Phenology of the spruce bark beetle *Ips typographus* in the UK under past, current and future climate conditions

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Summary

- The European spruce bark-beetle, *Ips typographus*, is a major pest of Norway spruce across mainland Europe; however, until 2018 it was considered absent from the UK. The finding of a breeding population of *I. typographus* in Kent, England, in 2018 and subsequent findings in pheromone traps across the southeast of England, has led to an urgent need to improve understanding of environmental suitability across the UK.
- Two distinct published phenological models for *I. typographus*, developed in Sweden and Austria, were adapted for use in the UK and validated against pheromone trap data collected at the original site of infestation and in the surrounding area from 2019 to 2022.
- Both models captured some, but not all, of the within-season variation in trap catches. One, the PHENIPS model, more accurately captured early season flight patterns. The climate in the southeast of England is mild enough to facilitate two generations of the beetle, whilst further north the pest is expected to be univoltine. At high-altitude in Scotland, there is insufficient thermal warming within a season for the completion of one annual generation.
- Phenological modelling does not explain why the pest failed to establish in England prior to 2018 including when a large amount of infested material was imported to sawmills in the 1940s. Under 2^{o}C and 3^{o}C global warming scenarios we might expect to see an increase in potential voltinism across the UK in the next few decades, increasing the risk of large outbreaks of *I. typographus* were it allowed to establish.

Keywords

Phenology, Mathematical model, *Ips typographus*, European spruce bark beetle, Climate change, Voltinism, Bark beetle

Societal impact statement

In 2018, a breeding population of the European spruce bark-beetle, *Ips typographus*, was discovered in woodland in southeast England. *Ips typographus* is a major forest pest in continental Europe, however, despite previous findings at ports and sawmills, this was the first recorded infestation in the UK. The number of generations per year (voltinism) varies with latitude and altitude. Applying a phenological model we find that the current climate in southern UK could support two generations, while temperature accumulation in parts of Scotland may be insufficient to support one generation. Global warming will increase voltinism and hence the risk of establishment.

Introduction

The European spruce bark beetle, *Ips typographus* (L.) (Coleoptera, Curculionidae), is considered the most destructive pest of Norway spruce (*Picea abies*) in Europe. An estimated 2.9 million m^3 per year of wood was lost to bark beetle (predominantly *I. typographus*) damage between 1950 and 2000 (Schelhaas et al., 2003) with the problem intensifying in many countries in the last 20 years (Hlásny et al., 2021). At low population densities, this tree-killing bark beetle species usually relies on recently dead, broken and felled, drought stressed or otherwise weakened trees (Schroeder & Lindelöw, 2002). However, under favourable conditions (following forest damage by storm and elevated temperatures, for example), populations of *I. typographus* can increase rapidly into an epidemic phase and disturb vast areas of healthy spruce forest (Wermelinger, 2004).

Until recently, the United Kingdom (UK) was considered free of *I. typographus* and was identified as a Pest Free Area (PFA) by the European Union (European Union (EU) Regulation 2016/2031). However, in December 2018 a breeding population of the pest was discovered in southeastern England in a woodland close to Ashford, Kent (Blake et al., 2024). The finding of active infestations of *I. typographus* followed intensive surveillance triggered by the capture of several beetles in a nearby monitoring billet trap. The trap was part of a network across the UK to demonstrate the absence of breeding populations of *I. typographus*, *I. amitinus* and *I. duplicatus* (Fielding et al., 1994). Breeding galleries were identified in windthrown and stressed Norway spruce and in log stacks waiting to be moved off the site. All life stages of the beetle were found, and old galleries demonstrated the beetles had been successfully breeding for several years. An intensive eradication program was initiated, with the aim of removing and destroying all potentially infested hosts before the 2019 spring swarming period. *Ips typographus* can overwinter under the bark and in soil and leaf litter (Annila, 1969) thus trap trees, billet piles and pheromone traps were put in place to capture emerging beetles and reduce the risk of onward spread of the pest. A demarcated zone was established encompassing woodland within 100km of the initial finding, and a ‘wider environment’ trapping study was initiated to determine whether the pest had spread out from the primary infestation site, including surveying for other breeding populations that may have been missed during winter surveillance. No new breeding populations were identified in 2019 and 2020 despite positive findings in pheromone traps away from the original site of infestation and intensive ground surveillance (Blake et al., 2024).

Continuation of the intensive surveillance strategy in 2021 and 2022 led to the discovery of several additional outbreaks of *I. typographus* in the counties of Kent and Sussex. All infestations were restricted to Norway spruce which were recently dead, dying, or left as harvesting residue, with no evidence found of breeding on healthy trees, and subject to official action to minimise the risk of onward spread (Blake et al., 2024). The current strategy, from Summer 2023, is to eradicate any breeding populations to mitigate against possible spread and establishment elsewhere in the UK where the pest could cause significant economic losses and ecological disturbance. The demarcated area has increased year-on-year in response to these new outbreak sites: in 2023 this encompassed the south-eastern counties of Kent, East and West Sussex, Greater London and Surrey as well as parts of Hampshire and Essex (Forestry Commission, 2023).

Around 75% of the roughly 725,000 hectares of spruce trees in Great Britain are grown in Scotland (Ditchburn & Brewer, 2014). A potentially important difference between spruce forestry in the UK and mainland Europe is the dominant species of spruce. In the UK, Sitka spruce (*Picea sitchensis*) accounts for over 90% of spruce grown, whereas in mainland Europe Norway spruce dominates (Durrant et al., 2016; Caudullo et al., 2016). Differences in the physical and chemical properties of the bark between Norway and Sitka spruce may affect host recognition by the beetle and response to attack by the host (Flø et al., 2018) as hypothesised for other spruce species (Lawson et al., 1996). However, in laboratory conditions *I. typographus* can successfully reproduce on Sitka spruce albeit with a significantly lower total offspring production than observed in Norway spruce (Flø et al., 2018; Økland et al., 2011).

Although there are no records of breeding populations of *I. typographus* in the UK prior to the finding in 2018, routine trapping has identified multiple incursions of *I. typographus* (Evans, 2021) that have generally been associated with imported timber. Notably, in the late 1940s large numbers of beetles were detected on spruce arriving from Germany for processing in British sawmills (Laidlaw, 1947). In this period, Germany was experiencing a large-scale outbreak due to a combination of shortage of labour to clear damaged wood and favourable weather conditions for beetle development (Schelhaas et al., 2003). Follow-up surveys at and near interception locations in the late 1940s found no evidence of breeding in the UK.

Typically, *I. typographus* is predominantly univoltine (one generation per year) across Fennoscandia (Annila, 1969; Bakke, 1983; Jönsson et al., 2007; Fritscher & Schroeder, 2022) and multivoltine, with two to three generations per year in Central Europe below 600m altitude (Berec et al., 2013; Doležal & Sehnal, 2007). A possible hypothesis for the failure of the pest to establish previously in the UK, despite repeated incursions, is that the environment is unsuitable for pest development. Increasing summer temperatures, drought and storms are positively correlated with epidemics of *I. typographus* in mainland Europe (Marini et al., 2017). However, host density, species composition, high rainfall and spring and summer temperatures may limit the ability of the pest to establish in the UK. Here, we use historic meteorology data to investigate the impact of air temperature on the potential voltinism of *I. typographus* in the UK. Two distinct phenological models, which use temperature to estimate the rate of insect development, are implemented to predict the number of generations of *I. typographus* within a breeding season (Baier et al., 2007; Jönsson et al., 2007).

The model by Baier et al. (2007), named ‘PHENIPS’, was developed as a decision support tool for the management of *I. typographus* in Austria. The PHENIPS model was parameterised using data collected from several sites within the Kalkalpen National Park, Upper Austria between 2001 and 2003. The site is mountainous with a wide variation in exposure to solar radiation according to slope, aspect and elevation ranging from 580 to 1200 meters above sea level. To enable localised predictions of insect voltinism, the model incorporates a complex topoclimatic model to obtain high resolution estimates of air and bark temperature. The model has been independently validated on data collected in the Bohemian Forest in the Czech Republic in 2010 and 2011 (Berec et al., 2013) and recalibrated, and simplified, for use with temperature data obtained from the INCA system (Integrated Nowcasting through Comprehensive Analysis) to support pest management in Slovenia (Ogris, 2020; Ogris et al., 2019).

The model by Jönsson et al. (2007) was developed to explore the potential impact of climate change on voltinism of the beetle in southern Sweden. It was parameterised using values extracted from published research studies on *I. typographus* populations in Fennoscandia (Annila, 1969; Harding & Ravn, 1983). An updated version of the model, validated using pheromone trap monitoring data from Sweden, Denmark and Norway, was published (Jönsson et al., 2011) in which the criteria for reproductive diapause were refined to include both photoperiodic and thermal cues and the threshold for swarming air temperature threshold was reduced from 20^{o}C to 16^{o}C.

Differences in model structure and parameters may be attributed in part to the methods used to develop the models, but they may also be driven by differences in the populations on which the models were based. The genetic structure of European populations of *I. typographus* is broadly split into a ‘northern’ and ‘southern’ group (Mayer et al., 2015). Recent research suggests that the most northerly populations may have adapted to the shorter warm season by avoiding shaded areas for breeding (Lindman et al., 2023) and producing one set of offspring per year with an obligate reproductive diapause to increase overwinter survival (Schebeck et al., 2022). Regular finds of *I. typographus* at ports (Evans, 2021), and cross channel wind-assisted spread (Inward et al., 2024a), provide dispersal pathways into the UK for both obligate and facultative diapausing populations. The UK has a temperate oceanic climate with relatively mild summers and winters compared to continental Europe thus it is unclear whether the phenology of the pest will be closer to that observed in Northern or Central Europe.

We compare the predicted development and swarming times of *I. typographus* using adaptations of the PHENIPS and Jönsson models (Baier et al., 2007; Jönsson et al., 2007, 2011). We use ERA5-Land meteorology data (Muñoz-Sabater et al., 2021) and pheromone trap data collected in the southeast of England between 2019 to 2022 as part of the ongoing monitoring for *I. typographus*. Overall, we conclude that the adapted PHENIPS model provides more accurate estimation of early onset and spring swarming than the Jönsson model for UK conditions. We use the PHENIPS model for further analysis to explore whether changes in temperature could explain why *I. typographus* did not successfully establish following multiple incursions in the late 1940s. We also analyse the likely impact of current weather conditions (2019-2022) on potential voltinism, were the pest to spread from the southeast of England under current conditions, and the possible long-term impact of global climate change (2^{o}C and 3^{o}C global warming) on potential voltinism across the UK.

