before rapidly decreasing towards the upper developmental threshold (DT_U) (Damos and Savopoulou-Soultani 2012). DT_L and DT_U vary amongst insect species,

but typically differ by about 20 °C from each other (Dixon et al. 2009). This relationship has been described with different functions primarily based on laboratory experiments conducted under constant temperatures (Rebaudo and Rabhi 2018), including numerous bark beetle species affecting Northern hemisphere forests (Bentz et al. 1991; Wermelinger and Seifert 1998; Peter 2014; Gent et al. 2017; Schebeck and Schopf 2017; Davídková and Doležal 2019).

In natural environments, however, constant temperature conditions are unlikely, as temperatures typically fluctuate over days and seasons. Therefore, oscillating temperatures more accurately reflect the habitat of most insects (Cloudsley-Thompson 1953; Ratte 1985). More specifically, oscillating temperatures differentially affect DR (Worner 1992; Colinet et al. 2015), either resulting in an increase (Chen et al. 2019), decrease (Butler and Trumble 2010; Fischer et al. 2011) or no change, compared to constant temperatures (Kingsolver et al. 2009). Most of these deviations can be explained by the rate summation effect, which accounts for temperatures differing from their mean during oscillation (Worner 1992). That means, that the consideration of a finer temporal resolution, e.g. hourly temperature, potentially result in altered average DR compared to daily mean temperature. Due to the convex shape of DR curves at DT_L and DT_U , and the concave shape at T_O , oscillations reduce DR at T_O and increase them at DT_L and DT_U (Hagstrum and Milliken 1991; Liu et al. 1995; von Schmalensee et al. 2021). Furthermore, exceeding harmful temperature thresholds during oscillation can cause stress, which reduces or entirely inhibits developmental progress (Colinet et al. 2015). Unfortunately, studies on the influence of fluctuating temperatures on DR are scarce, and completely lacking for bark beetles (Colinet et al. 2015).

Our current understanding of the temperature-dependent development and reproduction of *I. typographus* is based on laboratory experiments using constant conditions, determining a DT_L , T_O , and DT_U of 8.3, 30.4 and 38.9 °C, respectively (Wermelinger and Seifert 1998; 1999). Amongst the total developmental duration from egg to adult, pre-imaginal development (eggs, larvae, pupae) of individuals accounts for about 60%, and post-pupal development (maturation feeding of young beetles for development of gonads and flight muscles) for about 40% (Wermelinger and Seifert 1998). From an ecological perspective, however, the generation time of bark beetles additionally includes the successful attack by parental beetles, establishment of a nuptial chamber, mating, construction of mother tunnels, and oviposition (Wermelinger 2004; Danks 2013; Schebeck et al. 2023), which should also be accounted for when modelling phenology. Moreover, ontogenetic development under natural conditions is affected by extreme temperature fluctuations resulting from variations in air temperature and

exposure to global radiation (Nicolai 1986; Baier et al. 2007). The trunks of standing trees, and in particular of downed (e.g. wind-thrown) trees, are exposed to varying amounts of radiation depending on their orientation and position within a forest stand. Whilst temperatures within shaded parts of the trunks mostly resemble ambient air temperature, sun-exposed bark can reach temperatures above 50 °C (Annala 1969). These potential temperature fluctuations in its natural environment make *I. typographus* an ideal study system to test whether DR under constant temperatures are sufficient to predict development under natural conditions (Worner 1992; Wermelinger and Seifert 1998; Shi et al. 2016).

Hence, we studied the development of *I. typographus* under constant and oscillating temperatures in the laboratory. The experimental findings were subsequently applied to representative climate data in order to quantify the effect of natural temperature fluctuations on its development and voltinism. Our findings will not only contribute to the understanding of *I. typographus*' temperature-dependent development, but can also serve as an example for other bark beetles and insects in similarly fluctuating thermal environments. Determining the influence of fluctuating temperatures may furthermore improve predictions of the geographic range, population dynamics, and voltinism of insects in response to current and changing climates. Finally, our findings can contribute to the improvement of phenology models, which, as in the case of *I. typographus*, play a crucial role for risk assessment and mitigation of mass outbreaks (Baier et al. 2007; Jakoby et al. 2019; Ogris et al. 2019).

Material and methods

Experimental design

Our study aimed to determine DR, generation time and the relative duration of ontogenetic stages at different mean temperatures and diurnal temperature oscillations (i.e. fluctuations with constant magnitude and frequency). Previous laboratory experiments have shown developmental progress at constant mean temperatures between 12 and 33 °C (Wermelinger and Seifert 1998). Resulting DT_L has been reported to range between 5 and 8.3 °C (Annala 1969; Wermelinger and Seifert 1998; Štefková et al. 2017). Diurnal air temperature fluctuations typically vary between 0 and ± 10 °C at bark beetle-relevant sites across Germany, depending on season and location (Supplement 1a). Temperature fluctuations in the bark, the habitat of *I. typographus*, can be higher due to exposure to global radiation (Supplement 1b). Therefore, we conducted experiments to test temperature regimes with mean temperatures between 3 and 35 °C, and diurnal oscillations

with amplitudes up to ± 15 °C (Table 1, 2). All scenarios were conducted in separate incubators (Memmert ICH L 280) with temperature oscillations following diurnal sinusoidal curves.

Observing the ontogenetic stages of bark beetles during development can be challenging as it occurs under the bark. To overcome this obstacle, we applied two experimental approaches, phloem sandwiches and experimental logs, to study the pre-imaginal development and the entire generation time. Phloem sandwiches have been frequently used to observe the pre-imaginal development of bark beetle species (Wermelinger and Seifert 1998; Schebeck and Schopf 2017) as they allow repeated observations of the same individuals (for details see Supplement 2). Unfortunately, observations using this method are limited to approximately 40 days due to phloem desiccation and fungal growth (Wermelinger and Seifert 1998; Schebeck and Schopf 2017). Moreover, determining entire generation times is complicated, due to the surrounding Plexiglas sheets that hamper the emergence of young beetles. Phloem sandwiches were thus used to observe pre-imaginal development of at least 50 individuals per scenario on a daily basis for scenarios with mean temperatures ≥ 21 °C (Table 1). As breeding success and mortality rates varied, different numbers of phloem sandwiches were required to achieve the desired sample size. Pre-imaginal development in scenarios with mean temperatures ≤ 15 °C was observed using evenly colonised experimental logs (Wermelinger and Seifert 1998; Doležal and Sehnal 2007; Dworschak et al. 2014) by peeling of pre-defined bark stripes (Table 2, Supplement 2). Since the duration of the egg stage could not be determined using this method, additional phloem sandwiches were applied for scenarios with mean temperatures of 12 and 15 °C (Table 1). An additional trial was conducted at a constant temperature of 25 °C to compare D in logs with the sandwich method. Developmental progress in experimental logs was assessed once per week at mean temperatures ≤ 12 °C, and three times per week at 15 and 25 °C (Table 2). Finally, the proportion of pre-imaginal development from the entire generation time was determined for a subset of six scenarios (21, 25, and 30.4 °C; ± 0 and ± 8 °C), to account for the influence of mean temperature and temperature oscillation (Table 3). Three logs were colonised at each temperature regime with 100 beetles per scenario, and emerging young beetles were counted on a daily basis (Supplement 2).

