Predicting spruce beetle voltinism and flight times in western Canada using a model developed in the United States of America

K. P. BLEIKER[1], S. R. BRESCIA, AND B. H. VAN HEZEWIJK

ABSTRACT

The ability to predict voltinism and key phenological events such as flight times for forest pests can inform management decisions and aid in assessing the effects of climate change on outbreak risk of pest species. We assessed a spruce beetle voltinism model, developed for standing trees in Colorado, Utah, and Alaska, United States of America, for field sites in British Columbia, Alberta, and the Yukon, Canada. Spruce beetle preferentially attacks trees with compromised defenses, *e.g.,* recently downed trees, and populations that build up in sudden pulses of ideal breeding material will mass attack and kill healthy trees once preferred hosts are depleted. Modifications were made to the model interface in BioSIM, a software tool for running temperature-driven phenological models, to allow users to request voltinism predictions for six different height–aspect combinations on standing trees. Predicted and observed univoltinism for standing trees were similar. Furthermore, voltinism model predictions for ground level, north aspect on standing trees was similar to that observed on downed trees. For the period 2021–2050, the voltinism model predicts a high probability of univoltinism in downed trees east of the Rocky Mountains and in parts of central and southern British Columbia. In general, predictions of peak flight time were similar to those observed, but several 3–4 weeks differences occurred. Our data provide support for using the spruce beetle voltinism model to predict peak flight dates and voltinism in standing and downed trees in western Canada.

Keywords: *Dendroctonus rufipennis*; life cycle; univoltine; semivoltine; flight time

INTRODUCTION

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), is an eruptive bark beetle native to spruce forests, *Picea* spp. (Pinaceae), across Canada and the United States of America. Infestations are common in western coniferous forests, particularly in British Columbia, Canada, where outbreaks occur roughly decennially somewhere in the province (reviewed in Bleiker 2021). Spruce beetles prefer large-diameter trees with compromised defenses, *e.g.*, stressed, senescing, or recently downed trees (*e.g.*, Hard *et al.* 1983; Hard 1985, 1987); however, high-density populations will attack healthy trees once preferred hosts have been exhausted. Past outbreaks in British

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Columbia have been linked to sudden pulses in preferred breeding material, especially windfall, in susceptible stands that coincide with several years of warm summer temperatures (Safranyik *et al.* 1983, 1990; Safranyik 2011). Warm summer temperatures can shorten the usual two-year life cycle (semivoltinism, one generation every two years) to one year (univoltinism, one generation per year; *e.g.*, Massey and Wygant 1954; Werner and Holsten 1985; Reynolds and Holsten 1994; Berg *et al.* 2006; DeRose and Long 2012). A shift from semivoltinism to univoltinism has been linked to an increase in outbreak risk (Safranyik *et al*. 1990; Reynolds and Holsten 1994; Hansen and Bentz 2003; Berg *et al.* 2006).

In both the one- and two-year life cycles, adult beetles disperse to new host trees between mid-May and mid-July depending on the region and year, tunnel into the inner bark, and construct egg galleries at the phloem–sapwood interface (reviewed in Bleiker and Safranyik 2021). The larvae mine the phloem as they pass through four instars. In the one-year life cycle, eggs develop through to adults in the year of attack, and the new adults overwinter before emerging and dispersing to new host trees in the spring. In the two-year life cycle, eggs develop through to late-instar larvae the first summer, and the larvae overwinter in a putative diapause the first year (Dyer 1970; Dyer and Hall 1970; Hansen *et al.* 2011). The next summer, larvae complete development, pupate, and eclose to new adults that enter a putative diapause and overwinter the second year, before dispersing the following spring, two years after the tree was attacked (Bleiker and Meyers 2017; Bleiker and Willsey 2020; Bleiker and Safranyik 2021; but see Schebeck *et al*. 2017).

Adult beetles exhibit an interesting behaviour in that they may overwinter on the bole of standing trees where they developed or they may emerge in late summer or fall, drop to the base of the tree, and bore back under the bark and overwinter in gregarious feeding galleries, protected by the snowpack from extreme temperatures and woodpeckers (Massey and Wygant 1954, Knight 1961; Gray and Dyer 1972; Hansen and Bentz 2003). However, little is known about the tendency of adults to relocate for the winter. At warmer sites, parent beetles may re-emerge 3–4 weeks after establishing their first brood, reattack, and establish a second brood, and/or overwinter at the base of the tree with their progeny, emerge in the spring, and reproduce a second season (Massey and Wygant 1954; Hansen and Bentz 2003). In addition to the potentially complex relocation and reproduction behaviour of adults, trees may be attacked in more than one year, larvae may pupate late in the season, and a mix of life cycles may occur in the same tree, making it challenging to determine voltinism and the population growth rate (Robert and Bleiker 2021).