Materials and Methods

Overview

The work presented in this paper builds on published field data, phenological models, historic weather data and climate models to explore the voltinism of *I. typographus* in the past, present and future across the United Kingdom (UK). In this section, we provide a brief overview of: (i) our adaptation of two phenological models for *I. typographus* (Baier et al., 2007; Jönsson et al., 2007); (ii) the pheromone trap data collected from 2019-2022 within the demarcated zone in southeastern England which we use to determine how well the models predict flight times in a British context; and, (iii) the climate and weather data selected to investigate past, current and future voltinism of the pest across the UK. All plotting and analyses were conducted in MATLAB® 2022a using in-built functions and file-exchange functions CubeHelix (Stephen23, 2024) and The Climate Data Toolbox (Greene et al., 2019).

2.1 Phenological models

For ease of reference, we refer to the two previously published phenological models as the 'PHENIPS' model (Baier et al., 2007) and the 'Jönsson' model (Jönsson et al., 2007). Computer code was not available for either model from the original authors. It was therefore necessary to interpret the model structures from the published papers (Baier et al., 2007; Jönsson et al., 2007, 2011). To confirm our interpretation of the models, we shared schematic diagrams of our proposed model structures with the first authors of the original papers for comment (Anna Jönsson, Peter Baier *pers. comm. July 2019*).

Here we summarise our adapted versions of each model, which include minor alterations to the original published versions to enable use with the available meteorological data for the UK. In each case we model a maximum of two filial generations. For ease of reference, we use the following notation: F1 = first filial generation (offspring of overwintering beetles); F2 = second filial generation (offspring of F1); SB1 = sister brood (second brood of the overwintering beetles); SB2 = combined second generation of the offspring of the original sister brood (SB1) and the sister brood of the offspring of the first filial generation (F1).

PHENIPS model

Emergence and swarming of the overwintering generation are based on air degree days whilst all subsequent development is calculated using estimated bark degree days.

Estimated date of spring swarming and onset of infestation: 'Spring swarming' represents the initiation of flight activity in overwintering beetles, an early indicator of the presence of *I. typographus*. 'Onset of infestation' is the initiation of the first generation of offspring. The distinction between spring swarming and onset of infestation is supported by Ogris *et al.* (2019) who reported a time delay between spring swarming and onset of infestation in trap logs of between 7 and 52 days. Two criteria are required for each event: (i) minimum degree day (dd) accumulation of 60.5dd for spring swarming and 140dd for onset of infestation, where degree days are calculated using maximum daily air temperature starting from the 1st April with a baseline of 8.3°C; and, (ii) once the degree day requirement is met, spring swarming/ onset of infestation occur on the first day that the daily maximum temperature exceeds 16.5°C.

Development and swarming of offspring generations: The rate of development of *I. typographus* from egg to adult bark beetle is a function of the temperature within the maternal galleries (Wermelinger & Seifert, 1998). Baier *et al.* (2007) estimate under bark temperature using a non-linear function of air temperature and solar radiation where site specific climate data are estimated using their own topoclimatic model. Ogris *et al.* (2019), who adapted the PHENIPS model for use in Slovenia, use a simple linear model to transform air temperature reported by the INCA system (Integrated Nowcasting through Comprehensive Analysis) (Haiden et al., 2011) into bark temperature. The INCA system does not cover the UK and we cannot assume that the coefficients of the linear model are valid for other weather data sources. In the absence of a published formula relating any of the UK gridded air temperature data sources to bark temperature for Norway or Sitka Spruce, we focus on modelling development of *I. typographus* in the absence of insolation heating, i.e. within closed stands, and make the simplifying assumption that reported mean and maximum air temperature are adequate proxies for mean and maximum bark temperature. This follows from Baier et al. (2007) who state that “within closed stands, irradiation has negligible effect on bark temperature, which is then equivalent to air temperature”.

The degree day calculation for the rate of maturation from egg to adult beetle, originally proposed by Wermelinger and Seifert (1998), is a non-linear piecewise function of bark temperature. Details of the calculation, extracted from Baier et al. (2007), are provided in the supporting information (Methods S1). Each generation is assumed to be fully developed when the scaled accumulated maturation (relative to degree day requirement for full development: 557 bark dd) reaches one. However, swarming, and hence the start of the next distinct generation, can only occur on days where the maximum air temperature is at least 16.5°C. Parent beetles can lay a second (sister) brood of eggs with development of the second brood (SB1, SB2) initiated when the first set of offspring is halfway through development.

Reproductive diapause: The initiation of filial generations and second broods ceases when the daylength drops below 14.5 hours. Although there is some variation in when this daylength threshold is met across the UK, we make the simplifying assumption that the threshold is met on 18th August in all locations (based on daylight hours in London).

Overwintering: No further significant increase in thermal sum is assumed after the end of October. Only generations that have reached at least 60% of their total thermal development, at which point the initiated generation is assumed to have completed preimaginal development (Dworschak et al., 2014; Faccoli 2002; Schebeck et al., 2022), are considered able to overwinter successfully.

Jönsson model

The timing of spring swarming and the rate of development of each filial generation, differentiating between sunny and shaded conditions, up to a maximum of two generations (F1, F2) are estimated using air degree days (calculated by summing mean daily air temperature from the 1st January above a baseline of 5°C). In contrast to the PHENIPS model, the Jönsson model does not include the development of sister (second) broods.

Estimated date of spring swarming: Two criteria are required for spring swarming: (i) degree day accumulation requirement of 120 dd; and (ii) once the degree day requirement is met, swarming occurs on the first day that the daily maximum temperature exceeds 16°C.

Development and swarming of offspring generations: Following each swarming, a fixed period of seven days is assumed before eggs start to develop. Two distinct pathways are then followed to distinguish between differences in the microclimate in the breeding chambers, due in part to differences in sun exposure according to location in the forest, which are not captured by air temperature data. A lower temperature sum of 625dd is used to capture development in sun exposed bark and an upper temperature sum of 750dd for shaded locations. Swarming, and hence the start of seven-day period before egg development, can only occur on days where the maximum air temperature is at least 16°C.

Reproductive diapause: in the initial published version of the model, inhibition of summer swarming was modelled to depend only on temperature with a mean daily temperature drop below 15°C triggering reproductive diapause (Jönsson et al., 2007). Subsequently, photoperiod was included as an additional criterion with the daylength required to trigger diapause increasing with latitudinal gradient (Jönsson et al., 2011). Here we apply the same minimum photoperiod as used in the PHENIPS model of 14.5 hours (18th August).

Overwintering: The thermal sum for overwintering is assessed at the first time the mean day time temperature drops below 5°C or the end of the year, whichever occurs earlier. Only generations that have reached 100% of their total thermal development by this date are considered able to overwinter successfully.

Schematic diagrams for each model are provided in the supporting information (Figures S1 and S2).

2.2 Model evaluation

The performance of each phenological model when applied to the UK, was evaluated by comparing the predicted dates for swarming with pheromone trap data collected as part of the ongoing *I. typographus* eradication programme (Blake et al., 2024).

Field data

We divided the available *I. typographus* pheromone trapping data for 2019-2022 into three groups:

(i) 2019: Initial eradication site (Packing Wood, latitude: 51.08, longitude: 0.86): 145 traps were placed across the site following clearance of host trees to capture any remaining adult *I. typographus*.

(ii) 2019: Subset of 11 traps from the wider environment survey located within the ERA5-Land grid square containing Packing Wood (bounding box: latitude = [51.05,51.15], longitude = [0.82,0.92]).

(iii) 2019-2022: Wider environment survey complete data set: in 2019, 71 pheromone traps were set up across the wider region up to 100 km from Packing Wood to determine whether *I. typographus* had established elsewhere in southeastern England. In subsequent years the number of traps was increased (2020 – 74; 2021 – 80; 2022 – 125) and the trapping area was extended to cover all regions of England in 2022 (Figure 1 (a-d)). The majority of the wider environment survey traps were located within or close to stands of spruce, with half placed on Public Forest Estate and the rest in private woodlands. Traps were placed at a higher density in areas where there was evidence of *I. typographus* breeding from 2021 and some traps were added later in the season.

Traps placed at Packing Wood were emptied weekly. Wider environment study traps were emptied fortnightly (apart from a small number of locations where they were checked weekly) with traps divided into week A and week B collections. Traps were active across all sites from late March to the end of October in 2019, then active from late March to the end of September in subsequent years. The traps were black cross-vane traps (Witasek PflanzenSchutz GmbH, Austria), with diluted propylene glycol (E1520) (30% propylene glycol in water) used in the collection pots as a killing agent and preservative. The traps were set 1.5–2.0 m above the ground between two upright wooden poles and were baited with an *I. typographus* pheromone lure obtained from Pherobank BV (The Netherlands) (Blake et al. 2024). All samples were returned to the Forest Research laboratory at Alice Holt, Surrey, England, where they were sorted and the numbers of *I. typographus* recorded. Further details of the trapping program are given in Blake et al. (2024).

2.3 Gridded estimates of potential number of generations of *I. typographus* across the UK: past, present and future

Simulations to investigate spatial and temporal variation in the potential number of generations of *I. typographus* across different regions of the UK were run for three time periods:

(i) ***Current***: 2019-2022 to investigate whether the cooler climate in other parts of the UK compared with the southeastern England could limit establishment in other areas.

(ii) ***Historical***: 1945-1949 to investigate whether lower temperature during that time (in the context of climate change) could provide an explanation for the failure of the pest to establish in the UK historically despite the detection of large numbers of beetles on imported wood (as reported by Laidlaw (1947)).

(iii) ***Future***: 2025-2080 to explore how changes in climate, as predicted by climate models, could affect the potential number of generations across the UK.

Gridded air temperature data, 2m above ground, for each period were obtained from the following sources:

(i) 2019-2022: hourly values from ERA5-Land (Muñoz-Sabater, 2019). Resolution: 0.1°x0.1°

(ii) 1945-1949: hourly values from ERA5 (Hersbach et al., 2023). Resolution: 0.25°x0.25°

(iii) 2025-2080: daily mean and maximum from UKCP18 regional projections for the high emission representative concentration pathway (RCP) 8.5 (Met Office Hadley Centre, 2018). Resolution: 12km x 12km on the Ordinance Survey British National Grid.

The UKCP18 regional climate projection dataset consists of twelve ensemble members, covering a 100-year period (1981-2080) generated using the HadGEM3-GC3.05 global climate model (Met Office Hadley Centre, 2018). Each ensemble member (member identities: 1,4-13 and 15 (Met Office, 2021)) captures one possible future outcome that is consistent across climate variables at different times and spatial locations under the assumptions of the high emissions pathway RCP8.5. Any given simulation is not consistently warmer in each season and in each year than any other simulation. Here we plot the predicted number of generations in the first year the global mean surface temperature (GMST) exceeds 2°C and 3°C for each ensemble member (Barnes et al., 2024).

Results

Field data

Analysis of the wider environment survey data highlights three key features (i) the total trap catch is very low in comparison to reported catches in continental Europe; (ii) the date of spring swarming varies between years; and (iii) in three out of four years there is a clear second peak in trap catches in July/August. Adult *I. typographus* were identified at several trap sites in the southeast of England in all years since the introduction of the wider environment survey (Figure 1e-h). In 2022 the spatial extent of positive traps increased: however there was also an increase in the extent of the trapping area in comparison with previous years (Figure 1d,h).