Breeding material for the experiments was felled between May and August, and stored for no longer than 2 weeks to ensure good phloem quality, which has been shown essential for bark beetle development (Baier 1996). Beetles used in the experiments were obtained from a permanent rearing (Supplement 3). Bark temperatures inside phloem sandwiches and logs were monitored with data loggers (onset Hobo Pro V2) to compare microhabitat

Table 1 Mean developmental duration (D) in days, standard deviation (SD) and sample size (N) for different ontogenetic stages and the total pre-imaginal development of using phloem sandwiches

Scenario (°C)	N Phloem Sandwiches	N Eggs	D ± SD Eggs	N Larvae	D ± SD Larvae	N Pupae	D ± SD Pupae	N Pre-imaginal	D ± SD Pre-imaginal	Mortality rate (%)
12 ± 0	13	34	23.9 ± 2.2	0	NA	0	NA	0	NA	100
12 ± 4	13	23	22.9 ± 2.1	0	NA	0	NA	0	NA	100
12 ± 8	13	34	17.0 ± 2.5	0	NA	0	NA	0	NA	100
12 ± 15	10	532	15.2 ± 1.4	0	NA	0	NA	0	NA	100
15 ± 0	10	84	14.2 ± 1.9	0	NA	0	NA	0	NA	100
15 ± 4	10	74	11.8 ± 1.6	0	NA	0	NA	0	NA	100
15 ± 8	10	91	12.7 ± 1.4	0	NA	0	NA	0	NA	100
15 ± 15	10	162	10.8 ± 1.5	0	NA	0	NA	0	NA	100
21 ± 0	8	170	5.7 ± 0.9	18	17.0 ± 3.2	18	5.2 ± 0.6	46	27.7 ± 2.8	73
21 ± 4	9	255	4.8 ± 0.8	12	15.2 ± 1.8	12	5.3 ± 1.6	44	27.1 ± 1.8	83
21 ± 8	12	344	4.9 ± 0.8	2	20.0 ± 0.0	2	4.5 ± 2.1	87	27.4 ± 1.6	75
21 ± 15	21	238	6.1 ± 1.1	29	20.1 ± 4.0	28	5.1 ± 0.9	112	30.8 ± 3.0	53
25 ± 0	16	206	3.8 ± 0.7	2	8.5 ± 0.7	2	4.5 ± 0.7	62	20.3 ± 2.9	70
25 ± 4	16	311	3.8 ± 0.8	4	8.5 ± 0.6	2	4.0 ± 0.0	102	20.9 ± 2.6	67
25 ± 8	16	296	4.0 ± 0.8	7	10.0 ± 5.0	7	3.6 ± 0.8	109	22.9 ± 4.5	63
25 ± 15	21	158	6.3 ± 1.4	34	21.0 ± 5.7	32	4.9 ± 1.1	63	31.2 ± 4.1	60
30.4 ± 0	8	223	3.3 ± 0.7	32	8.0 ± 3	32	2.3 ± 0.6	99	14.1 ± 2.0	56
30.4 ± 4	12	277	3.4 ± 1.0	23	10.1 ± 1.9	23	3.0 ± 0.6	104	15.7 ± 1.2	62
30.4 ± 8	11	214	4.1 ± 1.0	29	10.6 ± 2.7	28	3.4 ± 0.7	89	18.5 ± 2.0	58
30.4 ± 15	28	37	7.6 ± 1.3	0	NA	0	NA	0	NA	100
33 ± 0	22	180	3.5 ± 1.1	4	9.5 ± 1.7	4	3.2 ± 1.7	11	16.6 ± 1.5	94
33 ± 4	22	79	4.3 ± 1.2	1	14.0 ± NA	1	3.0 ± NA	3	28.0 ± 8.9	96
33 ± 8	22	57	4.6 ± 1.0	0	NA	0	NA	0	NA	100
35 ± 0	10	0	NA	0	NA	0	NA	0	NA	100

'NA' indicates occasions, where D could not be obtained. Scenarios up to mean temperatures of 15 °C were conducted to complement log experiments with D for the egg stage

Table 2 Transition point (TP) in days and standard deviation (SD) for different ontogenetic stages of *Ips typographus*, total number of individuals examined (N), and control interval for each scenario using experimental logs

Scenario (°C)	N	TP ± SD L1	TP ± SD L2	TP ± SD L3	TP ± SD Pupae	TP ± SD Young beetles	Control interval	D Pre-imaginal
3 ± 0	1018	NA	NA	NA	NA	NA	weekly	NA
6 ± 0	1183	NA	NA	NA	NA	NA	weekly	NA
6 ± 4	647	51.9 ± 5.3	55.0 ± 4.0	NA	NA	NA	weekly	NA
6 ± 8	845	22.0 ± 1.8	47.6 ± 1.6	87.7 ± 1.4	NA	NA	weekly	NA
9 ± 0	1098	56.0 ± 3.2	62.8 ± 2.3	75.2 ± 2.3	NA	NA	weekly	NA
9 ± 4	818	47.1 ± 1.5	53.2 ± 1.2	64.6 ± 1.0	NA	NA	weekly	NA
9 ± 8	919	29.8 ± 1.6	44.2 ± 0.9	53.1 ± 1.0	93.4 ± 1.1	123.5 ± 2.7	weekly	121.1
9 ± 15	177	NA	NA	NA	NA	NA	weekly	NA
12 ± 0	1057	15.8 ± 0.8	29.4 ± 1.0	51.5 ± 1.3	77.6 ± 0.9	99.4 ± 0.8	weekly	107.5
12 ± 4	1060	14.2 ± 0.1	26.7 ± 0.6	39.6 ± 0.6	63.6 ± 1.1	85.9 ± 2.0	weekly	94.6
12 ± 8	1669	12.1 ± 0.6	18.6 ± 0.7	24.4 ± 0.7	47.3 ± 0.4	59.0 ± 0.5	weekly	63.9
12 ± 15	358	8.3 ± 1.6	16.4 ± 1.2	27.4 ± 1.1	46.5 ± 0.2	59.1 ± 0.9	weekly	66
15 ± 0	689	4.8 ± 0.3	8.3 ± 0.4	17.2 ± 0.5	31.3 ± 0.5	43.2 ± 0.5	M, W, F	52.6
15 ± 4	437	7.1 ± 0.5	9.1 ± 0.4	15.1 ± 0.8	30.8 ± 0.6	45.6 ± 0.7	M, W, F	50.3
15 ± 8	683	4.1 ± 0.4	10.1 ± 0.6	15.7 ± 0.9	27.8 ± 0.7	35.1 ± 0.5	M, W, F	43.7
15 ± 15	574	6.2 ± 0.5	9.4 ± 0.6	16.3 ± 0.8	25.5 ± 0.7	36.8 ± 0.6	M, W, F	41.4
25 ± 0	795	2.0 ± 0.1	4.5 ± 0.2	6.0 ± 0.2	12.3 ± 0.2	15.5 ± 0.3	M, W, F	17.3

'M', 'W', and 'F' indicate Monday, Wednesday, and Friday, respectively. 'NA' indicates occasions, where TP were not reached. Pre-imaginal developmental duration (D) was calculated as the duration from larvae to young beetles assessed with logs plus the duration of the egg stage from phloem sandwiches (Table 1)

Table 3 Mean developmental duration (D) in days and standard deviation (SD) of generation times of *Ips typographus*, the total number of investigated individuals (N), and the proportion (%) of pre-imaginal development (assessed using phloem sandwiches, cf. Table 1) from generation time

Scenario (°C)	Total emerged beetles (N)	D ± SD	Proportion of pre-imaginal development (%)
21 ± 0	379	53.3 ± 8.6	51.9
21 ± 8	467	56.4 ± 9.3	48.6
25 ± 0	626	39.8 ± 7.6	51.0
25 ± 8	383	41.2 ± 5.2	55.6
30.4 ± 0	540	28.1 ± 2.9	50.2
30.4 ± 8	381	34.4 ± 2.8	53.8

temperatures with the incubator settings (Danks 2013). Experiments on pre-imaginal development were conducted in constant darkness since photoperiod has no influence on DR, and diapause is expressed only in the adult stage (Doležal and Sehnal 2007). In contrast, the experiments on generation time were conducted under permanent light to ensure the emergence of young beetles.

Data analyses

For all scenarios with phloem sandwiches (12, 15, 21, 25, 30.4, 33 °C; ± 0, ± 4, ± 8, ± 15 °C) and logs measuring generation times (21, 25, 30.4 °C; ± 0, ± 8 °C), D and standard deviation (SD) were calculated for the ontogenetic stages and the total pre-imaginal development. Since each observation of the logs measuring pre-imaginal development (3, 6, 9, 12, 15 °C; ± 0, ± 4, ± 8, ± 15 °C) consisted of a unique set of individuals, D of distinct individuals could not be obtained. Instead, the shift in distribution towards the subsequent developmental stage was observed, from which D with SD could be determined. To this end, all observed individuals were grouped based on whether they had reached a certain developmental stage (1) or not (0), thus enabling binomial regression, and the determination of the transition points and SD via bootstrapping. To prevent delays in stage distribution caused by ongoing oviposition, only individuals from the first 60 mm of mother tunnels were included. To obtain thresholds to distinguish between larval instars, the R-package 'mclust' (Scrucca et al. 2016) was used to fit multiple Gaussian distributions on head capsule widths (Annala 1969).

