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A degree day model for predicting voltinism of the invasive balsam woolly adelgid (Hemiptera: Adelgidae) in northern Utah

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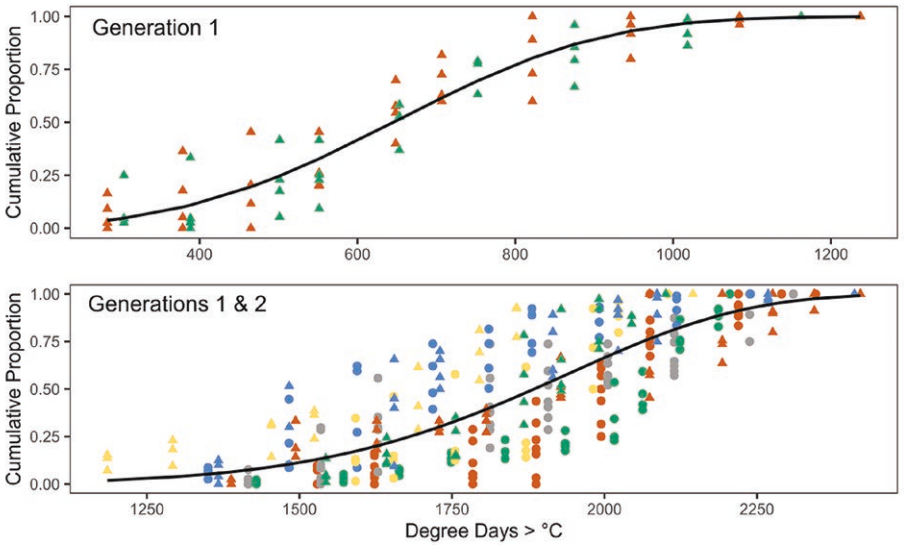
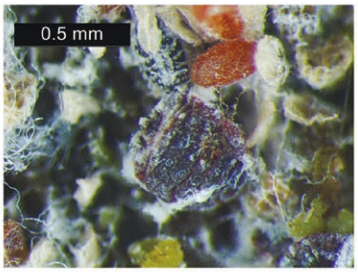
Balsam woolly adelgid, *Adelges piceae* (Ratz.) (BWA), invasive in North America, was first detected on subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] in several northern Utah counties in 2017. BWA phenology is known to vary by elevation and climate; a degree-day (DD) model focused on population expansion into the Intermountain West is needed. Bark samples were collected weekly from infested subalpine fir in early summer through late fall at 5 northern Utah sites from August 2020 to December 2022. At a single site, additional samples were collected biweekly to monthly during winter and spring. The presence of live individuals of all life stages in winter through early summer samples confirmed that life stages other than crawlers can successfully overwinter in northern Utah. Two generations were observed at all sites. Degree-day models were developed by fitting proportional adult counts and local air temperatures to Weibull distributions. Model fit was optimized with a 0 °C lower threshold, 30 °C upper threshold, and 1 Jan biofix. Completion of the first generation required 1,104 DD and 2 generations required 2,412 DD. Using the models and historical (1980 to 2020) temperatures, study sites were predicted to have thermal suitability for 2 generations at least 2 to 3 decades prior to detection in northern Utah, depending on site. Although upper estimates of future (2025 to 2099) predictions forecast a doubling of generations by 2060, knowledge of potential dormancies that may be disrupted in a changing climate is needed. The degree-day model will be a useful tool for predicting thermal suitability for future BWA expansion.

Keywords: phenology, invasive species, climate change, subalpine fir

Graphical Abstract

Degree-day models for balsam woolly adelgid (*Adelges piceae*) generations





Introduction

Balsam woolly adelgid, *Adelges piceae* (Ratz.) (Hemiptera: Adelgidae) (BWA), is an invasive pest of true firs (*Abies spp.*) in North America. Native to south-central Europe, BWA was first detected in North America in Brunswick, Maine in 1908 (Kotinsky 1916, Havill et al. 2021) and is now established on the east coast from south-eastern Canada to North Carolina, and in the Pacific Northwest of the United States and British Columbia, Canada (Zilahi-Balogh et al. 2016, Poland et al. 2021). Inland range expansion is ongoing with confirmation in Coeur d'Alene, Idaho in 1983 (Livingston et al. 2000), Montana in 2008, and in 7 northern Utah counties in 2017 (Davis et al. 2020). Balsam woolly adelgid infestations in Utah were extensive in 2017 suggesting its presence in subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] stands for at least a decade (Davis et al. 2020), contributing to recent fir mortality (Rideout et al. 2023). Within 10 yr of monitoring in Idaho, BWA-caused mortality increased from 0% to 20%, exceeding 50% in some stands (Davis et al. 2022). Subalpine fir is a critical species for maintaining healthy watersheds, providing wildlife habitat and forage, and sustaining recreational tourism industries throughout the Intermountain West.

In North America, BWA is parthenogenic and exhibits an anholocyclic life cycle with 3 instars, and in rare forms, 4 instars may be found (Balch 1952). The first instar, the crawler, is the only motile stage and is responsible for dispersal, usually by wind (Balch 1952). The crawler is also believed to be the overwintering life stage, though other life stages entering winter have been reported (Balch 1952, Tunnock and Rudinsky 1959). The crawler stage has been hypothesized to enter a winter diapause (Amman 1970, Greenbank 1970), although factors influencing induction and termination have not been investigated. Once hatched from the egg and settled in a prospective feeding site on a tree, the crawler inserts its stylets into the bark and begins feeding on parenchyma cells. The settled crawler begins exuding white, waxy threads colloquially called "wool," molts through 2 sessile nymphal stages, and upon reaching the adult stage is characterized by a heavy wool covering. Difficult to recognize when populations are low, higher densities of woolly masses contribute to population detection. Feeding by BWA leads to restricted water flow and reduced photosynthesis in the host tree, often presenting as drought-like symptoms (Mitchell 1967, Puritch 1973).

