

# Modelling geographical variation in voltinism of *Hylobius abietis* under climate change and implications for management

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- Abstract**
- 1 *Hylobius abietis* develop in conifer root-stumps and emerging adults attack replanted trees. Development is largely semi-voltine and this is an important determinant of economic impact, influencing the length of a fallow period or the frequency of chemical control.
  - 2 A simulation model followed a generation of weevils through the life cycle to predict voltinism based on temperature in the root-stump microhabitat modelled from air temperature. Daily air temperatures for representative U.K. locations simulated from the U.K. Climate Projections 2009 Weather Generator for the 2030–2070s were used to predict the potential effect of climate change on voltinism.
  - 3 The life cycle currently takes 2–3 years in the north and west (N&W) of the U.K. but, in the south and east (S&E), a 2-year cycle predominates. From the 2030s onwards, a predominant 2-year life cycle in the N&W was predicted to reduce economic impact in this region. In the S&E, however, the predicted 1–2-year cycle would be unlikely to reduced the period over which pest management was required.
  - 4 Changes in voltinism to the 2070s revealed different temporal patterns, emphasizing the importance for management of modelling local, as well as regional scale variation in the effects of climate change in Europe.

**Keywords** Day-degrees, developmental temperature thresholds, fallow period, microhabitat temperature, pine weevil.

## Introduction

Climate change has the potential to alter the distribution, abundance and, importantly, the impact of forest pests (Ayres & Lombardero, 2000; Pinkard *et al.*, 2010; Chen *et al.*, 2011; Evans *et al.*, 2011). Range expansion can influence pest impact and invasive pests often cause damage whenever they are introduced into a new area (Pimentel *et al.*, 2000; Cudmore *et al.*, 2010). For many widely distributed native pest species, however, the influence of climate on local pest impact is likely to be as or more important than range expansion itself.

Predicting the effect of climate change on abundance and damage is complicated by possible interactions between direct and indirect effects on population dynamics (Ayres & Lombardero, 2000). Characteristics of the life cycle, such as overwintering diapause or the need for close synchrony with the host, may limit the extent to which a warming climate

can influence the number of generations per year (van Asch & Visser, 2007; Bale & Hayward, 2010). Species with more flexible life cycles, unrestricted by obligatory diapause or seasonal food availability, have the potential to develop during much of the year and so benefit from warmer winters, as well as summers. In addition, insects in ‘protected’ microhabitats, feeding in bark or wood or below ground for example, will be buffered to a greater or lesser extent from climatic extremes predicted to occur as the climate warms (Pincebourde & Casas, 2006; Jenkins *et al.*, 2009). Bark beetles and weevils, which are serious pests of temperate forestry not only develop largely within protected microhabitats, but also their population dynamics are strongly influenced by both climatic factors and forest management (Långström & Day, 2004; Wermelinger, 2004). Understanding their response to climate change is therefore of considerable practical significance.

The present study focuses on the pine weevil *Hylobius abietis* (L.), adults of which can kill replanted conifers, predominantly pine and spruce, in the U.K. and elsewhere in northern Europe, causing significant economic loss (Långström & Day, 2004).

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Cycles of clearfelling and replanting influence both weevil abundance (through the availability of root-stump breeding sites), and the intensity of damage to young transplants during subsequent adult emergence (Eidmann, 1985; Långström & Day, 2004). The life cycle normally takes 1–3 years, and adult emergence at a single site can occur over  $\geq 2$  years. Local climate influences the length of the life cycle and thus is a key determinant of how long replanted clearfells remain vulnerable to attack.

Juvenile stages develop in the bark of root-stumps below ground, with prepupal development influenced by a temperature-induced facultative diapause (Christiansen, 1971; Inward *et al.*, 2012). Adults typically emerge in the autumn to feed above ground before overwintering in the soil or litter layer. Females are synovigenic, with egg development occurring after they re-emerge to feed in the spring. Reproductively mature weevils disperse during late spring–early summer to new clearfells where oviposition occurs (Solbreck & Gyldberg, 1979; Tan *et al.*, 2011).

Delayed re-planting is widely used in pest management but, in northern regions, this may require a fallow period of  $\geq 4$  years, with insecticidal protection of plants usually necessary for shorter fallow periods (Långström & Day, 2004). Both the length of the life cycle and the seasonal duration of adult activity are likely to be affected by climate change, with resulting effects on economic impact and pest management. The main aim of the present study is to predict the duration of development and timing of activity of pine weevil as the climate of the U.K. warms, and how this might affect management of this important pest. Modelling the relationship between air temperature and that of conifer root-stumps enables temperatures in the larval microhabitat to be predicted from air temperatures. Data on key cycle parameters are used to model development in the current climate and that predicted for the 2030s, 2050s and 2070s by the U.K. Climate Projections Weather Generator 2009 (UKCP09) (Jones *et al.*, 2009). Although the primary emphasis is on modelling the effect of climate change in the U.K., the model should be more widely applicable to pine weevil populations in Europe.

## Materials and methods

### *Measuring and predicting temperature in the weevil microhabitat*

Temperature measurements were made at 17 sites across the U.K., representing a range of environmental conditions under which pine and spruce trees are planted. Scots (*Pinus sylvestris* L.) and Corsican pine (*Pinus nigra* ssp. *laricio* (Poiret) Maire) predominated in the South and East and Sitka spruce [*Picea sitchensis* (Bong.) Carr.] predominated in the North and West. Experimental sites (see Supporting information, Table S1) had been clearfelled up to 6 months previously and were on level or moderately sloping ground with minimal shading by surrounding mature trees. At each site, air and root-stump bark temperatures were measured within an area (6 × 6 m) maintained clear of brash and vegetation with minimal disturbance to the soil surface and litter layer (see Supporting information, Fig. S1).