Hansen *et al*. (2001) developed a voltinism model for spruce beetles that predicts stand-level proportions of univoltine spruce beetle brood from ambient air temperatures. Funnel trap data collected at sites were used to estimate the peak flight date, which served as a starting point, or biofix, for the phenology model. The model was built from temperature data and insect development that was sampled on the north and south aspects near ground level (~0.3 m), at 1.8 m, and at 4.6 m on standing, infested trees in a multiyear study in Utah, Colorado, and Alaska, United States of America. Voltinism predictions were weighted by the amount of habitat at each location using taper equations (Hansen *et al*. 2001; Hansen, personal communication). The model was subsequently updated with data from additional sites and years (sites in Utah, Colorado, Washington, and Arizona) and a temperature-based rule to generate the biofix (*i.e.,* peak flight date) developed from emergence cage data from southern Utah (the adult emergence model; Hansen, personal communication). The updated version of the model is available in BioSIM, a free software tool designed to run temperature-driven simulation models to forecast phenological events (https://cfs.nrcan.gc.ca/projects/133).

In the current study, we assessed the performance of the spruce beetle voltinism model in BioSIM (Hansen *et al.* 2001; Hansen, personal communication) against data from field sites in British Columbia, Alberta, and the Yukon, Canada, to determine its potential for use in western Canada. In addition, we initiated modifications to the model interface in BioSIM to improve its applicability, including predicting univoltinism in downed trees, which are where many outbreaks originate. A model that predicts univoltinism and peak flight date would be invaluable for management and operational control decisions and in assessing the effects of a changing climate on the outbreak risk of this important pest species in spruce stands throughout western Canada.

METHODS

Model interface adjustments

The current version of Hansen's model in BioSIM predicts stand-level voltinism by integrating the predicted voltinism at three bole heights (ground, 1.8 m, 4.6 m) and two aspects (north, south). The BioSIM code was altered to output the proportion of univoltine beetles at each of the six height–aspect combinations. An additional modification allows users to specify the observed date of peak flight as the biofix. The modified model code is available on GitHub (https://github.com/RNCan/WeatherBasedSimulationFramework/tree/master/wbsModels/SpruceBeetle).

Observed *versus* predicted univoltinism

Observations of the proportion of univoltine beetles were available at three site-years from previous field work and experiments: Prince George, in northern British Columbia, 2017 (53.53° N, –122.48° W; 779 m); Duffey Lake, in southern British Columbia, 2019 (50.38° N, –122.34° W; 1155 m); and Peace River, in northern Alberta, 2019 (56.62° N, –118.64° W; 868 m; Figure 1). In each case, emergence cages were used to capture any re-emerging parents or new brood; parent beetles were distinguished from new brood based on timing of emergence. At each location, the proportion of univoltine beetles remaining under the bark was determined in the late fall or winter after development had ceased and before any winter-associated mortality had accrued, which could potentially confound the measurement. The proportion of univoltine beetles within a population was calculated for each site-year at the stand level by pooling data across a minimum of three sample trees. Stand-level proportion of univoltine beetles within a population was similar to that calculated at the tree level and then averaged across trees (unpublished data).

The observed proportion of univoltine beetles for the three site-years came from different types of hosts and stands (Table 1). The observations from Prince George and Duffey Lake came from infested logs that were hung in cages at 3 m on standing trees, but we noted that the stand at Prince George was more open than the stand at Duffey Lake. The stand at Duffey Lake where the logs were hung had a dense, closed canopy with a heavily shaded understorey. We expected that the Prince George observation would be best predicted by model output averaged for north and south aspects at 1.8 and 4.6 m, and Duffey Lake, due to its shaded nature, would be similar to the average of the north aspect at 1.8 and 4.6 m. The Peace River observation was from infested logs lying on the ground or just off the ground. Attacks were on the bottom and lateral sides of the logs because spruce beetle avoids surfaces with direct exposure to solar radiation. Thus, observations in felled trees in Peace River were expected to be best predicted using model output for the north aspect at ground level (~0.3 m). The altered BioSIM model was used to predict the proportion of univoltine beetles for each aspect (north, south) by height (ground, 1.8 m, 4.6 m) combination for each of the three site-years and the averages calculated as stated above.