Previous studies have shown that BWA seasonality is temperature-dependent and varies with elevation and climate. Three BWA generations were reported in North Carolina (elevation ~1,500 m) (Arthur and Hain 1984) and between 2 and 4 generations in the US Pacific Northwest (elevations 70 to 1,200 m) (Tunnock and Rudinsky 1959, Mitchell et al. 1961). In continental New Brunswick, Canada (elevation ~100 m), between one and 3 generations of BWA were observed (Greenbank 1970). In the western United States, minimum fall temperatures and wet conditions in the spring (Hrinkevich et al. 2016) and warm summer temperatures and/or generally wet conditions (Hicke et al. 2023) were associated with greater tree mortality due to BWA. Northern Utah is characterized by high elevations with warm, arid summers and cold winters with substantial snowfall. Using remotely sensed imagery of BWA impact in northern Utah and downscaled climate data, Campbell et al. (2023) predicted that higher minimum summer temperatures and fewer chilling degree days in autumn were associated with greater BWA infestation severity. Knowledge of the direct effects of temperature on BWA phenology and voltinism will further our understanding of BWA population dynamics and the potential for continued spread into true fir stands throughout Utah and surrounding states.

The goals of this field study were to describe BWA phenology in northern Utah and develop a degree day model for estimating life stage timing and voltinism. Degree day models are widely used for predicting critical life history events such as the timing of insect life stages and voltinism and have been developed for multiple invasive forest insects (Smyers et al. 2021, Haynes et al. 2022) including the congener species hemlock wooly adelgid (*Adelges tsugae* (Annand)) (Tobin and Turcotte 2018). We sampled BWA from infested trees in 5 subalpine fir stands across a range of elevation and latitude, and developed degree day models for BWA adults using air temperatures measured within each stand. The models were used to predict the number of annual generations expected in historical and future climate scenarios.

Materials and Methods

Phenology Sampling

This study was conducted at 5 BWA-infested subalpine fir stands located within the Uinta-Wasatch-Cache National Forest (Table 1). Sampling began in August 2020 at Rock Canyon, Laketown,

Table 1. Location information for balsam woolly adelgid phenology study sites, 2020 to 2022, shown in order of ascending elevation. All sites were located within the Uinta-Wasatch-Cache National Forest, Utah.

Site	Elev. (m)	Lat.	Lon.	Aspect	Slope (%)	Years Sampled
Green Canyon	2,039	41.804	−111.702	NW	50	2020, 2021, 2022
Big Mountain Pass	2,274	40.829	−111.651	N	45	2021, 2022
Laketown	2,326	41.725	−111.377	N	14	2020, 2021, 2022
Farmington Canyon	2,339	40.981	−111.809	NE	22	2021
Rock Canyon	2,456	41.674	−111.41	SE	24	2020, 2021, 2022

and Green Canyon and in June 2021 at Big Mountain Pass and Farmington Canyon. All sites except Farmington Canyon were sampled through December 2022. Due to limited sampling ability caused by low BWA populations, Farmington Canyon was discontinued in June 2022. Winter and spring access to sites was restricted due to snow; therefore, weekly samples were collected from all sites from ~1 June through ~30 November. In 2021 and 2022, winter and early spring samples were also collected biweekly to monthly at Green Canyon, which was accessible by skis or snowshoes, and in 2022, sampling began at the Big Mountain Pass site on 10 May.

Four or 5 BWA-infested subalpine fir trees with low to moderate infestation levels were randomly chosen at each site. For each sample, 6.45 cm^2 (2.54 cm × 2.54 cm) of bark was removed using a 2.54 cm width wood chisel (DeWalt Industrial Tool Company, Towson, MD, USA). Samples were placed in individual 50 ml centrifuge vials (VWR International, Radnor, PA, USA) and returned to the USDA Forest Service Rocky Mountain Research Station in Logan, Utah. Bark samples were collected from 2 bole heights (the tree base and 1 m above the base) and 2 aspects (north and south) on individual trees such that samples from every aspect/height combination were obtained in each sampling interval. We acknowledge that sequential bark removal from individual trees could influence tree physiology. To minimize this effect, new trees within the same stand were identified and sampled each year beginning ~ 1 June. Based on limited preliminary sampling showing similar life stage densities on previous-year and new-year trees, we assumed BWA life stage progression was similar among trees within the same stand. Sampling occurred on 27 trees at 5 study sites in 2021 and 16 trees at 4 study sites in 2022.

On each bark sample, adelgid life stages (egg, instars 1 to 3, adult) were counted with the aid of a stereoscope (magnification 25×). We did not observe more than 3 instars or sexuparae (ie winged individuals) in our samples. Life stage was determined by size and shape (Balch 1952). Settled crawlers often appear similar to second-instar nymphs with darker coloration; therefore, all crawlers (unsettled and settled) and second instars were grouped as "early instars" for analyses. Collection tubes were rinsed with distilled water to remove adelgids that dislodged from bark samples during transport. Adelgid life stages in the rinsate were counted in a petri dish and added to the sample total counts.

Small adjustments in protocols for processing bark samples and designation of living adelgids led to methodology improvements during the study period. In 2020 and 2021 all samples were stored in 95% ethanol. In 2022, bark samples were processed immediately after collection or stored at 5 °C for no more than 3 days before processing and all individuals were assessed as live or dead. Live and dead status of individuals in 2022 samples was determined following Mech et al. (2018) for hemlock woolly adelgid. Briefly, individual adelgids were removed from the bark and observed for movement of stylets or body; if neither was observed, the adelgid was pierced and exuding hemolymph was observed for appropriate viscosity and color. If the adelgid exhibited movement or the hemolymph was fluid and deep purplish-red, the adelgid was considered alive. If no movement was observed and the hemolymph was dry, the adelgid was determined to be dead. Living eggs were defined by reddish-brown coloration and intact oval shape; dead eggs were determined by a lack of color and a shriveled appearance. In 2021, the living status of adelgids in ethanol-stored samples was examined only by body piercing and hemolymph observation. This was not done for 2020 samples. The bodies of adelgids found in the rinsate from collection tubes were pierced to observe exuding hemolymph for viscosity and color, and living status was assigned as for bark samples.

To visualize temporal dynamics in lifestage timing within a generation, we normalized weekly sample data of live counts for each life stage in 2021 and 2022 using z-score analyses across the sampling range for each individual tree. Z-scores among trees were then averaged for a given sample date at each site and a local polynomial regression (LOESS, R Core Team 2022) was fit to the standardized values to visually enhance trends.

A minimum of 15 adults from each field site were identified and confirmed to species level using the morphology of slide-mounted specimens and PCR amplification of the DNA barcode (Utah State University, Utah Plant Pest Diagnostics Laboratory) using methods described in Havill et al. (2021). Each of our isolates matched sequence accession numbers for *Adelges piceae*. Voucher specimens have been deposited in the Utah State University Insect Collection.