Developmental rate models

Both linear and nonlinear models can be used to describe DR (Rebaudo and Rabhi 2018). Here, we used linear regressions to calculate DT_L for the various ontogenetic stages and the total pre-imaginal development for different temperature amplitudes (± 0 , ± 4 , ± 8 , ± 15 °C). Observations with temperatures above 25 °C were excluded, to avoid distortions from data points outside the linear relationship between temperature and DR. Additionally, nonlinear models were compared for DR of complete pre-imaginal development with the R-package ‘devRate’ (Rebaudo and Regnier 2023). The package simultaneously calibrates 25 different nonlinear DR models, including Logan-6 (Logan et al. 1976), Lactin-1 and Lactin-2 (Lactin et al. 1995), and Briere-2 (Briere et al. 1999), which have been applied to multiple arthropods. The models’ performance was evaluated based on their root mean square errors (RMSE) (Damos and Savopoulou-Soultani 2012).

We also tested whether the rate summation effect (Worner 1992) accounts for all deviations under fluctuating temperatures using DR under constant temperatures (Hagstrum and Milliken 1991; von Schmalensee et al. 2021). Thus, the integrals of DR based on a diurnal sinusoidal temperature curve were calculated for mean temperatures between 0 and 50 °C and for all studied amplitudes (± 4 , ± 8 , ± 15 °C). If the rate summation effect would indeed explain all deviations, observations should align with the integral curves.

Implications for development under natural conditions

Based on the DR curves from the laboratory experiments, the effect of temperature fluctuations and global radiation on DR under natural conditions was assessed. To facilitate data processing, missing DR for temperature amplitudes outside the experimental scenarios were linearly interpolated, creating a matrix with DR for mean temperatures between 0 and 40 °C and amplitudes up to ± 25 °C (Supplement 7). To represent the natural conditions for *I. typographus* development, daily raster data for temperature (mean, minimum, maximum) and global radiation (sum) (Dietrich et al. 2019) were used covering bark beetle-relevant sites across Germany over a 12-year period (2009–2020; Supplement 6a). Subsequently, mean and maximum bark temperatures at all sites were calculated according to Baier et al. (2007) for a range of global radiation from 0% (complete shade) to 100% (complete sun), in order to compare the development in different microhabitats. Daily temperature amplitudes were calculated by subtracting radiation-specific maximum bark temperatures from respective minimum temperatures. Daily, site-specific DR

were finally calculated using microhabitat temperatures (mean and amplitude) and the interpolated DR. The effect of microhabitat-dependent differences was analysed by plotting the averaged temperature-dependent DR curves for these global radiation categories. Moreover, the impact of temperature fluctuations on *I. typographus* voltinism, as opposed to diurnal mean temperatures, was quantified at three representative sites at different elevations (315, 815, and 1370 m a.s.l.) and over the respective 12-year period in south-western Germany (Supplement 6b, c). This was achieved by calculating the cumulative differences between DR under fluctuating and constant temperatures for each elevation, radiation, and year, and then averaging these values across all years for the two categories (elevation and radiation).

Results

Developmental progress was observed in all scenarios with mean temperatures between 9 and 33 °C when temperature extremes during oscillation did not exceed 40 °C, or fall below -5 °C (Table 1, 2). At 9 °C, D could only be obtained for the ± 8 °C scenario, whilst the individuals exposed to smaller amplitudes did not complete pre-imaginal development before the end of the experiment after 5 months (Table 2). At 6 °C developmental progress was only observed at ± 8 °C, and pre-imaginal development did not complete either. For each scenario with completed pre-imaginal development, an average of 77 individuals were studied using the sandwich method, and 867 individuals using the log method, i.e. approximately 50 individuals per bark stripe (Supplement 2, full datasets in Table 1–3). Mortality rate in phloem sandwiches was on average 65% in scenarios with mean temperatures between 20 and 30 °C, requiring a minimum of eight samples to approach the target of 50 individuals (Table 1). Generation time in experimental logs was determined by an average of 463 beetles per scenario (Table 3). Combined DR data from logs and phloem sandwiches were used, because pre-imaginal D was almost identical between the two methods at 25 °C (Fig. 1). Since temperature measurements within the samples differed only slightly from incubator settings (Supplement 5), the latter were used as temperature data for the analyses.

Pre-imaginal developmental duration

Pre-imaginal D (i.e. egg, larval and pupal development) ranged from 2 weeks at a constant temperature of 30.4 °C to 17 weeks at 9 ± 8 °C (Table 1, 2). Temperature oscillations differently affected D depending on mean temperatures and amplitudes. Temperature oscillations reduced D (i.e. increased DR) at low mean temperatures (≤ 15 °C), whereas

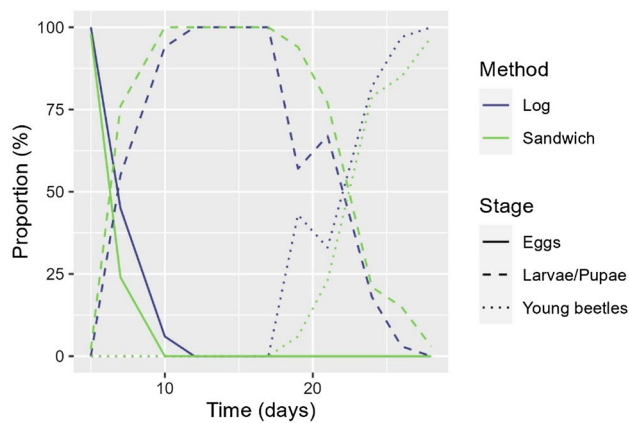


Fig. 1 Comparison of the proportions of ontogenetic stages of *Ips typographus* over time between experimental logs and phloem sandwiches at constant 25 °C. Colours indicate the methods, and line types indicate the respective ontogenetic stages. To make the data of the two methods comparable, the individual-based data of the phloem sandwiches were transformed into proportional data

they increased D (i.e. reduced DR) at high temperatures (> 21 °C). D was most affected by oscillations in scenarios temporarily exceeding T_O (30.4 °C), e.g. 25 ± 8 °C. At 30.4 °C, oscillations led to a significant difference between D of all three scenarios ($\pm 0, \pm 4, \pm 8$ °C) ($p < 4.9e-16$, Unpaired-Wilcoxon-test), with approximately 30% higher D at ± 8 °C compared to constant temperatures. At 33 °C, even a small amplitude of ± 4 °C almost doubled D, whilst all individuals died at an amplitude of ± 8 °C (Table 1). Also at low temperatures, substantial effects of oscillations on D were observed. At 12 °C, an amplitude of ± 8 °C reduced D to 59% compared to constant temperatures, and exposed to 9 ± 8 °C, approximately 50% of individuals completed pre-imaginal development within 121 days, whilst in the ± 0 and ± 4 °C scenarios, development was still incomplete (predominately in the larval stage) by the end of the experiment after 5 months. In scenarios completely within the range between DT_L and T_O (8.3 and 30.4 °C, respectively; Wermelinger and Seifert 1998) oscillations did not affect D, e.g. scenarios at 21 °C with amplitudes up to ± 8 °C ($p > 0.37$, Unpaired-Wilcoxon-test; Table 1).