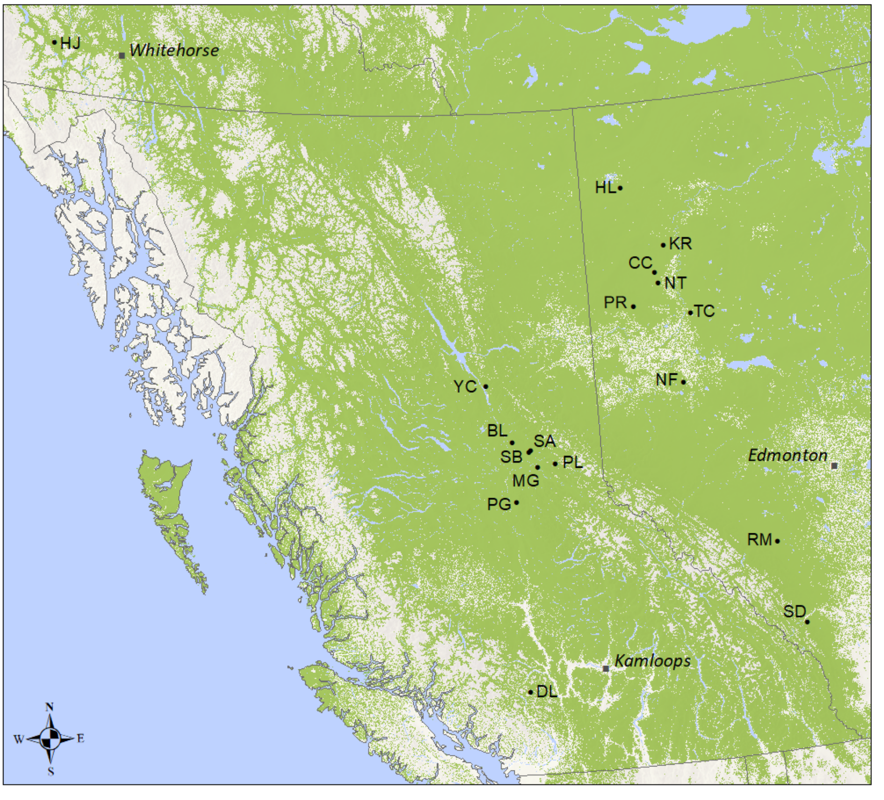

Figure 1. Location of field sites in western Canada (British Columbia, BC; Alberta, AB; the Yukon, YT) where spruce beetle voltinism or peak flight date were observed with the distribution of *Picea* spp. shown in green. Each site is labelled with a two-letter code: BL, Bear Lake, BC; CC, Chinchaga, AB; DL, Duffey Lake, BC; HL, Hay Lake, AB; KR, Kemp River, AB; MG, McGregor, BC; NF, New Fish Creek, AB; NT, Notikewin, AB; PL, Pass Lake, BC; PG, Prince George, BC; PR, Peace River; RM, Rocky Mountain House, Alberta; SA, Seebach A, BC; SB, Seebach B, BC; SD, Sibald, AB; TC, Three Creeks, AB; YC, Tony Creek, BC; HJ, Haines Junction, YT. Data for each site are noted in Supplementary material, Table S1.

Table 1. Observed and predicted proportion of univoltine beetles generated by the spruce beetle voltinism model in BioSIM for spruce beetles developing at three sites in British Columbia (BC) and Alberta (AB). Observed proportions were expected to be similar to the underlined proportions generated by the model (see text). The model generated the biofix (peak flight date), and for the Duffey Lake site the model was rerun with a later flight date based on local knowledge of when the flight occurs at that site (see text). N = North. S = South.