Temperatures were measured by Tinytag™ data loggers (model TGP-4520; Gemini Data Loggers Ltd, U.K.) fitted with dual thermistor probes recording at 20-min intervals from March 2008 to February 2009. Air temperature was measured at 1.5 m above ground level in a ventilated thermometer screen (see Supporting information, Fig. S1). The temperature of root-stump bark was measured on a single representative root-stump at depths of 10 and 30 cm below ground level, inserting probes from a soil pit on the north side of the root-stump. Pits were backfilled to maintain the natural soil horizons. The latitude, longitude and altitude of each site, tree species, time of felling and the cross-section area and height of the root-stump projecting above the ground were recorded. Local rainfall data and, where available, sunshine hours were obtained from the nearest Meteorological Office recording station.

Temperatures over the recording period were used to develop a recursive model to predict daily mean root-stump bark temperature from the mean air temperature calculated from the minimum and maximum air temperatures. The model  $S_t = \alpha S_{t-1} + \beta T_t$  related the current day's ( $t$ ) predicted root-stump temperature to that predicted for  $t-1$  and the current day's mean air temperature, where  $S_t$  was the predicted root-stump temperature and  $T_t$  was the mean air temperature on day  $t$ . It was assumed that the relationship between the observed ( $s_t$ ) and predicted ( $S_t$ ) root-stump temperature was  $s_t = S_t + e_t$ , where  $e_t$  represented independent normal errors. The parameters  $\alpha$  and  $\beta$  were estimated by maximum likelihood using R (R Development Core Team, 2012) and the 'bbmle' package (Bolker & R Development Core Team, 2012). The model was fitted separately to data from each of the 17 sites for depths of 10 and 30 cm. No suitable model related differences in parameter values between sites to local environmental factors such as root-stump size, rainfall or sunshine hours. A single model was therefore used over all sites for each depth. Parameters were adjusted to use the mean of the minimum and maximum air temperature simulated by the Weather Generator (WG) (see below) and constrained to sum to one to maintain stationarity over the period of the simulations. The resulting parameters for 10 cm were  $\alpha = 0.77$  and  $\beta = 0.23$  and, for 30 cm,  $\alpha = 0.91$  and  $\beta = 0.09$ . Root-stump temperatures predicted by the model represent a smoothed or averaged representation of what would be observed in the field. However, because the life cycle simulation model in which they were used averaged across the weevil population developing over 1–3 years, this smoothing would have little effect.

### *Predicting weather variation under climate change*

Regional variation in temperature up to the 2070s was assessed from U.K.-wide maps produced by the UKCP09 WG (<http://ukclimateprojections.defra.gov.uk/21708>). These maps were used as a basis for selecting two to four representative conifer forest sites in each of five regions. Using the UKCP09 WG (version 2) (Jones *et al.*, 2009), daily minimum and maximum air temperatures were simulated for a total of 12 sites, each of which corresponded either to an experimental field

site or was within 25 miles of one. Site names and locations on the UKCP09 WG 5-km grid are provided in the Supporting information (Table S2). Daily air temperatures were predicted for the baseline data (1961–1990), incorporated by default as a ‘control’ in WG simulations, and for the 2030s (2020–2049), 2050s (2040–2069) and 2070s (2060–2089) using the medium emissions scenario (A1B) (Jones *et al.*, 2009). The daily mean air temperature determined as the mean of the minimum and maximum air temperatures in the WG data was used to predict root-stump temperature at depths of 10 and 30 cm. The temperature at 20 cm was calculated as the mean of that at 10 and 30 cm. These microhabitat temperatures provided the basis for modelling future seasonal development of weevils across the U.K. Temperature differences from the baseline data to the present time were assumed to have had little effect on development relative to that predicted for the 2030s onwards, and so, for convenience, the baseline data were referred to as the current climate.

### Predicting weevil seasonal development and activity

**Life cycle simulation model, parameters and assumptions.** A life cycle simulation model was developed to follow a generation of weevils from egg to adult oviposition and to determine voltinism, as well as the seasonal timing of development and activity. The model is described in the Supporting information (Appendix S1). It was programmed in R (R Development Core Team, 2012) using R 2.15.0 for Mac OS (Apple Inc., Cupertino, California) and also run under Windows XP (Microsoft, Redmond, California). The model runs through life cycle ‘stages’ 0–10, which were grouped into a series of independent modules (Table 1). Stages 1–9 correspond to those in Table 2, with stages 0 and 10 referring, respectively, to the start time of oviposition in the first generation and to egg selection for the start of subsequent generations. A default population size of 1000 females was used to adequately describe variation in weevil development, with all individuals ‘passing’ through all modules in order. By modelling a fixed population size, the distribution of the key duration times was estimated on the assumption that they were independent of mortality. For the main stages in the life cycle, development or other activity was described by a set of parameters, based on temperature and/or time in days, derived largely from published data from laboratory and field studies in northern Europe (Table 2). Many parameters were

experimentally derived, although some, including threshold temperature for adult activity and duration of maturation feeding, were less precisely defined in the literature. Other parameters were not defined in the literature but were included in the model to account for observed characteristics of the life cycle, such as the timing of transition from the prepupal to the pupal stage, or to define an overwintering period. For parameters where experimental data were available, statistical models were fitted to the data and used in the simulation model.

Development of eggs, larvae and pupae at different depths was specified by the required number of day-degrees (DD) above the developmental threshold temperature. Individual DD requirements for any stage, which were independent of those of other stages and independent between generations, were generated from normal distributions with the appropriate means  $\pm$  SD (Inward *et al.*, 2012).

In prepupae, a facultative diapause results in a nonlinear relationship between development time and temperature, with no obvious developmental threshold temperature (Eidmann, 1963; Inward *et al.*, 2012). Prepupal development was therefore expressed as the number of days required at a given temperature, based on the model of Inward *et al.* (2012), which predicted development under constant temperatures using a log-logistic distribution with a logistic response function. It was assumed that, under varying temperatures, the number of days required for development was related to mean temperature over the period. To estimate individual prepupal stage duration, a deviate was generated from a log-logistic distribution with the required shape parameter but with unit scale. This deviate was then transformed to the required number of days for any given mean temperature. Bounds were placed on the minimum and maximum number of days based on values observed in experiments (D. Inward, unpublished data) and the interval searched to find the first day on which the required number of days was satisfied.