Relative duration of ontogenetic stages

Averaged over all scenarios and methods, pre-imaginal development (egg, larva, pupa) comprised $52 \pm 3\%$ (Table 3) of the generation time, independent of mean temperature ($F_{1,4} = 0.32$, $p = 0.602$) and amplitude ($F_{1,4} = 0.55$, $p = 0.500$). The relative duration of eggs accounted for $23 \pm 3\%$ of the total pre-imaginal development, larvae for $57 \pm 6\%$, and pupae for the remaining $20 \pm 4\%$ (Fig. 2). Mean temperature positively correlated with the relative

duration of larval development, increasing by 0.38% per 1 °C ($F_{1,19} = 5.17$, $p = 0.035$), and consequently reducing the relative duration of eggs ($F_{1,19} = 4.68$, $p = 0.043$) and pupae ($F_{1,19} = 2.5$, $p = 0.13$). In contrast, amplitude had no significant influence on the relative duration of egg ($F_{1,19} = 0.04$, $p = 0.836$), larval ($F_{1,19} = 0.54$, $p = 0.472$), and pupal development ($F_{1,19} = 0.79$, $p = 0.385$). The three larval instars L1–L3, as defined by head capsule width with thresholds of 575 μm and 773 μm (Supplement 4), accounted for 19, 26 and 55%, respectively, of total larval D (Fig. 2).

Developmental rate models

To find the most appropriate DR model, 25 different model types included in the R-package ‘devRate’ (Rebaudo and Regnier 2023) were compared. Logan-6 was selected as the most suitable nonlinear model for the observed data up to ± 8 °C, as it converged in all cases with the overall lowest RMSE (Table 4, Fig. 3). However, the Logan-model failed in fitting the data at ± 15 °C, as the observations did not represent the typical shape of DR curves (Fig. 3). Therefore, a polynomial model (Harcourt and Yee 1982), which can adapt more flexibly to different distributions, was chosen as the best alternative (Table 4, Fig. 3).

To determine DT_L of pre-imaginal development for all temperature amplitudes, linear regressions were calculated for data from scenarios with mean temperatures between 12 and 25 °C. Except for ± 15 °C, RMSE were low, indicating almost perfect linear correlations between temperature and DR (Table 4, Fig. 3). DT_L were 8.9, 8.0, and 4.4 °C for ± 0 , ± 4 , and ± 8 °C, respectively, reflecting an increase in DR with amplitude (Fig. 3). Note that DT_L for ± 15 °C (5.5 °C) is not meaningful, because the observations at scenarios with ± 15 °C do not follow a linear trend as temperature minima of -6 °C were lethal, hindering developmental progress below mean temperatures of 9 °C (Fig. 3).

The influence of oscillating temperatures on D is also reflected in the DR models (Fig. 3). There was no effect as long as temperature oscillated between DT_L and T_O (indicated by grey bars in Fig. 3), but deviations occurred when temperatures oscillated beyond these limits. This resulted in an increase in DR in the proximity of DT_L and a decrease at T_O . Interestingly, the regressions based on observations under oscillating temperatures exceed the predicted DR, based on the rate summation effect (Worner 1992), under the premise of non-lethal temperature maxima and minima (Fig. 3b–d). For example, DR at 30.4 ± 8 °C was 0.054 compared to a rate summation of 0.037 (Fig. 3c). This indicates that beetles can sustain higher DR under short, repetitive exposures to adverse temperature conditions during oscillation, which would be detrimental or even lethal under long-term exposure. At the same time, DT_U decreased from 35 °C under constant temperatures to less than 30 °C at an

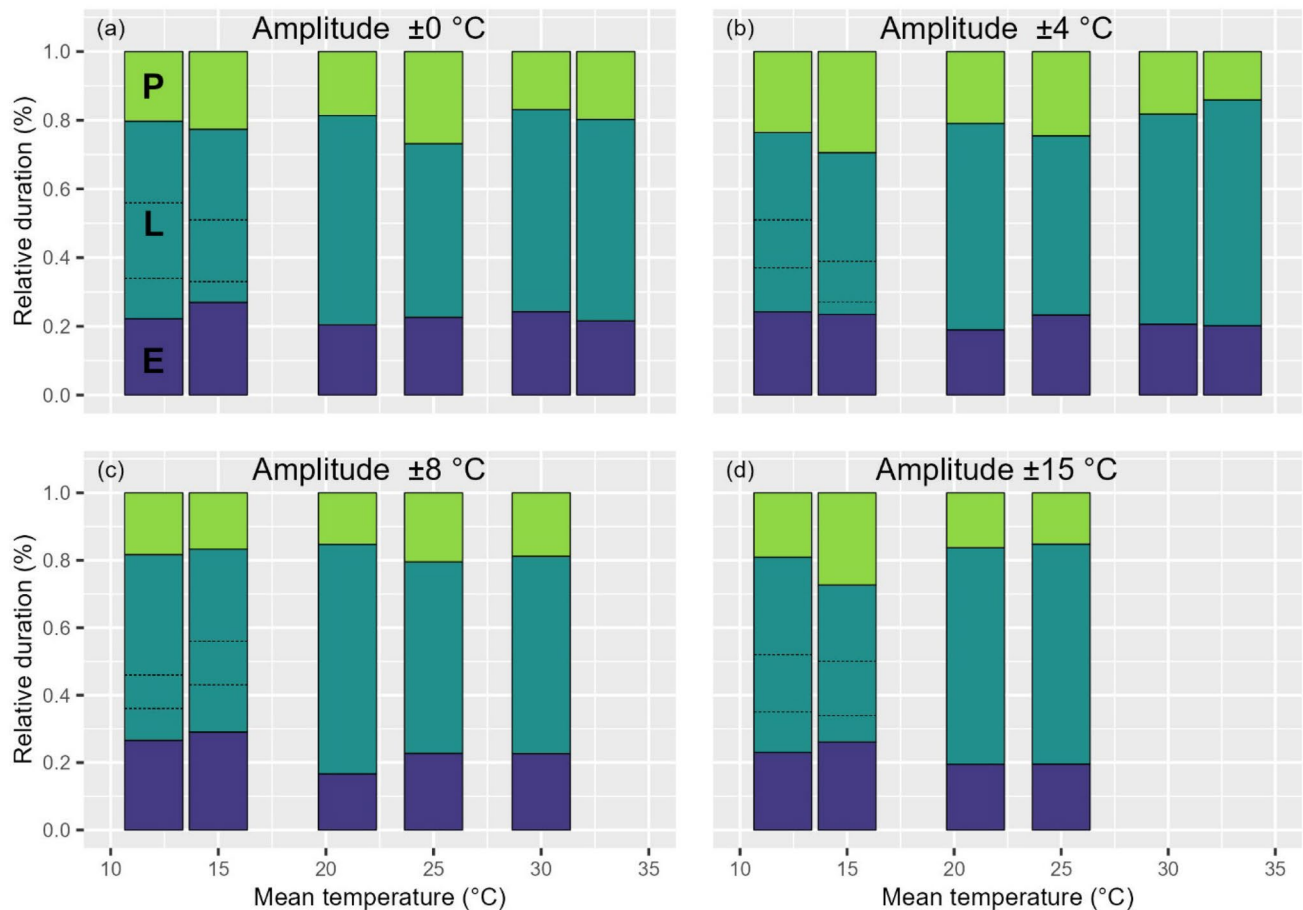


Fig. 2 Relative duration of the egg (E), larval (L), and pupal (P) stage of the total pre-imaginal developmental duration of *Ips typographus* for different temperature scenarios (a–d). Dashed lines within the lar-

val stage indicate the different instars L1–L3 determined by head capsule widths (Supplement 4)

Table 4 Root mean square errors (RMSE) of the best performing developmental rate (DR) models, that are included in the R-package ‘devRate’ (Rebaudo and Regnier 2023) and fitted on the DR data of *Ips typographus* from both the phloem sandwiches and logs. Models were separately fitted for each diurnal amplitude

Amplitude	Logan-6	Lactin-1	Lactin-2	Harcourt Yee	Linear
± 0 °C	0.194	0.354	NA	1.026	0.047
± 4 °C	0.180	0.250	0.142	0.528	0.021
± 8 °C	0.124	0.510	NA	0.848	0.029
± 15 °C	NA	0.443	NA	0.078	0.487

amplitude of ± 15 °C due to heat-induced mortality (Fig. 3a, d).