				Predicted proportion of univoltine beetles						
				At 4.6 m		At 1.8 m		At ground level		Whole tree
Site	Host and stand description	Observed proportion of univoltine beetles	Biofix	N	S	N	S	N	S	
Prince George, BC, 2017	Logs at 3 m Open canopy, gaps	0.94	1 June	0.86	0.93	0.71	0.85	0.34	0.55	0.83
Duffey Lake, BC, 2019	Logs at 3 m Closed canopy, heavy shade	0.08	23 May	0.55	0.75	0.33	0.54	0.09	0.20	0.55
			22 June*	0.18		0.08				
Peace River, AB, 2019	Downed trees	<0.01	27 May	0.33	0.54	0.17	0.33	0.04	0.09	0.36

*Peak flight date estimated based on local knowledge of site and date of observed peak flight in the recent past.

Observed *versus* predicted peak flight date

Because peak flight date is an important input for the voltinism model, we assessed the accuracy of this component separately using an independent set of funnel trap data from 2015 to 2023 collected in western Canada (Figure 1). Observed dates of peak flight were determined based on an assessment of the number of spruce beetles caught in pheromone-baited funnel traps for 15 site-years and on field observations that identified the week that trees were mass attacked for an additional site-year (Supplementary material, Table S1; Figure S1). Trap catches were usually collected weekly. It is common for parent beetles at some sites to re-emerge after establishing an initial brood, which can lead to a second flight several weeks after the first (*e.g.,* Massey and Wygant 1954; Knight 1961; Lawko and Dyer 1974; Safranyik et al. 1983; Hansen and Bentz 2003). Therefore, we identified the first notable peak in the average number of beetles caught per day, and the date of peak flight was taken as the mid-point between that date and the date of the previous collection. One exception was at site Seebach B, where there was a very small peak followed by a second peak that was several times larger; the latter was taken as the peak flight date (Supplementary material, Figure S1).

Predicted peak flight dates were obtained by running the voltinism model in BioSIM for each of the 16 site-years. Input for the model included hourly temperature data for the year of flight, as well as for the previous year, interpolated between the four nearest Environment Canada weather stations. In cases where weather data was missing, BioSIM uses interpolated values based on a database of 1980–2010 climate normals for temperature.

To assess the sensitivity of the voltinism predictions to variation in peak flight date, we performed a set of model simulations in which peak flight date was systematically varied from 1 May to 6 July for each site-year. For each set of simulations, the voltinism of beetles in whole standing trees and of beetles from ground level on the north aspect was predicted. The ground level–north aspect prediction was expected to represent the conditions experienced by beetles attacking downed (*e.g.,* windthrown) trees. For each site-year, the difference in voltinism when using the observed peak flight date *versus* the modelled peak flight date was calculated for both standing trees and downed trees.

Future predictions for univoltinism and peak flight in western Canada

To facilitate near-term risk analyses for spruce beetle under a changing climate and to provide operational-scale predictions for voltinism and peak flight date, we generated model predictions at 1000 random points in western Canada between longitudes –156° and –110° and between latitudes 47° and 64°. For each point and year between 2021 and 2050, the voltinism model was run using projected climate normals data under the greenhouse gas concentration scenario RCP4.5 (Canada–USA 2021-2050 ESM2 RCP45). Means and standard deviations were calculated across years for both peak flight date and voltinism. Continuous prediction surfaces were generated in BioSIM using universal kriging, with elevation (30 arc-second resolution) as an external drift variable.

RESULTS

The predicted and observed proportions of univoltine beetles within populations of spruce beetles were similar for Peace River: the model predicted 0.04 univoltine for the north aspect at ground level and we observed < 0.01 univoltine in downed trees (Table 1). At Prince George, the predicted proportion of univoltine beetles averaged across north and south aspects at 1.8 and 4.6 m was within 0.1 of that observed at 3 m. However, at Duffey Lake, the proportion observed to be univoltine was 0.08, and the predicted proportion for the north aspect averaged across 1.8 and 4.6 m was 0.44 (Table 1). We noted that the biofix for Duffey Lake was extremely early (23 May 2019); we did not observe the flight in 2019 but did in 2017, when it occurred in the third week of June, which is typical for this high-elevation site, based on our experience at this location. We reran the model with 22 June as the biofix, and the predicted proportions for the north aspect at 4.6 m and 1.8 m were 0.18 and 0.08, respectively (Table 1).