To prevent overwintering of eggs and pupae in the model, eggs taking longer than 40 days to develop were not selected to initiate the next generation and pupae taking longer than 60 days were reassigned to the prepupal stage, thus maintaining model population size. These times approximate to the maximum duration observed at 10 °C in laboratory experiments (D. Inward, unpublished data). The time requirement for development of overwintering prepupae would normally be accumulated before the end of winter in the current climate, but pupation does not appear to start until around mid-June (Bejer-Petersen *et al.*, 1962; Moore *et al.*, 2004), when mean root-stump temperature at the site studied by Moore *et al.* (2004) was estimated to be 12.5 °C. This was taken as a threshold temperature for transition to the pupal stage.

Adult emergence, spring re-emergence, feeding and oviposition were based on a threshold temperature of 9 °C. Inactive adults may be above or below ground and, because the relative differences between air and soil/root-stump temperature vary during the day and seasonally, the threshold was defined as both the mean air and the 10-cm root-stump temperature exceeding 9 °C. Temperatures above or below the threshold are referred to as ‘warm’ or ‘cold’ days, respectively. Emergence/re-emergence was triggered by five

**Table 1** Independent modules and associated life cycle stages in the simulation model

Module	Life cycle stages
1	Initial oviposition and egg development (stages 0 and 1)
2	Dispersal, oviposition and egg development (stages 8, 9, 10 and 1)
3	Larval development (stage 2)
4	Prepupal and pupal development (stages 3 and 4)
5	Emergence and, if required, overwintering (stage 6)
6	Maturation feeding (stage 7)

For stage descriptions, see Table 2 and text.

**Table 2** Key parameters and definitions used in the life cycle model

Life cycle stage	Location and definition	Key source references
1. Egg	RS at 10 cm. DT $8.0 \pm 0.08^\circ\text{C}$ DD $110 \pm 0.8$	Inward <i>et al.</i> (2012); Pye and Claesson (1981)
2. Larva	RS 50% at 10 cm, 50% at 30 cm. DT $4.5 \pm 0.39^\circ\text{C}$ DD Scots pine = $660 \pm 15.8$ Sitka spruce = $767 \pm 22.2$	Inward <i>et al.</i> (2012).
3. Prepupa	RS at 20 cm. Duration predicted from logistic model. Moulting to pupal stage when mean root-stump temperature $\geq 12.5^\circ\text{C}$	Eidmann (1963); Moore <i>et al.</i> (2004); Inward <i>et al.</i> (2012).
4. Pupa	RS at 20 cm. DT $7.3 \pm 0.18^\circ\text{C}$ DD $219 \pm 3.7$	Inward <i>et al.</i> (2012).
5. Adult melanization	RS at 20 cm. 21 days	Bejer-Petersen <i>et al.</i> (1962); Moore <i>et al.</i> (2004)
6. Emergence, overwintering and re-emergence	RS or AG. Adult emergence/re-emergence after five consecutive days where mean 10 cm root-stump and mean air temperature $> 9^\circ\text{C}$ . After summer solstice, overwintering initiated after 10 consecutive days where mean air and mean 10 cm root-stump temperature $< 9^\circ\text{C}$ . Overwintering may occur as adult in pupal cell	Munro (1928); Christiansen and Bakke (1971); Nordenhem (1989); Örlander <i>et al.</i> (1997)
7. Maturation feeding	AG. Mean of 20 days (minimum 12 days) when mean air and mean root-stump temperature $> 9^\circ\text{C}$	Nordenhem (1989); Wainhouse <i>et al.</i> (2001); Wainhouse <i>et al.</i> (2004); Thorpe and Day (2008)
8. Dispersal	AG. After egg maturation, when maximum air temperature $\geq 18.5^\circ\text{C}$	Solbreck and Gyldeberg (1979)
9. Oviposition	RS. When mean air and mean 10-cm root-stump temperature $> 9^\circ\text{C}$ after dispersal. Oviposition rate declines linearly to zero over 78 days, with a mean of 1.2 eggs/day	Bylund <i>et al.</i> (2004)

RS, root-stump; AG, above ground; DT, development threshold temperature; DD, day-degrees.

consecutive warm days, and overwintering was triggered by 10 consecutive cold days, based on temperature patterns typically observed around the end of weevil activity in the late autumn and its resumption in the spring in the current climate.

The time for egg maturation was accumulated by counting (as whole days) those days on which the temperature exceeded  $9^\circ\text{C}$ . Egg development normally occurs after overwintering and there is a presumed facultative reproductive diapause as found in related species (Clark, 1975; Trudel *et al.*, 2002). However, under the experimental conditions in the field, some individuals can mature eggs without overwintering (Tan *et al.*, 2010). As the climate warms, adult weevils may remain active into the late autumn, with the potential to mature eggs without overwintering. The model therefore allows a user-defined percentage of weevils to enter reproductive diapause. Egg maturation takes longer in the autumn than the spring (Tan *et al.*, 2010), and so a parameter in the model (*nfv*, the notional feeding value) allowed the proportion of a day accumulated towards the total required to be varied in any given month. Weevils with mature eggs dispersed when the flight threshold temperature was reached and began oviposition the next day. The life cycle was complete at the end of oviposition or at the overwintering signal. When egg maturation was incomplete or temperatures remained below the flight threshold at the start of overwintering, weevils were assumed to accumulate further 'maturation days' as necessary in the following spring before dispersal and oviposition.