The total annual catches in the wider environment survey remained low in the years 2019 to 2022, with a total beetle count of 1560, 850, 7500 and 4255 respectively. The highest individual trap counts per fortnight in these years were 138, 46, 786 and 158 respectively. For comparison, average weekly catches of between 600 and 1,700 beetles are typical in one location in epidemic periods in continental Europe with tens of thousands of beetles caught per trap over the main flight periods (Kuhn et al., 2022).

The number of *I. typographus* captured varied within each season, with clear peaks visible each year (Figure 1i-l). The timing of the peaks varied from year to year but was relatively consistent between trap sites. In 2021 no beetles were trapped until late May, which is late compared with 2019, 2020 and 2022 when beetles were caught earlier in the season.

In 2019 a total of 8586 beetles were also trapped in, and close to, the primary outbreak site - just under half of these beetles were caught in the week of 17-23rd April and a second smaller peak in the week of 15-21st May (Figure 2 – shorter horizontal bars – traps emptied weekly). The number of beetles caught in the eleven wider environment survey traps located in the same ERA5 grid square as the original site of infestation, was 330 with a peak of trap count of 62 (Figure 2: longer horizontal bars – traps emptied fortnightly).

Model validation: primary infestation site 2019

Adapted PHENIPS model

The predicted date of onset of swarming aligns with the first peak in pheromone trap catches at the primary infestation site and in the surrounding wider environment traps (Figure 2a: early swarming). Beetles were predicted to be sufficiently developed to take flight during an early short period of warm weather in mid-April.

The model indicates that beetles were fully developed by the 30th April in 2019, however, the predicted onset of infestation is delayed until the 18th May, since the maximum daytime temperatures in the first few weeks of May were below the threshold required for flight. The predicted date of onset of infestation coincided with a second, smaller peak in the primary infestation site data and a second peak in the surrounding wider environment data (Figure 2a: onset of infestation). No further peaks were observed at the primary infestation site; however, the surrounding wider environment data align with the predicted swarming of the first filial generation (Figure 2a: F1 swarming).

Model projections indicate that there was sufficient thermal sum for a second (sister) brood (SB1) and a second filial generation (F2) to complete development at the outbreak site in 2019, however this was predicted to occur after the reproductive diapause so swarming of these would not be expected (Figure 2a: reproductive diapause, SB1, F2). The model prediction is consistent with data from both the primary infestation site and the surrounding wider environment traps, whereby few beetles were trapped from mid-August onwards.

Adapted Jönsson model

The predicted date of spring swarming aligns with the first peak in pheromone trap catches at the primary infestation site and in the surrounding wider environment traps (Figure 2b: spring swarming). However, further peaks in trap counts in the week of 15-21st May at the primary infestation site, and between 15th May and 10th June in the wider environment data, are not explained by the model. The completion of the first filial generation is predicted to occur slightly earlier than the final peak in beetle catches in the surrounding wider environment traps (Figure 2b: F1 swarming). The model forecasts that two generations would have completed development in both sunny and shaded sites before overwintering (Figure 2b: F1, F2).

Overall, the PHENIPS model appears to perform better than the Jönsson model for the 2019 initial site of infestation and surrounding wider environment survey data sets (Figure 2).

Model validation: wider environment trap data 2019-2022

Both phenological models were run on climate data from 2019-2022 in all grid squares in which at least ten beetles were trapped in the given year. For clarity of presentation, we compare the model runs with the combined wider environment pheromone trap data for each year (shown as red horizontal bars in Figures 3 and 4).

Adapted PHENIPS model

In each year, the predicted number of generations of *I. typographus* was consistent across all modelled ERA5-Land grid squares. Two filial generations (F1, F2) and a sister brood of the first filial generation (SB1) were predicted in all years; in addition, in 2020 and 2022 sister broods of the second filial generation (SB2) were predicted (Figure 3a-d).

The predicted date of onset of swarming aligned with the first increase in pheromone trap counts in all years except 2021. In 2021, the initial increase in trap counts aligned more closely with the predicted onset of infestation - this could be explained by a period of cooler weather between predicted spring swarming and onset of infestation (Figure 3c).

The second peak in trap count, observed in all years except 2021, broadly aligns with the predicted date of emergence of the first filial generation (F1): in 2019 and 2020 the peak pheromone catch occurred slightly before the predicted completion of development, however relatively large numbers of beetles continued to be trapped with overlap between model prediction and observations (Figure 3a,b). The early peak might be explained by insolation heating of bark at forest edges which could enable those beetles to develop more rapidly. In 2021 the model predicted there would be sufficient thermal sum remaining for a second filial generation however very few beetles were caught in the traps (Figure 3c).

Adapted Jönsson model

The adapted Jönsson model predicted two complete generations of *I. typographus* in both sunlit and shaded locations from 2019-2022 across all modelled ERA5-Land grid squares (Figure 4a-d).

The Jönsson model does not distinguish between the onset of swarming and of infestation and instead predicts the date of spring swarming. The predicted date of spring swarming aligned with the first increase in pheromone trap counts in 2019 (Figure 4a); however, in 2020 and 2021 the predicted swarming date of late March to early April was earlier than indicated by the wider environment trap counts (Figure 4b-c). In 2022, there was wide variation in the predicted date of spring swarming from different grid squares – however the first peak in trap counts match the later predictions of early May (Figure 4d).

There is strong alignment between predicted date of swarming of the first filial generation and pheromone trap data in 2019 and 2020 (Figure 4a,b). The correspondence was less evident for 2022, in which there was wider variation in modelled developed across the study area (Figure 4d). In 2021 the model neither explained the pheromone trap data as spring swarming nor as first filial generation swarming (Figure 4c).

Choice of model for national gridded predictions

The adapted PHENIPS model was selected for further analyses based on its superior performance in matching the field data from 2019-2022. The Jönsson model is also disadvantaged for UK conditions by accumulating day degrees from 1st January leading to the potential to predict swarming dates during unusual warm days in early spring and much earlier than reported in mainland Europe.

Gridded estimates of potential number of generations of *I. typographus* across the UK

Present: 2019-2022

There is a clear spatial pattern in the predicted number of generations of *I. typographus* using the adapted PHENIPS model, with the most generations in the southeast and fewest in the north of the UK (Figure 5). Two full generations (F1, SB1, F2) would be possible in the south of England where degree day accumulation is more rapid than for the rest of the UK. An additional sister brood of the second filial generation (SB2) is also predicted to be sufficiently developed in the southeast of England for overwintering in 2020 and 2022 (Figure 5). In contrast, Scotland and Northern England would have been expected to experience only a single generation (F1) of offspring, had overwintering beetles been present, with the possibility of a sister brood (SB1) near the coast and in low lying areas.

Although at least one filial generation could develop sufficiently to overwinter across most of the UK (Figure 6 row 1), in much of Scotland the filial generation (F1) may not complete development before the 31st October (Figure 6 row 2). Where development is complete, this may occur too late for further swarming and additional generations of the beetle (Figure 6 row 3). In general, all stages were reached slightly earlier in 2020 and 2022 than in 2019 and 2021 (Figures 5,6)

Past: 1945-1949

The adapted PHENIPS model showed broadly similar patterns and year to year variation for the period 1945-1949 (Figure 7) compared with 2019-2022 (Figure 5), suggesting that the climate in these years was as amenable to the development of *I. typographus* as in more recent years. We note that most of southern and central England experienced sufficiently warm air temperatures during the spring and summer for two full generations with sister broods (F1, SB1, F2, SB2) to have developed in 1947.

Future: 2°C and 3°C global warming above pre-industrial levels

Among the UKCP18 RCP8.5 ensemble members, predictions vary for when global warming is predicted to reach ≥ 2°C above pre-industrial levels, with estimates ranging from 2029 (members: 4, 11 and 15) to 2045 (member: 12). Coupling the adapted PHENIPS model with each of 12 ensemble members yields varying results (Figure 8). In the worst-case scenarios, global warming of 2°C is predicted to lead to optimum temperature conditions for two generations of *I. typographus* across most of the UK (F1, SB1, F2, SB2), whilst for the majority of UKCP18 ensemble members, the spatial variation in environmental suitability is close to the maps generated using the 2019-2022 ERA5-Land data (*cf* Figure 5 and Figure 8). The effects are exacerbated for a 3°C threshold: more than half of the scenarios predict one full generation and a sister brood in all areas except high lying areas of Scotland and two full generations with sister broods across most of southern and central England (Figure 9).

Discussion

Phenological models are important tools in the management of *Ips typographus* providing both information on when swarming is likely to occur and the number of generations per season. In this paper we compared the predicted dynamics of *I. typographus* using two phenological models (Baier et al., 2007; Jönsson et al., 2007) with pheromone trap data collected in the southeast of England from 2019-2022 (Blake et al., 2024). Analysis of the pheromone trap data showed clear peaks in the trap data with the timing and number of peaks varying between years. Our implementations of the PHENIPS (Baier et al., 2007) and 'Jönsson' (Jönsson et al., 2007) models predicted that two generations of *I. typographus* could occur in all the locations in the southeast of England where the pest was trapped. The adapted PHENIPS model, however, more consistently captured the timing of early season peaks in trap counts than the 'Jönsson' model.

Using the adapted PHENIPS model we explored the potential voltinism of the pest under historic, present day and future climate conditions. The current climate is warm enough to support two full generations of the pest in the southeast of England with at least one generation feasible in most areas of the UK. Differences in temperature between the mid-twentieth century and early twenty-first century were insufficient to explain why the pest has not previously established within the UK. The failure of *I. typographus* to establish historically, despite multiple opportunities, may instead be due to a combination of other environmental factors, including host availability and vigour; the 'Allee' effect, whereby arriving populations are too low in number for viable establishment (Liebhold and Tobin, 2008); or chance. Under 2°C and 3°C global warming scenarios we might expect to see an increase in potential voltinism across the UK in the next few decades, increasing the opportunity for founder populations of *I. typographus* to establish in new areas. However, the likelihood and scale of outbreaks of the pest will also depend on a range of other known and unknown factors including host species distribution, forest management and differences in host-pest response between Sitka and Norway spruce.

The choice to use pre-existing models was driven initially by a request from government sources for a rapid analysis to address two key questions after the initial report of the pest in the southeast of England: how many generations of *I. typographus* could occur in one breeding season within the area that the breeding population was detected; and could the timing of spring swarming, onset of infestation and of swarming of filial and sister generations be estimated to support planning of control and monitoring programs. The PHENIPS model was simplified by removing the topoclimatic model, incorporated into the original model to capture temperature variation across a mountainous terrain, and by using air temperature as a proxy for bark temperature in all stages of development. As more data become available at a finer temporal resolution, further calibration of the adapted PHENIPS model for use with ERA5-Land data will become viable. A key feature not currently included in the adapted PHENIPS model is the impact of insolation heating on local variation in under bark temperature between sunny and shady sites. This might be captured either by incorporating solar radiation data, as used in the original PHENIPS model, or by reducing the degree day requirements in sunny locations as proposed by Jönsson et al. (2007).