Degree Day Model

A shielded air temperature probe (Campbell Scientific, Inc., Logan, UT) was installed at each site to record hourly air temperatures. Temperature data prior to the installation of dataloggers were extrapolated from at least 2 weather stations within 50 km and of similar elevation to each site (https://download.synopticdata.com/). Linear regressions were performed using the associated weather station and site-observed maximum and minimum temperature data (lm function, R Core Team 2022), and the regression parameter values were used to estimate missing daily maximum and minimum temperatures. Daily hourly temperatures were then estimated using a sinewave function (MATLAB R2022, Math Works 2022).

Degree days (DD) were calculated from hourly data for each year and site using trapezoid integration (trapz function, MATLAB R2022) with an upper and lower threshold. Accumulations were calculated using a 1 Jan biofix (DD_0), a common date used in insect phenology models for initiating heat accumulation calculations. Because no developmental thresholds have been determined for BWA, eleven lower developmental thresholds (T_0) between 0 °C and 10 °C were tested. The upper developmental threshold temperature (T_1) was kept constant at 30 °C because degree day calculations indicated that the DD for BWA were relatively insensitive to variations in T_1 over a range of 20 °C to 30 °C, and temperatures at each study site rarely exceeded 30 °C. Support exists for using these methods of testing when an empirical biofix or laboratory-tested developmental

threshold have not been established for a species (Akotsen-Mensah et al. 2011, Dupuy et al. 2017, Mo and Stevens 2021).

All life stages were evaluated for use in a degree day model; however, the adult stage was chosen for the final model due to its reliability for accurate identification and prevalence in bark samples. Analysis of z-scores suggested that 2 generations, one in late spring to early summer and the second in late summer and fall, occurred at all sites. Separate models for each generation were therefore developed, and generation start and end dates for each site year were chosen by visual estimation of the standardized life stage data. Cumulative live adult proportions were calculated as the count per date by tree, divided by the total count for that tree across the date range for each generation. Data collected in 2021 and 2022 (with live vs dead adult designation) from all sites were used to estimate parameters for the first and second generations combined (Gen1&2). The first generation (Gen1) was modeled using 2022 data from the Green Canyon site, which was accessible in winter and spring, and the 2022 Big Mountain Pass site which was first sampled on 10 May. The 3 other sites were not accessible until June.

The cumulative Weibull distribution was used to model the cumulative DD required for cumulative adult proportions (P) within each generation:

$$P = 1 - \exp\left(- \left(\frac{DD}{\lambda} \right)^{k} \right) \quad (1)$$

where λ (scale parameter) and k (curve shape parameter) are to be estimated (Elzhov et al. 2016, nlsLM function, R Core Team 2022). Separate fits were conducted for each of the 11 T_0 datasets for each generation. The residual standard error (RSE) from Weibull model fittings was used to select the most descriptive T_0 for accumulating DD to predict the development of each generation.

The cumulative DD (cumDD) at which a given proportion (P) of adults may be present was determined by taking the inverse of the cumulative Weibull distribution function, Equation (1), using the estimated parameters for each generation:

$$cumDD = \lambda * (-\log(1 - P))^{1/k} \quad (2)$$

Independent data from the 2020 site-years (with no live vs dead designation) were used to compare observed cumulative proportions and model predictions from the Gen1&2 model using linear regression (lm function, R Core Team 2022). Due to limited early spring site accessibility and associated data, we were unable to evaluate the Gen1 model with an independent dataset.

Predicting Historical and Future Voltinism

Historical daily maximum and minimum temperatures for each study site were generated using BioSIM (Régnière et al. 2017) for the years 1980 to 2020. BioSIM generates site-level daily maximum and minimum temperatures based on nearby weather stations, adjusting for latitude, elevation, and topography. BioSIM-estimated maximum and minimum temperatures were regressed with observed temperatures at each site for the years 2020 to 2022, and parameter estimates were used to predict daily maximum and minimum temperatures at each site for the years 1980 to 2020. Hourly temperatures were estimated from daily maximum and minimum temperatures based on a sinewave function, and degree days were estimated based on numerical trapezoidal integration as previously described.

To project future temperatures (2025 to 2099) for each study site, we used data from ten Global Climate Models (GCMs) parameterized under the most aggressive scenario in assumed fossil fuel use, RCP 8.5 (from the Multivariate Adapted Constructed Analogs (MACAv2)) (Abatzoglou and Brown 2012). Mean daily maximum and minimum temperatures were calculated across GCMs; total annual DD were calculated using the resulting temperature datasets with the methods previously described and averaged across GCMs.

Historical and future trends in voltinism were predicted using the Gen1&2 model based on the assumption that at least one, a partial second, or two full generations would be completed each year. Using cumDD estimations for either historical or future climates, the proportion of a generation less than or equal to 2 generations was estimated using equation (1) and estimated parameters for the Gen1&2 model. For future years with cumDD greater than the requirement for 99% completion of Gen1&2 (ie 2 generations), we developed upper and lower probabilities for additional generations as described herein.

For an upper probability, we assumed additional generations required cumDD based on 99% completion of Gen1 (ie the first generation) observed in this study (1,104 DD). For a lower probability, we assumed the probability of 2 additional generations required cumDD based on 99% completion of Gen1&2 (2,412 DD) (ie 2 generations). These assumptions were meant to encapsulate the upper and lower range of probability for generations beyond the two observed in our study.

Results

Phenology Sampling

Among the sample counts for which living status was assigned (2021 and 2022), live individuals of each life stage or group (ie N1 & N2) were present on the majority of sampling dates (Fig. 1) including in late fall, winter, and the first spring sampling dates at Green Canyon, the only winter-accessible study site (Fig. 1A). Despite finding live individuals of all life stages throughout the year, 2 peak periods of adults, which varied among site-years, were observed in standardized counts. These results suggest BWA is bivoltine at the study sites examined. The first adult peak occurred in early summer and the second peak in late summer and fall (Fig. 1).