Model predictions for each site and scenario were based on five generations, 100 realizations of the WG, each comprising daily predictions for the 30-year period, and 100% of the

population entering reproductive diapause. To examine the effect of possible adaptive changes in weevil reproductive development as the climate warms, the model was rerun for the 2070s with reproductive diapause in only 50% of individuals. The model ran until the required number of generations had been completed. For the first generation, the day of the year (1 January = day 1) on which egg development started was assumed to follow a normal distribution with a mean  $\pm$  SD of  $171 \pm 10$ , and was centred on the approximate timing of peak oviposition currently observed in the field (Nordlander *et al.*, 1997). The next generation was initiated by random selection of an egg from those laid by each individual in the previous generation. Approximately five generations were required to minimize the influence of oviposition timing in the first generation on voltinism. In each generation, the value of life cycle parameters for each individual was chosen at random from the appropriate statistical distribution (see Supporting information, Table S3). There was no correlation between generations and individuals may complete the final generation in different calendar years. Population statistics were accumulated over the different years of the final generation, which, in the weather stationary situation provided by the WG (i.e. with no trend across the 30-year run of each climate change projection), represents an equivalent picture of the monthly distribution of weevil development and activity. The model was used to predict voltinism, as well as the monthly distribution of adult emergence and the start of oviposition.

Voltinism was determined by the number of winters, defined as passing through 1 January, during development from egg–adult oviposition. Life cycles varied from  $< 1$ –3 years



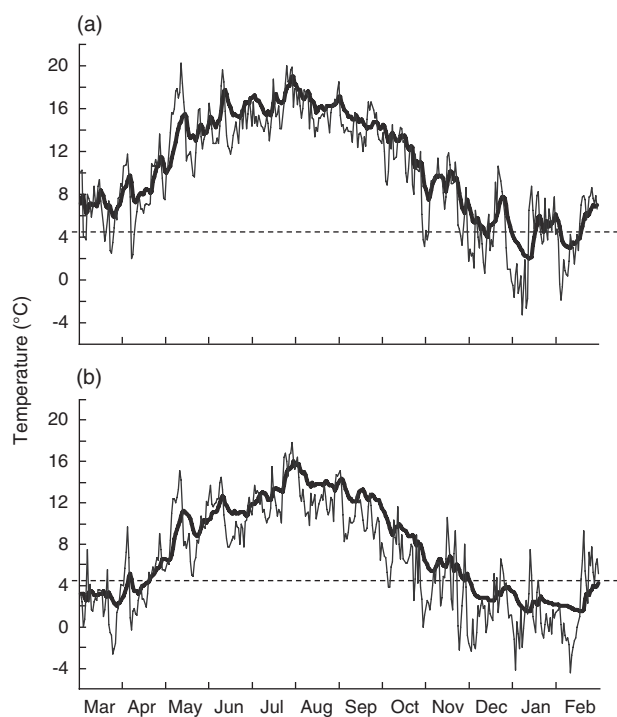
corresponding to 0–3 winters, respectively. A generation time of < 1 year was only possible when reproductive diapause was set at < 100% in the model. Predictions were also made for the mean of the potential first day of overwintering after the summer solstice and the mean occurrence of the first potential day of re-emergence after overwintering, which together define the period when weevils were inactive. For each scenario, predictions were based on WG simulations averaged over all years and realizations (i.e. for a given scenario, 30 years  $\times$  100 realizations).

The 'sensitivity' of the model to changes in the value of the less clearly defined parameters or those introduced to define seasonality was tested for the different scenarios. Only single parameter values were varied in tests based on five generations and 10 model runs.

## Results

### *Measuring and predicting temperature in the weevil microhabitat*

Annual variation in air and root-stump temperature shows that, in the larval microhabitat, temperatures were buffered relative to air temperature (Fig. 1). At the example southern site, root-stump temperatures remained above the larval development threshold temperature through much of the winter and early spring, in contrast to that at the Scottish site.



**Figure 1** Variation in daily mean air temperature and root-stump temperature at a depth of 30 cm from March 2008 to February 2009. (a) Site 2 in southern England and (b) site 15 in Scotland (see Supporting information, Table S1). —, Air temperature. —, 30-cm root-stump temperature. ..., Larval developmental threshold temperature.

### *Predicting weevil seasonal development and activity*

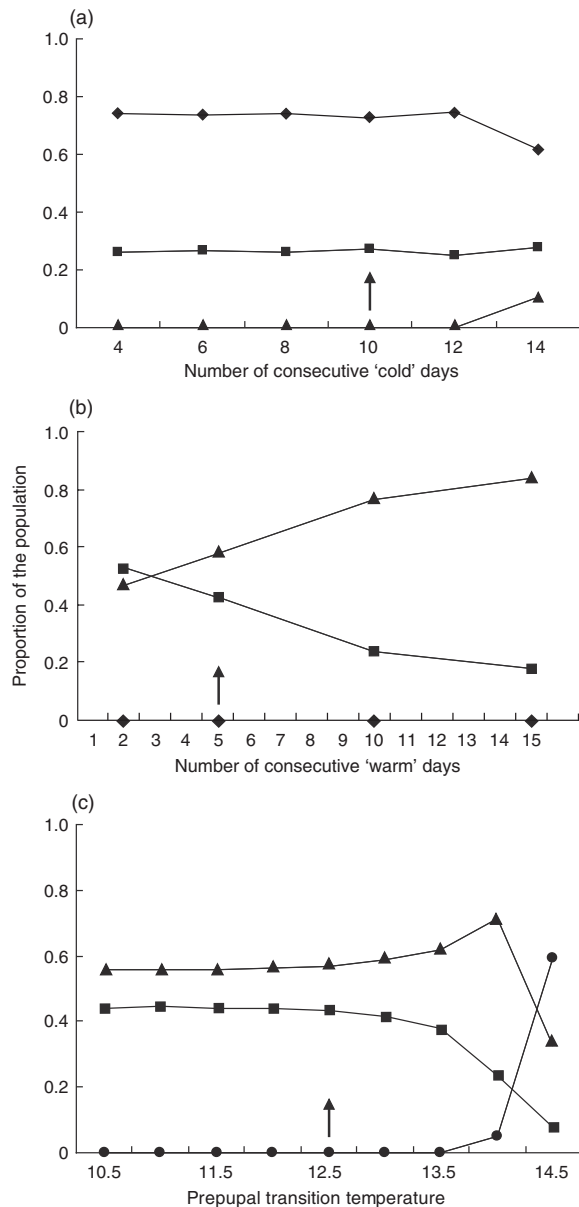
*Varying parameter values in the simulation model.* The effect on predicted voltinism of varying the values of parameters that were not defined experimentally was tested in model runs. Parameters with a low temperature requirement were tested in the warm climate predicted for southern England in the 2070s, and those requiring higher temperatures, in the current climate of the north of Scotland. Increasing the number of consecutive days of cold weather required to initiate overwintering increased the likelihood that, in a warmer climate, some individuals would not receive an overwintering signal in some years. For the 10 days used in the model, this occurred in < 7% of years for any site in the 2070s and was highest at the New Forest site. Small effects on predicted voltinism were only evident at the highest number of consecutive days used (Fig. 2a). The number of consecutive warm days to initiate adult emergence in the current climate at Lairg had a larger effect on voltinism, which was most evident when the number of days was increased from 5 to 10 days (Fig. 2b). Varying the threshold temperature for transition from the prepupal to the pupal stage at Lairg affected voltinism only at the highest temperatures (Fig. 2c). Varying the parameter  $n_{fv}$ , which changed the length of the period required for maturation feeding, had no effect on voltinism when reproductive diapause was set at either 100% or 50%.