By comparing model predictions, using gridded weather data encompassing trap locations, we implicitly assumed that the peaks in trapped beetles were driven by local population dynamics. However, frequent interceptions at ports of *I. typographus* (Evans, 2021), presumed to be hitchhikers on cargo ships, active flight and long-distance dispersal on wind currents from continental Europe could mean that some, or even all, beetles trapped did not develop locally (Blake et al., 2024; Inward et al., 2024a). Distinguishing between sources is complicated by the relatively low frequency trap data (fortnightly) in the wider environment study in comparison with relatively small spatial shifts in predicted emergence dates driven by warmer air temperatures at the sites of potential sources populations in continental Europe. In addition, beetles which dispersed in summer, overwintered without breeding, then swarmed in spring, would be indistinguishable in the traps from beetles crossing the channel in spring flights (Inward et al., 2024a) at this low sampling frequency. The failure, despite intense surveillance, to find any breeding populations of *I. typographus* in the UK in 2019-2020 (Blake et al., 2024) supports the hypothesis of a continental origin of trapped beetles. Ongoing work, which will be reported in a follow-up paper, aims to combine the UK Met Offices Numerical Atmospheric-dispersion Modelling Environment (NAME) with daily trap data. The alignment between the adapted PHENIPS model predictions and the 2019 data at and near the primary site of infestation adds some confidence that the adapted PHENIPS model can be used to predict voltinism across the UK.

The application of the PHENIPS model to historic data from 1945-49 suggests that air temperature was sufficiently warm for the completion of one to two generations per year across most of England. In this context and given the reported import of large quantities of infested wood (Laidlaw, 1947), the failure of *I. typographus* to establish anywhere in the UK prior to the finding in 2018 suggests that other factors may have limited population growth. Afforestation programmes since the 1940s have more than doubled the UK woodland area, with Sitka spruce expanding at a similar rate when averaged across GB, potentially increasing the chance of founder populations finding suitable host (Ditchburn & Brewer, 2014; Locke, 1970). However, the total area of Norway spruce in GB has almost halved reducing the availability of the most suitable host in some areas.

The main species of spruce grown in the UK is Sitka spruce, whereas the main host in Europe is Norway spruce. Differences in response mechanisms between Sitka and Norway spruce may be sufficient to reduce the risk of establishment, however *I. typographus* will feed on Sitka spruce in laboratory environments (Flø et al., 2018; Økland et al., 2011). In addition, the host range of *I. typographus* is wider within *Picea* than usually reported, with outbreaks known from *P. jezoensis, P. glehnii, P. orientalis* and *P. obovata* across the Palaearctic (Akkuzu et al. 2009; Du et al. 2022; Trubin et al. 2022; Yamaoka et al. 1997). It is currently unknown if differences in tree volatiles, tree defences and changes to pheromone production would impact the long-term success of *I. typographus* on Sitka spruce.

The relatively low density of host in the southeast of England, in the areas with the best environmental suitability, in comparison with areas where there have been population eruptions in continental Europe, may also explain the failure of *I. typographus* to establish and spread in the UK historically. A further factor, and area for further investigation, which may have protected UK forestry is the role of drought in weakening host trees and thus enabling *I. typographus* to establish. Sitka and Norway species are generally grown in different environments in the UK, with Sitka in regions with higher, more consistent rainfall (Savill, 2019). However, the effects of drought are relative to the tree species involved and the environment in which it has grown (Xenakis et al., 2021) and climate change could lead to an increase in drought-stressed Sitka which is likely to be attacked just as readily as drought-stressed Norway spruce. The recent finding of *Ips typographus* breeding in a small block of Sitka spruce in West Sussex, near to a larger block of infested Norway spruce, shows the beetle is capable of attacking Sitka in the field (Inward 2024b).

Cooler temperatures within the forest blocks (driven by a combination of local climate, altitude and canopy density affecting sun-exposure to tree trunks) may have a more significant impact on the survival of *I. typographus*, as may localised humidity and attacks by entomopathogenic fungi (Luz & Fargues, 1999). Small populations of *I. typographus* are at a high risk of extinction if suitable, weakened but live host material is not available year-on-year as there are too few beetles to overwhelm healthy tree defences (Kärvemo et al., 2016). The wide distribution of positive findings across the southeast of England since intensive surveillance began in 2019 suggests that *I. typographus* may have been entering the southeast via wind borne dispersal over a longer period, but lack of consistent material across years within individual forests may have led to local extinction and protected the region against large-scale outbreaks.

The predicted voltinism of *I. typographus*, generated using the adapted PHENIPS model, varies regionally with the most generations in the southeast of England and fewest in northern Scotland. For historic and recent projections, only the first filial brood is predicted to have been capable of developing sufficiently to overwinter across most of Scotland, and in some areas this first brood is only partially developed. Considering these factors (single generation, partial development), we might conclude that *I. typographus* would be unlikely to establish long-term in northern and high-altitude regions of Scotland. However, in the worst-case scenarios for the impact of global warming on UK temperatures, two generations of *I. typographus* could be possible throughout Scotland by 2034. Furthermore, *I. typographus* is already present in parts of Scandinavia with significantly colder winters and similar summer temperatures (Mayer et al., 2014). Under climate warming, the proportion of years and area over which the climate would be sufficiently warm to enable development of at least two filial generations with sister broods is predicted to increase over time. In this paper, we have focussed on the relationship between temperature and potential voltinism. It is possible that other differences between the UK and infested areas in mainland Europe including the predominance of Sitka spruce, low forest density in England and a maritime environment could provide some protection from large outbreaks. However, if the pest is allowed to establish in the UK then the opportunity for local adaptation, population build up and spread will increase. Good surveillance is an essential component in mitigating against the impact of *I. typographus*. Initial spread may be hard to detect with breeding populations causing minimal damage enabling populations to increase until environmental conditions trigger the switch between endemic and epidemic phases. Recent interceptions of *Ips typographus* in Scotland (Scottish Forestry, 2023) demonstrate the clear need for vigilance across the UK.

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Author Contribution

C.R.W. planned and carried out the project with advice from C.A.G. and M.B.. C.R.W., M.B. and C.A.G. wrote the manuscript. M.B. supplied the pheromone trap data.

Data availability statement

The data that support the findings of this study are available on request from Max Blake. The data are not publicly available due to privacy or ethical restrictions.

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Conflict of interest statement

No conflict of interest is declared.

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Figures

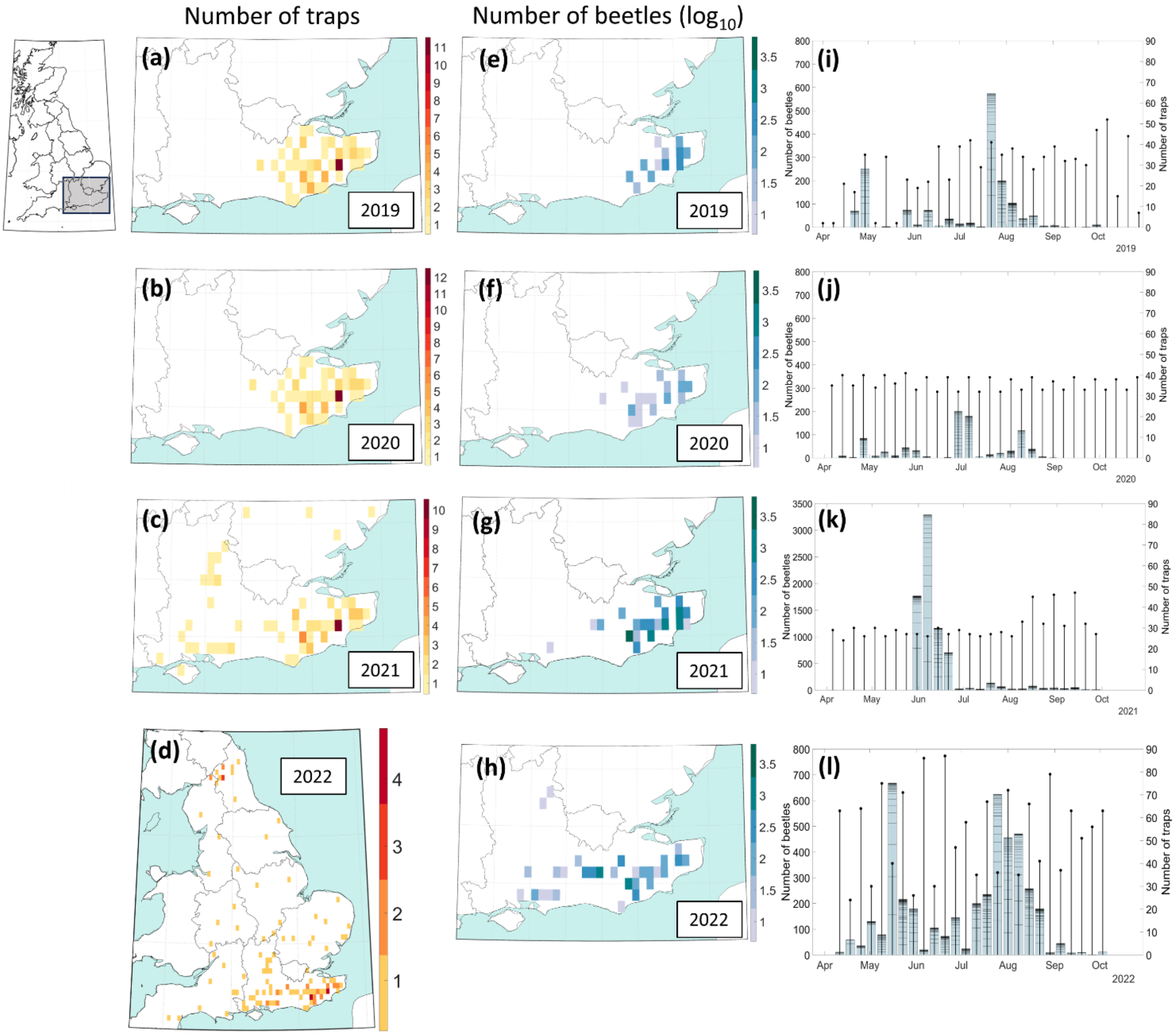


Figure 1*: Results of wider environment surveillance programme for* Ips typographus *in England 2019-2022: (a-d) number of traps in each ERA5-Land grid square; (e-h) total number of beetles (log10) trapped in each grid square (note squares where the total number of beetles was less than 10 are not plotted); (i-l) total beetle count (bar plot) and number of traps (stem plot) in each week. Graduations on the bar plots divide the total weekly beetle count into individual trap data. Note the plotted data do not include the trap data from the original site of infestation (Packing Wood) in 2019 whereby traps were used to lure beetles that had overwintered in forest litter following the intensive eradication action. Note also, for clarity, the upper limit for the 'number of beetles' in subplot k (2021) is higher than for other years.*