Degree Day Model

Cumulative DD varied among study sites and were greatest at Big Mountain Pass, Laketown, and Farmington Canyon. Green Canyon and Rock Canyon, the lowest and highest elevation sites, respectively (Table 1) (Fig. 2), were the coolest each year suggesting that environmental factors in addition to elevation influenced microclimate at each site. Based on RSE from Weibull model fits, we chose a lower threshold of T_0 = 0 °C, accumulated from 1 January, to estimate parameters for both the Gen1 (λ = 716.1299 ± 12.04, k = 3.5400 ± 0.2784, RSE = 0.1105, DF = 72) and Gen1&2 (λ = 1976.9391 ± 10.1332, k = 7.6772 ± 0.4243, RSE = 0.1859, DF = 353) models (Fig. 3). Both models gave reasonable results when evaluated with data used to develop each model (ie observed vs model-predicted regression) (Gen1: Adj R^2 = 0.9074, DF = 72; Gen2: Adj R^2 = 0.7275, DF = 353). Using the independent data collected from 3 sites in 2020 with no live and dead determination, 85% of the variation among observed and predicted cumulative adult proportions based on observed DD was explained for the Gen1&2 model predictions (Adj R^2 = 0.855, DF = 161). Given the limited sampling in spring due to access restrictions, independent data was not available for testing the Gen1 model. However, given that 90% of the variation in cumulative adult proportions was described by

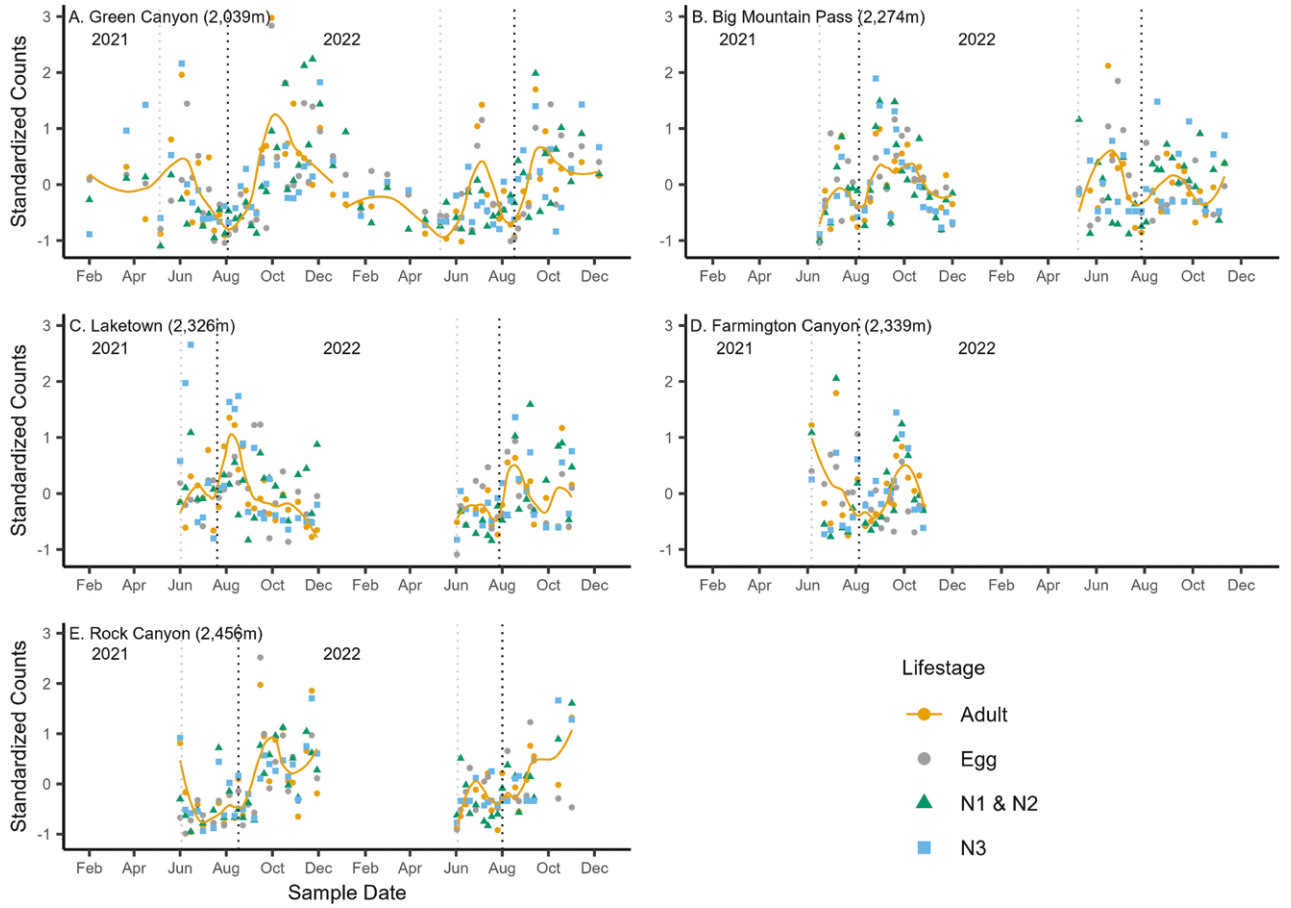


Fig. 1. Standardized counts for balsam woolly adelgid life stages at 5 northern Utah study sites in the Uinta-Wasatch-Cache National Forest, 2021 to 2022. Due to morphological similarity between settled crawlers (N1) and second instar nymphs (N2), these 2 life stages were combined. Light dotted line is the estimated beginning of the first generation and dark dotted line is estimated beginning of the second generation.

the model when evaluated with the data used in model development (Adj R^2 = 0.9074, DF = 72), we used the model for estimating future voltinism trends, acknowledging the lack of model evaluation.

Overall, models predicted 50% and 99% completion of Gen1 by 646 and 1,104 DD > 0 °C, respectively; and 1,885 and 2,412 DD > 0 °C for both generations combined (Gen1&2), respectively (Table 2). These results suggest that completion of the first and second generations combined required slightly more than twice the cumDD > 0 °C of the first generation. The 2 coolest sites, Green Canyon and Rock Canyon, had on average 366 fewer cumulative DD than the 3 warmer sites (Fig. 1), and also had fewer sample trees wherein cumulative proportion of second generation adults reached 1.0 within 2,412 cumDD > 0 °C (Fig. 3). These results suggest fewer individuals experienced enough heat units to complete the second generation at the cooler sites.

Predicting Historical and Future Voltinism

Results from the Gen1&2 model using estimated historical temperatures for the 5 study sites indicated that temperature suitability for 2 BWA generations varied among years and sites (Fig. 4). Thermal suitability for slightly more than two generations occurred most frequently during the 1980 to 2020 time period at the warmest sites, Farmington Canyon and Big Mountain Pass. Less than 2 generations were often predicted for the 2 coolest sites, Green Canyon and Rock Canyon, particularly prior to 1995 and again between 2008 and 2011.