Implications for development under natural conditions

Based on the results described above, the most appropriate DR models resulting from the laboratory experiment

were chosen to apply to regional climate data, i.e. a mixture of the linear and nonlinear regressions for amplitudes up to ± 8 °C, and a polynomial model for ± 15 °C. Daily site-specific DR were calculated using mean bark temperatures and amplitudes. To visualise developmental progress under natural conditions, the resulting DR (see Supplement 7) were plotted against the daily mean temperatures and fitted with regression lines for different amounts of radiation representing different microhabitats (Fig. 4). DR was represented by an optimum curve for all radiation exposures, except for the fully shaded scenario, for which the measured conditions did not exceed T_0 . At low temperatures, global radiation led to faster development by increasing mean temperatures. At higher temperatures, however, global radiation shifted T_0 towards lower mean temperatures and consequently reduced maximum DR, as increasing temperature amplitudes lead to exposure to lethal temperatures. As a result, complete shade resulted in the slowest development at mean temperatures below 15 °C, but DR notably increased in the

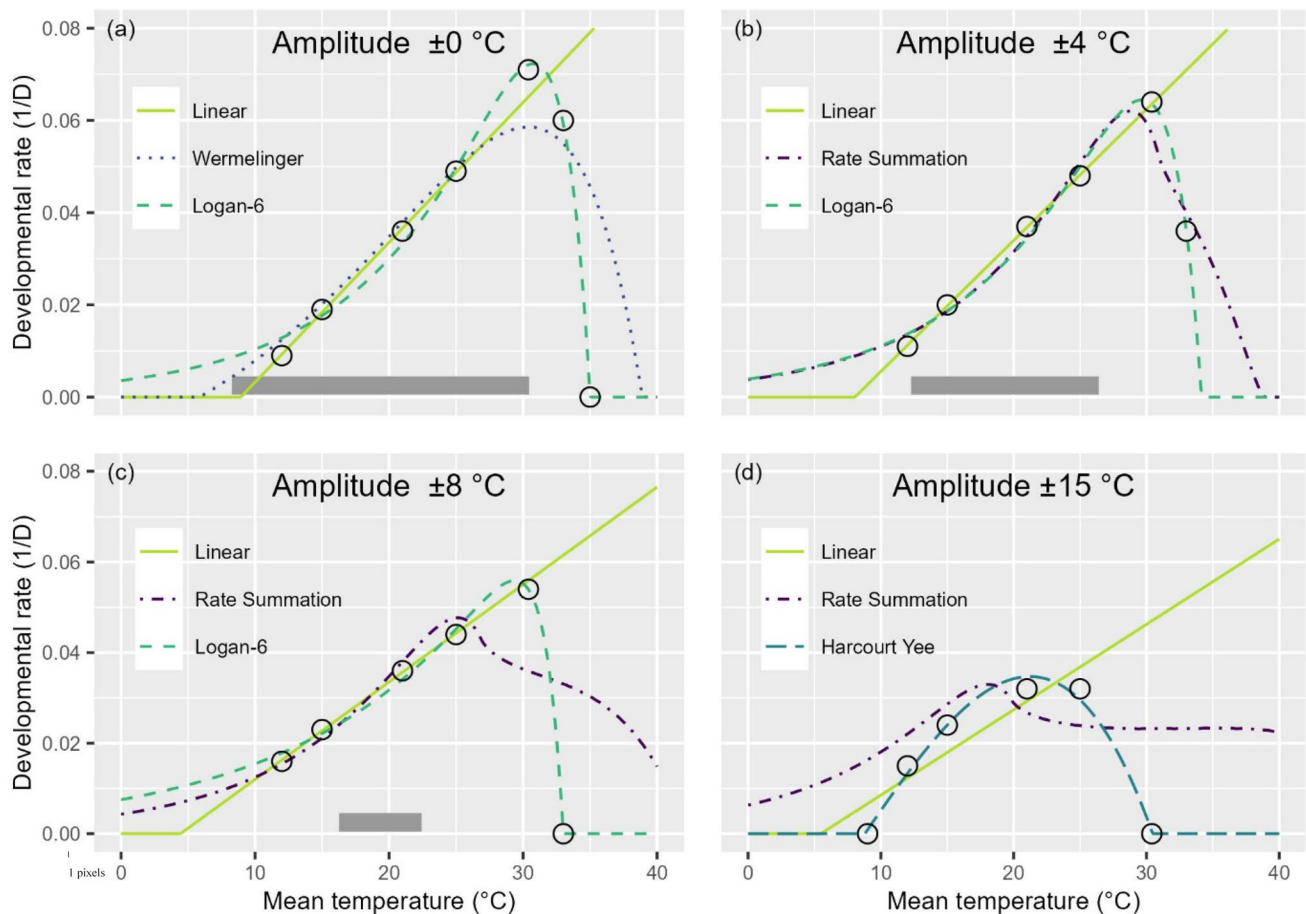


Fig. 3 Mean developmental rates (DR) for pre-imaginal development of *Ips typographus* (circles) and corresponding linear and nonlinear regressions for different temperature amplitudes (a–d). The line “Wermelinger” under constant temperature (a) shows the commonly used regression from Wermelinger and Seifert (1998). “Rate Summation” at amplitudes of ± 4 , ± 8 , and ± 15 °C represents the integral of

DR at constant temperatures along a diurnal sinus curve of the given amplitude, and “Logan-6” (a–c) and “Harcourt Yee” (d) are the fitted regressions of the respective models. Grey bars indicate the range of mean temperatures for which the respective temperature oscillation stays between DT_L (8.3 °C) and T_O (30.4 °C) determined under constant temperatures (Wermelinger and Seifert 1998)

shade at higher temperatures, surpassing all other curves above 21 °C.

The effects of fluctuating temperatures on *I. typographus* voltinism, compared to diurnal mean temperatures, were investigated at three different elevations by calculating the cumulative deviation in DR between April and October over a 12-year period. Notable differences in respective DR were revealed across all years and microhabitats (Fig. 5). In particular, the combination of low elevations and 100% solar radiation resulted in an average reduction of -1.75 potential generations (Fig. 5a). Such drastic negative effects decreased with elevation (Fig. 5b, c) and shading (Fig. 5a–c), even leading to a small positive effect of up to $+0.25$ potential generations in all fully shaded microhabitats and the semi-shaded microhabitat at high elevation.

Discussion

The effect of oscillating temperatures on developmental progress and the relative duration of ontogenetic stages of *I. typographus* was quantified under controlled conditions within a range of 3–35 °C and amplitudes up to ± 15 °C. DR were significantly affected by oscillations with an increase at low temperatures and a decrease around T_O and DT_U , whilst the relative duration of ontogenetic stages remained unaffected. The application of our experimental findings to meteorological data indicated that natural fluctuations in bark temperature, caused by air temperature and global radiation, notably alter DR and the resulting number of potential annual generations.

In our experiments, developmental progress occurred under constant temperatures between 9 and 33 °C, with

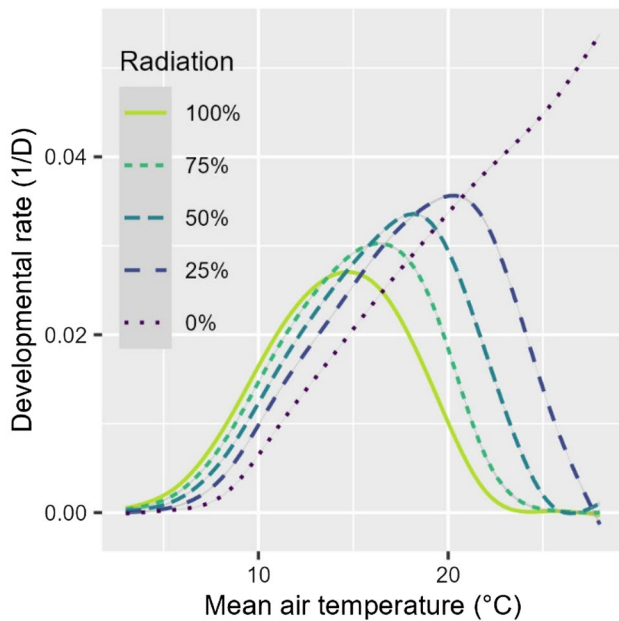


Fig. 4 DR curves for different radiation exposure based on temperature and global radiation data at *Ips typographus*-relevant sites across Germany (Dietrich et al. 2019) (details in Supplement 6). Bark temperatures were calculated according to Baier et al. (2007) and DR resulting from the laboratory experiment

the shortest D at 30.4 °C (Fig. 3a), which is consistent with earlier studies (Annala 1969; Wermelinger and Seifert 1998). However, no developmental progress was observed

at 35 °C, although an earlier study predicted a DT_U of 38.9 °C based on experimental observations between 12 and 33 °C (Wermelinger and Seifert 1998; see Fig. 3a). This discrepancy confirms previous reports of DR models predicting incorrect developmental thresholds due to their rather mathematical nature than biological plausibility (Damos and Savopoulou-Soultani 2012). Furthermore, our findings suggest that developmental progress at constant 5 °C (Štefková et al. 2017) is highly improbable. In the mentioned study, development was inferred from the percentage of developmental stages in already colonised logs. Since parental beetles were included in the calculation, it is possible that the observed proportional shift is due to mortality of developing stages, rather than their developmental progress.