For the 16 site-years of flight data, the mean (standard deviation) of the absolute differences between predicted and observed peak flight dates was 9.6 (10.1; Supplementary material, Table S1). The three site-years with the greatest differences were in the same area (Pass Lake 2A022, Seebach A 2022, Seebach B 2023): the predicted flight was 23–34 days before the observed peak flight at these site-years. Excluding these sites, the mean (standard deviation) of the absolute difference between observed and predicted was 5.14 (3.16), with the maximum difference being 11 days (Figure 2).

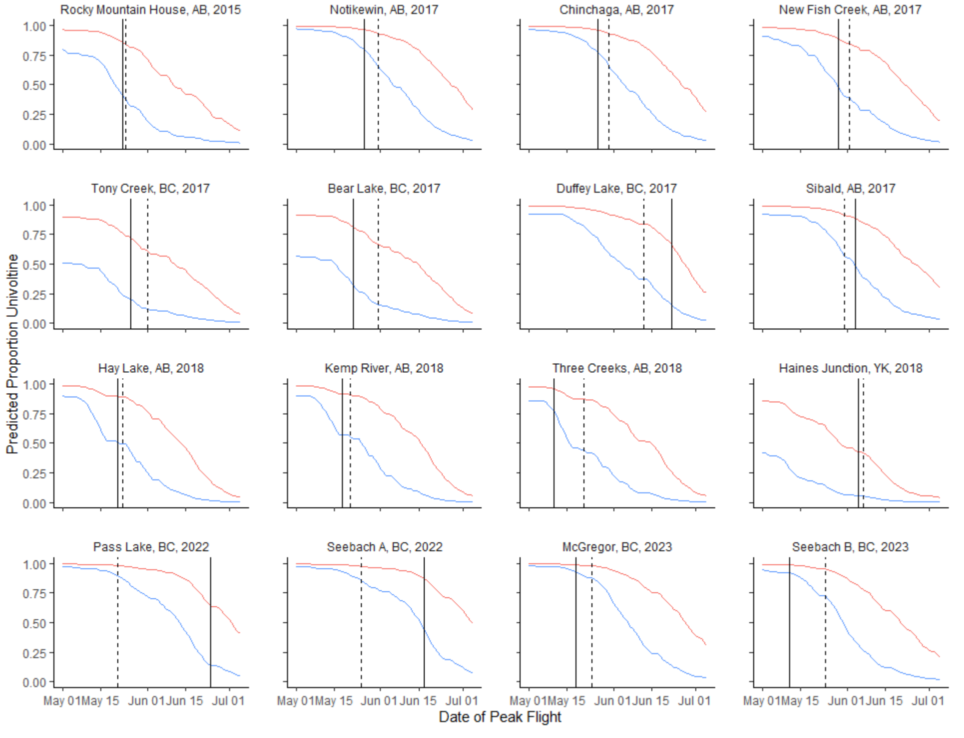

Figure 2. The effect of peak flight date on the proportion of a spruce beetle population predicted to be univoltine in standing trees (red line) and downed trees (blue line) at 16 site-years using the spruce beetle voltinism model in BioSIM (see text). The voltinism model predicts peak flight date (dashed black line), based on a temperature rule, and uses this date as the biofix. Observed peak flight dates (solid black line) are based on funnel trap catches, except for Duffey Lake, which was based on field observations of attacked trees (see text). Univoltinism in downed trees was inferred from the north aspect of standing trees at ground level (see text).

The sensitivity analysis revealed that for standing trees at least, model predictions for univoltinism were not severely affected by errors associated with using model predictions of peak flight rather than estimates from trapping data (Figure 2; Supplementary material, Table S1). For standing trees, the absolute difference in proportion of univoltine beetles between the two methods averaged only 0.07. However, in downed trees represented by north aspect–ground level, the average difference was 0.17. At Pass Lake, using the modelled peak flight date overestimated the proportion of univoltine beetles in downed trees by 0.75 (Figure 2).

Significant areas in western Canada have, or soon will have, climates warm enough to support a one-year life cycle for spruce beetles developing in standing trees (Figure 3A). Univoltine development dominated in standing trees in river valleys, across the central plateau in British Columbia, and east of the Rocky Mountains. The area where univoltinism is expected to dominate on average in downed trees was greatly contracted compared to standing trees (Figure 3A, B). Predominately univoltine populations were most likely in downed trees in river valleys and at lower elevations in the central and southern interior of British Columbia, as well as east of the Rocky Mountains. The model also predicted that peak flight occurs, on average, between mid-May (day 140) and mid-June (day 170), with limited deviation from this timing throughout the interior plateau, at lower elevations in northern British Columbia, and east of the Rocky Mountains (Figure 4A, B). The flight is predicted to occur later at high elevations in the Rocky Mountains and Coast Mountains. Most of the among-year variation in peak flight date was associated with elevation, not latitude (Figure 4B).