For future voltinism projections, if we assume that additional generations beyond those observed in this study are similar in their thermal requirements to Gen1 (upper probability), at least 3 generations were predicted for all sites beginning in 2025 using forecasted temperatures (Fig. 5A). We term this an upper probability due to the lower DD requirement of a single generation (Gen1) compared to Gen1&2 models combined. By 2060, the upper probability was 4 annual generations at the majority of sites and years. By the end of the century the warmest site, Big Mountain Pass, was predicted to have a high probability of 5 generations and the coolest sites, slightly more than 4 (Fig. 5A). Assuming additional generations require degree day accumulations like Gen1&2 (lower probability), the probability of 2 additional generations increases throughout the century, with the warmest site, Big Mountain Pass, having the greatest probability of 2 complete additional generations or 4 generations annually (Fig. 5B).

Discussion

BWA Phenology and Degree Day Model

This study addresses findings for BWA phenology exclusively on subalpine fir in northern Utah. As observed in previous research (Tunnock and Rudinsky 1959, Greenbank 1970), BWA DD requirements on other tree species in western North America could vary from those presented herein. Individuals of all BWA life stages were found on bark samples from most sample dates, indicating the

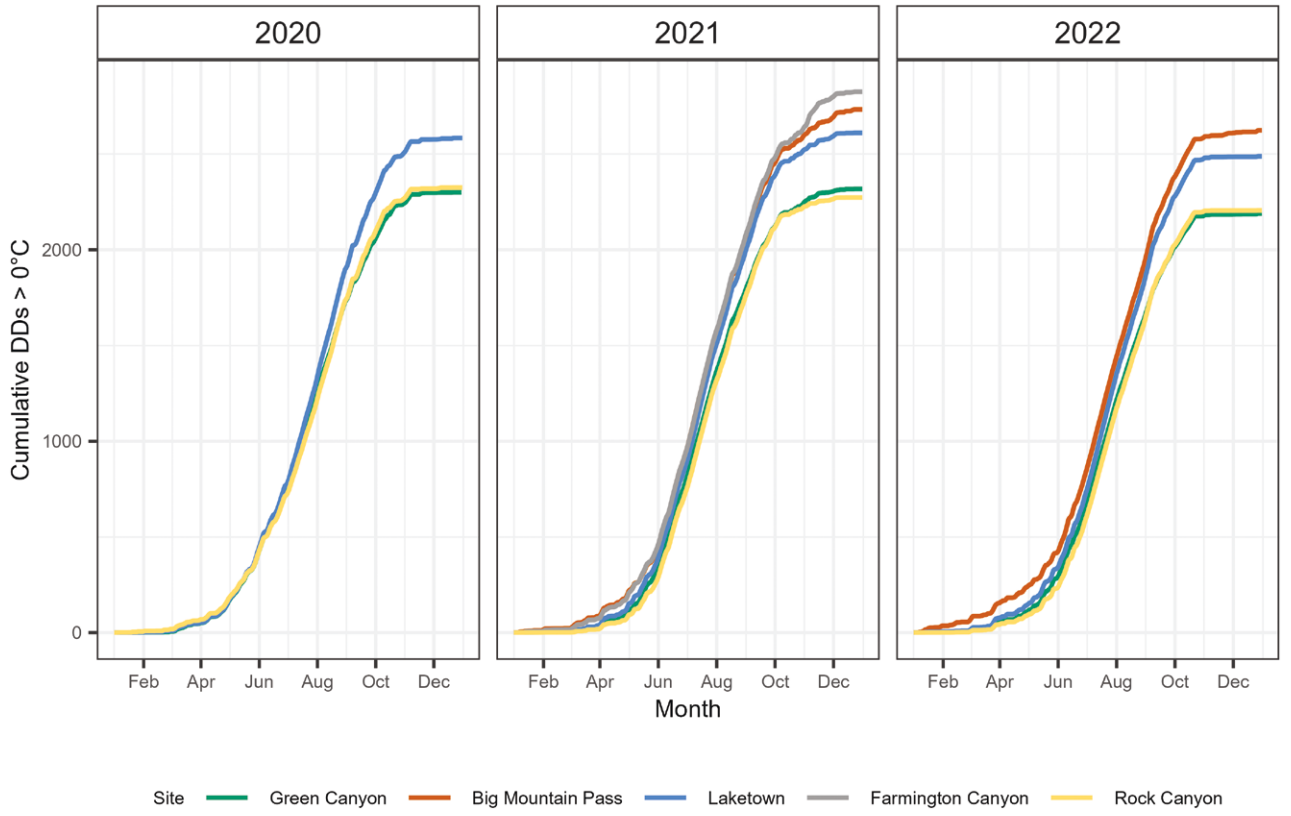


Fig. 2. Cumulative degree days (DD) above 0 °C with an upper development threshold of 30 °C and 1 Jan biofix for 5 northern Utah study sites in the Uinta-Wasatch-Cache National Forest, 2020-2022.

presence of overlapping cohorts. In most cases, one or two life stages dominated within a sample period. Although overlapping cohorts can create challenges in estimating the number and timing of generations, 2 distinct adult peaks were evident annually at all sites (Fig. 1). Variability in timing of life stages, including adults, varied by site likely due to differences in DD accumulations (Fig. 2). These results support 2 generations of BWA in northern Utah, concurring with previous observations at mountainous elevations in the US Pacific Northwest (Ragenovich and Mitchell 2006) and coastal British Columbia (McMullen and Skovsgaard 1972). The presence of live individuals of all life stages in winter samples and spring samples at the Green Canyon site lends support to overwintering success of more than the crawler stage (N1) in northern Utah.

The regional degree day model developed herein predicts that 99% completion of 2 generations (2,412 cumDD) required slightly more than twice the cumDD (2,208) for one generation (1,104 cumDD). Depending on the site, the second generation started in late July and early Aug and would include a period in mid to late Aug when crawlers are hypothesized to estivate (Balch 1952). Little is known about estivation in BWA, but it is hypothesized to last from 2 to 8 weeks, increase resistance to adverse weather conditions, and is associated with morphological changes in appearance without molting (Amman 1970, Greenbank 1970). Limbu et al. (2022) and Weed et al. (2016) demonstrated an extended development time in the crawler stage of the congener species hemlock woolly adelgid suggesting an estivation that was induced by temperatures above 20 °C. Induction of a potential BWA crawler estivation in Aug may explain the slightly higher cumDD required for the second generation. The observed overlapping cohorts may also be due to variation in the manifestation of estivation (Tobin et al. 2002, Bernardini and DI Russo 2004). For example, if only a proportion of individuals estivate, non-estivating individuals in the cohort may continue to develop and attain the adult stage at an earlier time. The observed developmental progression varied among sites and years indicating estivation may be facultative and that variation in factors such as microclimate may play a significant role (Tauber et al. 1986).