### *Geographical variation in voltinism and adult activity*

Pine and spruce can co-occur in some areas, as for example in north-east Scotland and south-west England. Development on pine and spruce was compared at Lairg and at Cookworthy, for each scenario (Fig. 3). The slower development of weevils on spruce (Table 2) had the largest effect on predicted voltinism at the colder northern site in the current climate, with the effect declining as the climate warmed.

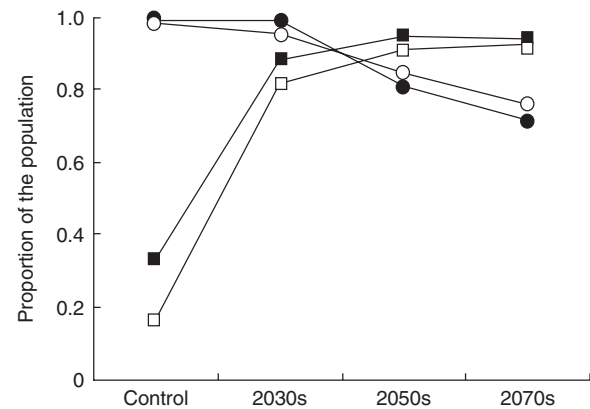
In the current climate, weevils were predicted to have a predominantly 2-year life cycle in the south and east of England (S&E) but, in Wales, the north of England and Scotland (N&W), a 2- or 3-year cycle predominated (Fig. 4). By the 2030s, voltinism in the N&W was predicted to be similar to that currently seen in the S&E, with a 2-year cycle predominating. In the S&E, the model predicted a marked increase in the proportion of the population with a 1-year cycle.

Predicted changes in voltinism to the 2070s show differences in response between the two broad geographical regions, although with some variation between sites within each region. Four main patterns of change were evident (Fig. 5), with sites displaying similar patterns grouped together for the S&E (groups 1 and 2) and the N&W (groups 3 and 4) as: group 1 – New Forest; group 2 – Thetford, Forest of Dean, Checkendon, Cookworthy and Sherwood; group 3 – Dunkeld and Llanwrst; and group 4 – Waun, Kielder, Lairg, Fiunary. In group 1, there was a progressive decline in the predominant 2-year cycle and a corresponding increase in a 1-year cycle so that, after the 2050s, a 1-year cycle predominated. The slower rate of change predicted for group 2 forests indicated that a 1-year cycle was not likely to predominate until after the 2070s. In group 3, there was relatively little effect of climate change, with a 2-year life cycle in > 70% of the population



**Figure 2** The effect on predicted voltinism of variation in parameters used in the life cycle model, the values of which were not experimentally defined. (a) The number of consecutive cold days (parameter t6O days) to initiate adult overwintering in the New Forest in the 2070s. (b) The number of consecutive warm days (parameter t6E days) that would initiate adult emergence at Lairg in the current climate. (c) The threshold temperature (parameter t4i) for transition from the prepupal to the pupal stage at Lairg in the current climate. Parameters are given in the Supporting information (Appendix S1). Arrows indicate default values. Life cycle duration (voltinism) was 1 (◆), 2 (■), 3 (▲) or 4 (●) years.

throughout the period, with the 3-year cycle disappearing in the 2030s. In group 4, the predominant 3-year cycle in the current climate decreased to a low level by the 2030s, with a corresponding marked increase in the proportion with a 2-year cycle so that, from the 2030s, > 80% of the population had a 2-year cycle.



**Figure 3** Proportion of *Hylobius abietis* with a 2-year life cycle when developing on pine (closed symbols) or spruce (open symbols) at Lairg (■) and Cookworthy (●) in the current climate and 2030s to 2070s. An increase in the proportion of weevils with a 2-year life cycle at Lairg was associated with a decrease in the 3-year life cycle. At Cookworthy, a decline in the 2-year cycle was associated with a proportional increase in a 1-year cycle.

Allowing reproductive development in 50% of adults without overwintering increased the proportion of the population with a 1-year life cycle, with a corresponding decrease in the 2-year cycle. By the 2030s, the proportion with a 2-year cycle among the four groups decreased by a mean of 35.8% (range 26.3–40.7%) compared with the default 100% reproductive diapause.