In comparison with other bark beetle species, our observations resemble the temperature-dependent development of *Ips duplicatus* (Davídková and Doležal 2019) that inhabits a similar habitat and thermal environment. However, DT_L of other bark beetle species are slightly higher (Schebeck and Schopf 2017) or lower (Bentz et al. 1991; Gent et al. 2017). Such differences can be explained with different evolutionary trajectories through historical distribution ranges and adaptations to resulting biotic (i.e. trophic interactions, interspecific competition) and abiotic (i.e. temperature) conditions.

In summary, the observed effects of temperature fluctuations on developmental rates can be explained by four concepts, also applicable for insects in general: First, the rate

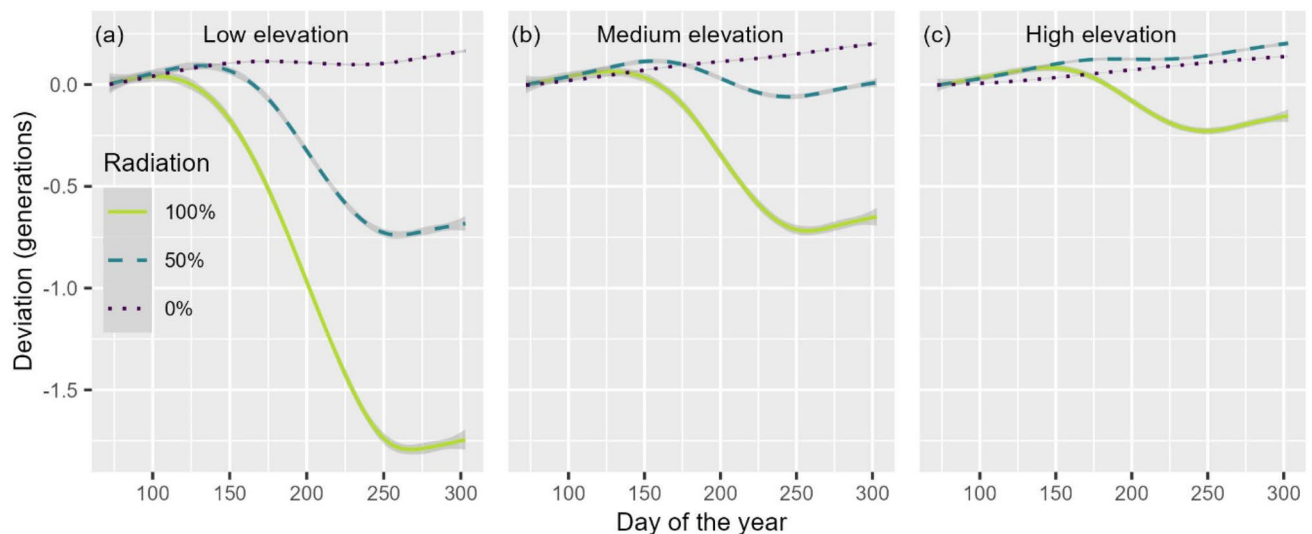


Fig. 5 Deviation of development prediction accounting for temperature fluctuations from development under constant temperatures, i.e. diurnal mean at different elevations (Low = 315 m, Medium = 815 m, High = 1370 m a.s.l.; see Supplement 6) and radiation levels (100% = complete sun, 50% = semi-shade, 0% = complete shade). The mean deviation for the period April to October for the years 2009–

2020 is shown. A deviation of 0 indicates no difference between fluctuating and constant temperature, whilst -1 indicates a reduction of one potential *Ips typographus* generation due to temperature fluctuations. Developmental rates were calculated based on results of the laboratory experiment and bark temperatures (mean and amplitude) according to Baier et al. (2007)

summation effect accounts for temperatures differing from their mean during oscillation, which subsequently affects DR (Worner 1992). Second, insects can sustain higher DR when exposed to disadvantageous temperature conditions for short periods (Damos and Savopoulou-Soultani 2012). Third, constant temperatures predict unrealistic DR near the developmental thresholds, as developmental progress is too slow to be measurable (Régnière et al. 2012; Shi et al. 2016). Both concepts two and three result in DR above the values predicted by the rate summation effect (Fig. 3b–d). One solution to address these limitations are approaches based on maximum likelihood, by allowing the use of censored observations (Régnière et al. 2012; McManis et al. 2018). Finally, lethal temperature thresholds of roughly 42 °C and –6 °C hindered any development, thus reducing DT_U under oscillating temperatures (Fig. 3b–d) and increasing DT_L under strongly oscillating temperatures (Fig. 3d). As a consequence, taking temperature fluctuation into account is important for accurately predicting the development of *I. typographus* and other insects that are exposed to extremely variable temperatures within their habitat. However, considering the rate summation effect alone would also provide fairly accurate estimates based on constant temperatures for many insect species in less variable habitats (von Schmalensee et al. 2021), as it was shown to improve the prediction accuracy of developmental rates for multiple species by > 40%, when compared to predictions based on diurnal mean temperatures (Hagstrum and Milliken 1991).

Under natural conditions, the predicted effects of temperature fluctuations on *I. typographus* are most relevant for sun-exposed areas in summer. Hence, developmental progress and resulting generations per season are significantly overestimated in these occasions when considering DR based on constant temperatures (Fig. 5; cf. Hlásny et al. 2011). For example, whilst constant 30 °C in the laboratory results in 30 days to complete one generation (Fig. 3a), natural fluctuation increases generation time to 40 days in the shade and even hinders developmental progress entirely in the sun due to exposure to lethal temperatures (Fig. 4). This is reflected in *I. typographus* behaviour to avoid sun-exposed parts of trunks in summer at lower elevations (Annala 1969). To a smaller degree, developmental progress and the number of generations per year are underestimated under cool and shaded conditions. The effect of temperature fluctuations should thus be considered when using thermal sums in field studies (Dworschak et al. 2014; Fritscher and Schroeder 2022; Lindman et al. 2023), as they lead to a reduction in required sums under low temperatures and an increase under high temperatures compared to constant temperatures.

Ultimately, our findings contribute to a further improvement of phenology models for *I. typographus*, e.g. Phenips (Baier et al. 2007), BSO (Jakoby et al. 2019),

and Rity-2 (Ogris et al. 2019). Phenips and Rity-2 only partly account for the effect of temperature fluctuations according to the rate summation effect. Furthermore, all of these models can be improved at temperatures exceeding DT_L or T_O , by accounting for the duration of adverse conditions and lethal temperature thresholds (Régnière et al. 2012), for which our study provides accurate predictions. Additionally important for predictive modelling is the quantification of the entire generation time instead of individual developmental duration (from egg to adult) for development under natural conditions. By combining our observations on the relative duration of ontogenetic stages with an earlier study (Wermelinger and Seifert 1998), we revealed that the entire generation time of *I. typographus* is 15% longer than individual development, which can be attributed to colonisation, mating, and oviposition, and directly affects potential annual generations. For forest pest insects, such as *I. typographus*, phenology models are crucial for risk assessment and forest ecosystem models (Netherer and Nopp-Mayr 2005; Seidl et al. 2012). Whilst risk assessment models facilitate timely management measures, like infestation control, debarking or removal of infested trees, as well as long-term silvicultural planning to mitigate eruptive outbreaks, forest ecosystem models allow simulation studies with a broader ecological perspective.