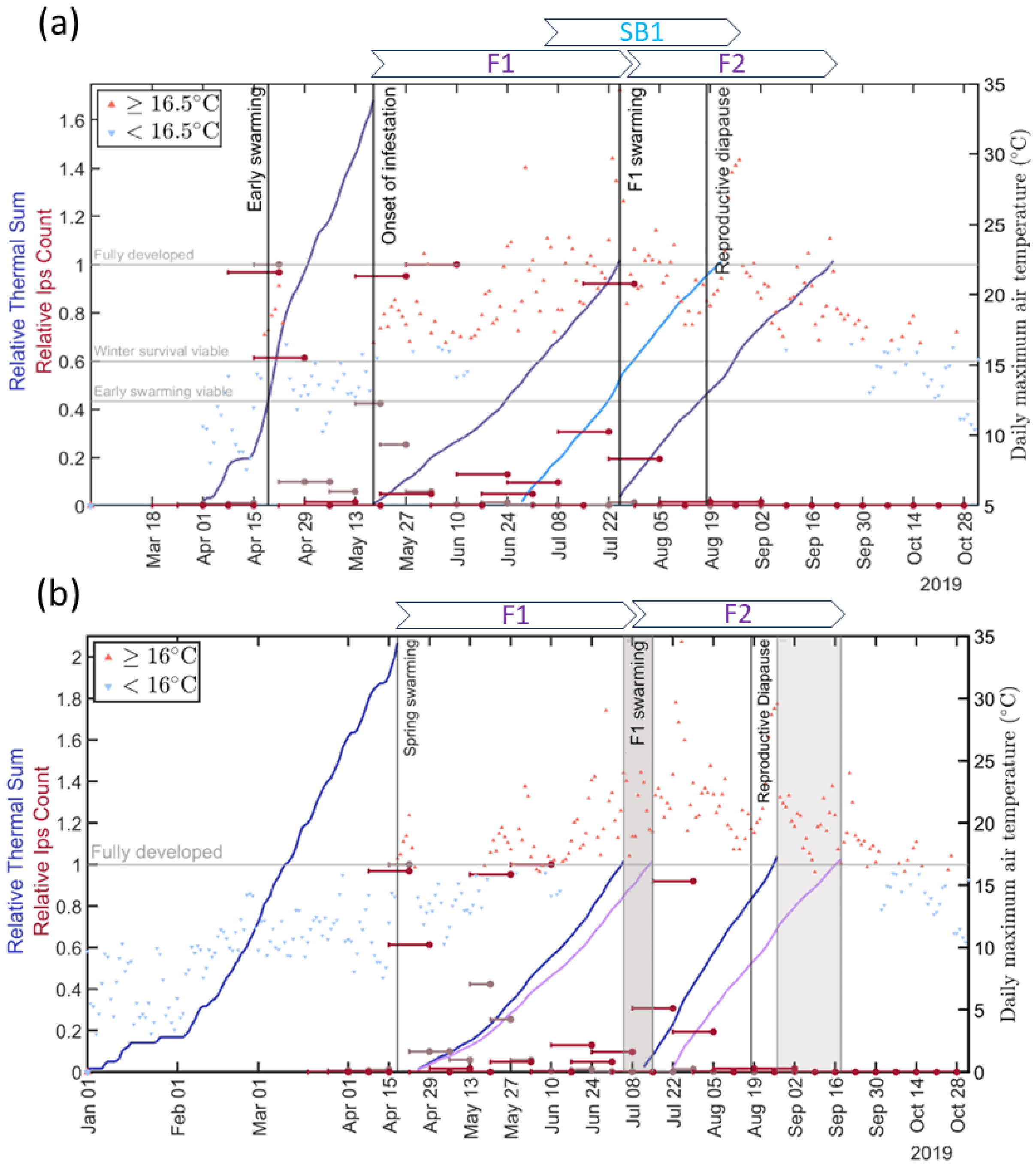


***Figure 2**: Comparison of predicted development of* Ips typographus *[(a) adapted PHENIPS model and (b) adapted Jönsson model] with trap count data from: (i) Packing Wood (shorter, 7-day, horizontal lines); and (ii) all other traps within the ERA5 grid square that contains Packing Wood (longer, 14-day, horizontal lines). Plots show modelled degree-day accumulation for overwintering adults and for each generation (PHENIPS: two filial generations (F1, F2) and one sister brood (SB1); Jönsson: two filial generations (F1, F2) distinguishing between shaded (light purple) and sunny sites (dark blue)). Trap data are illustrated by a circle, indicating the day of collection, and extending in a horizontal line backwards for the duration traps were in the field. Trap values are scaled relative to the peak trap count for each data set (Packing Wood: 4172; Wider Environment: 62). Maximum daily temperature, colour coded according to whether it was warm enough for swarming to occur, are plotted in the background (red = above swarming temperature threshold; blue = below swarming temperature threshold).*

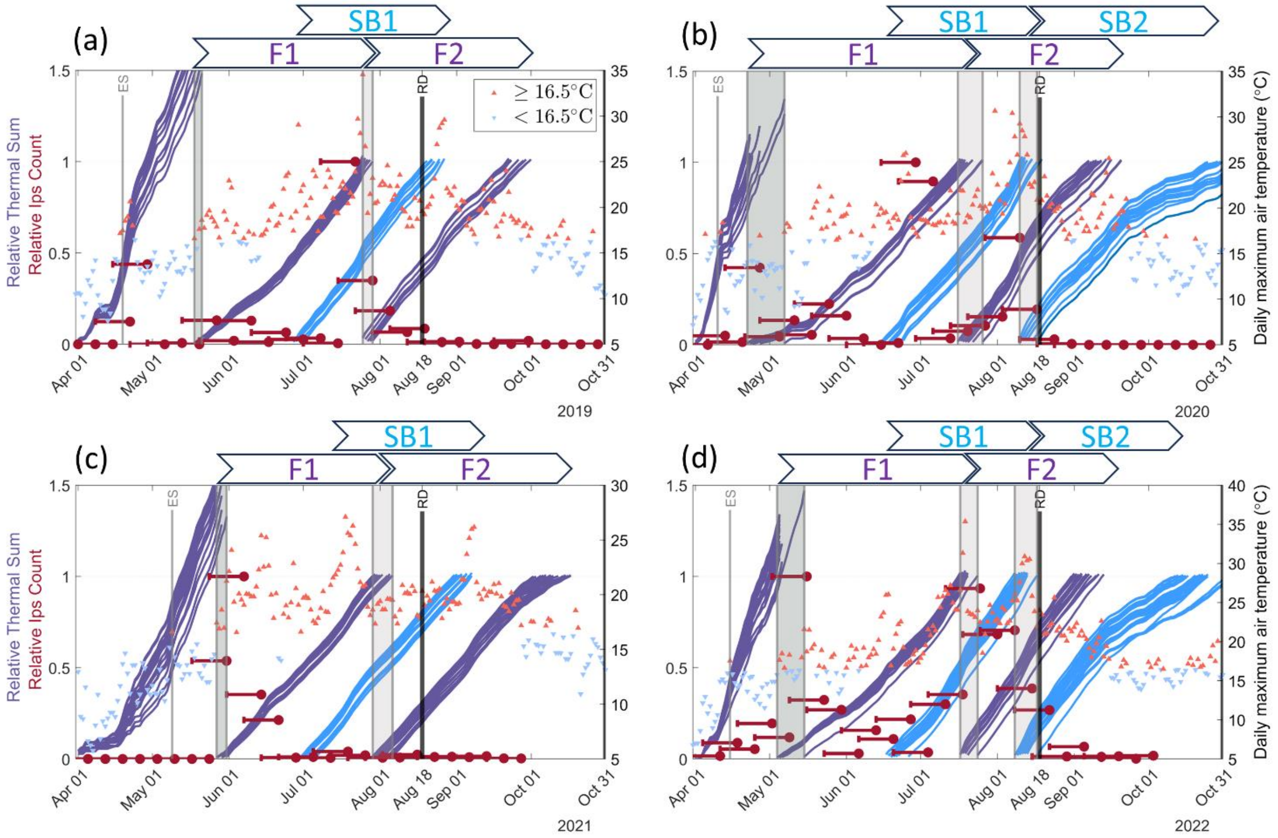


***Figure 3**: Comparison of predicted development of* Ips typographus *2019-2022 using the adapted PHENIPS model with the combined trap data from the Forest Research Wider Environment Study. Plots show modelled degree-day accumulation for overwintering adults and for each filial (F1, F2) (purple/ darker lines) and sister brood generation (SB1, SB2) (blue/ lighter lines). Degree-day accumulation, calculated using ERA5-Land data, is plotted for each grid square in which there were at least ten beetles trapped for the plotted year. Trap data were combined for all trap sites and illustrated by a circle, indicating the day of collection, and extending backwards for the duration traps were in the field (14 days). Trap values are scaled relative to the peak trap count (138 (2019), 46 (2020), 786 (2021) and 158 (2022)). Maximum daily temperature for all modelled ERA5 grid squares, colour coded according to whether it was warm enough for swarming to occur, are plotted in the background. The first vertical line in each plot gives the earliest predicted date of spring swarming across all grid squares (ES). Shaded regions show the range in the dates of predicted onset of infestation and of predicted swarming of any generations completing development prior to the reproductive diapause (RD), across all ERA5-Land grid squares in which there were at least 10 beetles trapped.*