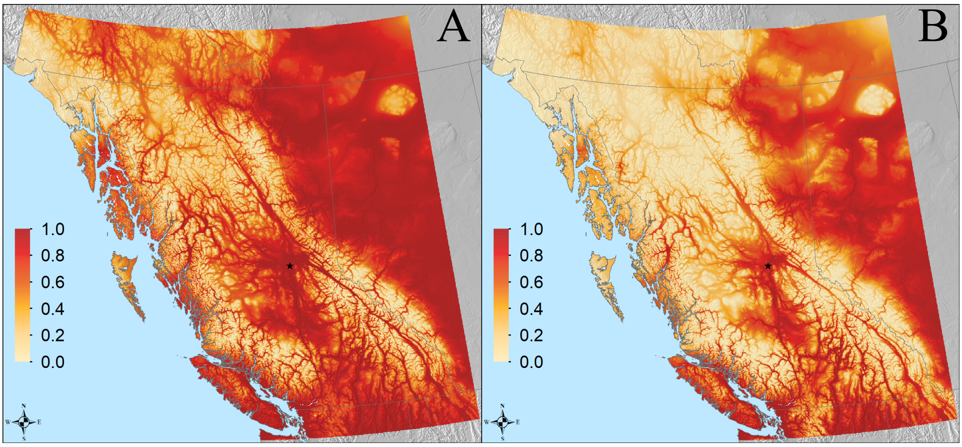

Figure 3. Mean proportion of spruce beetle predicted to be univoltine in standing (A) and downed trees (B) in western Canada using the spruce beetle voltinism model in BioSIM for the period 2021–2050. The proportion of univoltine beetles for downed trees was inferred from that predicted for the north aspect at ground level on standing trees (see text). The black star represents the city of Prince George.

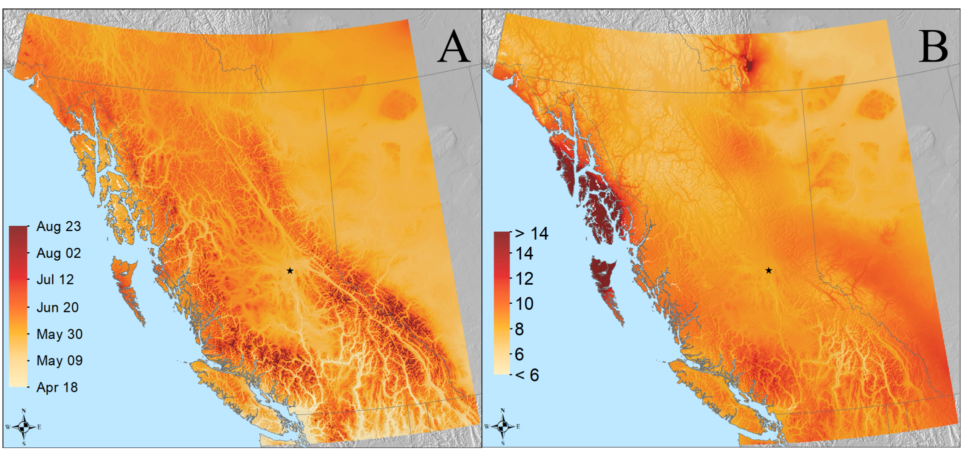

Figure 4. Mean predicted peak flight date (A) and variation in mean peak flight date represented by standard deviation from the mean (B) for spruce beetle in western Canada predicted by the spruce beetle voltinism model in BioSIM for the period 2021–2050 (see text).