Four BWA generations were observed on *Abies grandis* (Doug.) at a low-elevation Oregon site, requiring 1,157 and 2,083 DD for one and two generations, respectively (Tunnock and Rudinsky 1959). Our estimated values for northern Utah only differ from the low Oregon site by 53 DD for one generation (Gen1), but we estimated 329 more DD were required for 2 generations (Gen1&2). Greenbank (1970) found that univoltine and bivoltine populations on *Abies balsamea* (L.) Mill in New Brunswick required 710 and 1,915 DD, respectively, using T_0 = 0 °C. Greater DD requirements were estimated for northern Utah compared to New Brunswick (394 more DD for Gen1 and 497 more DD for Gen1&2) and these differences were greater than that found between northern Utah and Oregon. Estimated differences may be due to differences in performance and development of BWA subspecies (*A. piceae canadensis* in New Brunswick versus *A. piceae piceae* in Utah and Oregon) (Havill et al. 2021) on the different host tree species. Additionally, degree day accumulations at our study sites highlight that factors other than just elevation influence thermal conditions important for BWA. Farmington Canyon, one of the highest elevation sites, had the greatest DD accumulations, whereas Green Canyon, one of the lowest elevation sites, had the lowest DD accumulations (Fig. 2). Factors including aspect, slope, shading, and stand density likely contribute to variation in heat accumulation within BWA-infested true fir stands.

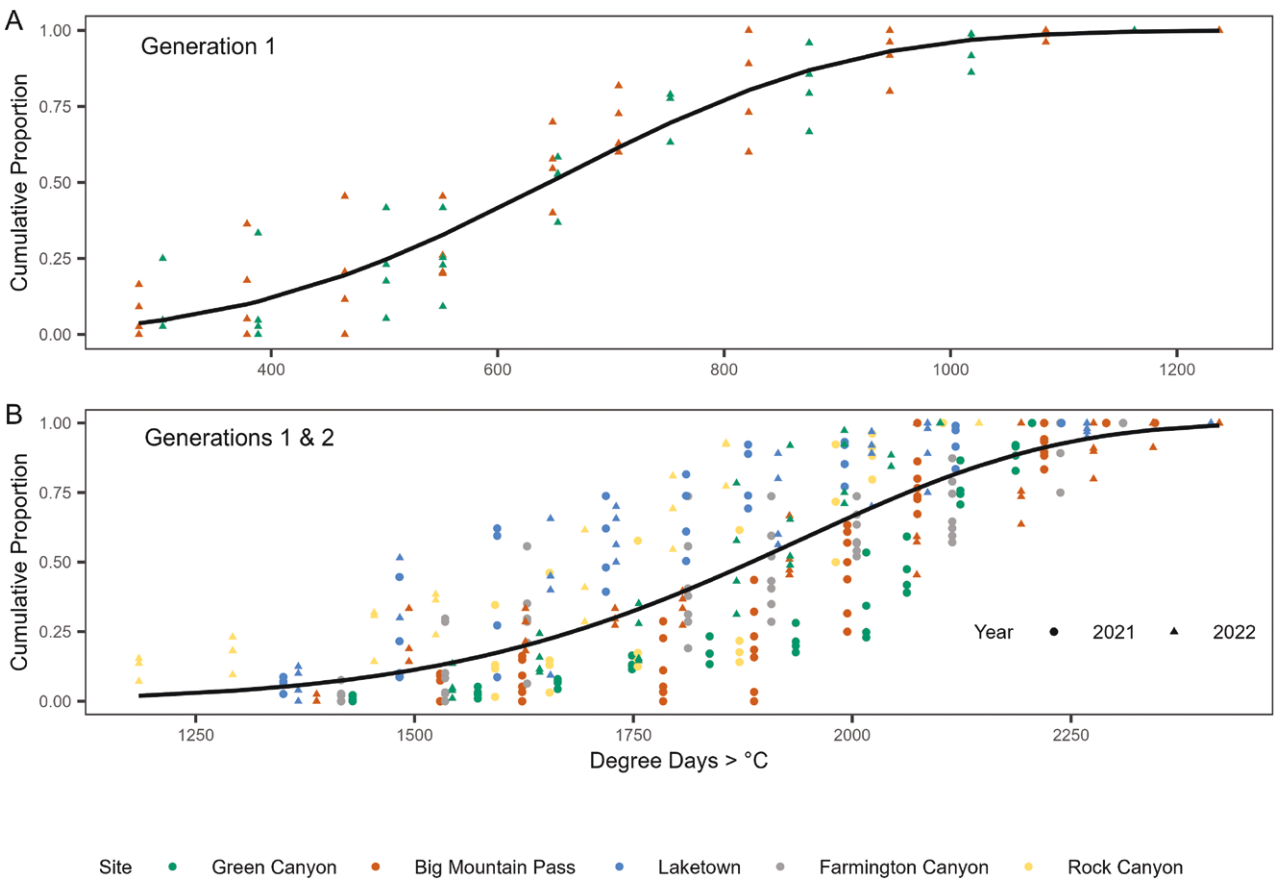


Fig. 3. Observed adult balsam woolly adelgid cumulative proportions fitted to a Weibull distribution and observed cumulative degree days (1 Jan biofix, 0 °C lower developmental threshold, and 30 °C upper developmental threshold) for (A) generation 1 (Gen1) and (B) generations 1 and 2 combined (Gen1&2) at 5 northern Utah study sites (2021 and 2022). The generation 1 model (Gen1) was only fitted to 2022 data from the Green Canyon and Big Mountain Pass sites due to limited spring access at other sites.

Table 2. Model predicted degree day accumulations from 1 Jan (T_0 = 0 °C, T_1 = 30 °C) corresponding to cumulative proportion of balsam woolly adelgid adults in the first generation (Gen1) and the first and second generations combined (Gen1&2) at 5 northern Utah study sites, 2021 to 2022.