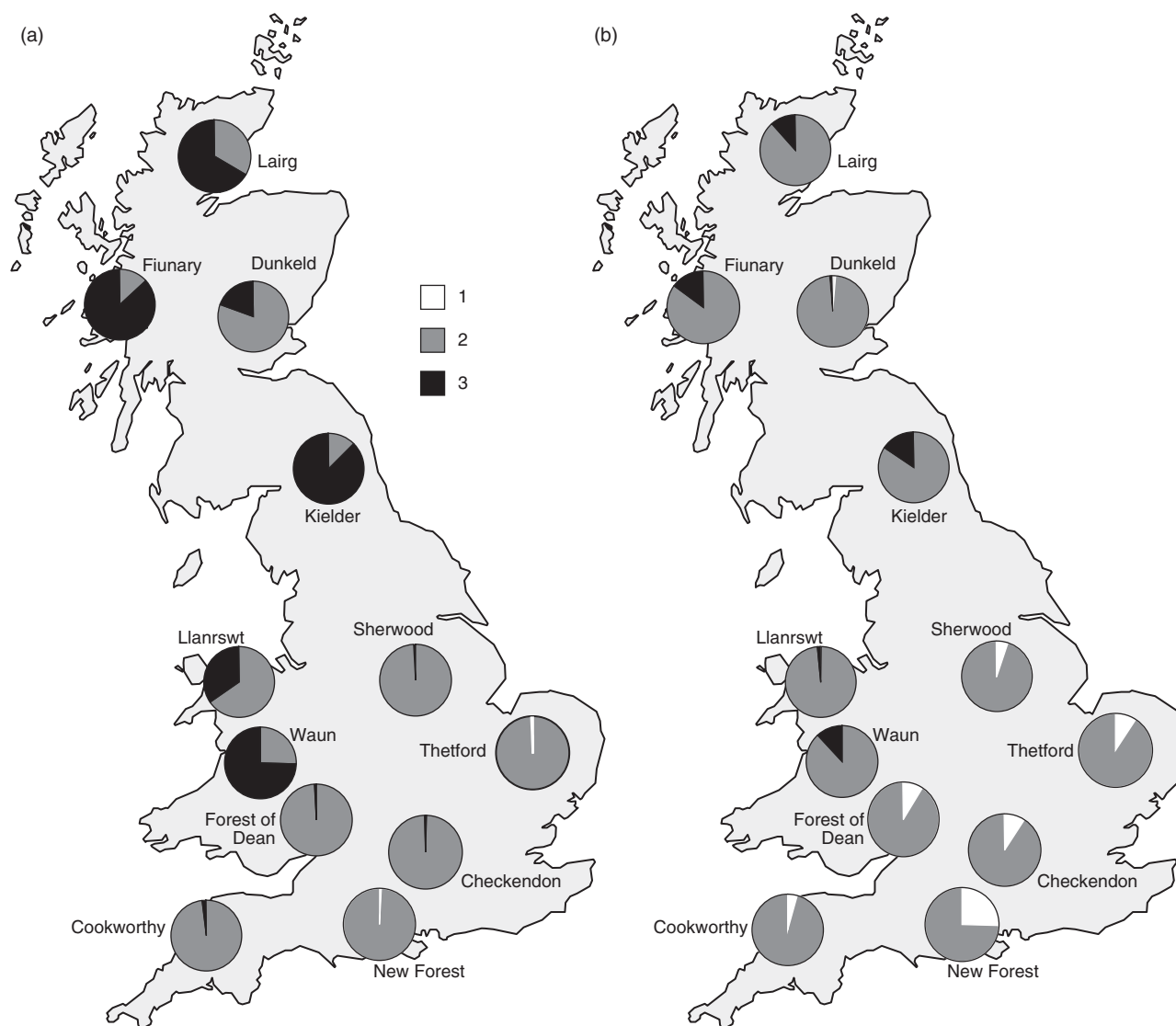
The predicted effect of climate change on the monthly timing of adult emergence and dispersal (1 – proportion ovipositing in each month) from emergence sites is shown in Fig. 6. In the current climate (Fig. 6a), emergence occurs somewhat earlier in the S&E, with a corresponding earlier dispersal after overwintering. Emergence in both groups was advanced by the 2030s, with 63–87% of emergence occurring by July in contrast to the 12–29% currently predicted. With increasing warming, emergence tends to occur over a longer period in populations from the S&E, with emergence in the N&W tending to occur in advance of that in the S&E by the 2070s. There was a corresponding earlier dispersal in the subsequent spring, with 3–59% remaining by May in the 2030s compared with 46–99% in the current climate.

When 50% of weevils reproduce without reproductive diapause, emergence and dispersal in the 2070s was much more spread out, so that only 54–60% had emerged by July, and 36–50% had still to disperse by May of the next year (Fig. 6b).

The length of the overwintering period when weevils are inactive varies between the N&W and S&E. In the current climate, it lasts for > 6 months in the N&W and approximately 5 months in the S&E but, by the 2070s, it was only predicted to extend for approximately 4 months and 2 months, respectively (Fig. 6a).

## Discussion

Pine weevil has a predominantly semi-voltine life cycle and the model accurately reflects currently observed geographical