DISCUSSION

The spruce beetle voltinism model developed by Hansen *et al*. (2001; Hansen, personal communication) can be used to predict both proportion univoltinism in standing and downed trees and peak flight date in western Canada with some caveats and local knowledge. Quantifying the proportion of univoltine beetles in a population requires knowing the timing of attack, sampling after development ceases in the fall, quantifying the number of new adults that relocate in the late summer and through the fall to overwinter, and distinguishing parent beetles from brood beetles (Massey and Wygant 1954; Knight 1961; Gray and Dyer 1972; Hansen and Bentz 2003; Robert and Bleiker 2021). We attempted to extract additional reports of univoltinism to validate the model from Canadian Forest Service historical Forest Insect and Disease Survey reports (https://www.exoticpests.gc.ca/documents; Nealis *et al.* 2016). Unfortunately, most reports appeared to be based on limited under-bark checks made at one point in time, and it was usually unclear if the observations were from standing or downed trees. In each case, we were uncertain as to how, where, or when the determinations were made and, as a result, did not use these reports to validate the model. The model was tested against the three observations of voltinism and 16 site-years of flight data in which we had confidence.

The proportion of univoltine beetles within a population was within 0.1 of that observed, once the appropriate parameters were selected: flight date, bole height, and aspect. Predictions of peak flight time were usually close to observed peak flight times, but in several cases, predicted peak flight time was 3–4 weeks earlier than the observed peak flight time, a difference that greatly affected univoltinism, especially in downed trees (Figure 2). Fluctuating temperatures, such as a warm period in May followed by a week or two of cool weather and rain in June, and variability in overwintering sites could confound the adult emergence model's ability to accurately predict peak flight date in some cases. A period of warm weather typically initiates spruce beetle to start flying in mid- to late-May, with peak flight occurring in May or early June in most of western Canada. However, some sites, especially higher-elevation windward sites, retain a substantial snowpack through much of June that could prevent adults that overwintered in downed hosts or at the base of trees from emerging in May despite favourable air temperatures. For most locations, the threshold temperature of the adult emergence model (Hansen, personal communication) represents the peak flight date well, which is likely because spruce beetle overwinters in the adult stage before dispersing, such that adults can emerge rapidly in the spring once temperatures warm.

The modifications made to the model's user interface in BioSIM, which allow users to specify aspect (north, south), height (ground, 1.8 m, 4.6 m), and alter the biofix (*i.e.,* peak flight date), improved its accuracy and expanded its potential application. Although only one observation was made for downed trees, it seems reasonable to expect univoltinism in downed trees to be similar to the north aspect of standing trees at ground level. Spruce beetle avoids surfaces exposed to direct solar radiation, and attacks are often focused on the shaded undersides of felled trees (Mitchell and Schmid 1973). Fallen trees often rest on their branches just above ground level. Being able to predict the likelihood of univoltine development in downed trees would help forest managers to assess the risk of a spruce beetle outbreak following a disturbance that creates ideal breeding habitat. The origin of most outbreaks in western Canada can be traced to sudden pulses of ideal breeding material in susceptible stands that are followed by warm growing-season temperatures that promote univoltinism (Safranyik *et al*. 1983, 1990; Reynolds and Holsten 1994; Bleiker and Safranyik 2021).

Montane and subalpine boreal forests throughout central and southern British Columbia where white, Engelmann, and hybrid spruce are common may face increased risk of spruce beetle outbreaks due to the prevalence of univoltinism in the period 2021–2050. Overall, there was limited variation in the annual timing of the peak flight date, except for some coastal areas and at higher elevations. The high standard deviations (> 30) around peak flight date for Haida Gwaii and adjacent coastal areas may be due to some growing seasons not warming sufficiently to support flight until late in the summer in these locations. The relatively low variation in peak flight date through most of western Canada may be a consequence of the model's dependence on the number of days exceeding a relatively low threshold temperature, rather than on an average temperature or cumulative degree-days.

Based on our assessment, the spruce beetle voltinism model developed by Hansen *et al.* (2001; Hansen, personal communication) can be used to predict peak flight date and univoltinism in standing and downed trees in western Canada. Users should know the host and stand conditions and have a general knowledge of spruce beetle's flight period to use the model to predict voltinism at the stand level. The modifications made to the user interface in BioSIM allow users to improve the accuracy of predictions to potentially assess outbreak risk associated with disturbances, such as a spring windfall event, that produce ideal breeding habitat. At a regional scale, the model can be used to help managers assess the risk of spruce beetle outbreaks in the future under climate change.