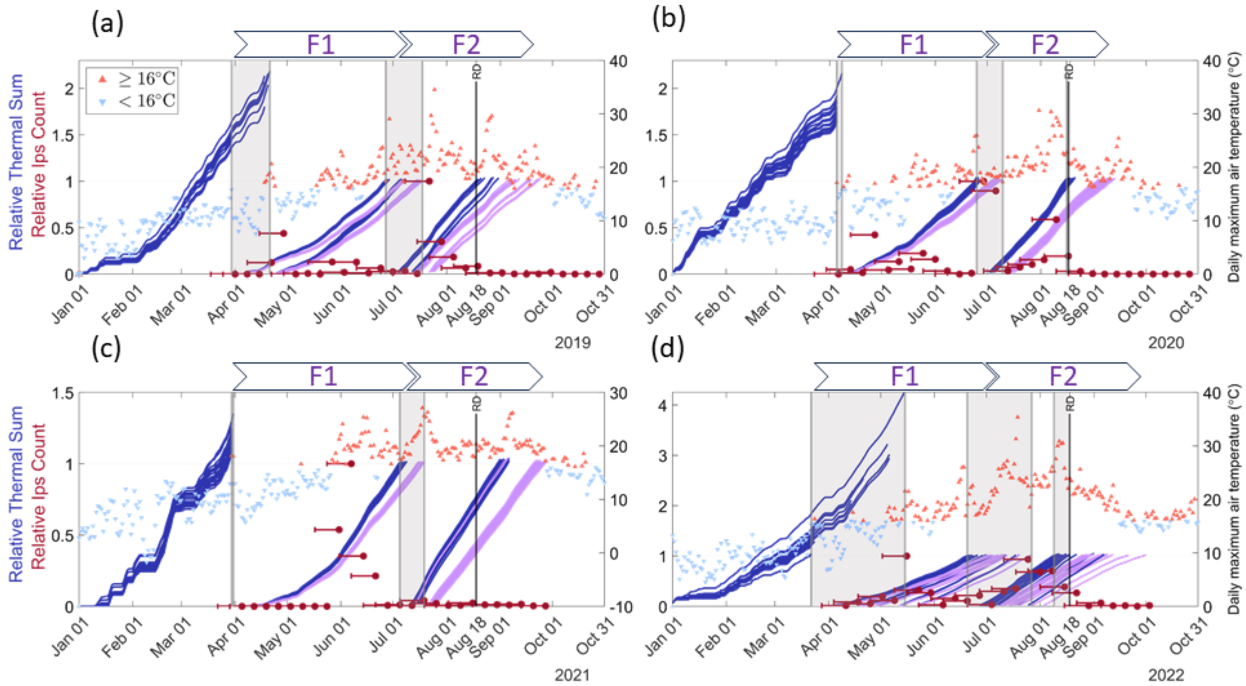


Figure 4*: Comparison of predicted development of* Ips typographus *2019-2022 using the adapted Jönsson model with the combined trap data from the Forest Research Wider Environment Study. Plots show modelled degree-day accumulation for overwintering adults and for each filial generation (F1, F2) in sunny (dark blue) and shaded (light purple) locations. Degree-day accumulation, calculated using ERA5-Land data, is plotted for each grid square in which there were at least ten beetles trapped for the plotted year. Trap data were combined for all trap sites and illustrated by a circle, indicating the day of collection, and extending backwards for the duration traps were in the field (14 days). Trap values are scaled relative to the peak trap count (138 (2019), 46 (2020), 786 (2021) and 158 (2022)). Maximum daily temperature for all modelled ERA5 grid squares, colour coded according to whether it was warm enough for swarming to occur, are plotted in the background. Shaded regions show the range in the dates of predicted spring swarming, and the date range over which each generation is predicted to swarm, across all ERA5-Land grid squares in which there were at least 10 beetles trapped.*

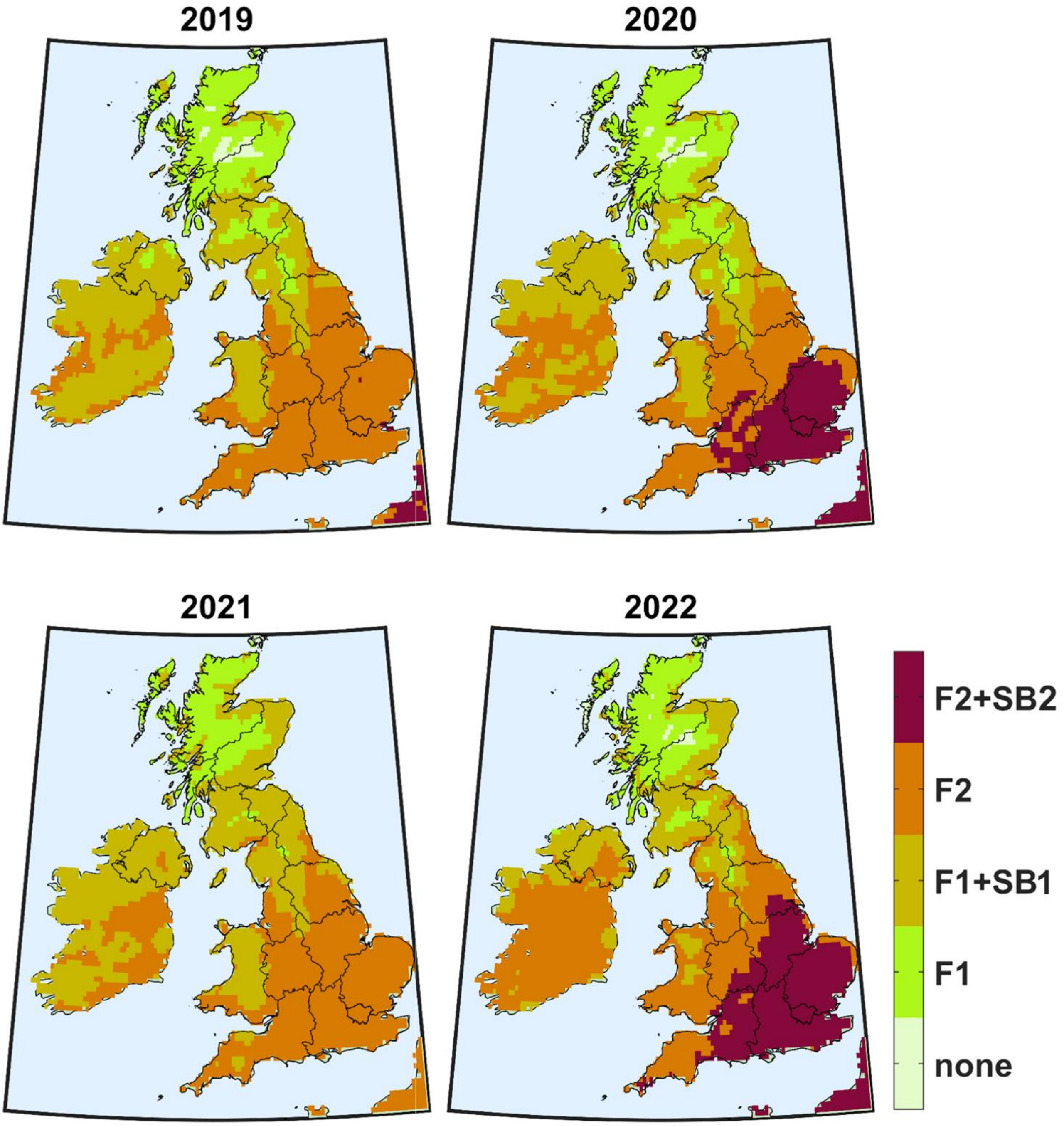


***Figure 5**: Estimated number of generations from 2019 to 2022 of* Ips typographus *theoretically possible in each region had the pest and suitable host been available. Estimates used ERA5-Land reanalysis temperature data for the adapted PHENIPS model. The number of generations is denoted: none = insufficient degree days for any offspring to overwinter; F1 = first filial generation; SB1 = sister brood of F1; F2 = second filial generation (offspring of F1); SB2 = sister brood of F2 and offspring of SB1. Each brood must be at least 60% of the way through the thermal sum required for complete development to overwinter successfully.*

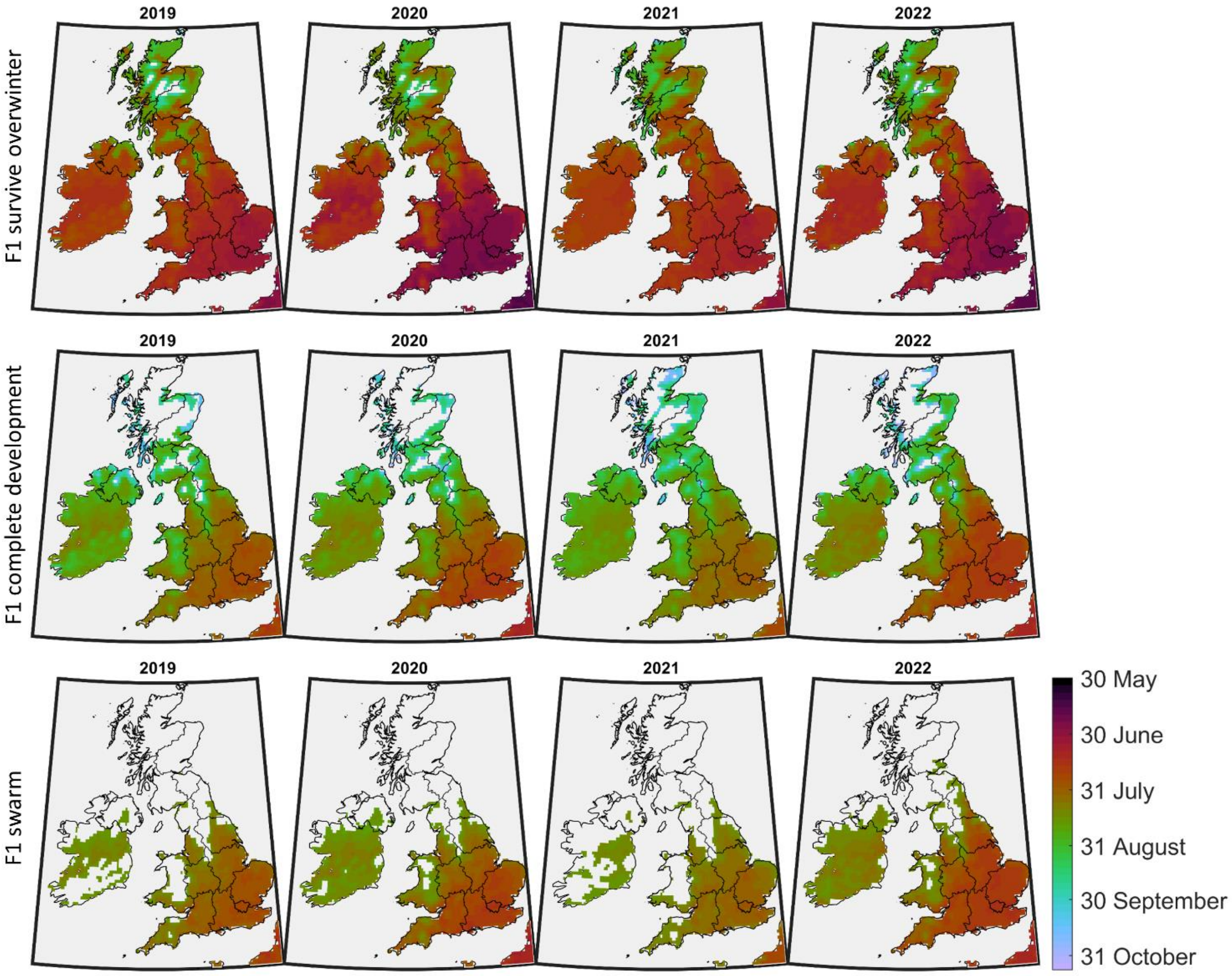


***Figure 6**: Predicted development of the first filial (F1) generation from 2019 to 2022 of* Ips typographus *theoretically possible in each region had the pest and suitable host been available. The maps in the first row show the date by which the F1 generation is predicted to be sufficiently developed to overwinter successfully. The maps in the second row show the date by which the F1 generation is predicted to be fully developed. The maps in the final row show the date on which swarming could first occur for the F1 generation. Not all stages of development are reached in all regions. Estimates were created using ERA5-Land reanalysis data to provide temperature data for the adapted PHENIPS model.*