	Cumulative proportion						
Generation	5%	25%	50%	75%	90%	95%	99%
Gen1	309	504	646	785	906	976	1,104
Gen1&2	1,343	1,681	1,885	2,063	2,204	2,281	2,412

In addition to summer estivation, Greenbank (1970) hypothesized that crawlers enter a diapause in the fall that increases resistance to winter temperatures. In New Brunswick, all life stages excluding the crawler were observed dying by prolonged exposure to temperatures below 0 °C and instantly below −20 °C in a region of study where mean annual minimum temperatures ranged from −20 to −25 °C (Greenbank 1970). Our finding that all life stages—not just the crawlers—can be found in winter and spring may be due to slightly warmer temperatures at our sites in northern Utah. The average minimum temperature across our sites and years during the study was −19.2 °C ± 1.1 °C, though temperatures fell below 0 °C for an annual average of 137 d (± 6.27). Variations in the thermal requirements of BWA subspecies may also be a factor in these differences (Hensen et al. 2018). Additional research on a potential winter diapause in the BWA crawler life stage and cold tolerance thresholds for all life stages is needed to further understand the dynamics of life stage activity over winter in the Intermountain West.

Predicting Historical and Future Voltinism

BWA was first detected in multiple Utah counties in 2017, including at the Farmington Canyon site, and estimated to have been in the state for at least a decade (Davis et al. 2020). Our upper probability estimates suggest that between 2000 and 2020, 12 years were thermally suitable for a partial third generation at the warmest sites, Farmington Canyon and Big Mountain Pass. Except for Rock Canyon, most years at the cooler sites between 2010 and 2020 were predicted to have at least 2 generations. Model predictions therefore suggest that at least 2 decades prior to detection in northern Utah, degree day accumulations were adequate for 2 generations at the warmest locations.

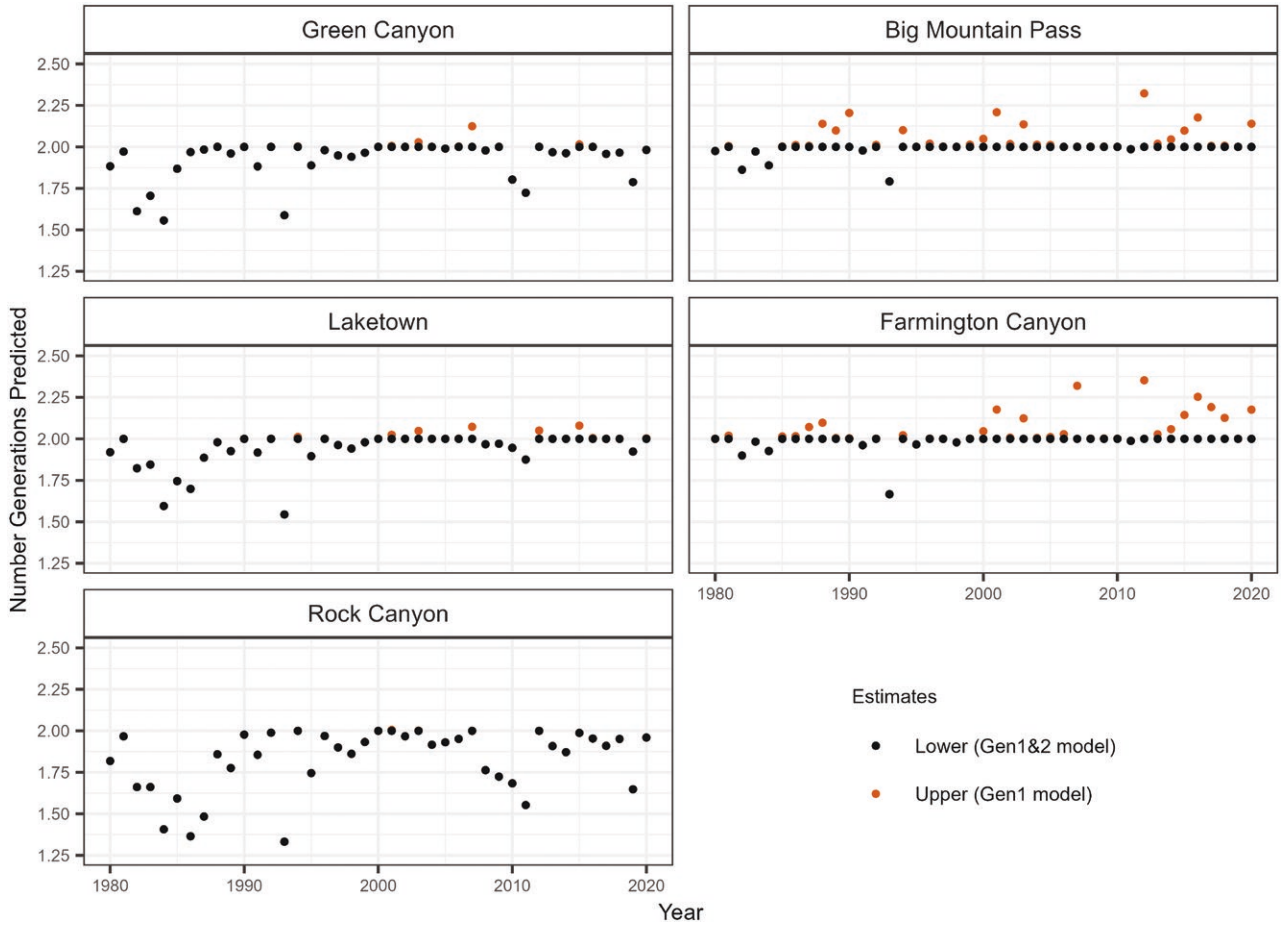


Fig. 4. Predicted historical annual generations of balsam woolly adelgid (BWA) at 5 northern Utah study sites in the Uinta-Wasatch-Cache National Forest from 1980 to 2020. Upper estimates for additional generations beyond 2 were based on predictions from a model for the first generation (Gen1). Lower estimates were based on model predictions for first and second annual generations combined using the Gen1&2 model.