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SUPPLEMENTARY MATERIAL

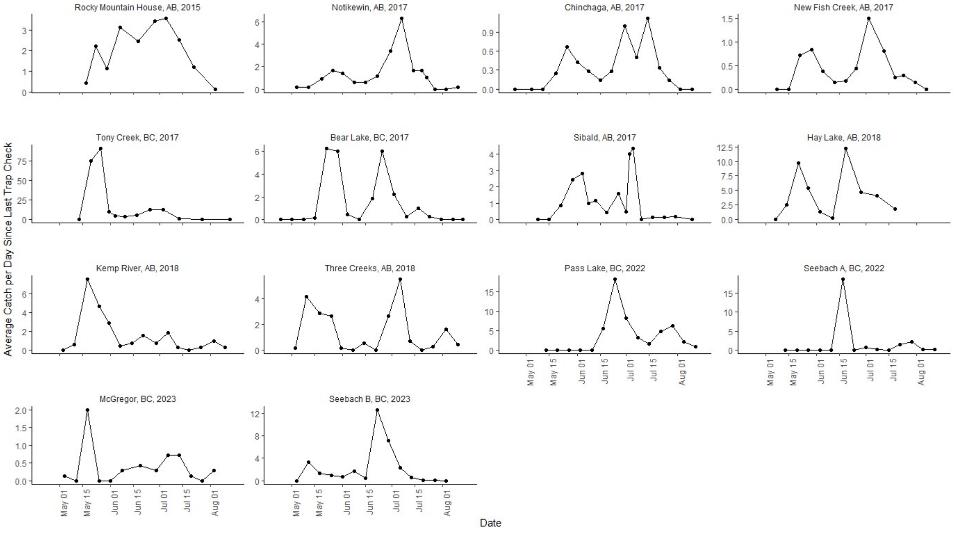

Figure S1. Mean number of spruce beetles caught per day in funnel traps for 14 site-years (also see Supplementary material, Table S1).

Supplementary material, Table S1. Sites and years at which the peak flight date for spruce beetle was observed and predicted using the voltinism model in BioSIM. The difference between the predicted proportion of univoltine beetles using the predicted and observed peak flight dates is also presented for standing and downed trees. Observed peak flight dates were taken from funnel trap catches (see Supplementary material, Figure S1), except for Duffey Lake, which was taken from field observations of mass attacked trees.

					Peak flight date (mo–dd)			Difference between proportion of univoltine beetles predicted using observed and predicted peak flight date	
Name (2-letter code), province or territory	Year	Latitude	Longitude	Elevation	Observed	Predicted	Difference	Standing trees	Downed trees
Bear Lake (BL), BC	2017	54.516	–122.499	867	05–22	05–31	–9	0.15	0.17
Chinchaga (CC), AB	2017	57.147	–117.904	606	05–26	05–30	–4	0.02	0.12
Hay Lake (HL), AB	2018	58.601	–118.666	371	05–21	05–23	–2	< 0.01	0.02
Kemp River (KR), AB	2018	57.580	–117.521	472	05–18	05–21	–3	< 0.01	0.01
McGregor (MG), BC	2023	54.086	–121.819	633	05–18	05–24	–6	< 0.01	0.05
New Fish Creek (NF), AB	2017	55.288	–117.418	785	05–29	06–02	–4	0.03	0.09
Notikewin (NT), AB	2017	56.974	–117.817	594	05–26	05–31	–5	0.03	0.14
Pass Lake (PL), BC	2022	54.139	–121.327	773	06–24	05–21	34	–0.34	–0.75
Rocky Mtn House (RM), AB	2015	52.461	–115.399	1138	05–23	05–24	–1	0.02	0.04
Seebach A (SA), BC	2022	54.372	–121.989	799	06–17	05–25	23	–0.10	–0.41
Seebach B (SB), BC	2023	54.354	–122.056	783	06–22	05–24	29	0.04	0.19
Sibald (SD), AB	2017	51.053	–114.942	1559	06–04	05–31	4	–0.03	–0.08
Three Creeks (TC), AB	2018	56.410	–116.967	606	05–10	05–21	–11	0.09	0.33
Tony Creek (YC), BC	2017	55.480	–123.210	816	05–26	06–01	–6	0.11	0.08
Duffey Lake (DL), BC	2017	50.376	–122.340	1155	06–22	06–12	10	–0.18	–0.21
Haines Junction (HJ), YT	2018	60.7804	–137.423	628	06–05	06–07	–2	< 0.01	< 0.01

AB, Alberta; BC, British Columbia; YT, Yukon