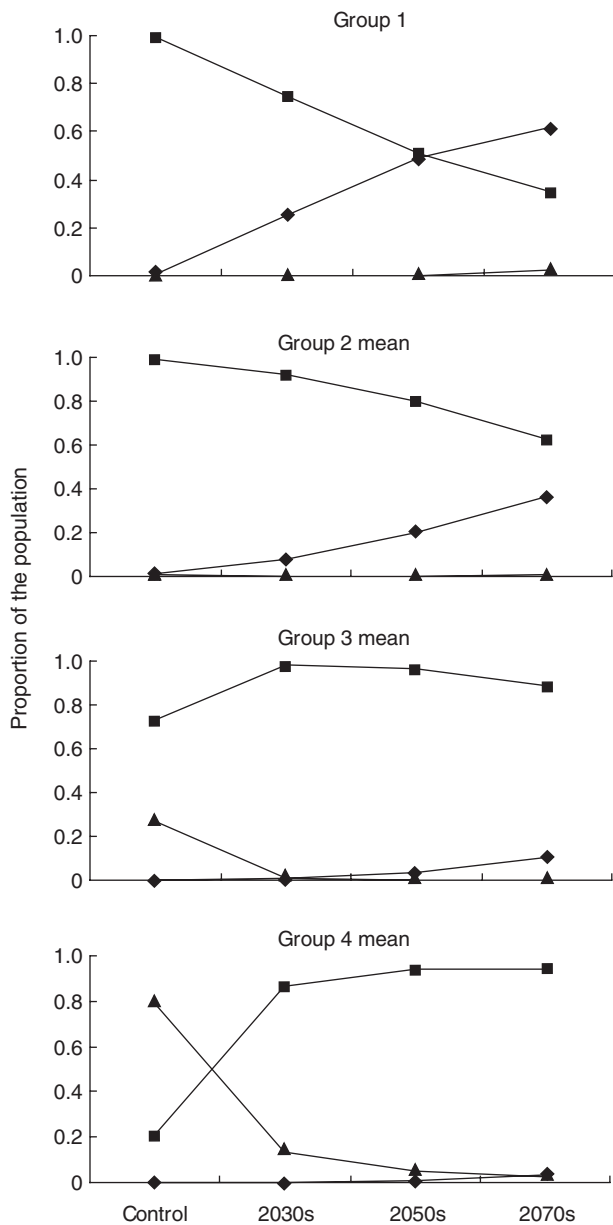


**Figure 4** Predicted geographical variation in voltinism of *Hylobius abietis* (a) current climate and (b) 2030s. Key indicates life cycle duration (voltinism) of 1, 2 or 3 years. Pie diagrams are positioned at the approximate location of the sample sites, which are georeferenced in the Supporting information (Table S2).

variation in voltinism. As the climate warms, however, the values of particular parameters used in the model could influence predicted changes in voltinism. In particular, parameters that define seasonality or influence the timing of key events, whose values are not known with any precision, could have a disproportionate influence if the model were sensitive to departures from default values. Varying the number of consecutive warm days required for weevil emergence or re-emergence in colder northern regions provides an illustrative example (Fig. 2b). This parameter influenced predicted voltinism in the north but not in warmer southern regions in the current climate. However, relatively large departures from the default value were needed to change predicted voltinism by more than 10%, and the influence would decline as the climate warmed. We conclude that the default parameters used in the model appropriately reflect weevil development and activity in the field and were not

likely to unduly influence predicted voltinism under climate change.

Geographical differences in voltinism influence current pest management by determining the number of seasons over which emergence occurs on clearfell sites and this is an important determinant of economic impact. In the N&W, it may be  $\geq 4$  years after clearfelling before all weevils have dispersed from sites because of lower temperatures and, to a lesser extent, slower development on spruce. A prolonged fallow period or insecticide treatment of transplants is therefore usually necessary to minimize mortality (Wainhouse *et al.*, 2007). By the 2030s, the increasing predominance of a 2-year cycle in the N&W, and the corresponding reduction in a 3-year cycle, should allow either a shorter fallow period or reduced insecticides input. Given that most of the U.K. conifer plantations occur in the N&W, this would have a



**Figure 5** Predicted variation in voltinism under climate change for forests grouped according to patterns of change over time (see text). Life cycle duration (voltinism) was 1 (♦), 2 (■) or 3 years (▲).

significant economic and environmental benefit. In the S&E, a shorter fallow period of 2–3 years is usually sufficient in the current climate, although this is not likely to change as the climate warms as a 2-year cycle predominates until 2070s. It is worth emphasizing, however, that predictions from the WG become increasingly uncertain into the future and, of course, modelling a more extreme climate change scenario could result in more marked changes in voltinism. Grouping the forests with similar changes in voltinism over time emphasizes the importance of geographical variation in climate change and local responses to it. As a guide to future management therefore,

it is important that the model is run using local climate change predictions.