When a worst-case GCM scenario (RCP 8.5) of future temperature projections was used to run the models, differences between upper and lower voltinism estimates were greater than the differences between upper and lower estimates from model predictions using historical temperatures. The greater differences in future predictions highlight the severity of future RCP 8.5 projections, entailing more than 4 °C in warming. Running the Gen1&2 model sequentially (lower probability) resulted in predictions of 2 generations through the middle of the century and several sites approaching 2 additional (4 annual) generations by the end of the century (Fig. 5a). If additional generations beyond two were predicted to develop sequentially based on the Gen1 model (upper probability), most sites were predicted to have 4 generations by 2060 and some approaching five generations by the end of the century (Fig. 5b). We acknowledge that the Gen1 model used for upper probability estimates was not evaluated with independent data, and therefore estimates could be enhanced with additional data focused on this generation. Considering both upper and lower probabilities, the number of BWA generations is predicted to at least double within the century at elevations between 2,000 and 2,500 m in northern Utah and the prevalence of partial generations will increase. Using similar RCP8.5 downscaled climate projections and a model based on remotely sensed data, Campbell et al. (2024) also predicted more severe BWA impact by 2060 in northern Utah subalpine fir locations.

Summer and winter dormancies have been hypothesized for BWA (Amman 1970, Greenbank 1970), although neither has been researched in depth. In species with winter dormancies, climate change can cause developmental traps wherein life cycle regulation decisions are disrupted, development proceeds, and subsequent mortality occur in life stages that have not evolved to survive winter. Low or zero fitness affects the abundance of the spring generation, with longer-term impacts on population persistence (van Dyck et al. 2015). In the one winter we sampled, however, multiple life stages survived suggesting a risk-spreading tactic. Additional winter sampling is needed to fully understand BWA thermal limitations. Summer dormancies can also be affected by a changing climate if induction cues are mismatched with seasonal temperatures (Forrest 2016). Without additional knowledge of potential BWA dormancies that could be disrupted with warming that exceeds historical variability, predictions of future population success will contain additional uncertainties beyond those inherent to our models and downscaled temperature projections. Additionally, our projections only include the effect of future temperatures on BWA voltinism. Clearly, host trees will also be affected by future changes in temperature and precipitation (Hartmann et al. 2022) which will indirectly influence BWA, and inclusion of these effects is needed. Indeed, subalpine fir is highly susceptible to mortality during drought (Bigler et al. 2007) and is predicted to decline in many areas within its range (Bell et al. 2014, Harris et al. 2023).

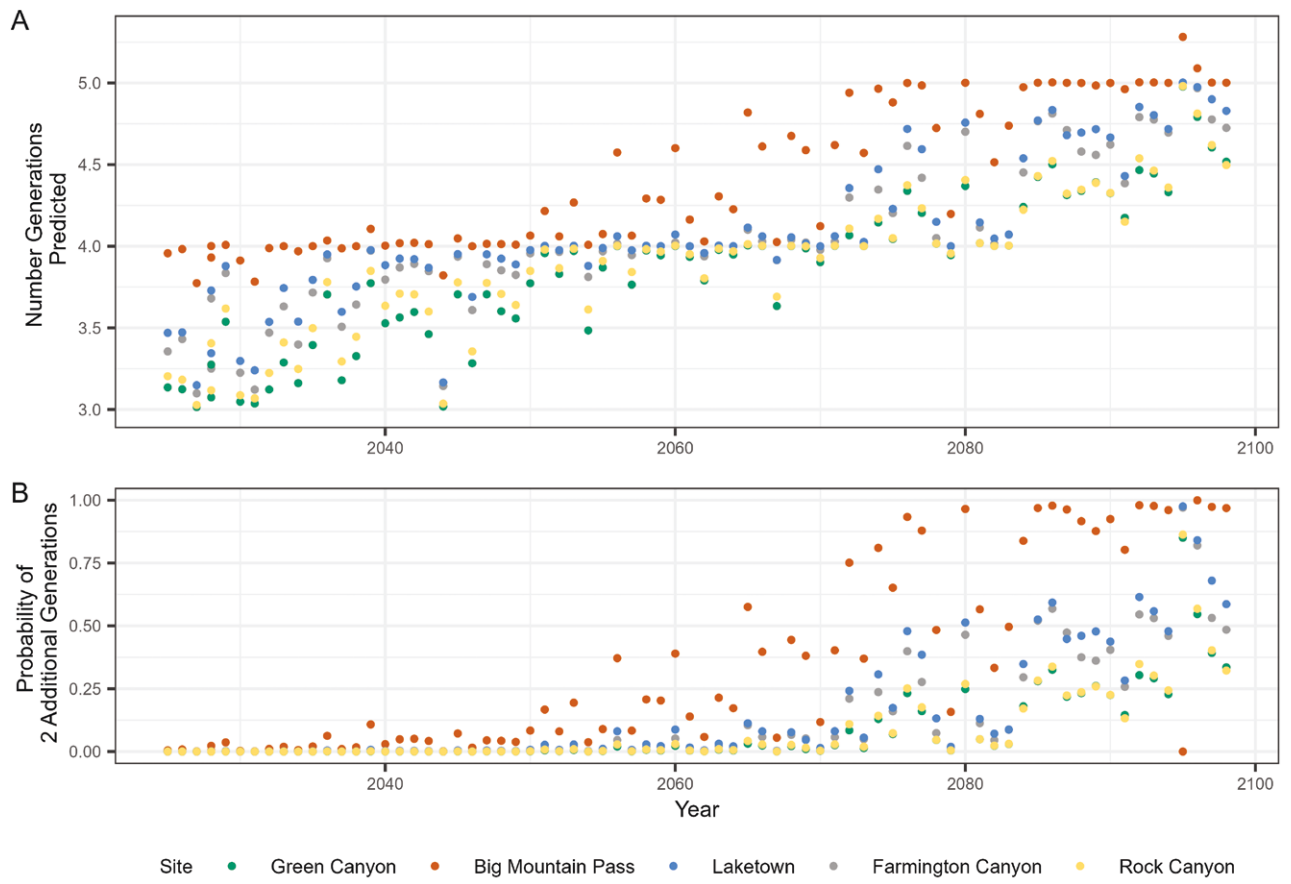


Fig. 5. Predicted future annual generations of balsam woolly adelgid (BWA) at 5 northern Utah study sites in the Uinta-Wasatch-Cache National Forest from 2025 to 2099. (A) Upper estimates for additional generations were based on a model predicting the probability of a single generation (Gen1) and (B) lower estimates were based on a model predicting the probability of 2 annual generations (Gen1&2).

BWA spread relatively slowly through the US Pacific Northwest potentially due to geographic barriers, but detection was also difficult due to the cryptic nature of the species (Davis et al. 2020). We acknowledge the need to include potential dormancy responses in models for predicting BWA performance in long-term future warming scenarios. In the near term, however, our models can be used to identify susceptible true fir stands in Utah and adjoining states of the Intermountain West that are thermally suitable for BWA and require additional monitoring.

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