Due to climate change, the distribution of most insect species expands and retracts simultaneously, because of temperature-dependent population dynamics and trophic interactions (Lehmann et al. 2020). Likewise, DR and the number of annual *I. typographus* generations will potentially increase in currently relatively cool environments, such as Northern Europe or medium to high elevations in Central Europe. In contrast, at low elevations in Central Europe, a further acceleration of generation dynamics appears to be typically limited by maximum summer temperatures (Fig. 5a) and can then only result from a climate-induced extension of the activity period of *I. typographus*. Additionally, *I. typographus* is forced to follow the climate-related retraction of spruce trees at low elevations and latitudes (Vacek et al. 2019), which renders potential temperature-dependent voltinism irrelevant at these sites. Furthermore, our findings suggest that accelerating effects of rising temperatures on distribution and reproduction of insects are less pronounced than predicted with constant temperature data, ultimately affecting temperature-dependent voltinism and distribution by reducing T_O .

Still, further research is necessary to investigate the development of *I. typographus* at sub-zero temperatures, which was not fully addressed in this study. This could help to determine the lower developmental limit and cold-induced mortality in different ontogenetic stages, ultimately enhancing DR predictions during winter. Furthermore, validation of our development projections under natural

conditions could be achieved through detailed field studies of temperature-dependent development rates in different microhabitats. We strongly encourage considering fluctuating temperatures, especially near developmental thresholds, when studying DR of insects. These insights will improve our understanding of climate change-related effects on development, voltinism, and distribution of insects, which finally contributes to the preservation of structure and functionality of forest ecosystems in a changing climate.

Author contributions

SH and MK developed the research ideas and the study design; SH collected and analysed the data; SH led the writing of the manuscript. All authors were involved in data interpretation, revised drafts and contributed to the final version of the manuscript.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10340-024-01758-1>.

Acknowledgements We want to thank the forest district Freiburg for supplying us with spruce logs for the experiments. Furthermore, we are very grateful to Jonathan Decker, Marlene Graf, and Felicitas Sander for their assistance in data acquisition. In addition, we would like to express our gratitude to Felicitas Sander and Stephan Kammen for providing graphical illustrations. Finally, we wish to thank the two anonymous reviewers for their constructive feedback, which significantly improved the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This research was funded by the Ministry of Food, Rural Affairs and Consumer Protection Baden-Württemberg (MLR).

Data availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Annala E (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Ann Zool Fenn* 6:161–208
- Baier P (1996) Auswirkungen der Baumvitalität auf die Brutbaumqualität der Fichte (*Picea abies* Karsten) für *Ips typographus* (Linné 1758)(Coleoptera, Scolytidae). *Entomol Gen* 21:27–35
- Baier P, Pennerstorfer J, Schopf A (2007) PHENIPS—a comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *For Ecol Manage* 249:171–186. <https://doi.org/10.1016/j.foreco.2007.05.020>
- Bentz BJ, Logan JA, Amman GD (1991) Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Can Entomol* 123:1083–1094. <https://doi.org/10.4039/Ent1231083-5>
- Briere JF, Pracros P, Le Roux AY, Pierre JS (1999) A novel rate model of temperature-dependent development for arthropods. *Environ Entomol* 28:22–29. <https://doi.org/10.1093/ee/28.1.22>
- Butler CD, Trumble JT (2010) Predicting population dynamics of the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae) resulting from novel interactions of temperature and selenium. *Biocontrol Sci Tech* 20:391–406. <https://doi.org/10.1080/09583150903551587>
- Chen W, Yang L, Ren L, Shang Y, Wang S, Guo Y (2019) Impact of constant versus fluctuating temperatures on the development and life history parameters of *Aldrichina grahami* (Diptera: Calliphoridae). *Insects* 10:184. <https://doi.org/10.3390/insects10070184>
- Cloudsley-Thompson JL (1953) LXIX: studies in diurnal rhythms—III. Photoperiodism in the cockroach *Periplaneta americana* (L.). *Ann Mag Nat Hist* 6:705–712. <https://doi.org/10.1080/00222935308654473>
- Colinet H, Sinclair BJ, Vernon P, Renault D (2015) Insects in fluctuating thermal environments. *Annu Rev Entomol* 60:123–140. <https://doi.org/10.1146/annurev-ento-010814-021017>
- Damos P, Savopoulou-Soultani M (2012) Temperature-driven models for insect development and vital thermal requirements. *Psyche* 2012:123405. <https://doi.org/10.1155/2012/123405>
- Danks HV (2013) Measuring and reporting life-cycle duration in insects and arachnids. *Eur J Entomol* 97:285–303. <https://doi.org/10.14411/eje.2000.046>
- Davidková M, Doležal P (2019) Temperature-dependent development of the double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836)(Coleoptera; Curculionidae). *Agric For Entomol* 21:388–395. <https://doi.org/10.1111/afe.12345>
- Dietrich H, Wolf T, Kawohl T, Wehberg J, Kändler G, Mette T, Röder A, Böhner J (2019) Temporal and spatial high-resolution climate data from 1961 to 2100 for the German National Forest Inventory (NFI). *Ann For Sci* 76:6. <https://doi.org/10.1007/s13595-018-0788-5>
- Dixon AFG, Honěk A, Keil P, Kotela MAA, Šizling AL, Jarošík V (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Funct Ecol* 23:257–264. <https://doi.org/10.1111/j.1365-2435.2008.01489.x>
- Doležal P, Sehnal F (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. *J Appl Entomol* 131:165–173. <https://doi.org/10.1111/j.1439-0418.2006.01123.x>
- Dworschak K, Gruppe A, Schopf R (2014) Survivability and post-diapause fitness in a scolytid beetle as a function of overwintering developmental stage and the implications for population dynamics. *Ecol Entomol* 39:519–526. <https://doi.org/10.1111/een.12127>
- Fischer K, Kölzow N, Hölte H, Karl I (2011) Assay conditions in laboratory experiments: is the use of constant rather than fluctuating temperatures justified when investigating temperature-induced