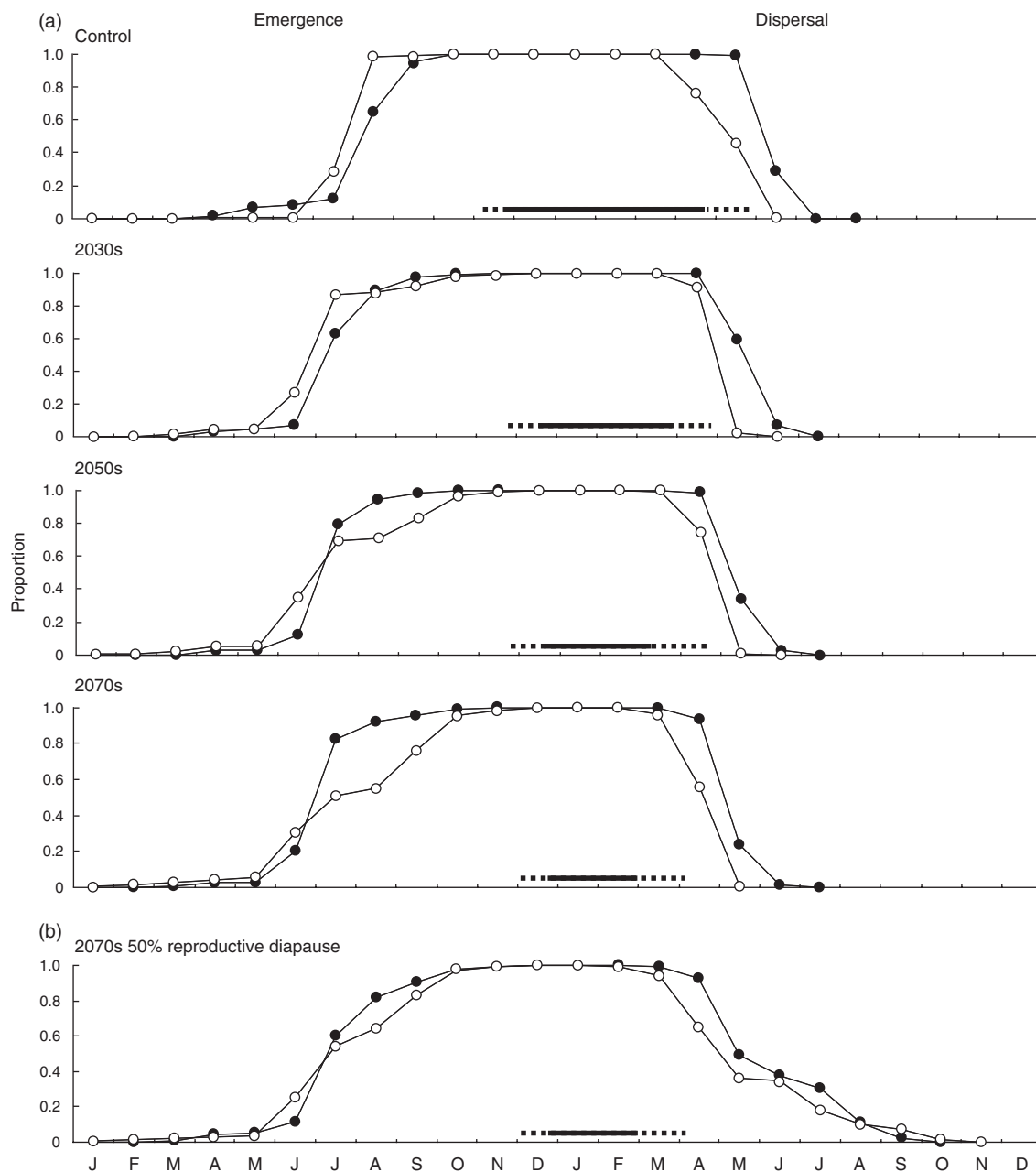
As the climate warms, earlier weevil emergence and later onset of overwintering increased the length of the summer–autumn feeding period by approximately 3 months by the 2070s. This provides scope for adaptive changes in weevil behaviour and development (Parmesan, 2006). One interesting possibility is that of egg maturation without reproductive diapause. Feeding in the summer–autumn period before overwintering can be important for wing muscle maturation, but there is normally little development of oocytes during this period (Tan *et al.*, 2010). There is some circumstantial evidence that egg development can occur in the field before overwintering (i.e. without reproductive diapause) (Tan *et al.*, 2010) and such ‘flexibility’ in the life cycle has been reported in the white pine weevil *Pissodes strobi* (Peck), in which reproductive diapause normally occurs (Trudel *et al.*, 2002). The potential influence of autumn maturation of eggs in pine weevil was tested by assuming that 50% of individuals develop without reproductive diapause. The resulting decrease in the proportion of the population with a 2-year life cycle allows for the possibility of a further shortening of the fallow period.

The potential effects of climate change on weevil abundance were not addressed in the model and would be difficult to predict. The main determinant of weevil abundance in managed forests is likely to remain the availability of root-stumps on recent clearfells. However, adults increase in size when larvae develop at higher temperatures (Inward *et al.*, 2012), in contrast to that seen in most insect species (Kingsolver & Huey, 2008). A warming climate could therefore result in larger more fecund adults that cause more damage to individual transplants and, in addition, maternal effects on egg size and subsequent larval survival could increase local population size (Wainhouse *et al.*, 2001). Pine weevil is usually characterized as a low density pest because young trees are sensitive to the removal of bark from the main stem and are easily killed, and each adult can damage several transplants during maturation feeding (Wainhouse *et al.*, 2004). Management is therefore usually required at relatively low population density levels, and insecticides are often applied prophylactically (Långström & Day, 2004). Possible changes in abundance should not therefore outweigh the pest management gains of a shorter life cycle.

Pine weevil is a significant pest of conifer plantation forestry throughout northern Europe and, because model parameters were derived from the wider European literature, model predictions should be applicable outside the U.K. In southern Europe, pine weevil appears to have less economic impact for reasons that are unclear (Långström & Day, 2004) but may result from differences in forest management or the effect of temperature on voltinism. However, warming of the climate in southern U.K. into the second half of this century was not predicted to reduce the period over which pest management was required, suggesting that the warmer climate of southern Europe may not be the main influence on pest status in that region.

In conclusion, the duration of the life cycle in pine weevil is predominantly semi-voltine and this is a key determinant of economic impact. In the north and west of the U.K.,





**Figure 6** The effect of climate change on the seasonal timing of adult emergence, expressed as cumulative proportion, and subsequent population decline as adults disperse to oviposition sites after overwintering. Predictions are for (a) current climate and 2030s to 2070s and (b) 2070s with 50% adults entering reproductive diapause. Data are the means for south and east (S&E) (groups 1 and 2) (○) and north and west (N&W) (groups 3 and 4) (●). The approximate duration of the overwintering period, when adult weevils are inactive, is indicated by the solid horizontal line for the S&E. The dotted line is the additional length of the overwintering period for adults in the N&W.

where most conifer plantations occur, the current 2–3-year life cycle requires a fallow period of at least 4 years or insecticidal protection of young transplants. As the climate warms, however, the simulation model predicts that, by the 2030s, a 2-year cycle will predominate, resulting in a shorter fallow period or reduced insecticide input. Predicted changes in voltinism to the 2070s revealed marked differences across the U.K. In the south and east, there was a progressive decrease

in a 2-year cycle and increase in a 1-year cycle but, in the north and west, voltinism changed little after the 2030s, with a 2-year cycle predominating. A reduction in the length of the overwintering period as the climate warms has the potential to increase weevil seasonal feeding activity. Possible adaptive changes in weevil behaviour, such as a reduction in the proportion of individuals with reproductive diapause, could have important effects on the weevil life cycle.

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## Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12043

**Fig. S1.** Example clearfell site within a forest where air and root-stump temperatures were measured. The thermometer screen recorded air temperatures comparable with Meteorological Office Stevenson screens (D. Inward unpublished data).

**Table S1.** Temperature measurement sites in the U.K. used in development of the root-stump temperature model.

**Table S2.** Sites used for UKCIP Weather Generator climate simulations for the 2030–2070s using the medium emissions scenario (A1B).

**Table S3.** Distribution models for key life cycle parameters.

**Appendix S1.** Simulation model description and default model parameter values.

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