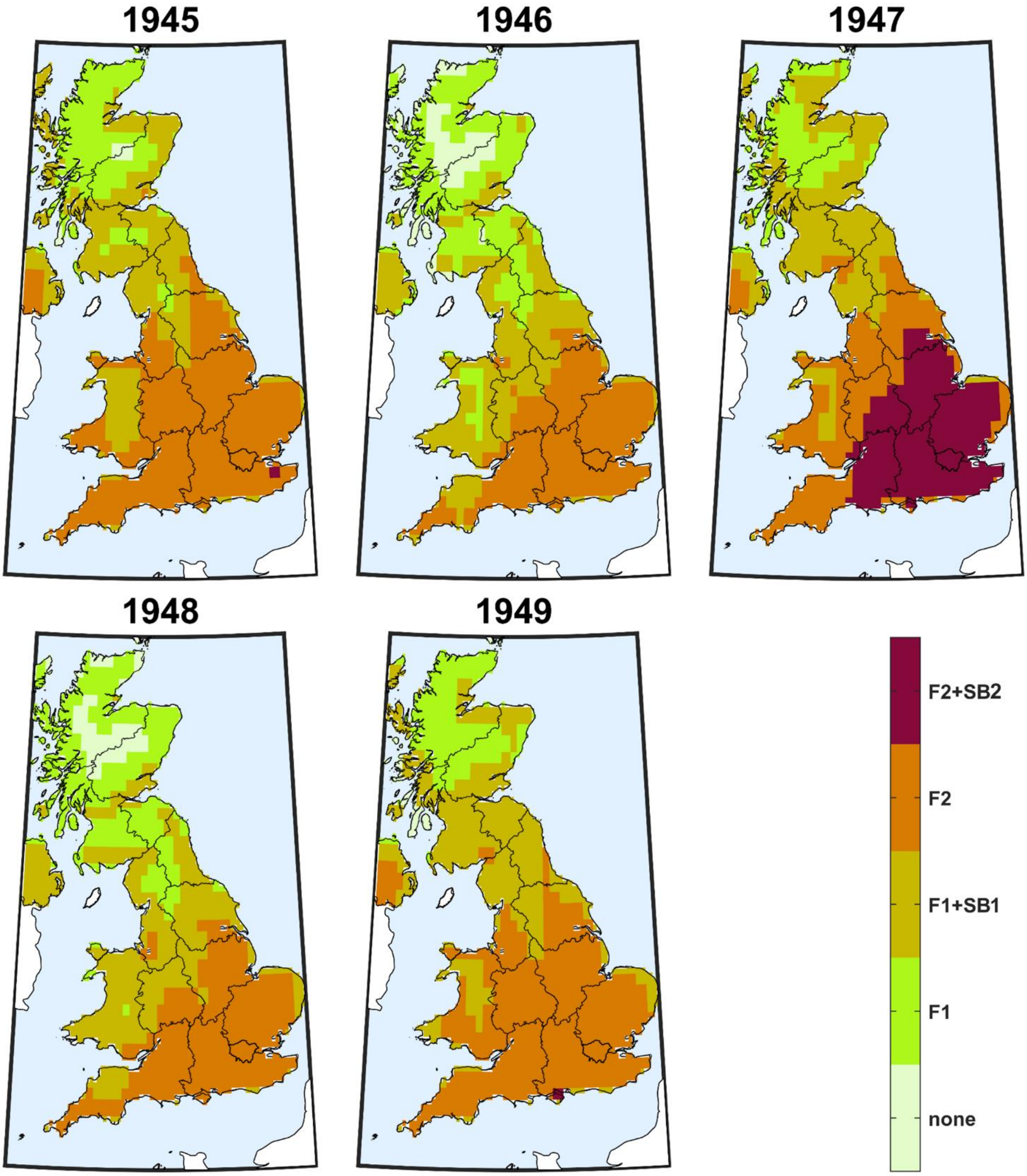


Figure 7: Estimated number of generations across the UK from 1945-1949 of Ips typographus *theoretically possible in each region had the pest and suitable host been available. Estimates were created using ERA5 reanalysis temperature data for the adapted PHENIPS model. The number of generations are denoted: none = insufficient degree days for any offspring to overwinter; F1 = first filial generation; SB1 = sister brood of F1; F2 = second filial generation (offspring of F1); SB2 = sister brood of F2 and offspring of SB1. Each brood must be at least 60% of the way through the thermal sum required for complete development to overwinter successfully.*

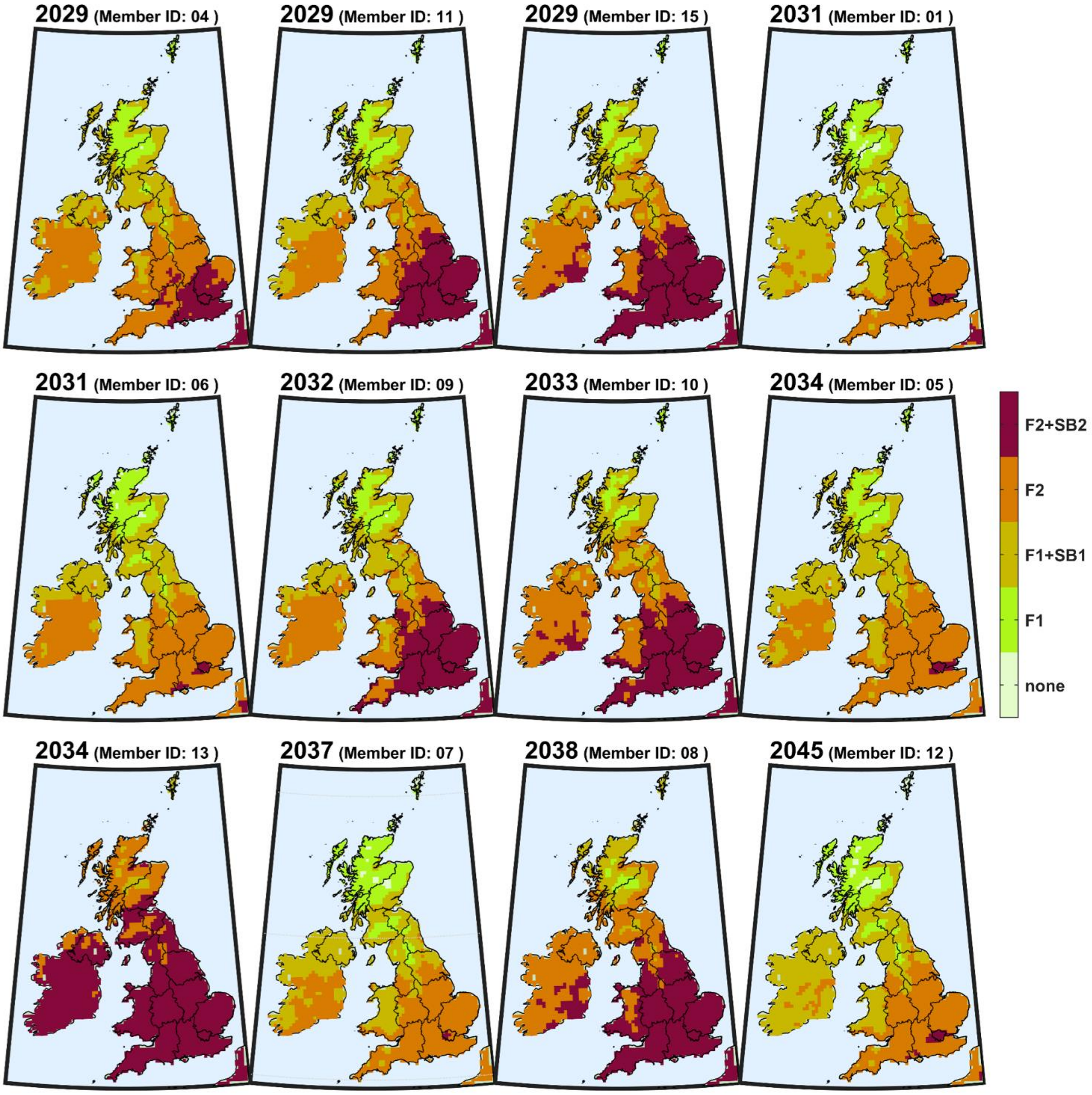


***Figure 8**: Variation across the UK and the Republic of Ireland in the projected number of generations of* Ips typographus *that could develop sufficiently within a season to overwinter (if the pest were present and suitable host were available) for each of the twelve UKCP18 model runs in the year that they first reach or exceed a global warming average of 2^{o}C above preindustrial levels. Estimates were created using daily mean and maximum temperature data generated by the twelve UKCP18 regional climate projections for the high emissions pathway RCP8.5 in the adapted PHENIPS model. The numbers of generations are denoted: none = insufficient degree days for any offspring to overwinter; F1 = first filial generation; SB1 = sister brood of F1; F2 = second filial generation (offspring of F1); SB2 = sister brood of F2 and offspring of SB1). Each brood must be at least 60% of the way through the thermal sum required for complete development to overwinter successfully.*