- plasticity? *Oecologia* 166:23–33. <https://doi.org/10.1007/s00442-011-1917-0>
- Fritscher D, Schroeder M (2022) Thermal sum requirements for development and flight initiation of new-generation spruce bark beetles based on seasonal change in cuticular colour of trapped beetles. *Agric For Entomol* 24:405–421. <https://doi.org/10.1111/afe.12503>
- Gent CA, Wainhouse D, Day KR, Peace AJ, Inward DJ (2017) Temperature-dependent development of the great European spruce bark beetle *Dendroctonus micans* (Kug.) (Coleoptera: Curculionidae: Scolytinae) and its predator *Rhizophagus grandis* Gyll. (Coleoptera: Monotomidae: Rhizophaginae). *Agric For Entomol* 19:321–331. <https://doi.org/10.1111/afe.12212>
- Hagstrum DW, Milliken GA (1991) Modeling differences in insect developmental times between constant and fluctuating temperatures. *Ann Entomol Soc Am* 84:369–379. <https://doi.org/10.1093/aesa/84.4.369>
- Harcourt D, Yee J (1982) Polynomial algorithm for predicting the duration of insect life stages. *Environ Entomol* 11:581–584. <https://doi.org/10.1093/ee/11.3.581>
- Hlášný T, Zajíčková L, Turčáni M, Holuša J, Sitková Z (2011) Geographical variability of spruce bark beetle development under climate change in the Czech Republic. *J For Sci* 57:242–249. <https://doi.org/10.5555/20113296908>
- Hogue JN, Hawkins CP (1991) Morphological variation in adult aquatic insects: associations with developmental temperature and seasonal growth patterns. *J N Am Benthol Soc* 10:309–321. <https://doi.org/10.2307/1467604>
- Jakoby O, Lischke H, Wermelinger B (2019) Climate change alters elevational phenology patterns of the European spruce bark beetle (*Ips typographus*). *Glob Change Biol* 25:4048–4063. <https://doi.org/10.1111/gcb.14766>
- Johnson DM, Haynes KJ (2023) Spatiotemporal dynamics of forest insect populations under climate change. *Curr Opin Insect Sci* 56:101020. <https://doi.org/10.1016/j.cois.2023.101020>
- Kingsolver JG, Arthur Woods H, Buckley LB, Potter KA, MacLean HJ, Higgins JK (2011) Complex life cycles and the responses of insects to climate change. *Integr Comp Biol* 51:719–732. <https://doi.org/10.1093/icb/11/5/719>
- Kingsolver JG, Ragland GJ, Diamond SE (2009) Evolution in a constant environment: thermal fluctuations and thermal sensitivity of laboratory and field populations of *Manduca sexta*. *Evolution* 63:537–541. <https://doi.org/10.1111/j.1558-5646.2008.00568.x>
- Lactin DJ, Holliday N, Johnson D, Craigen R (1995) Improved rate model of temperature-dependent development by arthropods. *Environ Entomol* 24:68–75. <https://doi.org/10.1093/ee/24.1.68>
- Lehmann P, Ammunét T, Barton M, Battisti A, Eigenbrode SD, Jepsen JU, Kalinkat G, Neuvonen S, Niemelä P, Terblanche JS (2020) Complex responses of global insect pests to climate warming. *Front Ecol Environ* 18:141–150. <https://doi.org/10.1002/fee.2160>
- Lindman L, Ranius T, Schroeder M (2023) Regional climate affects habitat preferences and thermal sums required for development of the Eurasian spruce bark beetle, *Ips typographus*. *For Ecol Manag* 544:121216. <https://doi.org/10.1016/j.foreco.2023.121216>
- Liu S-S, Zhang G-M, Zhu J (1995) Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. *Ann Entomol Soc Am* 88:107–119. <https://doi.org/10.1093/aesa/88.2.107>
- Logan J, Wollkind D, Hoyt S, Tanigoshi L (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. *Environ Entomol* 5:1133–1140. <https://doi.org/10.1093/ee/5.6.1133>
- Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, Grégoire JC, Hurling R, Nageleisen LM, Netherer S (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* 40:1426–1435. <https://doi.org/10.1111/ecog.02769>
- McManis A, Powell J, Bentz B (2018) Developmental parameters of a southern mountain pine beetle (Coleoptera: Curculionidae) population reveal potential source of latitudinal differences in generation time. *Can Entomol* 151:1–15. <https://doi.org/10.4039/tce.2018.51>
- Netherer S, Nopp-Mayr U (2005) Predisposition assessment systems (PAS) as supportive tools in forest management—rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *For Ecol Manag* 207:99–107. <https://doi.org/10.1016/j.foreco.2004.10.020>
- Nicolai V (1986) The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148–160. <https://doi.org/10.1007/BF00399052>
- Ogris N, Ferlan M, Hauptman T, Pavlin R, Kavčič A, Jurc M, De Groot M (2019) RITY: a phenology model of *Ips typographus* as a tool for optimization of its monitoring. *Ecol Model* 410:108775. <https://doi.org/10.1016/j.ecolmodel.2019.108775>
- Patacca M, Lindner M, Lucas-Borja ME, Cordonnier T, Fidej G, Gardiner B, Hauf Y, Jasinevičius G, Labonne S, Linkevičius E (2023) Significant increase in natural disturbance impacts on European forests since 1950. *Glob Change Biol* 29:1359–1376. <https://doi.org/10.1111/gcb.16531>
- Peter Z (2014) Effect of climate change on population dynamics of bark beetles: relationships between temperature and development rate of *Ips sexdentatus* (Boern.). M.Sc.-Thesis, Université de Lorraine, 32 pp
- Raffa K, Grégoire JC, Lindgren BS (2015) Natural history and ecology of bark beetles. In: Vega FE, Hofstetter RW (eds) *Bark beetles: biology and ecology of native and invasive species*. Elsevier, London, England, pp 1–40
- Ratte HT (1985) Temperature and insect development. In: Hoffmann KH (ed) *Environmental physiology and biochemistry of insects*. Springer Verlag, Berlin, Germany, pp 33–65
- Rebaudo F, Rabhi VB (2018) Modeling temperature-dependent development rate and phenology in insects: review of major developments, challenges, and future directions. *Entomol Exp Appl* 166:607–617. <https://doi.org/10.1111/eea.12693>
- Rebaudo F & Regnier B (2023) devRate: quantify the relationship between development rate and temperature in ectotherms. R-package version 0.2.4. <https://CRAN.R-project.org/package=devRate>
- Régnière J, Powell J, Bentz B, Nealis V (2012) Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *J Insect Physiol* 58:634–647. <https://doi.org/10.1016/j.jinsphys.2012.01.010>
- Schebeck M, Dobart N, Ragland GJ, Schopf A, Stauffer C (2022) Facultative and obligate diapause phenotypes in populations of the European spruce bark beetle *Ips typographus*. *J Pest Sci* 95:889–899. <https://doi.org/10.1007/s10340-021-01416-w>
- Schebeck M, Schopf A (2017) Temperature-dependent development of the European larch bark beetle, *Ips cembrae*. *J Appl Entomol* 141:322–328. <https://doi.org/10.1111/jen.12351>
- Schebeck M, Schopf A, Ragland G, Stauffer C, Biedermann P (2023) Evolutionary ecology of the bark beetles *Ips typographus* and *Pityogenes chalcographus*. *Bull Entomol Res* 113:1–10. <https://doi.org/10.1017/S0007485321000353>
- Scrucca L, Fop M, Murphy TB, Raftery AE (2016) mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. *The R Journal* 8:289–317
- Seidl R, Rammer W, Scheller RM, Spies TA (2012) An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecol Model* 231:87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>
- Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacciano G, Wild J, Ascoli D, Petr M, Honkaniemi J (2017) Forest

- disturbances under climate change. *Nat Clim Chang* 7:395–402. <https://doi.org/10.1038/nclimate3303>
- Shi PJ, Reddy GV, Chen L, Ge F (2016) Comparison of thermal performance equations in describing temperature-dependent developmental rates of insects: (I) empirical models. *Ann Entomol Soc Am* 109:211–215. <https://doi.org/10.1093/aesa/sav121>
- Stange E, Ayres M (2010) Climate change impacts: insects. Eiley, Chichester, England, Encyclopedia of life sciences (ELS). <https://doi.org/10.1002/9780470015902.a0022555>
- Štefková K, Okrouhlík J, Doležal P (2017) Development and survival of the spruce bark beetle, *Ips typographus* (Coleoptera: Curculionidae: Scolytinae) at low temperatures in the laboratory and the field. *Eur J Entomol* 114:1–6. <https://doi.org/10.14411/eje.2017.001>
- Vacek Z, Vacek S, Slanař J, Bílek L, Bulušek D, Štefančík I, Králíček I, Vančura K (2019) Adaption of Norway spruce and European beech forests under climate change: from resistance to close-to-nature silviculture. *Central Eur For J* 65:129–144. <https://doi.org/10.2478/forj-2019-0013>
- von Schmalensee L, Gunnarsdottir KH, Näslund J, Gotthard K, Lehmann P (2021) Thermal performance under constant temperatures can accurately predict insect development times across naturally variable microclimates. *Ecol Lett* 24:1633–1645. <https://doi.org/10.1111/ele.13779>
- Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus* — a review of recent research. *For Ecol Manage* 202:67–82. <https://doi.org/10.1016/j.foreco.2004.07.018>
- Wermelinger B, Seifert M (1998) Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L) (Col., Scolytidae). *J Appl Entomol* 122:185–191. <https://doi.org/10.1111/j.1439-0418.1998.tb01482.x>
- Wermelinger B, Seifert M (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. *Ecol Entomol* 24:103–110. <https://doi.org/10.1046/j.1365-2311.1999.00175.x>
- Worner SP (1992) Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. *Environ Entomol* 21:689–699. <https://doi.org/10.1093/ee/21.4.689>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.