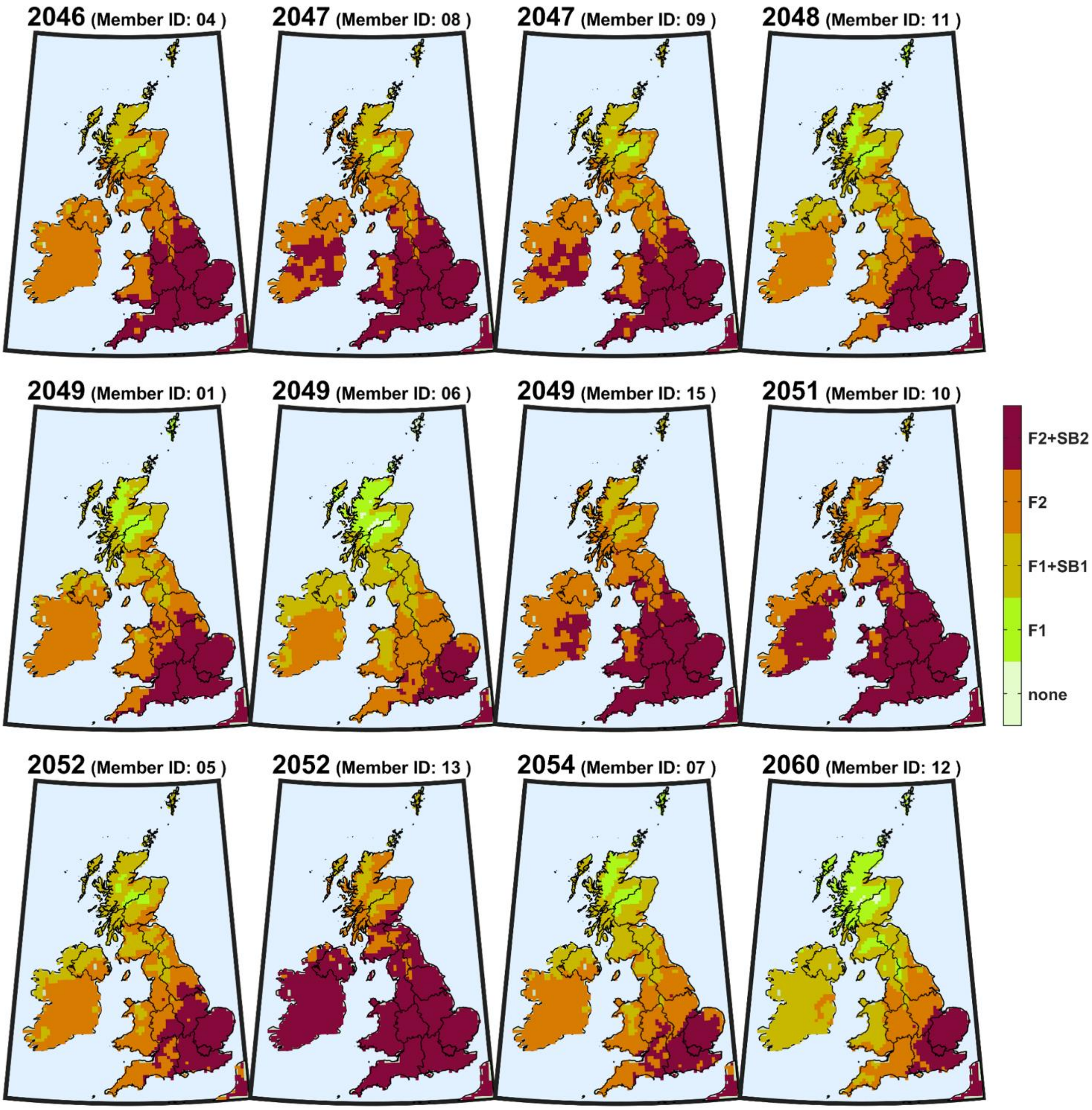


Figure 9*: Variation across the UK and the Republic of Ireland in the projected number of generations of* Ips typographus *that could develop sufficiently within a season to overwinter (if the pest were present and suitable host were available) for each of the twelve UKCP18 model runs in the year that they first reach or exceed a global warming average of 3ºC above preindustrial levels. Estimates were created using daily mean and maximum temperature data generated by the twelve UKCP18 regional climate projections for the high emissions pathway RCP8.5 in the adapted PHENIPS model. The numbers of generations are denoted: none = insufficient degree days for any offspring to overwinter; F1 = first filial generation; SB1 = sister brood of F1; F2 = second filial generation (offspring of F1); SB2 = sister brood of F2 and offspring of SB1. Each brood must be at least 60% of the way through the thermal sum required for complete development to overwinter successfully.*

Plants, People, Planet Supporting Information

Article title: Phenology of the spruce bark beetle Ips typographus in the UK under past, current and future climate conditions

Authors: Cerian R. Webb, Max Blake, Christopher A. Gilligan.

The following Supporting Information is available for this article:

Methods S1: Relationship between air temperature at 2m and effective temperature for the development of *Ips typographus* (adapted PHENIPS model)

This section describes the method used to calculate degree day accumulation from egg stage to emergence of mature filial beetles as implemented in the adapted PHENIPS model. The approach used is based on the description of the original PHENIPS model in the absence of the insolation heating (see Baier et al. (2007) section 2.3.2.1, equation 2 and Appendix A).

The effective daily temperature, T_{eff}, which determines the daily rate of development from egg stage to emergence of mature filial beetles, is modelled using a non-linear piecewise function of the mean daily air temperature, T. The relationship between T_{eff} and T varies according to three temperature thresholds: a lower development threshold, below which the naturally occurring temperature is too low for development ($DT_L = 8.3$°C); an optimal temperature for development ($T_{opt} = 30.4$°C); and an upper development threshold over which the temperature is too high for development ($DT_U = 38.9^o$C). The first threshold, $DT_L$is crossed if the daily mean daily air temperature exceeds DT_L , whilst $T_{opt}$and DT_U are crossed if the daily maximum air temperature (AT_{max}) is exceeded.

In summary:

If $T < DT_L$ there is no development and $T_{eff} = 0$.

If $T \geq DT_L$ and $\mathrm{A}T_{max} \leq T_{opt}$ degree day accumulation is the number of degrees above the threshold for development thus $T_{eff} = T - DT_L$.

If $AT_{max} > T_{opt}$ and $AT_{max} \leq DT_U$ then degree day accumulation is a reducing function of temperature captured using the nonlinear function (originally described by Wermelinger & Seifert (1998))

$$T_{eff} = \left(T_{opt} - DT_L\right)\left[e^{\alpha \times T} - e^{\left(\alpha T_{max} - \frac{T_{max} - T}{\beta}\right)} - \gamma\right]$$

Where $\alpha = 0.029, \beta = 3.592, \gamma = 1.247, T_{max} = 40.996$.

If $AT_{max} > DT_U$ there is no development and $T_{eff} = 0$.

Development is complete when the thermal sum reaches $K = 557dd$. The relative thermal sum, T_{sum}, is given by:

$$T_{sum} = \left(\frac{\sum T_{eff}}{K}\right)$$

Each generation is assumed to be fully developed when $T_{sum} \geq 1$, however swarming, and hence the start of the next distinct generation, can only occur on days where the maximum air temperature is at least 16.5^{o}C.

Development of the second brood starts when the parental generation is halfway through development i.e. $T_{sum} = 0.5$.

Fig. S1 Schematic diagram of the adapted version of the PHENIPS model

Figure S1: Schematic diagram summarising the key development stages of Ips typographus *modelled with PHENIPS (Baier et al. 2007). Air degree days are calculated using maximum daily air temperature above 8.3°C. Bark degree days are calculated using a non-linear function of bark temperature, which in the original paper was derived from solar radiation and air temperature data. In the adapted implementation, mean air temperature is used as a proxy for bark temperature. Swarming, which requires the degree day requirement to be met, only occurs on sufficiently warm days with a long enough photoperiod. Any broods laid must be at least 60% of the way through the thermal sum required for complete development to overwinter successfully. Early spring swarming does not result in new infestations.*

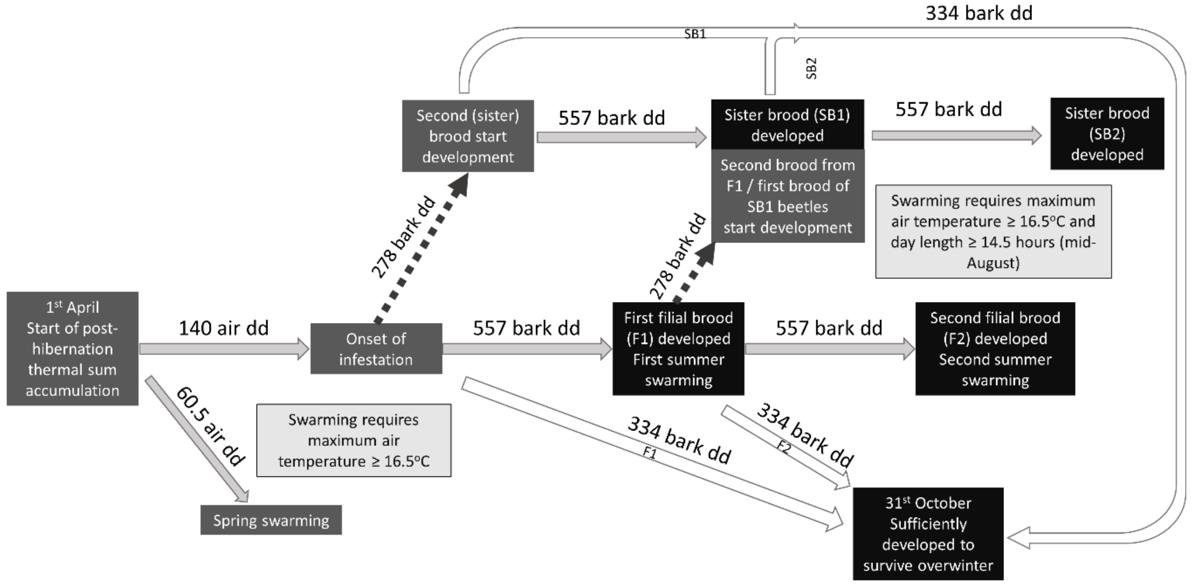
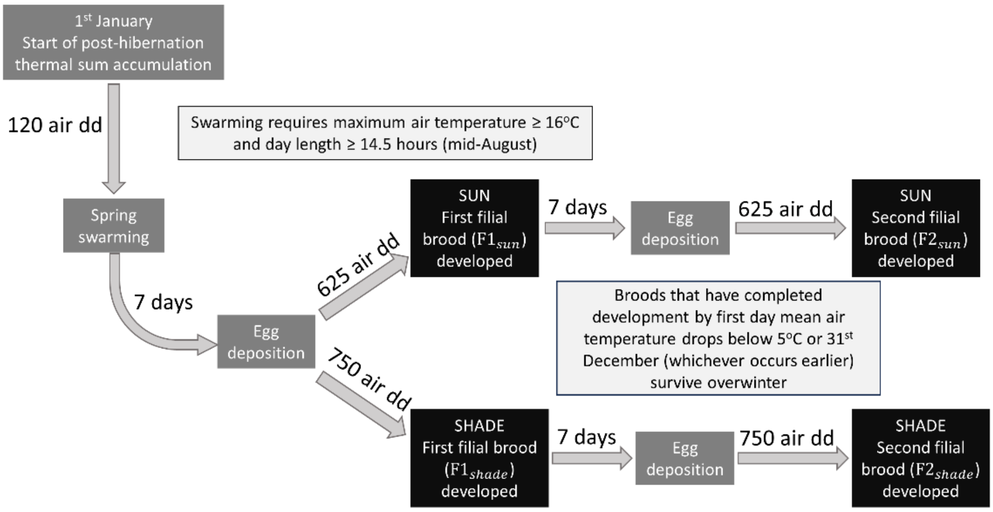


Fig. S2 Schematic diagram of the adapted version of the Jönsson model

Figure S2: Schematic diagram summarising the key development stages of Ips typographus *as modelled by Jönsson et al. (2007, 2011). Two potential filial generations are shown; however, the model allows for an additional generation which follows the same development pathway as previous generations. In the adapted implementation, the reproductive diapause is set as 18th August. Air degree days are calculated using mean daily air temperature above 5°C. Swarming requires the degree day requirement to be met and only occurs on sufficiently warm days. Any broods already laid must be 100% of the way through the thermal sum required for complete development to successfully overwinter. Sister broods are not included in the model.*



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